COLOR PERCEPTION

Physiology, Processes and Analysis

Darius Skusevich
Petras Matikas
Editors

NEUROSCIENCE RESEARCH PROGRESS SERIES

NOVA

NEUROSCIENCE RESEARCH PROGRESS SERIES

COLOR PERCEPTION: PHYSIOLOGY, PROCESSES AND ANALYSIS

NEUROSCIENCE RESEARCH PROGRESS SERIES

Current Advances in Sleep Biology
Marcos G. Frank (Editor)
2009. ISBN: 978-1-60741-508-4

Dendritic Spines: Biochemistry, Modeling and Properties
Louis R. Baylog (Editor)
2009. ISBN: 978-1-60741-460-5

Relationship between Automatic and Controlled Processes of Attention and Leading to Complex Thinking
Rosa Angela Fabio
2009. ISBN: 978-1-60741-810-8

Neurochemistry: Molecular Aspects, Cellular Aspects and Clinical Applications
Anacleto Paços and Silvio Nogueira (Editors)
2009. ISBN: 978-1-60741-831-3

Sleep Deprivation: Causes, Effects and Treatment
Pedr Fulke and Sior Vaughan (Editors)
2009. ISBN: 978-1-60741-974-7

Color Perception: Physiology, Processes and Analysis
Darius Skusevich and Petras Matikas (Editors)
2009. ISBN: 978-1-60876-077-0

NEUROSCIENCE RESEARCH PROGRESS SERIES

COLOR PERCEPTION: PHYSIOLOGY, PROCESSES AND ANALYSIS

DARIUS SKUSEVICH
AND
PETRAS MATIKAS
EDITORS

Nova Science Publishers, Inc.
New York

Copyright © 2010 by Nova Science Publishers, Inc.

All rights reserved. No part of this book may be reproduced, stored in a retrieval system or transmitted in any form or by any means: electronic, electrostatic, magnetic, tape, mechanical photocopying, recording or otherwise without the written permission of the Publisher.

For permission to use material from this book please contact us:
Telephone 631-231-7269; Fax 631-231-8175
Web Site: http://www.novapublishers.com

NOTICE TO THE READER

The Publisher has taken reasonable care in the preparation of this book, but makes no expressed or implied warranty of any kind and assumes no responsibility for any errors or omissions. No liability is assumed for incidental or consequential damages in connection with or arising out of information contained in this book. The Publisher shall not be liable for any special, consequential, or exemplary damages resulting, in whole or in part, from the readers' use of, or reliance upon, this material.

Independent verification should be sought for any data, advice or recommendations contained in this book. In addition, no responsibility is assumed by the publisher for any injury and/or damage to persons or property arising from any methods, products, instructions, ideas or otherwise contained in this publication.

This publication is designed to provide accurate and authoritative information with regard to the subject matter covered herein. It is sold with the clear understanding that the Publisher is not engaged in rendering legal or any other professional services. If legal or any other expert assistance is required, the services of a competent person should be sought. FROM A DECLARATION OF PARTICIPANTS JOINTLY ADOPTED BY A COMMITTEE OF THE AMERICAN BAR ASSOCIATION AND A COMMITTEE OF PUBLISHERS.

LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA

ISBN: 978-1-61761-866-6 (Ebook)

Available upon request

Published by Nova Science Publishers, Inc. ✝ New York

CONTENTS

PREFACE

There is no color without light, nor is there color perception without a sensory organ and brain to process visual input. This book discusses the complex impact of color action on the organism. It is shown that the perception of color depends on the action of irritants on other sensor systems and, vice versa, the action of color may exert exciting or inhibiting influence on the perception of sounds or smells. The mechanism of increasing realism of colored images is also discussed, as well as the epistemic role of color. Furthermore, this book examines whether there exist very large individual differences in the perception of color, and if so how these differences manifest themselves. Other chapters in this book discuss the role of visual processing in the regulation of adaptive behaviors, a review of image denoising, and the role of color in psychological functioning (i.e., the unconscious associations people have with color that could act as possible confounds).

Chapter 1 - In order to investigate a possible role of visual processing in regulation of adaptive behaviors, two behavioral experiments using color stimulus were performed. In the first experiment, hemispheric asymmetry of color processing was investigated by measuring reaction time to a stimulus presented either in the left or the right visual field responded by ipsilateral hand. The simple reaction time was shorter to a color stimulus presented in the right hemisphere in the right-handed participants, while no hemispheric asymmetry was found in color discrimination reaction time without verbal cues. In the second experiment, a modulatory effect of color on sensory-motor interaction was investigated using a prepulse modulation task. Amplitude of a startle eyeblink response elicited by an air-puff to the cornea was significantly inhibited by a shortly (100 ms) preceding color prepulse. A different amount of the inhibition was induced by different color prepulses. Yellow was more effective as compared to a blue prepulse. Although the exact neuronal pathways underlying the prepulse inhibition of the corneal blink response is not determined, a top-down pathway from the cortex to the brainstem nuclei via the amygdala seems to be involved in the sensory-motor interaction. The descending pathway seems to play a role in modulation of the startle responses. From these findings combined with other studies, a dual processing hypothesis of visual inputs will be proposed, where physical features of the stimulus are processed in the cerebral cortex with consciousness, while the psychological and biological meanings are processed mainly in the limbic system without consciousness. Traditionally, it was thought that these two processes are in series, while in the present model these processes are in parallel, in addition to the serial processing. Visual inputs are conveyed to the limbic system via the indirect cortical and the direct subcortical pathways. The cortical pathway further divided into two routs; one is from the inferotemporal cortex and the other is from the posterior parietal association cortex through the pulvinar nucleus of the thalamus.

Chapter 2 - There are two basic approaches to studying color: one of them considers the issue of the physical reasons of color, the other investigates color perception. According to the first, color is not an objective physical entity; the second approach has many experimental evidences of color influence on human organism, for example, changes of the emotional condition, blood pressure, accuracy of perception, etc. The considered question can be formulated as follows: how color, being a sign without a referent, can make a real impact on the organism? A working hypothesis is that color is a non-conventional objective sign. This hypothesis will be subjected to critical analysis from the point of view of psychology of development in order to ascertain whether the sign properties of color are innate or are formed by the influence of culture. Another topic is a role of color in the world cognition. This question was usually considered from the point of view of direct influence on the increase of the visual recognition accuracy. We will investigate a question of indirect influence of color by means of pre-setting of the nervous system to perception; this is possible thanks to the system character of perception.

Chapter 3 - There is no colour without light, nor is there colour perception without a sensory organ and a brain to process visual input. This chapter first reviews how the colour of objects is produced. Most commonly, this depends on so-called pigments, the molecular nature of which provokes strong absorption of part of the incident light falling on an object. Colour can also be produced by optical phenomena such as refraction, dispersion, interference or diffraction from ordered structures within objects. A wide variety of photonic microstructures are known in the living world and specific examples will be described in mammals, birds, fish and insects. Some of these structures reflect light in the near ultraviolet spectral region, particularly pertinent for certain birds, insects and fish which are sensitive to these wavelengths. A detailed account of a particularly elaborate structure present in the king penguin beak will be given to illustrate the extent to which evolutionary pressure leads to the elaboration of such structures to satisfy specific needs of birds or animals. Subsequently, the perception of colour in man and animals and its biological significance is dealt with. For man, this will include a discussion of the symbolic meaning of different colours. In many species, especially birds, the colours of plumage and parts of the skin have an important survival function. Such biological colourations may fulfil the role of ornaments that determine mate choice and reproduction of the species, or signal good health, allowing individuals to secure and maintain territorial dominance. Colour perception may also have an underlying survival function in man, but more complex explanations are needed to relate perception to such a function. The colour of an object in the visual field is known to determine the way in which humans perceive relations between objects and their background, particularly which objects appear nearer. This suggests that colour perception is important in processing information about the physical structure of the world. The colour red plays an important role in this process, since it drives mechanisms of visual selection which attract attention to, or away from, objects in the visual field. Psychophysical studies of colour perception in both animals and man help to understand these complex processes. Finally, colour perception in man may contribute either to rewarding psychological sensations of warmth, comfort and safety or to aversive sensations of coldness and discomfort, sensations which can strongly influence individuals in their daily social interactions.

Chapter 4 - Since the formulation of the Young-Helmholtz chromatic theory in the 19th century, it has generally been accepted that human colour vision is trivariant, i.e., it is possible to match any colour stimulus by mixing three primary stimuli in appropriate proportions. This resulted in the definition by the International Commission on Illumination in 1931 of the standard colorimetric observer for fields of 2° only three years after the definition of the standard photometric observer known as the V_λ luminous efficiency curve.Much progress has been made in the knowledge of colour vision since then, in such fields as physics, physiology, genetics, biochemistry, neuroscience, and psychology. That is why it is perhaps the time to raise our level of exigency a step when it comes to characterizing a chromatic observer. The question we should ask ourselves is not whether that figure of the standard colorimetric observer represents the average of the population, because this can indeed be done with successive corrections. Rather it is whether there exist very large individual differences in the perception of colour, and if so how these differences manifest themselves. This is of course apart from observers characterized as defective.In this chapter, we review the state-of-the-art in this field, and present our own latest research results concerning this question.

Chapter 5 - Classically, different physical attributes of the visual stimulus were thought to be solved in parallel by interdependent neuronal populations conveying information from the retina to the parietal and temporal cortical areas. According to this assumption, while neurons in the dorsal areas of the visual system were mainly related to the analysis of motion and spatial information, those located at the more ventral positions were mostly associated to shape and color processing. However, although this functional segregation between visual areas has been supported for several decades, there is also strong experimental evidence suggesting an alternative task-driven view of the visual system. According to this more recent perspective, neuronal responses in cortical visual areas can be simultaneously dependent on more than one single visual attribute. As far as color perception plays a central role in visual recognition, it could be assumed that color-sensitive neurons would be also involved in the analysis of some other critical visual attributes. In agreement with this idea, it has been shown that V1 double opponent cells respond to edges defined not only by chromatic and luminance differences, but also by the orientation of their receptive fields. Furthermore, results from many electrophysiological and neuroimaging studies have also demonstrated that color-sensitive neurons in V2 and V3, modulate their responses depending on diverse physical attributes of the stimulus such as the stimulus direction, orientation, luminance and shape, revealing the simultaneous contribution of magno- and parvocellular inputs from the Lateral Geniculate Nucleus (LGN) at different levels of the visual system. At higher visual areas, several authors have reported the existence of multi-sensitive neurons. Middle Temporal (MT) neurons, in the dorsal stream, are sensitive to motion spots defined by single or combined changes in texture and color. In the ventral stream, responses to both, color and orientation have been described in V4 and the inferotemporal cortex. Additionally, results from several studies blocking the magno- and parvocellular projections from the LGN to V4 have shown that these two channels can simultaneously contribute to neuronal responses at this level of processing. All these data evidence that even sharply-color-tuned neurons can show color-related responses modulated by many other visual attributes.

Chapter 6 – Colour composition divides colours into two types: unitary and binary colours. Colours which are not composed are said to be “unique” or “unitary” colours, whereas composed colours are always binary. Colour composition and the distinction between unitary and binary colours have played a major role in colour science and in the philosophy of colours. They have for example been invoked to introduce opponent-processes in the mechanisms underlying colour vision and have been used to criticize philosophers who defend a physicalist view on the nature of colours. Most philosophical or scientific theories suppose that colour composition judgments refer to the way colours appear to us. The dominant view is therefore *phenomenalist* in the sense that colour composition is *phenomenally* given to perceivers. This paper argues that there is no evidence for a phenomenalist view of colour composition and that a conventionalist approach should be favoured.

Chapter 7 – Image restoration has been a classical and significant topic of image processing, which refers to the techniques to reconstruct or recover an image from distortion (e.g. motion blur and noise) in different applications, such as satellite imaging, medical imaging, astronomical imaging, and family portraits. For motion blur, *image deblurring* techniques are used to estimate the actual blurring function and “undo” the blur to restore the original image. In cases where the image is corrupted by noise, *image denoising* methods are employed to compensate for the degradation the noise caused. In the past two decades, image denoising has been a fundamental and active research topic and widely used as a key step in a variety of image processing and computer vision applications, such as image segmentation, compression, object recognition, and tracking. This chapter focuses on image denoising, specifically for color image denoising and the application to color photo denoising.

Chapter 8 – Psychology is a discipline that prides itself on being an empirical science. As such, rigorous statistical and methodological controls must be used to ensure the validity of every result. Ostensibly, each submission for publication is peer reviewed, and needs to be replicated by other scientists in other locations to confirm or disconfirm the results. This is how a scientific discipline must operate if it wishes to produce meaningful, accurate results. When a discipline strays from these procedures, it leaves itself open to criticism and more importantly, to the possibility of inaccurate or misleading conclusions. All research needs to ascribe to these standards, regardless of how time consuming, inefficient, or difficult they may be.

One area of research that has failed to live up to these standards is the study of color and psychological functioning. The aesthetic property of color may at first consideration make it seem like a trivial topic for study, but recent research indicates exactly the opposite. Color has been shown to influence affect, cognition, and behavior. The degree and type of influence has varied from study to study, some more psychologically consequential (e.g. color and performance) than others (e.g. shoe color preference). None of these results, however, can be considered valid if they fail to live up the methodological rigors of science.

An in depth examination of the color research of the past and present makes it clear that most of the work fails to meet scientific standards. Too many studies have failed to take into account the three basic properties of color. Others have failed to consider the unconscious associations people have with color that could act as possible confounds. Stated differently, color used in an experiment may affect the experiment’s dependent variable in unwanted and unaccounted for ways. In either case, it is impossible to draw meaningful conclusions from these studies, as their results could be due to any number of variables. This is the primary argument that will be made throughout this chapter. The aim is not to criticize or demean the existing research or researchers. Rather, it is hoped that this analysis will lead to more systematic, scientifically valid empirical work on color psychology. By learning about and avoiding the mistakes documented in this chapter, researchers will be able to meaningfully add to the growing body of work in on color psychology.

Chapter 9 - Carotenoids are widely used in aquaculture to achieve natural coloring of salmon flesh, improvement of trade quality (color) of sea urchin roe and in aquaculture of Crustaceans.For salmon, it has been found, that the relationship between pigment content and color parameters is complex and nonlinear. Nevertheless, there is an evident correlation between the total concentration of carotenoids (mainly astaxanthin) and the red, most valued by consumers, color of a muscular tissue of salmon (i.e. the higher the pigment content the better). Assimilation of carotenoids in salmon usually does not exceed 10-15 per cent, and cost of astaxanthin makes up about 6-8 % from the cost of filleted fish. Thus, researches in this field are directed on improvement of feed composition increasing of carotenoid assimilation and search of new sources of these pigments; optimization of processing and storage conditions of production, allowing keeping natural color. Ability to reach desirable color of roe is crucial condition for commercial echinoculture. A number of studies were devoted to developing of composition of artificial feed giving desirable color characteristics. Considering macroalgae, the best results have been reached with species of Laminaria, Alaria, Palmaria, and Ulva. It has been proved great significance of carotenoids as essential micronutrients for sea urchin aquaculture. A promising source of carotenoids in aquaculture may be microalga Duneliella salina. Carotenoid content correlates with redness of the gonads, but unlike salmon, for sea urchins there is a certain optimum of the pigment concentrations in gonads, excess or, on the contrary, lack of the pigments lead to falling into less desirable for customers color grades.

Chapter 10 - A common problem among social scientists who group all members of a race/ethnicity together is that they assume that all of the life experiences of those individuals are the same, and thereby, overlook the prevalence of heterogeneity within ethnicities. One such example is a global phenomenon present in all cultures where there is skin tone variation—colorism. This longstanding ideology which suggests preference within ethnic groups is closely linked with skin color is often ignored. Recent research, however, has found that among Blacks, lighter skin has major implications in the job selection process—where one is better off if he/she is lighter-skinned. Due to issues of attractiveness and general levels of comfort, individuals tend to feel a lighter-skinned black is more competent or less threatening, respectively. Though many companies are now concentrating efforts on enhancing diversity—with race being one of the primary focuses—one has to wonder if these "advancements" in diversity are resulting in more lighter-skinned Blacks being hired over their equally-qualified darker-skinned counterparts. This research commentary intends to look broadly at the executive boards of corporate America to investigate if this "lopsidedness" is indeed present. It is expected that greater numbers of light-skinned Blacks will be found in these positions, which will support prior research and illustrate the need for greater discussion and future research regarding this very issue.

Short Communication 1 - In outer space habitats, where the weightlessness and isolation deeply influence human life, color perception, processing and reaction to color are subjects for analysis in Human Factors investigation. The "µgOrienting" project aims to improve the life quality in outer space by research on colors and other visual stimuli.

Short Communication 2 - In microgravity under weightlessness conditions, where 'Up' and 'Down' have no meaning, orientation is of primary importance. Instinctual reactions to color and symbols are investigated in the WIUD experiment to help implement Up and Down orientation in Outer Space Habitats.

In: Color Perception: Physiology, Processes and Analysis
Editors: D. Skusevich, P. Matikas, pp. 1-50
ISBN: 978-1-60876-077-0

Chapter 1

CORTICAL AND SUBCORTICAL PROCESSING OF COLOR: A DUAL PROCESSING MODEL OF VISUAL INPUTS

Hitoshi Sasaki
Department of Physiology and Biosignaling, Osaka University
Graduate School of Medicine, Yamadaoka, Japan

ABSTRACT

In order to investigate a possible role of visual processing in regulation of adaptive behaviors, two behavioral experiments using color stimulus were performed. In the first experiment, hemispheric asymmetry of color processing was investigated by measuring reaction time to a stimulus presented either in the left or the right visual field responded by ipsilateral hand. The simple reaction time was shorter to a color stimulus presented in the right hemisphere in the right-handed participants, while no hemispheric asymmetry was found in color discrimination reaction time without verbal cues. In the second experiment, a modulatory effect of color on sensory-motor interaction was investigated using a prepulse modulation task. Amplitude of a startle eyeblink response elicited by an air-puff to the cornea was significantly inhibited by a shortly (100 ms) preceding color prepulse. A different amount of the inhibition was induced by different color prepulses. Yellow was more effective as compared to a blue prepulse. Although the exact neuronal pathways underlying the prepulse inhibition of the corneal blink response is not determined, a top-down pathway from the cortex to the brainstem nuclei via the amygdala seems to be involved in the sensory-motor interaction. The descending pathway seems to play a role in modulation of the startle responses. From these findings combined with other studies, a dual processing hypothesis of visual inputs will be proposed, where physical features of the stimulus are processed in the cerebral cortex with consciousness, while the psychological and biological meanings are processed mainly in the limbic system without consciousness. Traditionally, it was thought that these two processes are in series, while in the present model these processes are in parallel, in addition to the serial processing. Visual inputs are conveyed to the limbic system via the indirect cortical and the direct subcortical pathways. The cortical pathway further divided into two routs; one is from the inferotemporal cortex and the other is from the posterior parietal association cortex through the pulvinar nucleus of the thalamus.

1. INTRODUCTION

Color is one of attributes of an object. However, color does not belong to the object itself, but is produced in the organism that receives it. Indeed, sight of mono- or dichromatic observers is so different from normal trichromatic sight. It is well known that a black and white stimulus can produce color sensation if it is presented in a certain spatio-temporal arrangement. Benham top is a famous example showing that color does not belong to the physical object itself, but depends on physiological and psychological events, which are produced in the visual system (Newton, 1672).

Color processing is a function of the visual cortex (Zeki, 1991; Corbetta et al., 1991; De Valois and De Valois, 1993; Ungerleider and Haxby, 1994). However, little is known about the hemispheric difference of the color processing. Moreover, there are few studies that examined functional meanings of color information. In the present study, two experiments were undertaken to answer these questions; one examined the hemispheric dominance of color processing, and the other examined the effect of color on modulating a startle reflex in normal human subjects.

Results of these experiments will clearly demonstrate that the right hemisphere has superiority in color detection in right-handed participants, and that color information modulates a startle reflex by a subcortical pathway to the brain stem, presumably via the limbic system. From these results and related findings, I propose a new hypothesis that the sensory inputs, in general, are analyzed and processed in two evolutionary different systems (limbic and neocortex) to elicit adaptive behaviors to maintain homeostasis of the organism. A visual stimulus, including color, is processed in two systems in parallel; one is a modality specific visual system and the other is a non-specific limbic system. In detail, local physical features of the stimulus are processed in the former system with consciousness, while the global psychological and biological meanings are processed mainly in the latter system without consciousness.

These two systems are in parallel in nature, with some interactions, and the outputs of the former system are transferred to the latter system.

2. EXPERIMENT 1: HEMISPHERIC ASYMMETRY IN COLOR PROCESSING

2.1. Background

2.1.1. Anatomical Asymmetry of Brain

Bilateral asymmetries have been found in the human brain—larger right than left prefrontal and larger left than right occipital lobe volume (Foundas et al., 2003). Asymmetry has been also reported in several subcortical structures. Amygdalar and hippocampal volume measurements indicate a right-greater-than-left asymmetry for right-handed normal participants (Jack et al., 1989; Szabo et al., 2001). These structural asymmetries suggest functional lateralization of various cerebral functions.

2.1.2. Hemispheric Lateralization of Cerebral Functions

It has been suggested that the left hemisphere plays an important role in linguistic and higher order cognitive processes, such as self recognition (McFie et al., 1950; Conway et al., 1999; Turk et al., 2002), whereas the right hemisphere is responsible for visuospatical perception and facial recognition (Kimura, 1969; Gazzaniga and LeDoux, 1978; Sergent et al., 1992; Haxby et al., 1994; Kanwisher et al., 1997; Barton et al., 2002; Corballis, 2003).

Several researchers have postulated lateralized function to each hemisphere. The right-hemisphere functions were referred to as "visuospatial," or "constructional" (Sperry, 1982). It has also suggested that the right hemisphere is specialized for the analysis of global-level information, and serves as an anomaly detector, while the left hemisphere tends to create a "story" to make sense of the incongruities (Ramachandran, 1998; Smith et al, 2002). Levy (1969) studied an organizational differentiation of the hemispheres for perceptual and cognitive functions and supposed that the left hemisphere is specialized for analytic and the right hemisphere is specialized for integrative processing. In addition, the left hemisphere is specific in logical processing, while the right one has superiority in emotion, music and holistic processing (Levy, 1969; Ladavas et al., 1984; Magnani et al., 1984; Patel et al., 1998). Little is known, however, about hemispheric asymmetry in color processing. In the first experiment we examined the hemispheric lateralization of color processing.

2.1.3. Hemispheric Asymmetry Using Reaction Time

Lateralized function in the cerebral hemisphere has been studied by using several methods, such as a same-different comparison task (Hannay, 1979), a list-learning procedure (Berry, 1990), tachistoscopic presentation (Malone and Hannay, 1978) and reaction time (Davidoff, 1976). These different methods reveal the different features of the cerebral function. However, the input information presented to either one of the hemispheres immediately transfers to the other hemisphere via the commisure fibers. The interhemispheric transfer time is estimated from 2 to 6 ms (Poffenberger, 1912; Berlucchi et al., 1971; Brizzolara et al., 1994; Brysbaert, 1994). Therefore, in order to detect a difference in the processing time between two hemispheres, a method with high time resolution should be used. The reaction time task has an advantage that it is sensitive to analyze the difference in time for information processing in the hemispheres.

2.1.4. Reaction Time Task Based Upon Double Crossed Projections

The optic nerve fibers originating from the nasal retina project to the contralateral visual cortex, while the others from the temporal retina project to the ipsilateral visual cortex, and the right motor cortex innervates the left hand and the left one innervates the right hand. Hemispheric dominance in color processing can be evaluated by using a reaction time task based upon these double crossed projections of the visual and pyramidal pathways features in human participants (Poffenberger, 1912; Berlucchi et al., 1971).

2.2. Experiment 1-1: Reaction Time Difference by Dominant and Non-Dominant Hands

2.2.1. Purpose

Hemispheric asymmetry can be evaluated based on the difference in reaction times to lateralized stimuli presented either in the left or the right visual field, and responded by the ipsilateral hand (Fig.1). The first experiment was designed to evaluate a difference of reaction times between the dominant and non-dominant hands using achromatic targets presented at the center of the visual field. The results of this experiment will serve as a control for difference of reaction time by different hand.

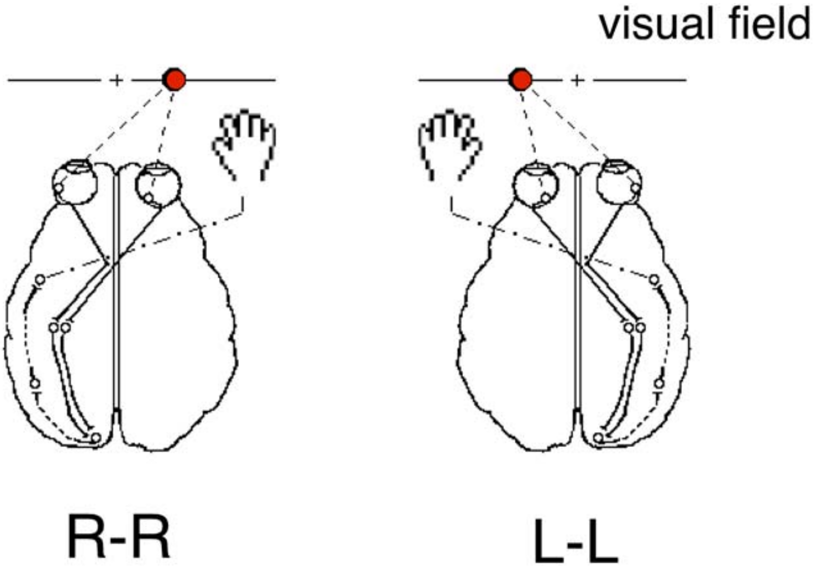


Figure 1. Schematic representation of experimental conditions used in Experiment 1. Reaction time was measured to a target presented in the right visual field by the right hand (R-R, left hemisphere) or the left visual field by the left hand (L-L, right hemisphere).

2.2.2. Methods

2.2.2.1. Participants

Ten right-handed undergraduate students (3 males and 7 females) with normal or corrected normal vision (mean age 19.5 years, SD 2.7) participated in the first experiment. Most of the participants were selected from ten groups of eight subjects each in a preliminary experiment, because they showed the smallest variability and the shortest reaction time in each group. In the preliminary experiment, thirteen simple reaction times to color stimuli (either red, green, blue or yellow) presented at the center of a cathode ray tube (CRT) display were recorded. No ‘ready’ signal was used in the preliminary experiment. All the participants were naive to this kind of behavioral experiment and the experiments were performed with the consent of each participant.

2.2.2.2. Apparatus

An achromatic solid circle with a diameter of 2 deg (x = 0.283, y = 0.320, CIE) was presented on a CRT display (Panasonic TX-D7P35-J, Japan, with a resolution of 800 x 600 dots at 60 Hz, 9300K). The luminous intensity of the target was 12, 14, or 18 cd/m^2 with a uniform gray background of 10 cd/m^2. The CRT display was placed at a distance of 57 cm from the participant's eye. All the visual stimuli were generated using a graphic generator (VSG Series Three, Cambridge Research Systems Ltd., England).

Reaction time was measured using a programmable logic controller (Keyence KV24AT, Japan). The experiments were automatically controlled by a computer (Power Macintosh 7300/180, Apple), using a hand-made program (HyperCard, Apple) and a serial/parallel interface.

Electro-oculogram (EOG) was recorded from two small electrodes with a diameter of 5 mm placed 2 cm above or below the lateral edges of right and left eyes. The signal was amplified with a time constant of 1.5 sec and with a high-cut filter at 60 Hz (Nihon Kohden, EEG-4316, Japan) and was recorded on a computer (Power Macintosh 7100/80AV, Apple) after being digitized at 400 Hz (MacLab, AD Instruments, Australia). If the amplitude of EOG exceeded 50 µV, which corresponded to an eye-movement of 3 deg in the visual angle, or if an eye blink occurred at the time of stimulus presentation, the trial was omitted from later analysis. In addition, trials with reaction times longer than 400 ms were omitted from later analysis. Thus about 10 % of the trials were omitted as error trials.

2.2.2.3. Procedures

Participants were seated in a sound-attenuated chamber, facing the CRT display. The participant's head was loosely restrained by using a chin rest, and the participant was asked to fixate at a small cross (0.5 deg, 0.5 deg) at the center of the CRT. An auditory 'ready' signal preceded the onset of the target stimulus by 1-4 sec (mean 2.5 sec), and the delays were delivered in a quasi-random order (Fig. 2).

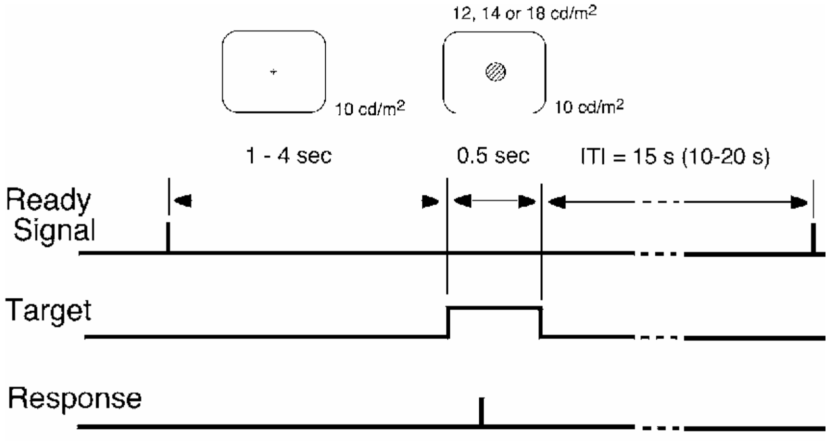


Figure 2. Schematic illustration of the time schedule for Experiment 1-1. A trial started with an auditory ready signal preceding 1-4 sec with a mean of 2.5 sec. A target was presented for 0.5 sec at the center of the CRT, where a small cross was presented as a fixation point. A total of 15 trials were performed with an intertrial interval of 10-20 sec with a mean of 15 sec. The target was a gray circle with a diameter of 2 deg at either12, 14 or 18 cd/m^2 with a gray background of 10 cd/m^2.

Two blocks of experiments were performed with an inter-block interval of about 5 min. In each block, participants were required to press the key as quickly as possible to each stimulus presented at the center of visual field (Fig. 3). Before starting each block, participants were instructed which hand to use and the order of hands used were randomized among the participants. Each block consisted of 15 trials with a randomized intertrial interval of 15 sec ranging from 10 sec to 20 sec. The median reaction time was calculated for each block for each participant. The mean value was then obtained for each condition (right or left hand).

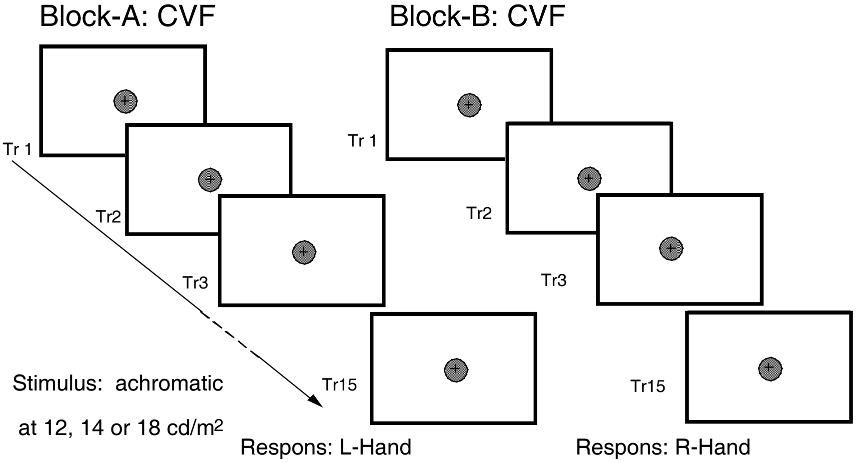


Figure 3. Schematic drawing of the procedure for Experiment 1-1. Two blocks, each consisting of 15 trials, were performed, using three different luminance stimuli (12, 14 or 18 cd/m^2) each for 5 trials. For both block-A and block-B, target was presented at the center of visual field (CVF). Response was made by the left hand (L-Hand) for block-A, and by the right hand (R-Hand) for block-B, respectively. Order of the blocks was randomized for each individual. Which block was performed had been informed before starting each block.

2.2.3. Results

There was no significant difference between the reaction times by the dominant (right) and non-dominant (left) hands (Fig. 4). Figure 5 shows reaction times by the dominant and non-dominant hands to three target luminance (12, 14 and 18 cd/m^2). Reaction time decreased gradually as a function of stimulus intensity. For both dominant and non-dominant hands, however, there was no significant difference between the reaction times of the right and left hands in any luminance condition. Similar results were obtained for the mean of these three luminance conditions, shown at the extreme right column in Fig. 2 (12-18 cd/m^2). Statistical analysis using analysis of variance (ANOVA) showed that only the effect of luminance was significant ($F(2,18) = 5.854$, $p < 0.01$), and both the effect of hands and the interaction between these two factors were not significant ($F(1,9) = 0.019$, N.S., $F(2,18) = 0.550$, N.S., respectively).

2.2.4.Discussion

The results of Experiment 1-1 show that the dominant hand has no advantage over the non-dominant hand for the simple reaction time task, in which triggering simple hand-movement-initiation is required. This finding is well consistent with previous studies (Hayes and Halpin, 1978; Annett and Annett, 1979; Adam and Vegge, 1991), thus confirming the validity of the present experimental procedures. The time required for the response selection and/or the motor control processes, which can be assumed to exist between stimulus presentation and the response (Schmidt and Lee, 1998), were also suggested to be similar between the reaction times by the dominant and non-dominant hands. This means that no correction is required when comparing reaction times by the dominant and non-dominant hands in the following experiments.

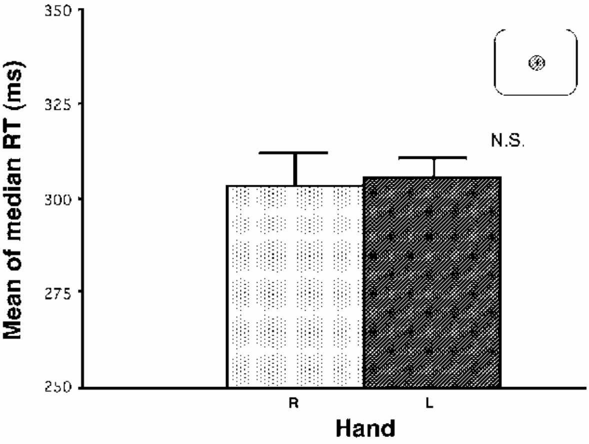


Figure 4. Simple reaction time by right (R, dominant) or left (L, non-dominant) hand to achromatic targets presented at the center of visual field in 10 right-handed participants. There was no significant difference between reaction times by dominant and non-dominant hands. Mean with SE.

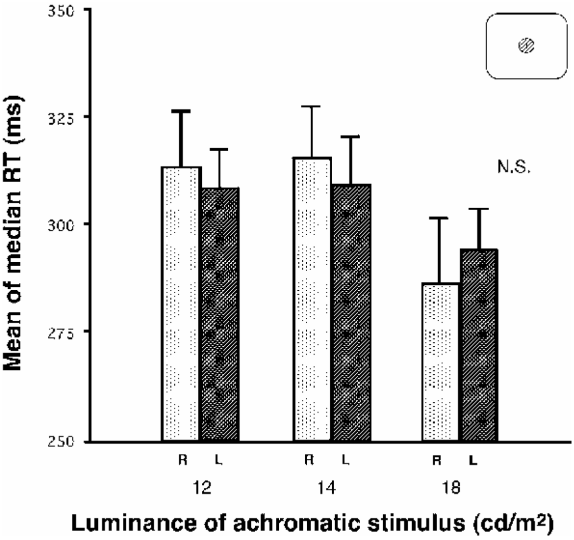


Figure 5. Simple reaction time by the right hand (R, dominant) or the left hand (L, non-dominant) to achromatic stimulus presented at the center of visual field in 10 right-handed participants. Means of median reaction time (mean with SE) were plotted against luminance of stimulus. There was no significant (N.S.) difference between reaction times by dominant and non-dominant hands to visual stimuli in each luminance level (12, 14, and 18 cd/m^2).

2.3. Experiment 1-2: Hemispheric Asymmetry of Color Detection in Right-Handed Individuals

2.3.1. Purpose

In this experiment, the hemispheric difference of color processing was evaluated by comparing reaction times of the right and left hands to chromatic stimuli presented to the ipsilateral visual field of right-handed individuals.

2.3.2. Materials and Methods

2.3.2.1. Participants

Ten right-handed undergraduate students (7 males and 3 females) with normal or corrected-to-normal vision (mean age 22.6 years, SD 6.1) participated in this experiment. All of these participants were selected from ten groups of eight subjects in the preliminary experiment as in Experiment 1-1.

2.3.2.2. Apparatus

One of three chromatic solid circles with a diameter of 2 deg (red, $x = 0.553$, $y = 0.313$, CIE; green, $x = 0.279$, $y = 0.577$, CIE; or blue, $x = 0.226$, $y = 0.151$, CIE) was presented on the CRT with a uniform gray background of 10 cd/m^2. All of these chromatic stimuli had the same saturation of 60%. The luminance of the chromatic stimuli was adjusted to gray of 10 cd/m^2 using the flicker photometry method so that it was equal for all participants, thus only the hue change served as a cue for the detection of the stimulus.

2.3.2.3. Procedures

Two blocks, each consisting of 15 trials, were performed, with an inter-block interval of about 5 min (Fig. 6). For each block, participants were asked to press the key either with the right hand for targets presented in the right visual field (R-R condition), or with the left hand for targets in the left visual field (L-L condition). Before starting each block the participants were instructed which hand to use depending on the side of stimulus presentation. Thus, there was no spatial cue for the response. The order of block was randomized among participants. In each trial, one of the three chromatic targets was presented at 4 deg horizontally from the fixation point in either right or left visual field (Fig. 7). The rest of the procedure was the same as in Experiment 1-1.

2.3.3. Results

Figure 8 shows the reaction times to the chromatic targets in R-R and L-L conditions. In the right-handed participants, reaction time in L-L (320±9 ms, mean ± SE) was shorter than that in R-R (303±9 ms, mean ± SE). Since there was no significant difference between reaction times to the target colors (red, green and blue), data were collapsed across cued color. Statistically significant difference was observed between reaction times in L-L and R-R (time difference was 17 ms, $t(9) = 3.171$, $p < 0.05$). The significant difference was still apparent if the analysis included only six right-handed participants who participated in both Experiments 1-2 and 1-4 ($t(5)=6.544$, $p < 0.01$). Shorter reaction time in L-L was consistently observed in each of the three colors. These data show that right hemisphere is dominant in the detection of chromatic stimulus among right-handed participants.

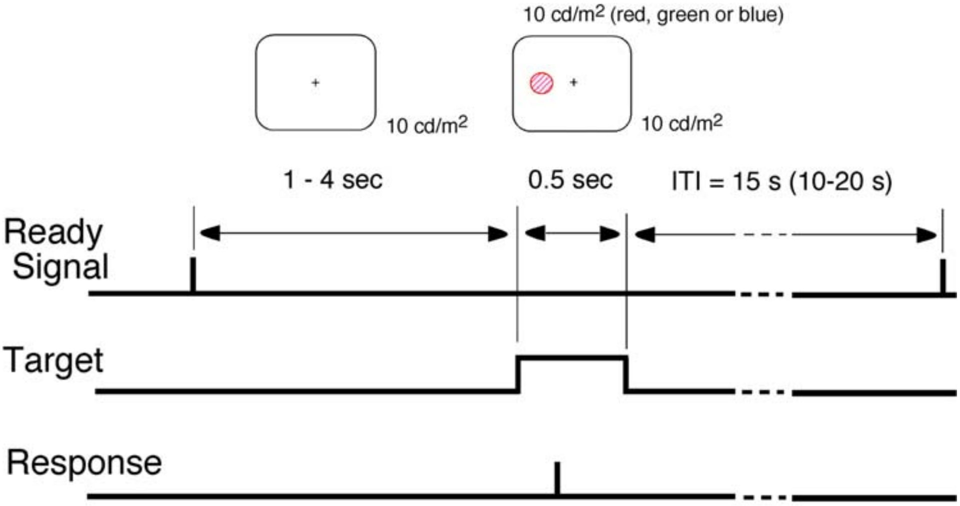


Figure 6. Schematic illustration of the time schedule for Experiment 1-2. A trial started with an auditory ready signal preceding 1-4 sec with a mean of 2.5 sec. A target was presented at 4 deg lateral to the fixation point, either left or right visual field for 0.5 sec. A total of 15 trials were performed with an intertrial interval of 10-20 sec with a mean of 15 sec. The target was a 2-deg chromatic circle of either red, green or blue with a gray background of 10 cd/m^2.

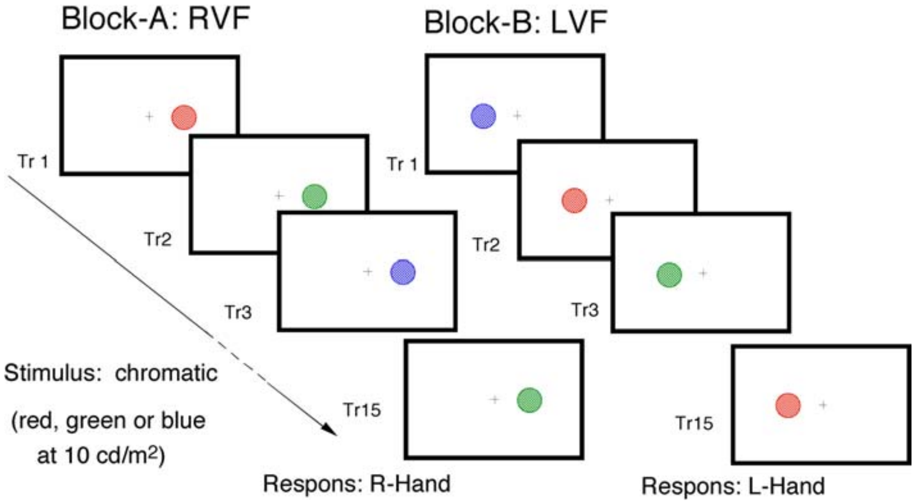


Figure 7. Schematic drawing of the procedure for Experiment 1-2. Two blocks, each consisting of 15 trials, were performed, using three different chromatic stimuli (red, green or blue) each for 5 trials. For block-A, target was presented in the right visual field (RVF), and for block-B in the left visual field (LVF). Response was made by the right hand (R-Hand) for block-A, and by the left hand (L-Hand) for block-B, respectively. Orders of the chromatic stimuli and of the blocks were randomized for each individual. Which block was performed had been informed before starting each block.

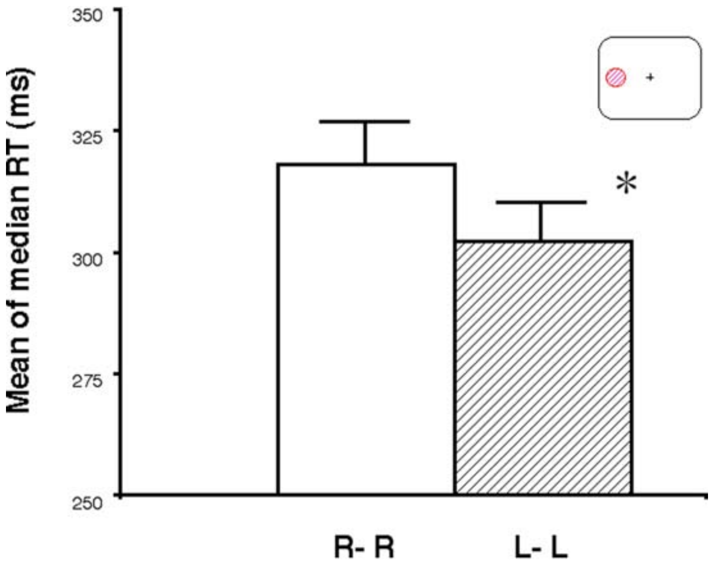


Figure 8. Simple reaction time by the right hand to chromatic targets presented in the right visual field (R-R), and by the left hand to targets presented at the left visual field (L-L) in 10 right-handed participants. Mean of median reaction time in L-L was significantly faster than in R-R (* $p<0.05$). Mean with SE.

2.3.4. Discussion

Clear right hemisphere dominance in color detection was observed among the right-handed individuals. A time difference of the color processing between right hemisphere and left hemisphere was 17 ms. This time difference cannot be ascribed to the difference of hands, or motor process, because there was no significant difference between reaction times by the dominant and non-dominant hands (Experiment 1-1). Thus, the time difference should be ascribed to the difference in the processing of visual stimuli.

In the present study, we found hemispheric asymmetry in detection of chromatic stimuli in normal subjects, not in patients. Present findings seem to be in good harmony with previous results, in which color discrimination is specialized for the right hemisphere (Davidoff, 1976; Pennal, 1977). However, in these prior studies, the target color stimuli were presented on a dark background of different luminance. Therefore, appearance of the target was inevitably accompanied by a change in luminance, in addition to a change in hue. As it has been known that the salience of stimulus is one of the important variables that affect reaction time (Schmidt and Lee, 1998), if more than two attributes of a stimulus change simultaneously, the more salient attribute may overshadow the effects of the other (Sutherland and Mackintosh, 1971; Rescorla and Wagner, 1972; see Christman, 1989). In contrast, in the present study, we used color stimuli with the subjectively equated luminance as the background to control all attributes as equal, except for hue.

Consistent with the present results, it has been reported that deficits in color detection in the contralateral visual field are more frequently observed in patients with a lesion of the right postero-occipital cerebral areas than the left ones (Scotti and Spinnler, 1970). Cortical color blindness has been also reported in patients with impairment of the left visual field (Albert et al., 1975). These findings imply that RH is dominant in the detection of color among the right-handed individuals. However, to elucidate the neural mechanisms underlying the asymmetric processing in color detection, further studies should be done including recording of cortical activity during color detection task, and using methods with high time resolution.

2.4. Experiment 1-3: Hemispheric Asymmetry of Color Detection in Left-Handed Individuals

2.4.1. Purpose

In this experiment, the hemispheric difference of color processing was evaluated by comparing reaction times of the right and left hands to chromatic stimuli presented to the ipsilateral visual field of left-handed individuals.

2.4.2. Methods

2.4.2.1. Participants

Eight left-handed mail subjects (7 undergraduate students and one researcher) with normal or corrected-to-normal vision (mean age 25.1 years, SD 9.3) participated in this experiment. All of these left-handed participants were selected based on an assessment of the handedness score using a modified Edinburgh Laterality Inventory (Oldfield, 1971), which included 7 items: write, eat, throw, tooth brushing, drive, key, and hammer. For each item, right-handed responses were scored as 0, left-handed ones as 1, or both hands as 0.5. The total score of the left-handed participants ranged from 2.0 to 7.0 (4.6±1.6, mean ± SD), while that of the right-handed ones was 0.

2.4.2.2. Apparatus and Procedures

The experimental apparatus and procedures for this experiment were similar for the Experiment 1-1 and 1-2, excepting that color stimuli were used to examine the effect of dominant hand on the simple reaction time.

2.4.3. Results

Figure 9 shows that there was no significant difference between the simple reaction times by dominant and non-dominant hands in the left-handed participants.

There was no significant difference between simple reaction times in R-R and L-L conditions among the left-handed participants (Fig. 10 right, R-R 325±5 ms, mean ± SE; L-L 324±9 ms, mean ± SE; t(7) = 0.179, N.S.). However, it might be assumed that right hemisphere is more specialized in color detection among the left-handed individuals with low left-handedness score, while symmetrical processing occurs among the typical left-handers with high score. In order to ascertain this possibility, we performed the correlation analysis. No significant correlation between the handedness scores and reaction time differences (R-R – L-L) was observed（r = 0.006, p = 0.990, N.S.）.

2.4.4. Discussion

A more symmetrical hemispheric processing was observed among left-handed individuals compared to right-handed individuals. It is well known that language cerebral dominance is lateralized in the left hemisphere in 88-96% of right-handed individuals and in

43-76% of left-handers (Pujol et al., 1999; Springer et al., 1999; Khedr et al., 2002). It has been suggested that the hemispheric specialization of brain functions is less clear among left-handers than among right-handers (Zangwill, 1962, Bryden et al., 1982). Consistent to this concept, the present study showed that color detection was less clearly lateralized among the left-handed participants than among the right-handed participants

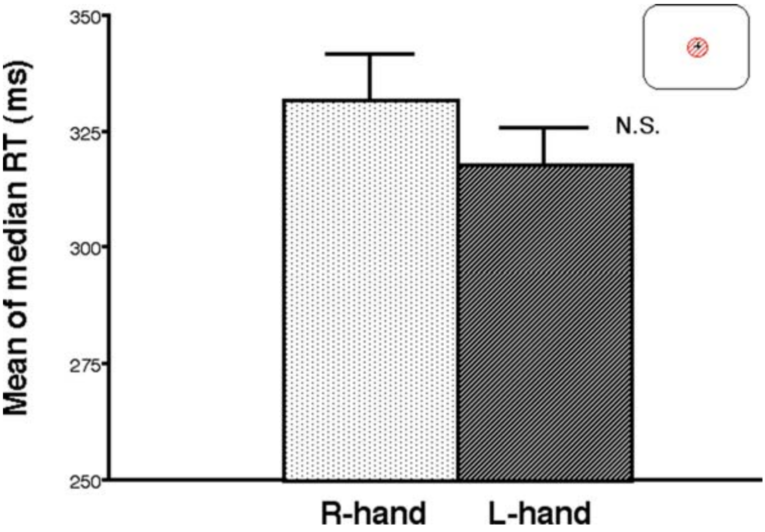


Figure 9. Simple reaction times to target stimuli presented at the center of visual field, responded by the right hand (R-hand, non-dominant) and the left hand (L-hand, dominant) in 8 left-handed participants. There was no significant difference between reaction times by dominant and non-dominant hands. Mean with SE.

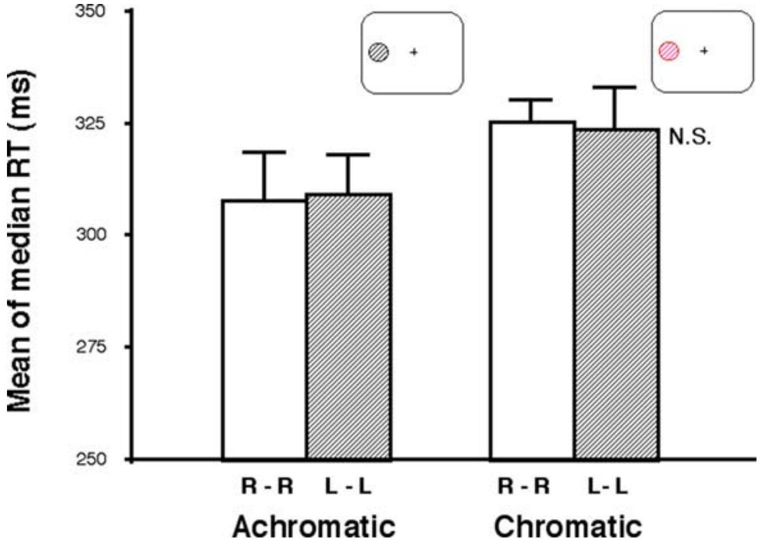


Figure 10. Simple reaction times to lateralized stimuli, responded by the right hand to targets presented in the right visual field (R-R), and by the left hand to targets presented in the left visual field (L-L) in 8 left-handed participants. Target stimulus was achromatic (left, 20 cd/m^2) or chromatic (right). There was no significant difference between reaction times in R-R and L-L both to achromatic and chromatic stimuli. Mean with SE.

2.5. Experiment 1-4: Hemispheric Asymmetry of Non-Color Detection in Right- and Left-Handed Individuals

2.5.1. Purpose

This experiment was designed to identify the critical factor for the asymmetry observed in Experiment 1-2. We determined whether the asymmetry observed in the detection of color might also be found in the detection of achromatic stimuli or not. If the asymmetry was lost using achromatic stimuli, it should therefore be ascribed to color processing and not to other factors.

2.5.2. Methods

2.5.2.1. Participants

Twelve right-handed (6 males and 6 females, mean age 20.5 years, SD 2.8) and eight left-handed undergraduate students participated in the present experiment. Six right-handed subjects were the same individuals who participated in Experiment 1-1, while the other six subjects were those who participated in Experiment 1-2. All left-handed subjects were those who participated in Experiment 1-3.

2.5.2.2. Apparatus

An achromatic solid circle with a diameter of 2 deg (x = 0.283, y = 0.320, CIE) was presented on the CRT with a uniform gray background of 10 cd/m^2 (Fig. 11). In the six right-handed participants who participated in Experiment 1-1, luminance of either 12, 14, or 18 cd/m^2 was tested, while in other six right-handed participants who participated in Experiment 1-2, as well as in the eight left-handed participants, only a luminance of 20 cd/m^2 was used.

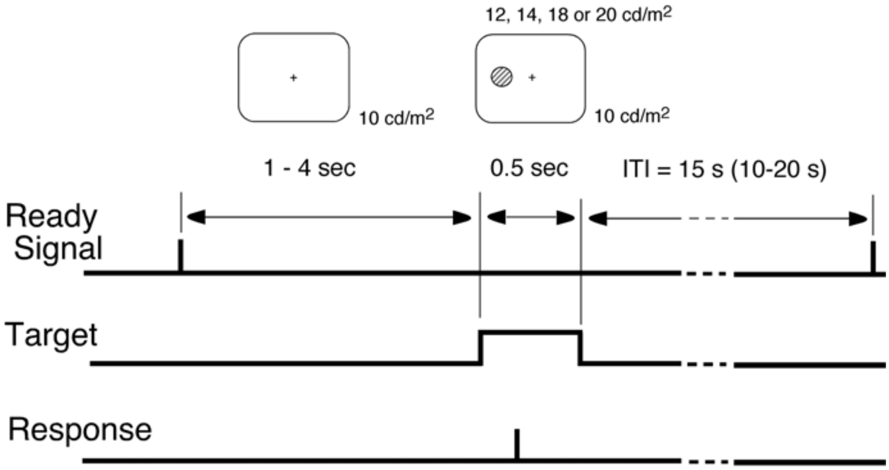


Figure 11. Schematic illustration of the time schedule for Experiment 1-4. A trial started with an auditory ready signal preceding 1-4 sec with a mean of 2.5 sec. A target was presented at 4 deg lateral to the fixation point. either left or right visual field for 0.5 sec. A total of 15 trials were performed with an intertrial interval of 10-20 sec with a mean of 15 sec. The target was an achromatic circle with a diameter of 2 deg, either 12, 14, 18 or 20 cd/m^2 with a gray background of 10 cd/m^2.

2.5.2.3. Procedures

The reaction times to achromatic stimuli presented in either right hemisphere or left hemisphere were recorded. In each block, the achromatic target was presented either on the right or the left visual field, at 4 deg horizontally from the fixation point (Fig. 12). Other experimental settings and procedures were the same as in Experiment 1-2.

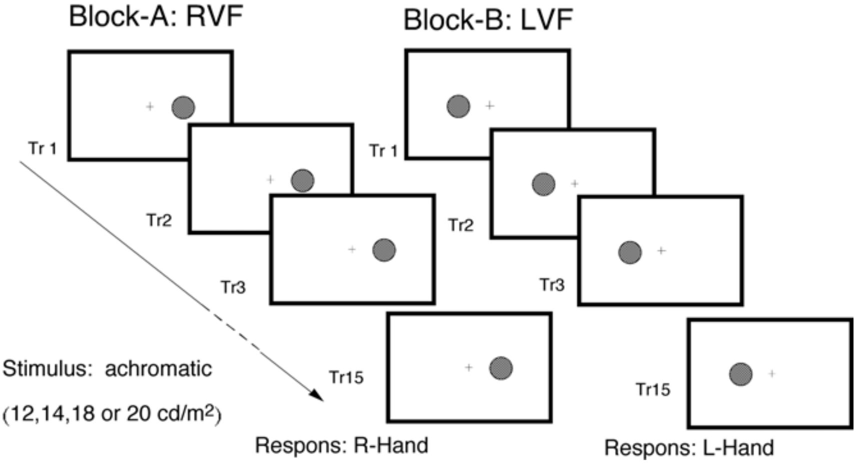


Figure 12. Schematic drawing of the procedure for Experiment 1-4. Two blocks, each consisting of 15 trials, were performed, using three different chromatic stimuli (red, green or blue) each for 5 trials. For block-A, target was presented in the right visual field (RVF), and for block-B in the left visual field (LVF). Response was made by the right hand (R-Hand) for block-A, and by the left hand (L-Hand) for block-B, respectively. Order of the blocks was randomized for each individual. Which block was performed had been informed before starting each block.

2.5.3. Results

As the stimulus luminance increased, the reaction time to the achromatic stimulus decreased in the right-handed participants (Fig. 13). There was a statistically significant difference between the mean reaction time of 12, 14, 18 cd/m^2 (N = 6) and the mean reaction time at 20 cd/m^2 (N = 6), in R-R and L-L conditions ($t(10) = 3.221$, $p < 0.01$; $t(10) = 2.686$, $p < 0.05$), respectively. However, at any target luminance, no significant difference was found between the reaction times to the achromatic stimuli among the right-handed participants in RR and LL conditions (W12 $t(5) = 0.697$, N.S.; W14 $t(5) = 0.188$, N.S.; W18 $t(5) = 1.057$, N.S.; W20 $t(5) = 0.464$, N.S.), even after these data were pooled ($t(23) = 0.704$, N.S.). Similarly, there was no significant difference between the reaction times to the achromatic stimuli among the eight left-handed participants in R-R and L-L conditions (308±11 ms, mean ± SE; 309±9 ms, mean ± SE, respectively; $t(7) = 0.192$, N.S., Fig. 10 left).

2.5.4. Discussion

2.5.4.1. Effect of Luminance on Hemispheric Asymmetry

The decrement of reaction time with increasing luminance of target stimulus observed in Experiment 1-4 is well consistent with previous results. It has been known that reaction time depends on the intensity or salience of the stimulus (Lit et al., 1971; Jaskowski, 1982; Adams and Mamassian, 2004).

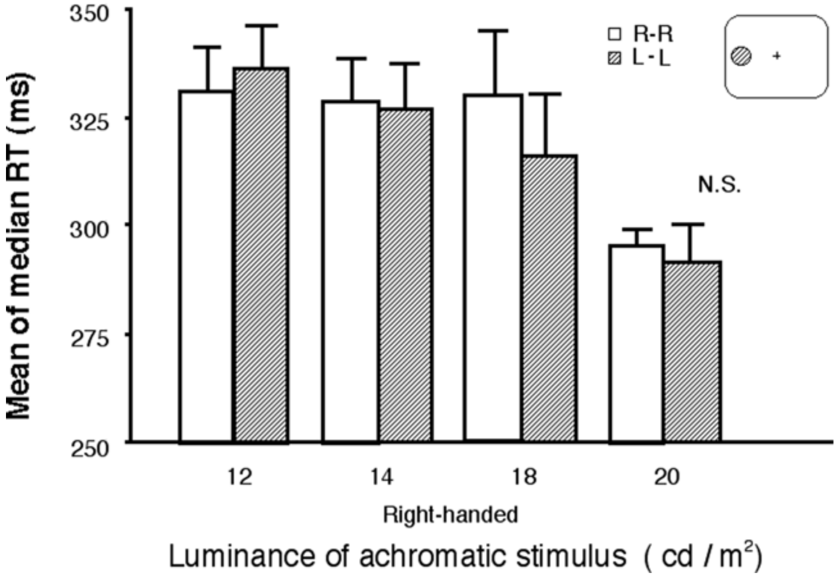


Figure 13. Simple reaction times to achromatic stimuli presented either in the right visual field responded by the right hand (R-R; open bars) or the left visual field responded by the left hand (L-L; hatched bars) in right-handed participants (n=6; 12, 14 or 18 cd/m^2, n=12; 20 cd/m^2). In any case there was no significant difference between reaction times in R-R and L-L. Mean with SE.

Although there are many studies examining hemispheric asymmetry of luminance processing, only a few studies have explicitly examined the effects of stimulus luminance (see review by Christman, 1989). Christman (1990) varied luminance within a temporal integration task involving the identification of digits and found that increases in luminance tend to preferentially benefit left hemisphere. Sergent (1982) varied luminance in a task requiring subjects to judge the gender of laterally presented faces and found a shorter reaction time in right hemisphere for low luminance (0.8 mL) and in left hemisphere for high luminance stimuli (12.0 mL). More recently, Corballis et al. (2002) found in split-brain patients that luminance discrimination was processed equivalently by the two hemispheres. Thus, there is no general consensus regarding whether there is hemispheric asymmetry in the detection speed of the achromatic patch stimulus used in the present study. Since we have used chromatic stimuli with constant luminance (Experiment 1-2), luminance itself does not seem to be an important factor for right hemisphere advantage in the present experiment. No significant asymmetry was observed in the luminance detection task in Experiment 1-4. Therefore, the asymmetry obtained in Experiment 1-2 can be ascribed to color processing.

2.5.4.2. Effect of Contrast on Hemispheric Asymmetry

One might argue that stimulus contrast might affect the hemispheric asymmetry found in Experiment 1-2. Stimulus contrast, however, has been shown to benefit either left hemisphere, right hemisphere processing, or no hemispheric difference depending on the task characteristics (Christman, 1989). No asymmetry was found in Experiment 1-4, where the contrast changed with the luminance. Both luminance and contrast, therefore, does not seem to contribute considerably to the right hemisphere advantage in color detection.

2.5.4.3. Effect of Practice on Visual Field Difference

In Experiment 1-4 no significant hemispheric difference was observed, which shows that the right hemisphere superiority observed in Experiment 1-2 was due to the detection of color. However, there is a possibility that the lack of asymmetry found in Experiment 3 might be due to practice effects. Most participants in the present study were assigned to two experiments. Half of the subjects had participated in Experiment 1-2 and the other half had participated in Experiment 1-1. There are general carry-over effects in psychological experiments. And in a visual half-field paradigm, visual field differences sometimes disappear with practice. Therefore, the observation that there was no hemispheric difference in Experiment 1-4 might be due to the practice effect.

This possibility can be examined by making two comparisons. First is the comparison of reaction times between R-R and L-L in the two groups. No significant difference was observed between reaction times in R-R (292±3.4 ms, mean ± SE) and L-L (289±11.3 ms, mean ± SE) in the 6 right-handed subjects who participated in Experiment 1-2 ($t(5)=0.464$, $p = 0.6621$). Similarly, no significant difference was observed between reaction times in R-R (329±14.5 ms, mean ± SE)) and L-L (326±11.3 ms, mean ± SE)) in the 6 right-handed subjects who had not participated in Experiment 1-2 ($t(5)=0.362$, $p = 0.7323$). Second is the comparison of the mean reaction time difference between RR and LL in these two groups. The difference of reaction times between R-R and L-L was 3.8±8.3 ms (mean ± SE) in the 6 subjects who participated in Experiment 1-2, and was 3.7±10.6 ms (mean ± SE) in the 6 subjects who had not participated in Experiment 1-2. No significant difference was observed between the mean differences ($t(10)= 0.012$, $p = 0.9904$). These two comparisons rule out the practice effect as an explanation.

2.5.4.4. Effect of Subject Number Size

In Experiment 1-4 no hemispheric asymmetry was observed to the achromatic targets in the right-handed participants, while clear asymmetry was found to the chromatic targets in Experiment 1-2. It seems impossible that the null results in Experiment 1-4 might be ascribed to a small number of subjects, because no asymmetry could be observed even in a larger size of subject ($N= 24$), in comparison to the size of subject in Experiment 1-2 ($N= 6$ or 10). Consistent with this view, the effect size (Dunlap et al. 1996) for the null results was smaller ($d= 0.025$) than those were obtained in Experiment 1-2 ($d= 0.678$, 0.198; $N= 6$, 10, respectively). These findings reject the possibility that a relative small number size of participants is responsible for the null results in Experiment 1-4.

2.6. Experiment 1-5: Hemispheric Asymmetry of Color Discrimination with Verbal Cue in Right-Handed Individuals

2.6.1. Purpose

In the next, we examined the hemispheric asymmetry of color discrimination. Detection and discrimination require different neural processing, thus different group of neurons are involved in the two processes (Schmidt and Lee, 1998).

2.6.2. Methods

2.6.2.1. Participants

Ten right-handed undergraduate students (5 males and 5 females) with normal or corrected-to-normal vision (mean age 23.0 years, SD 1.0) participated in the present experiment. All of these participants were newly selected from ten groups of eight subjects in the preliminary experiment as in Experiment 1-1.

2.6.2.2. Apparatus

One of three chromatic solid circles with a diameter of 2 deg (red, $x = 0.553$, $y = 0.313$, CIE; green, $x = 0.279$, $y = 0.577$, CIE; and blue, $x = 0.226$, $y = 0.151$, CIE) were presented at 4 deg from the center of the CRT with a uniform gray background of 10 cd/m^2 as in Experiment 1-2. The luminance of the chromatic stimuli was adjusted using the flicker photometry method as described in Experiment 1-2.

2.6.2.3. Procedures

The subjects were required to press a key quickly after they perceived the color that was not told before each session. For example, if the designated color was red, then target colors were green and blue. Each block consisted of 15 trials, 5 trials each for 3 conditions (target color was either non-red, non-green, or non-blue) with a randomized intertrial interval of 20 sec ranging from 15 sec to 30 sec. A total of 6 blocks, 3 blocks for L-L and 3 blocks for R-R were performed with a quasi-random order. Mean correct response rate was 94.8±1.03 % (± SE).

2.6.3. Results

Figure 14 shows that the mean discrimination reaction time was significantly shorter in R-R than L-L condition (367.2±20.98 ms vs. 385.6±21.15 ms, mean ± SE, paired-t(9)=2.718, $p<0.05$). The left hemispheric superiority in color discrimination based on the verbal cues was found in 8 of 10 participants (Fig. 15). These findings suggest that right-handed participants have left hemispheric predominance in color discrimination task with verbal cues.

2.6.4. Discussion

The discrimination reaction time was longer than the simple reaction time. This is consistent with a view that a serial processing of signal detection and discrimination and that the discrimination needs more process than the detection of color (Schmidt and Lee, 1998). The present finding that the discrimination reaction time was shorter in left hemisphere than in right hemisphere might suggest that the left hemisphere is dominant in color discrimination. However, before draw a conclusion, we must consider about effect of verbal processing in the present discrimination task. It is well known that the verbal processing is dominant in the left hemisphere (LeDoux et al., 1977; Gazzaniga et al., 1977), although it is also clear that there are complementary specializations of the right hemisphere (Sperry, 1982). Thus, the present finding that the discrimination reaction time was shorter in left hemisphere might be associated mainly with language processing in the left hemisphere.

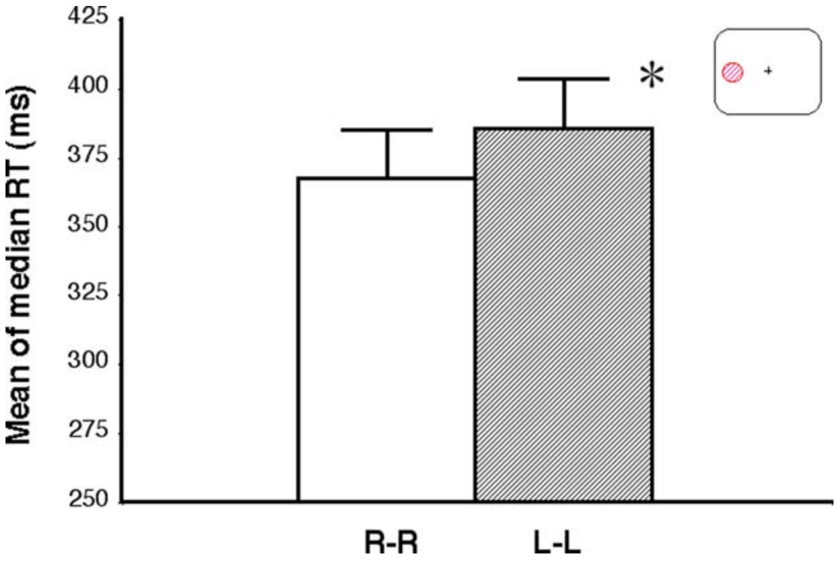


Figure 14. Discrimination reaction times to chromatic stimuli presented either in the right visual field responded by the right hand (R-R) or the left visual field responded by the left hand (L-L) in 10 right-handed participants. The discrimination task involved verbal cues. The subjects were required to press a key if the color was not told before each session (non-matching). Mean reaction time was significantly shorter in R-R than L-L (* p<0.05). Mean with SE.

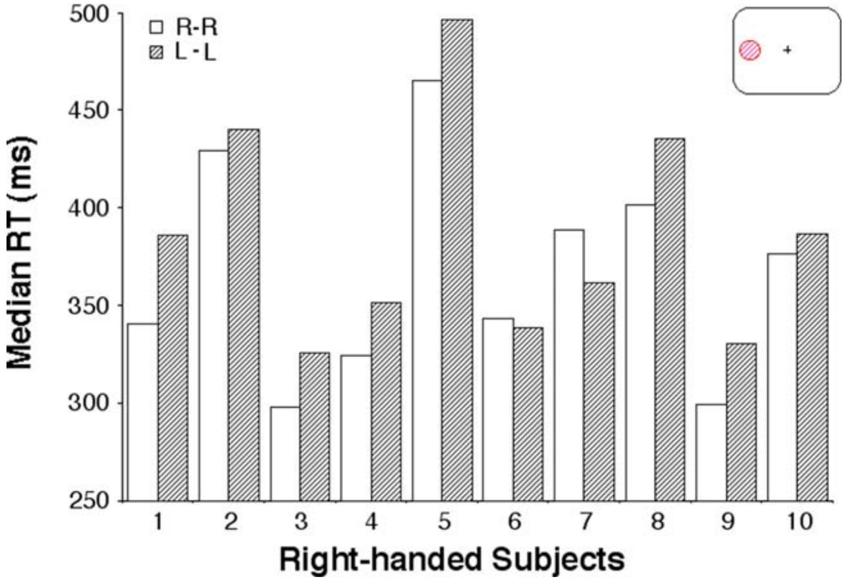


Figure 15. Discrimination reaction times with verbal cues to chromatic stimuli presented either in the right visual field responded by the right hand (R-R) or the left visual field responded by the left hand (L-L) in each of 10 right-handed participants. In 8 of 10 participants, discrimination reaction time was shorter in R-R than L-L.

2.7. Experiment 1-6: Hemispheric Asymmetry of Color Discrimination without Verbal Cue in Right-Handed Individuals

2.7.1. Purpose

In this experiment, hemispheric lateralization in color discrimination was examined using a task which dose not requires verbal processing.

2.7.2. Methods

2.7.2.1. Participants

Eight right-handed undergraduate students (7 males and 1 female) were participated in the present experiment (mean age 22.0 years, SD 2.2). All of these participants were newly prepared. The participants were required to press a key when two stimuli were different in hue or luminance.

2.7.2.2. Apparatus

Two of three chromatic circles (red, x = 0.553, y = 0.313, CIE; green, x = 0.279, y = 0.577, CIE; and blue, x = 0.226, y = 0.151, CIE) or two of three achromatic ones (12, 14 and 18 cd/m^2) were presented at 4 deg lateral to the center of the CRT either in the left or right visual field with a uniform gray background of 10 cd/m^2. The diameters of circles were 2 deg. The chromatic stimuli had the same saturation of 60%. The luminance of the chromatic stimuli was adjusted to gray of 10 cd/m^2 using the flicker photometry method.

2.7.2.3. Procedures

Participants were required to press a key as fast as possible when the two stimuli presented simultaneously were different either in hue (chromatic stimuli) or luminance (achromatic stimuli). Response was required to be done using the ipsilateral hand to the visual field. Which hand to use was instructed before starting each block.

A block consisted of 48 trials; 36 chromatic and 12 achromatic trials with a quasi-random order. Four trials were performed for each condition. For a chromatic trial, one of nine conditions (RR, RG, RB, GR, GG, GB, BR, BG and BB), and for an achromatic trial, one of three conditions (14-12 cd/m^2, 14-14 cd/m^2, and 14-18 cd/m^2) was tested.

A total of four blocks (discrimination reaction time with R-R or L-L, and simple reaction time with R-R or L-L condition) were performed for each participant with a quasi-random order. Discrimination reaction times longer than 600 ms and simple reaction time longer than 400 ms were omitted from later analysis. Other procedures were the same as in Experiment 1-2. Data from one subject was omitted from later analysis for achromatic stimuli, because he made no response to achromatic stimuli in L-L condition.

2.7.3. Results

Although the discrimination reaction time to chromatic stimuli was tend to be shorter in the left hemisphere (386.7±11.2 ms, mean ± SE) than in the right hemisphere (409.6±17.5 ms, mean ± SE), the difference was not statistically significant (paired-t(7)=1.722, p=0.1286) (Fig. 16). Similarly, although a net discrimination time which was obtained by subtracting simple reaction time from the discrimination reaction time was tend to be shorter in the left hemisphere (R-R: 123.3±10.8 ms, mean ± SE, L-L: 150.8±20.1 ms, mean ± SE), no statistically significant difference was found (paired-t(7)=1.867, p=0.1041) (Fig. 17). As for achromatic stimuli, there was no significant difference in achromatic discrimination reaction time (R-R: 514.7±10.1 ms, mean ± SE, L-L: 520.4±17.7 ms, mean ± SE, paired-t(6)=0.361, p=0.7303), or even after the net discrimination time was calculated (R-R: 258.3±12.4 ms, mean ± SE, L-L: 273.9±18.7 ms, mean ± SE, paired-t(6)=0.647, p=0.5414). From these findings we could not find any significant hemispheric asymmetry in color discrimination.

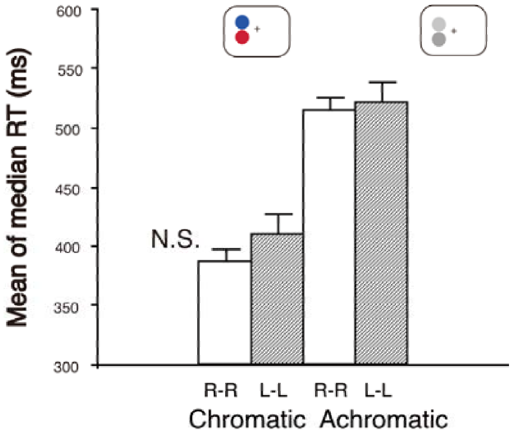


Figure 16. Discrimination reaction times without verbal cues to lateralized stimuli presented either in the right visual field responded by the right hand (R-R) or the left visual field responded by the left hand (L-L) in 8 right-handed participants. The discrimination task was not dependent on verbal cues. There was no significant difference between the reaction times both to chromatic and achromatic stimuli. Mean with SE.

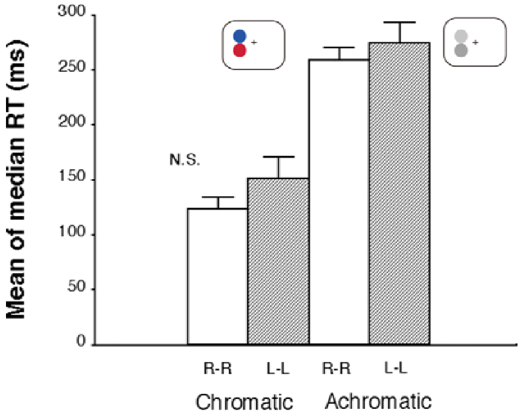


Figure 17. Net discrimination times to stimuli presented either in the right visual field responded by the right hand (R-R) or the left visual field responded by the left hand (L-L) in 8 right-handed participants. The discrimination task was not dependent on verbal cues. The net discrimination time was calculated by subtracting simple reaction time from discrimination reaction time. There was no significant difference between the net discrimination times both to chromatic and achromatic stimuli. Mean with SE.

2.7.4. Discussion

Although clear asymmetry was found in the color detection (Experiment 1-2), no hemispheric difference was observed in the color discrimination reaction time without using language cues. Consistent with this, Danilova and Mollon (2009) recently reported that no asymmetry in color discrimination. However, before draw a conclusion we should consider a possibility that a longer reaction time has a larger variation. Both in Experiments 5 and 6, discrimination reaction time was longer than simple reaction time. This may easily obscure a subtle difference in reaction time and make it difficult to detect any difference in discrimination reaction time. To elucidate a small but definite difference in reaction time, it is important to adopt some explicit and refine methods to reduce individual variation (Sasaki et al. 2008). The net discrimination time, however, showed a slight tendency of shorter reaction time in left hemisphere (R-R) than right hemisphere (L-L) for chromatic stimuli, no significant difference was found. These findings suggest that color detection is specialized for the right hemisphere, while color discrimination is not specialized for any hemisphere.

It was shown that emotional stimuli are perceived more efficiently by the right hemisphere than by the left hemisphere (McKeever and Dixon, 1981; Smith et al., 2004; Sato and Aoki, 2006). And the right hemisphere plays an important role in producing emotions (Ladavas et al., 1984). Effect of right amygdala in discriminating emotional faces without primary visual cortices has been suggested (Pegna et al., 2005). A subcortical pathway to the right amygdala, via superior colliculus and pulvinar of the thalamic nucleus, provides a rout for processing unconscious identification of affective expressions in parallel to a cortical route necessary for conscious identification (Morris et al., 1999).

Verbal and non-verbal communication is important for social behaviors in humans. The non-verbal communication includes gestures, eye contact, and expression of emotion, such as disappointment, fear, pleasure, and surprise. Because the right hemisphere is closely related to emotion, as described above (Ladavas et al., 1984), it is suggested that the right hemisphere plays an important role in the non-verbal communication, by contrast the verbal communication in the left hemisphere.

3. EXPERIMENT 2: PREPULSE INHIBITION OF STARTLE BLINK RESPONSE USING COLOR PREPULSE

3.1. Background

In the second experiment, contributions of color stimulus to modulation of the corneal blink reflex were examined in healthy human subjects.

3.1.1. Startle Response

A sudden intense stimulus produces a startle response in many species of animal (Landis and Hunt, 1936; see Davis, 1984). Startle response is one of defensive reflex to protect from harmful or noxious stimulus.

In human studies, eyeblink reflex was usually recorded as the startle response (Graham, 1975; Lipp and Siddle, 1998). The blink reflex elicited by a corneal stimulation is a component of the startle response, as well as the acoustic startle blink reflex (Krauter, 1987;

Flaten and Elden, 1999) and the electrically elicited blink reflex (Rossi et al., 1995; Miwa et al., 1998). A relatively weak trigeminal stimulus evokes electromyographic (EMG) activities in the olbicularis occili muscles, while an intense stimulus elicits EMG activities in the other muscles such as masseter and sternocleidomastoid muscles, in addition to the olbicularis occili. The former is the blink reflex and the latter is termed as the startle response (Valls-Solé et al., 1999).

3.1.2. Prepulse Inhibition

A weak stimulus, which itself dose not produce a startle response, presented 30-500 ms prior to a startle stimulus reduce a magnitude of the startle response. This phenomenon is called as prepulse inhibition (PPI, see Hoffman and Ison, 1980) and is widely observed in many animal species including humans (Carlson and Willott, 1996; Swerdlow et al., 1990; Linn and Javit, 2001; Lipp et al., 1994), but excluding hamsters (Sasaki et al., 1988, 2007).

PPI is impaired in humans suffered from schizophrenia (Swerdlow et al., 1994) or Huntington's disease (Swerdlow et al., 1995). Impairment of PPI is also observed in rats after mesolimbic dopamine receptors activation (Hoffmann and Donovan, 1994; Caine et al., 1995; Ralph et al., 1999), and in mouse lacking the metabotrophic glutamate receptors (Brody et al., 2004), providing an important cue to study the mechanisms for these psychiatric disorders.

Neural circuits of PPI have been widely documented using auditory startle responses in rats. It has been assumed that the PPI occurs at the pontine reticulo-spinal neurons (the caudal pontine nucleus, PnC, see Koch, 1999). However, it is still open about the pathway from where the visual prepulse reach its effect on the PnC neurons. Fendt et al. (1994) showed that PPI decreased significantly, although not completely, after lesion of the superior colliculus, suggesting that the descending pathway from the superior colliculus to the brain stem is the main pathway which provides the inhibitory inputs to the PnC. On the other hand, Ison et al. (1991) showed that the lack of visual PPI after decortications by using bilateral application of KCl in rats. More recently, bilateral entorhinal cortical lesions reduced PPI in rats (Goto et al., 2002). These findings suggest a possibility that the cortical areas may critically participate in the mechanism of PPI.

3.2. Purpose

It is well established that color information is preferentially processed in the inferior occipito-temporal visual areas, especially around the fusiform gyrus (Zeki, 1991; Corbetta et al., 1991). The purpose of present study is to examine whether the visual cortical areas are involved in human PPI circuit, using color stimulus as the prepulse.

3.3. Methods

3.3.1. Participants

Twenty undergraduate students (18 male and 2 female) with normal or corrected normal vision (mean age 21.9 years, SD 3.1) participated the present experiment. All participants provided informed consent and were assigned randomly to one of four groups consisting of five individuals.

Each participant received two different chromatic stimuli and one achromatic stimulus as the prepulse; Group R-G (red and green), Group G-Y (green and yellow), Group Y-B (yellow and blue), and Group B-R (blue and red). The achromatic prepulse was common for all of these experimental groups. For example, a participant in Group R-B received red, blue and the achromatic prepulse, in a quasi-random order.

This experimental paradigm was adopted, in order to reduce a total experimental time, which is useful for preventing decrease of PPI within an experimental session and is good for robustness of the results (Quednow et al., 2006).

The record of one participant from Group G-Y was discarded prior to analysis due to insufficient blink amplitude, especially on the later trials. A psersonal report after the experiment, showed that this participant was drowsy during the experimental session.

3.3.2. Apparatus

The participant seated in an isolated dim experimental room with an ambient illumination level of 0.5 lx, facing to a CRT display (Panasonic TX-D7P35-J, resolution 800 x 600 dots at 60 Hz, 9300K) placed at a distance of 57 cm. The participant's head was loosely restrained by using a chin rest, and the participant was asked to fixate at a small cross (0.5 deg, 0.5 deg) presented at the center of the CRT. The background illumination level of the CRT was the same as the ambient level.

3.3.3. Prepulse

Four chromatic stimuli (red, 0.553, 0.313, CIE; green, 0.334, 0.531, CIE; blue, 0.230, 0.147, CIE; and yellow, 0.456, 0.410, CIE) and one achromatic stimulus (0.283, 0.320, CIE) were used as the visual prepulse. Main wavelength of these chromatic stimuli was 635 nm (red), 548 nm (green), 463 nm (blue), or 580 nm (yellow), respectively. All of these chromatic stimuli had the same saturation of 60%. Luminance of the chromatic stimuli was adjusted to be equal to 10 cd/m^2 of gray in each participant, by the flicker photometry method. And the luminance of the achromatic stimulus was 10 cd/m^2. The shape of the visual prepulse was a square and the size of the stimulus was 10 deg x 10 deg in the visual angle. It was presented at the center of the CRT for 20 ms (Fig. 18). These visual stimuli were generated by a graphic generator (VSG Series Three, Cambridge Research Systems Ltd.), which was controlled by a computer (Power Macintosh 7300/180, Apple), using a hand-made program (HyperCard, Apple).

3.3.4. Startle Stimulus

A 50-ms air puff (0.2 MPa, a flow of 2 l/min) directed to the cornea of the left eye was used as a startle stimulus. Distance between the top of a nozzle which was attached at the end of the air-way and the surface of the cornea was about 5 cm. Delivery of the air puff was controlled by a solenoid bulb (AB31-02-3-H3A, DC-48V, CKD, Nagoya, Japan) which was placed at the midway of the air-way from the compressed air source and the nozzle. Opening of the bulb was controlled by combination of two stimulators (SEN-1101 and SEN-3201, Nihon Kohden). The lead interval between the prepulse and the delivery of the air puff was 100 ms (Fig. 18). This lead interval was chosen because the most sufficient PPI was obtained in a preliminary experiment using the achromatic prepulse ranging 50-200 ms intervals.

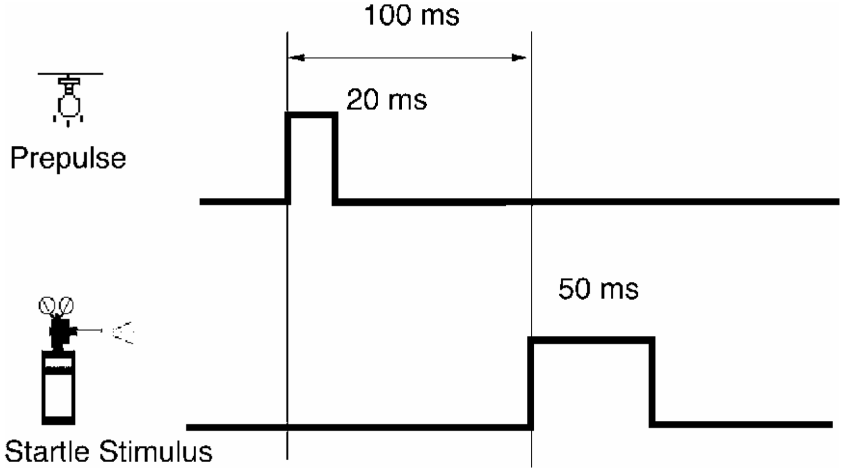


Figure 18. A schematic drawing of experimental procedure for prepulse inhibition. Startle blink responses were elicited by an air-puff to the corneal surface (0.2 MP, 2 l/min, for 50 ms duration). One of four chromatic stimuli (red, green or blue, matched to gray of 10 cd/m^2 by flicker photometry, with saturation of 60 %) or an achromatic stimulus of 10 cd/m^2 was used as prepulse for 20 ms duration. The lead interval of prepulse and the startle stimulus was 100 ms.

3.3.5. Recordings Of Blinking

A differnce in the electrical potentials between the cornea and the retina caused by eye and/or eyelid movements during blink was detected in the EOG records (Collewijn et al., 1985; Stern and Dunham, 1990;Veltman and Gaillard, 1996; Kong and Wilson, 1998). Two Ag-AgCl surface electrodes with a diameter of 5 mm, placed 1 cm lateral and 1 cm below the lateral edge of the left eye were used to record the EOG. The signals from these electrodes were differentially recorded with a ground electrode attached on the forehead (Fz). The signal was amplified (EEG-4217, Nihon Kohden) with a low pass filter at 60 Hz, and with a low cut filter at 0.5 Hz (time constant of 0.3 sec). The EOG recordings lasted for 1 sec in each trial, from 100 ms before and 900 ms after the onset of the startle stimulus and was digitized at 400 Hz (MacLab, A/D Instruments), then stored on a hard disk of a computer (Macintosh Centris 660AV, Apple).

3.3.6. Procedures

In each group, 5 participants received a total of 45 trials with a mean intertrial interval of 15 sec, ranged from 10 to 20 sec. Only the startle stimulus was presented in the first 5 trials for habituation. Following the ituation trials, the participant received 40 test trials, with or without the prepulse (Fig. 19). Four different groups received different pairs of the prepulse. Three types of prepulse; one gray, and two different color prepulses were presented with a fixed lead interval of 100 ms. This value was chosen because a dominant inhibition was observed at this lead interval in our preliminary experiment. Participant's behaviors were always monitored by a video-camera system.

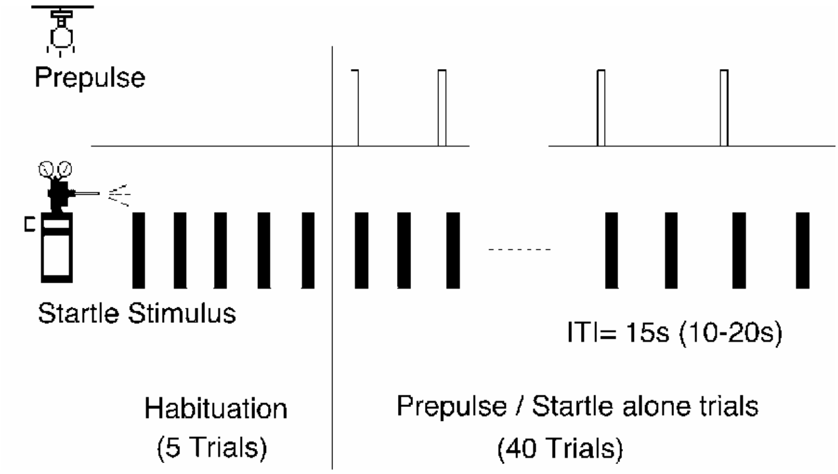


Figure 19. An experimental session was consisted of 45 trials with a mean intertrial interval of 15 sec (10-20 sec). In the first five trials, only startle stimulus was presented as control trials. In the following trials, startle stimulus was presented with or without prepulse. The lead interval of prepulse and the startle stimulus was 100 ms.

3.4. Results

3.4.1. Measurements of the Response Amplitude

The EOG recordings of corneal blink elicited by the air-puff was composed of two positive deflections with a latency at 80 ms and 150 ms, respectively, followed by a large negative deflection at 300 ms (Fig. 20). The early positive deflection was sharp and small in amplitude as compaired to the second positive deflection. The early component is consisted of high frequency activities, presumably EMG activities of the orbicularis occuli muscles. A peak-to-peak amplitude of the second positive and the large negative components was measured for the amplitude of the startle response.

Figure 21 shows a typical example of blink responses in one session (Group R-B). A total of 45 trials were displayed in a line. Although slight decrement in the blink amplitude was noted during the habituation trials, relatively consistent amplitudes were recorded throughout the session. In most trials without preceding prepulse (marked by filled circles), a clear blink response was elicited by the air puff. On the contrary, remarkable decrease in the amplitude was observed in the prepulse trials (marked by open circles) as compared to the non-prepulse trials.

3.4.2. Typical Example of PPI of the Blink Response

Figure 22 shows superimposed traces of 5 trials each, excluding the first 5 trials. A filled circle indicates the onset of the air puff and an open circle indicates the onset of the prepulse. The left column shows recordings in the early half and the right column shows ones in the late half of the session. The second five traces marked 7-24 show the recordings without prepulse from 7th to 24th trials. In these five trials, a slight decrease in the blink amplitude was noted as compared to the control trials. A remarkable decrease in the amplitude was found in the following prepulse trials. A similar decrease of the blink amplitude in the prepulse trials was observed in the late half of the session. As compaired to the five trials without prepusle (29-44th trials), the blink amplitude was small in prepulse trials either in 26-32th, 33-38th, or 39-45th trials.

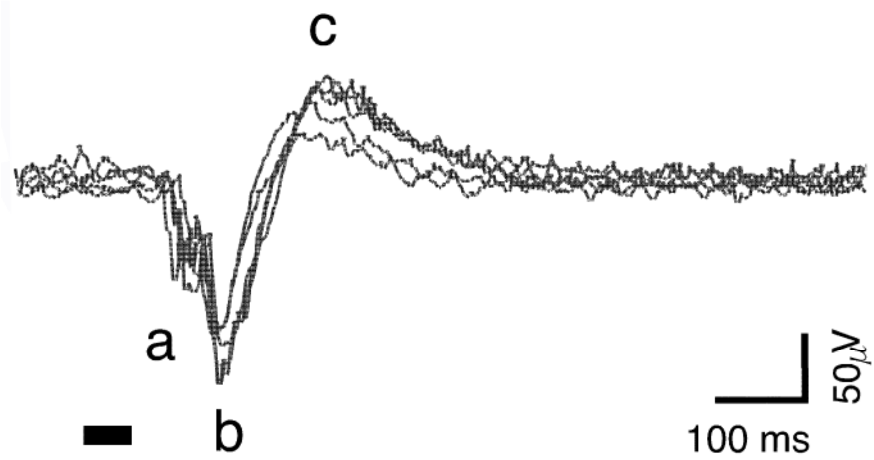


Figure 20. A typical waveform of corneal blink response elicited by air-puff to the corneal surface. Five recordings were superimposed from 100 ms before and 900 ms after the onset of air-puff. The thick bar indicates duration of the air-puff for 50 ms. A waveform of the blink response consisted of two positive deflections (a and b) and a large negative one (c). A peak-to-peak amplitude (b-c) was measured as the startle amplitude.

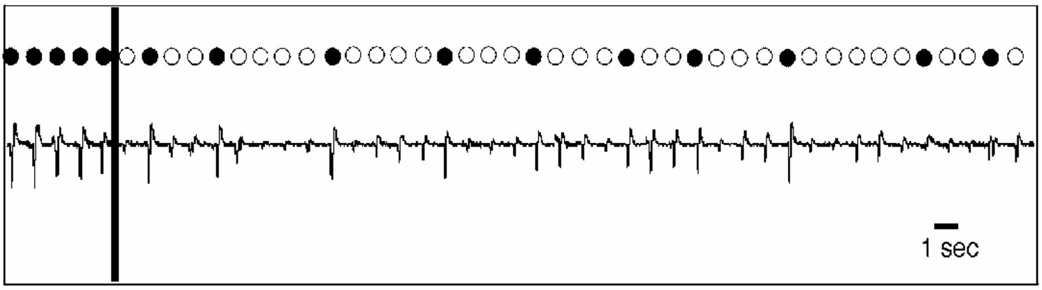


Figure 21. A sequence of blink responses consisting of 45 trials in an experimental session of Group R-B. Each trial was sampled for a 1-sec epoch. Open circles indicate trials with the prepulse, and filled circles indicate trials without prepulse. Vertical line indicates end of the habituation period. Red and blue prepulses are not distinguished here. Amplitudes of the blink responses decreased in the prepulse trials as compared to those in no prepulse trials.

3.4.3. Responses to Chromatic and Achromatic Prepulses

Effect of prepulses on the startle amplitudes was examined using % inhibition as an inhibition index, calculated by the following equation:

% inhibition = (mean amplitude in prepulse trials)/(mean amlitude in non-prepulse trials) x 100

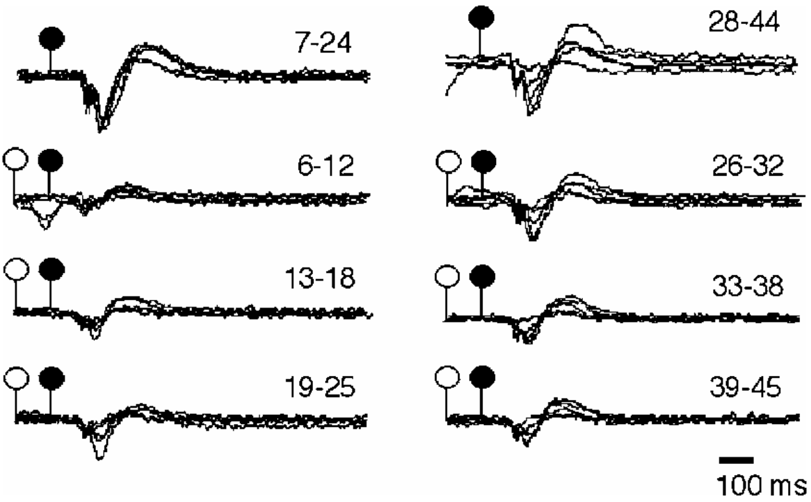


Figure 22. Inhibition of the startle blink amplitude by the chromatic prepulse in the same session as shown in Fig. 21, excluding the first 5 trials. Each group of traces is superimposition of 5 recordings for 1-sec period, from 100 ms prior and to 900 ms after the onset of the air-puff. The open circle and the filled circle indicate the onsets of the prepulse and the air-puff, respectively. The number at the right of traces indicates a rage of trial number, in which the recordings were obtained.

Figure 23 shows effect of the chromatic and achromatic prepulses on the startle blink responses. Control amplitude (OFF) was the mean amplitude in the non-prepulse trials, excluding the first 5 trials for habituation. All of these prepulses inhibited the startle amplitude in every group (Fisher's PLSD, $p<0.05$). There was a difference in the effect of chromatic prepulses on the startle responses. Significant difference was found between decrease of the amplitude by the blue and the yellow prepulses in Group G-Y (Fisher's PLSD, $p<0.01$).

3.5. Discussions

3.5.1. Three Types of Blink Reflexes

Blink reflex is essential to protect the eye against corneal drying and damage (Magladery and Teasdall, 1961; Evinger et al., 2002). Blinking is classified into three types according to its motor aspect: spontaneous, voluntary and reflexive blinking (Bour et al., 2000). The reflexive blinking can be elicited by at least three different types of stimulation in humans.

1) A glabella tap (Pearce, 2008) or electrical stimulation of the supraorbital branch of the trigeminal nerve elicits EMG responses in the orbicularis oculi muscle, and evokes the blink reflex. The electrically elicited blink reflex recorded from the orbicularis oculi muscle is formed by three components: the two principal ones, R1 and R2, and a third, R3 (Esteban, 1999). Kugelberg in 1952 recorded the early-latency R1 and the late-latency R2 EMG responses from orbicularis oculi (Pearce, 2008). Cruccu et al. (1986) examined the R2 and the corneal reflex, which will be described below, in normal subjects and found some different behaviors in habituation and recovery cycle. The corneal reflex habituated significantly to repetitive stimulations at a rate of 0.2–1 Hz but was more resistant than the late component of the blink reflex (R2). And the corneal reflex was less affected by the preceding impulse. From

these results they suggest that the corneal reflex is relayed through fewer intramedullary synapses than R2.

2) An intense auditory or visual stimulus evokes the blink reflex. A light flash stimulation evokes the photic early and late responses (Mukuno et al., 1983), and the photic responses were impaired by bilateral occipital lobe lesions (Mukuno et al., 1983). Auditory stimulus also elicits a blink reflex, which is usually considered as the most representative and consistent response of the startle response in humans (Valls-Solé et al., 1999). It was suggested that the physiological characteristics and a brainstem circuitry of the auditory blink reflex may be different from those of the auditory startle response (Valls-Solé et al., 1999). Auditory blink reflexes were considered when auditory stimuli induced responses limited to the orbicularis oculi and auditory startle responses were considered when the responses were induced in other muscles, such as masseter and sternocleidomastoid muscles (Valls-Solé et al., 1999).

3) A reflex contraction of the human orbicularis oculi muscles can be evoked also by stimulation of the cornea ("corneal reflex") (Fig. 24). The corneal reflex can be elicited by a light mechanical touch to the cornea and the response is bilateral blinking (Ongerboer de Visser, 1980). Mechanical touch and an air-puff to the cornea have been used to produce the corneal reflex (Mukuno et al., 1983, Celebisoy et al., 2000; VanderWerf et al., 2007).

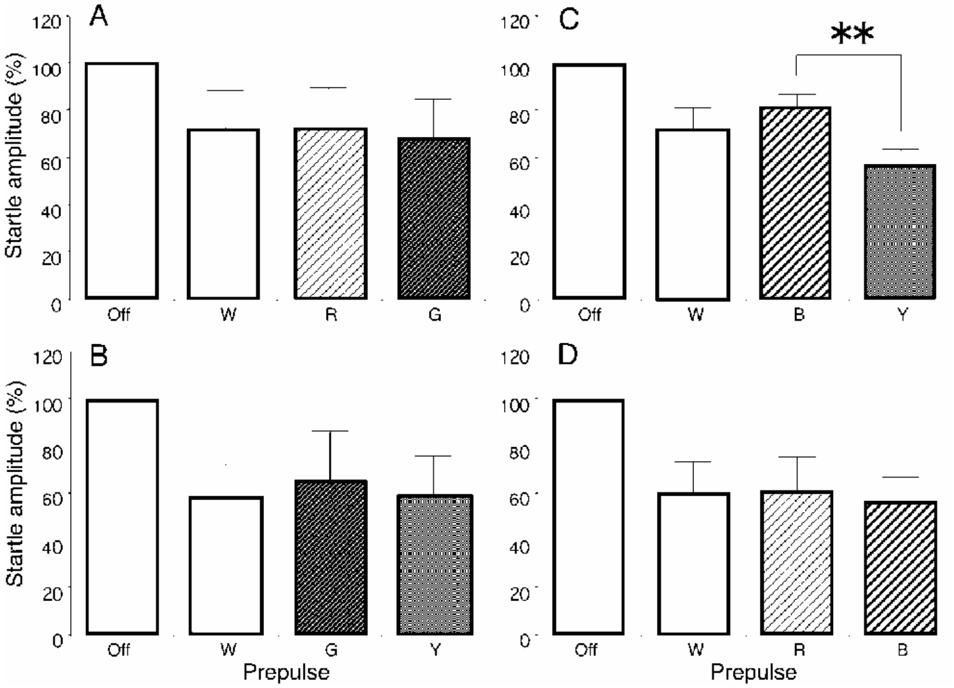


Figure 23. Effect of color prepulse on the amplitude of blink response. Mean blink amplitudes with the chromatic and the achromatic prepulses in the four groups; Group R-B (A), Group G-Y (B), Group Y-B (C), and Group B-R (D). Each chromatic prepulse, as well as the achromatic one, significantly decreased the blink amplitude (in all groups $p<0.05$). In addition, significant decrease in the amplitude was observed between blue and yellow prepulses (** $p<0.01$).

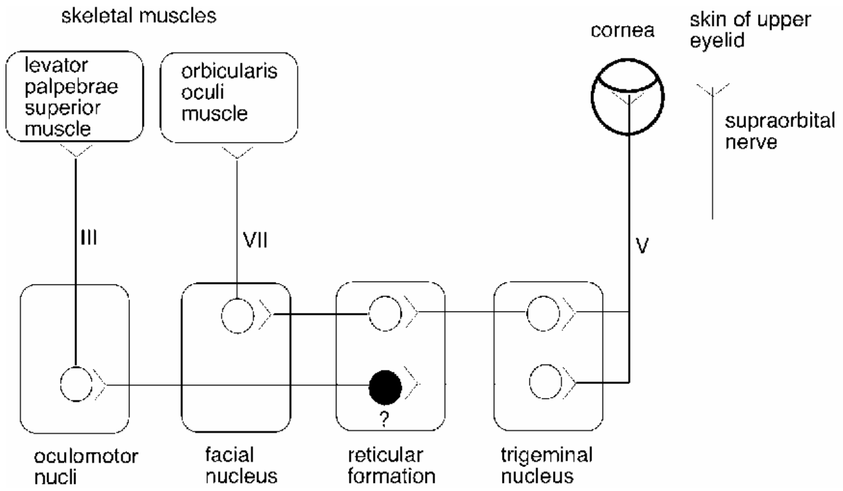


Figure 24. Schematic drawings of neural pathways underling the corneal reflex. A mechanical stimulus applied to the surface of the cornea or the skin of the upper eyelid elicits action potentials in the trigeminal nerve (afferent pathway). They are transmitted to the facial neuron (efferent pathway) through multisynaptic relays in the reticular formation and elicit contraction of the orbicularis occuli muscles. At the same time, inhibition of the oculomotor neuron (efferent pathway) probably via an inhibitory interneuron located in the reticular formation elicits relaxation of the levator palpebrae superior muscles. These responses in the skeletal muscles cause the eyelid closure. V: trigeminal nerve, VII: facial nerve, III: oculomotor nerve.

3.5.2. Eyelid and Eye Movements During Blinking

During a blinking, both eyelid and eye movements occur. Eyelid movement during blinking is mainly mediated by the levator palpebrae superioris and orbicularis oculi muscles (Evinger et al., 1991; Schmidtke and Buttner-Ennever, 1992; Esteban et al., 2004). The inhibition the electrical activity of the levator palpebrae superioris muscle precede and outlast the reciprocal contraction of the orbicularis oculi (Björk and Kugelberg, 1953). During blinking stereotypical eye movements occur. In normal human subjects, the eyeball rotates from a straight-ahead position nasally downward, then followed by laterally upward movement during blinking (Evinger et al., 1984; Bour et al., 2000; Collewijn et al., 1985; Riggs et al., 1987; see VanderWerf et al., 2007). These eye movements during blinking have been termed as Bell's phenomenon. However, Bell's phenomenon did not occur during short blinks (Collewijn et al., 1985). On the other hand, the lid closing over the eye causes a difference in the corneal-retinal potential that is evident in the electro-oculogram (EOG) (Stern and Dunham, 1990). Therefore, the EOG can be used for recordings of blinking (Veltman and Gaillard, 1996; Kong and Wilson, 1998).

The neuronal mechanisms initiating the eyelid and eye movement during blinking is not well understood. Recently, however, new evidence was obtained showing that specific areas in the lateral medullar reticular formation are involved in eyelid and eye movements during blinking (Smit et al., 2005, 2006).

Neural circuits for the blink reflex elicited by the electrical stimulation of the supraorbital nerve have been reported. The trigeminal afferent limb reaches the facial efferent limb by means of a long and complex pathway located at the brainstem bulbopontine level (Esteban, 1999). The corneal reflex circuit has three components: (1) primary cornea afferents; (2)

second order trigeminal complex neurons; and (3) orbicularis oculi motoneurons (Henriquez and Evinger, 2007)(Fig. 24).

3.5.3. Neural Circuit for PPI

It has been suggested that the PPI mediating circuit for auditory startle response in rats is consist of the superior colliculus, PPTg, and Pnc, where the prepulse exerts inhibitory effects on the auditory startle response (Koch, 1999; Fendt et al., 2001). The auditory evoked potentials can be recorded in the PPTg with a latency of 13 ms in rats (Ebert and Ostwald, 1991). Although the effective lead interval between prepulse and the startle stimulus depends upon the intensity of prepulse, it ranged about from 20 ms to 500 ms in rats (Hoffman and Searle, 1965) and from 30 ms to 500 ms in human eyeblink response (Graham, 1975). These facts mean that the subcortical PPI mediating pathway from the superior colliculus to the Pnc plays an important role in PPI at a relatively short lead interval (Fendt et al., 2001). PPI at a longer lead interval should be mediated by other neural circuits with more synaptic connections. Consistent with this suggestion, PPI decrement after bilateral lesions of the superior colliculus was not complete but some residual PPI still remained (Fendt et al.,1994).

3.5.4. Effect of Change in Luminance

In the present experiment, visual prepulse was presented on the black background of the ambient illumination level. Thus the appearance of the prepuse on the CRT was accompanied by the change in luminance as well as the change in chroma. The presentation of the achromatic stimulus elicited only the luminance change, while the presentation of the chromatic stimuli elicited both changes in the luminance and the chroma. The effect of chroma itself as the prepulse seems to be weak as compaired to the luminance, because the amount of the inhibition caused by the chromatic prepulse was similar to that elicited by the achromatic prepulse of 10 cd/m^2. In addition, in our preliminary experiment using the chromatic stimuli that produced only change in chroma without accompanying change in luminance, no significant PPI was observed. However, these findings do not necessarily imply that the luminance is always more effective than chroma, because it has been shown that the effect of the PPI depends on the intensity of the prepulse (Reijmers and Peeters, 1994; Blumenthal, 1996) and because the intensity of the chromatic and the achromatic prepulses were not changed systematically in the present experiment. Moreover, in the present results, there was the significant difference in the effect of inhibition between chromatic stimuli. The startle amplitude was more inhibited by the yellow prepulse than the blue one. These findings show that not onl the luminance but also the hue was importantly involved in the PPI.

3.5.5. Cortical Contributions to PPI

The color information is processed in the cortex around the fusiform cortex (Corbetta et al., 1991; Zeki et al., 1991). Therefore, the present findings suggest that the visual cortex is involved in the visual PPI at least in human startle response elicited by the corneal stimulus. It has been suggested that the ventral stream of visual information from the striate cortex to the fusiform cortex is responsible for the processing of color, as compared to the dorsal stream, which engages in the processing of positional cues of the stumulus (Rozenzweig et al., 1999). The ventral stream of the visual information will transmit to the amygdala via the inferotemporal cortex. The neurons in the amygdala project to the PPTg through the accumbens and the ventral pallidum (Koch, 1999). These indirect projections may exert an inhibitory influence on the PPTg. Consistent with this view, it was reported that the central nucleus of the amygdala modulates blink reflex sensitivity in the rabbit (Whalen and Kapp, 1991). Results of several lesion studies are also in line with the view described here. Lesions of the inferotemporal cortex caused sever impairements in the PPI. Reduced PPI with entorhinal cortex lesions has been reported in rats (Goto et al., 2002). Additionaly, quinolinic acid lesions of the basolateral amygdala significantly reduced PPI without significantly changing startle amplitude (Wana and Swerdlow, 1996). Moreover, blockade of the dopamine receptors in the basolateral amygdala disrupted PPI in a dose-related manner in the rat (Stevenson and Gratton 2004). Furthermore, it has been suggested that the medial prefrontal cortex is involved in the PPI circuit (Koch, 1999). Therefore, it is possible for the visual activity to reach the PPTg via these cortical areas. Although the precise neural circuitry for the PPI of the human corneal reflex is still remained to be determined, the present findings suggest that the visual cortex is critically involved in the visual prepulse circuit in the human PPI.

4. PARARELL PROCESSING IN THE VISUAL SYSTEM

4.1. Two Visual Pathways

Visual signals starting from the retina are transmitted to the visual cortex via two different pathways; one is the geniculostriate pathway and the other is the extrageniculostriatel pathway. The geniculostriate pathway conveys the visual signal to the striate cortex (primary visual cortex, area 17) by the relay cells of the dordal necleus of the lateral geniculate nucleus. While the extrageniculostriate pathway conveys the visual signal to the extrastriate visual cortex (secondary visual cortex, area 18/19) via the neurons in the superior colliculus and the pulvinar nucleus of the thalamus. The lateral posterior nucleus of the thalamus in rodents is a homology of the pulvinar in monkeys and a homology of the lateral posterior nucleus- pulvinar complex in cats (see Sasaki et al., 2008).

Schneider (1969) posturated a separation between cording of location and identification of a visual stimulus; the retino-tectal and the geniculo-striatal pathways, respectively. The geniculostriate pathway serves for object perception and the extrageniculostriate pathway plays an important role in the visually guided orientation of eye, head, and body to the stimulus, and in detection of the brightness change (Sasaki et al., 2008). Involvement of the extrageniculostriate system in processing of the global features of a stimulus, such as brightness, contrast and intensity, rather than the detailed, local features, which is responsible for the geniculostriate system, has been suggested (Sasaki et al., 2008).

4.2. Two Visual Streams

Two paralell visual streams in the cortex are well known. The cortical flow of visual information starting at the striate cortex diverges into two streams; dorsal and ventral streams (Ungerleider and Miskin, 1982). The dorsal visual pathway is concerned to processing of spatiotemporal informations, visually guided action while the ventral pathway is involved in processing of color and object cognition (Goodale and Milner, 1992; Ungerleider et al., 1998).

The geniculostriate pathway in monkeys is composed of magno-, parvo-, and konio-cellular channels, each receives afferent projections from M (parasol), P (midget) and small bistratified retinal ganglion cells, respectively (see Rodieck, 1998). These channels correspond to motion, form and color processing (see Nicholls et al., 1992; Sincich and Horton, 2005). Extentions of the mago-cellular and parvo-cellular pathways are suggested to be responsible for the dorsal and the ventral streams, respectively (Livingstone and Hubel, 1998).

In cats and rodents, X-type (alpha) retinal ganglion cells project selectively to the dorsal part of the lateral geniculate nucleus, thus contribute to the geniculostriate system, while W-cells (gamma) project to the superior colliculus, which is a part of the extrageniculostriate system. Y-cells (beta) project both to the lateral geniculate nucleus and the superior colliculus by bifurcating fibers (Hoffmann, 1973; Boycott and Wassle, 1974; Fukuda and Stone, 1974).

X-cells have relatively large size of receptive field and thus X- system is involved in analysis of detailed features of a stimulus, while Y-cells have relatively fast conduction velocity and thus Y- system plays a role in analysis of movements of the stimulus, respectively (see Sasaki et al., 2008). X- and Y- system correspond to the parvo-cellular and mago-cellular systems in monkeys, respectively (Rodieck et al., 1985), although an debate has been exist about which cell classes in the monkey are most like to cat ganglion cell classes (Shapley and Perry, 1986).

The global features of a stimulus are essential for action to the stimulus, and less important for the object perception, which requires more detailed features of the stimulus. Consistent with this view, the extrageniculostriate system contributes to an analysis of global features of a stimulus, and W-cells are mainly involved in the extrageniculostriate system (Sasaki et al., 2008). As compared to the X- and Y-systems, W-system is consisted of a heterogenus group of non-X and non-Y systems. From the evidence that the W-system has relatively slow conduction velocity and relatively low spatial resolution as compared to the X- and Y-systems, it is reasonable to consider that the W-system is an evolutionaly old system. It seems probable that the limbic system, which is also an evolutionaly old brain structure, receives the sensory inputs via the primitive sensory pathways.

It has shown that there is a heavy projection from the superior colliculus to the pulvinar-lateral posterior complex (cat, Graybiel,1972; rat, Perry, 1980; hamster, Mooney et al., 1984). Tectal cells which project to the pulvinar-lateral posterior complex located in the superficial layers of the superior colliculus, are innervated by W-type retinal axons (Hoffmann, 1973; Nagata and Hayashi, 1979). These suggest that W-system may convey visual information to the limbic system.

Table 1 summarizes three systems for a visual signal analysis. Dorsal and ventral streams are consisted of Y-cell (mogno-cellular) and X-cell (parvo-cellular) systems, respectively. The dorsal stream is involved in the analysis of spatio-temporal features, while the ventral stream plays important roles in the analysis of figure and color. Thus the dorsal stream is concerned with information about ’where’ (Ungerleider and Miskin, 1982) and vision for ’action’ (Goodale, 1993), while the ventral stream is concerned with information about ’what and vision for ’perception is concerned with information about ’where’ and vision for ’action’. On the other hand, the subcortical pathway from the superior colliculus to the amygdala via the pulvinar nucleus involves W-cell, and is concerned with the analysis of biological meanings (appetitive or aversive) and psychological meanings (pleasant or unpleasant) to produce emotion without acknowledged perceptual awareness.

Table 1. Three levels of analysis for a visual signal.

pathway	cell type	information	analysis		output
dorsal stream	Y-cell (magno)	where	spatio-temporal□ conscious detectoion	=>	action□
ventral stream	X-cell (parvo)	what	figure-color□ conscious detection	=>	perception□
SC-Pul-Amy	W-cell	how	appetitive-aversive pleasant-unpleasant	=>	emotion

SC: superior colliculus, Pul: pulvinar nucleus, Amy: amygdala

4.3. Three Hierarchies of the Brain

In evolutionary lower animals such as planarian, adaptive behaviors are controlled by a primitive type of information processing mechanism which is termed as taxis. Planarian is the multicellular organism and belongs to the flatworm. It has a very simple nervous system and is one of the most primitive animals that has a brain (Agata et al., 1998; Agata, 2008; Aoki et al., 2009). Planarian shows approaching movements to a feed such as a block of lever of the chicken (positive chemo taxis) and escaping movements from a bright light (negative photo taxis). Former is necessary to obtain food, and the latter is useful for escaping from predators. Both of these are primitive types of adaptive behavior.

Innate programmed behaviors in vertebrate are consisted of reflex and instinctive behaviors. Many reflexes elicit defensive or appetitive responses to stimuli incoming from outside and thus contribute to our survival. These reflexes are the bases for the conditioned responses in higher level of adaptive behavior (Pavlov, 1928). The center of the reflex arch located in the spinal cord or the lower brain stem. More integrated but still automatically regulated adaptive behaviors such as food-intake, regulation of body temperature, and sexual behaviors are controlled by activities of the hypothalamus, which innervates both the autonomic nervous system and the endocrine system (Fig. 25). Conscious behaviors are closely related to activities of the cerebral cortex, which developed later in evolution. These stratified behaviors seem to have close relation to a triune brain model to explain evolution of human brain (McLean, 1970). In this model human brain is consisted of three hierarchies (triune brain) from inside to outside.

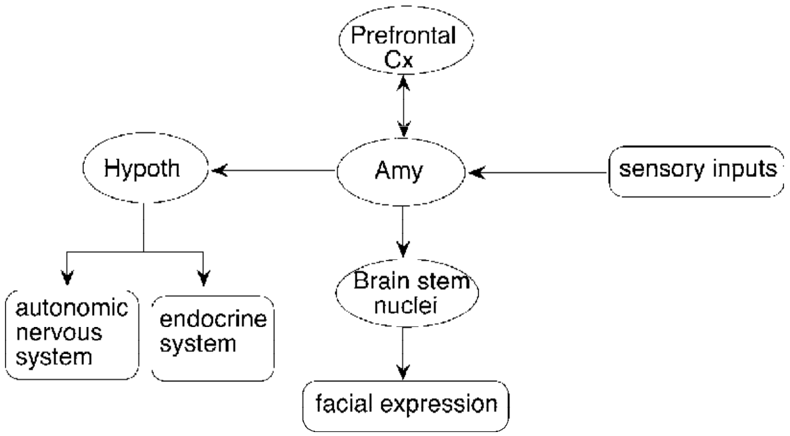


Figure 25. Sensory afferents to the amygdala (Amy) are transmitted to at least three different structures. Aversive or appetitive values are transffered to the hypothalamus (Hypoth) for homeostatic regulation by the automatic nervous system and the endcrine system. The emotional consequences are expressed outside as a facial expression via the brain stem nuclei, such as the facial nucleus. The activity of the amygdala is interacted with those in the prefrontal cortex (prefrontal Cx).

4.4. Limbic System

Limbic system situated deeply inside the human brain, corresponding its function is a primitive judgment of the incoming stimulus. Whether a stimulus is aversive (dangerous, harmful) or necessary for the organism is estimated by the limbic system, especially in the amygdala. As a result of the judgment, a behavioral strategy whether 'approach to' or 'avoid from' the stimulus is determined.

Appetitive and aversive stimuli are well defined in behavioral studies in animals (Sasaki and Yoshii, 1984; Sasaki et al., 1993). It has been demonstrated that the amygdala is involved in the processing of emotional stimuli (Zald, 2003). Lesion studies have shown that the amygdala is critical for fear and anxiety in rats (Davis, 1992a, 1992b; Falls and Davis, 1995; Malkani and Rosen, 2001). Lesions of the amygdala disrupted fear conditioning measured with fear-potentiated startle in rats (Hitchcock, 1987; Campeau, 1995; Campeau and Davis, 1995). Functional imaging studies showed that the amygdala make evaluative judgments on appetitive and aversive stimuli (LaBar et al., 1998; Büchel et al., 1998; Sabatinelli et al., 2005). Thus, it is suggested that the amygdala processes knowledge about stimuli and plays a crucial role in processing affective information conveyed by sensory stimuli (Adolphs, 1999; Sander et al., 2003; Williams et al., 2004).

A scale for judgment to an incoming stimulus is ranged from danger, noxious, aversive, dislike to likelihood, appetitive, affective, and needs. This scale is not fixed but flexible in a certain range, and it is depending on the drive level of the organism. For example, food is very attracting objects for a hungry animal but is neutral for a saturated animal. If the stimulus is noxious or aversive, avoidance behavior will take place, and at the same time negative emotion will be produced automatically and unconsciously. If the stimulus is attractive, approaching behavior and positive emotion will be induced.

Aversive stimulus induces a negative emotion at the amygdala and elicits the autonomic and endcrine responses at the hypothalamus, to prepare for danger and to alert the incoming danger (Fig. 25).

These primitive types of adaptive responses are performed subcortically without consciousness, and the consequence of the responses will be perceived and interpreted at the level of cerebral cortex. This is very similar for a case of somatic reflex to a noxious stimulus. Withdrawal of hand or foot to a noxious stimulus is controlled by spinal reflexes. The ascending sensory information is transmitted to the cortex, and then a series of events occurred are perceived later.

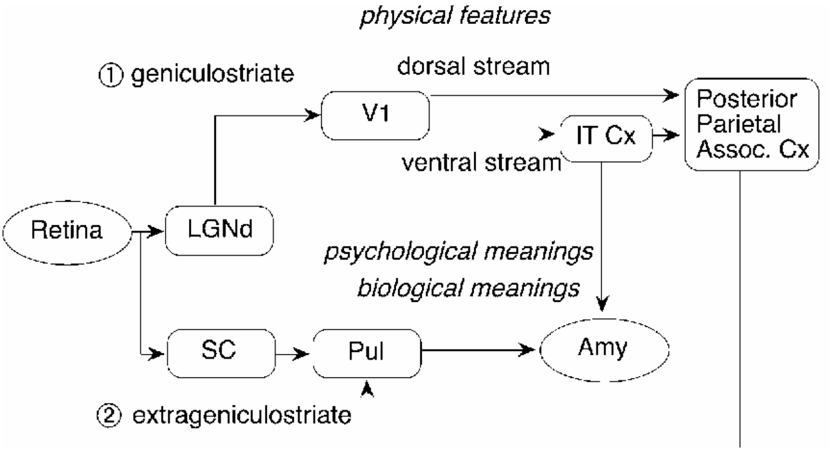


Figure 26. Visual pathways for analysis of physical features and of biological meanings of the stimulus. The former is processed by the geniculostriate pathway which branch off into dorsal and ventral streams. These pathways exert modulatory effects on producing emotion at the amygdala (Amy) via direct or indirect top-down pathways. The latter is processed by the extrageniculostriate pathway through the superior colliculus (SC) and the pulvinar nucleus of the thalamus (Pul) to the amygdala. These two systems are in pararell, thus the visual inputs are processed by the dual pathways to the amygdala. LGNd: dorsal part of the lateral geniculate nucleus of the thalamus, V1: primary visual cortex, IT Cx: inferotemporal cortex, SC: superior colliculus, Pul: pulvinar nucleus of the thalamus, Amy: amygdala.

4.5. Dual Processing Circuits of Visual Inputs

Visual signal is processed not only in the visual system but also in the limbic system, which is non-specific to the visual processing. Amygdala is the core center for analyzing biological meanings of the stimulus in order to judge whether a stimulus is positive or negative for the organism (Klüver and Bucy, 1939; Rolles, 1999).

Visual afferents to the amygdala are conveyed through either the inferotemporal visual cortex or the posterior thalamic nuclei (Fig. 26). Visual pathways to the amygdala have been well documented in rats. Substantial projections to the amygdala from the lateral posterior thalamic nucleus were found by several retrograde tract tracing techniques (Doron and Ledoux, 1999). In addition, injections of anterograde tracer biotinylated dextran amine into the lateral posterior thalamic nucleus resulted in heavy labeling in two amygdala-fugal cortical areas: temporal cortex area 2 and dorsal perirhinal cortex, and moderate labeling in the lateral amygdaloid nucleus (Shi and Davis, 2001).

A visual stimulus can be transmitted to the amygdala in rats via either geniculocortical (dorsal part of the lateral geniculate nucleus -> primary visual cortex, secondary visual cortex -> temporal cortex area 2 /perirhinal cortex) or extrageniculocortical (lateral posterior thalamic nucleus -> secondary visual cortex, temporal cortex area 2 /perirhinal cortex) pathways, or direct thalamo-amygdala projections (lateral posterior thalamic nucleus -> lateral amygdaloid nucleus). These visual pathways to the amygdala are suggested to be included in fear conditioning using a visual cue as conditioning stimulus (Shi and Davis, 2001).

Projections of the perirhinal cortex to the amygdala have been reported both in rats and monkeys (Shi and Cassell, 1999; McDonald et al., 1999; Suzuki, 1996b). It has long been appreciated that the cortex of the temporal pole in monkeys has interconnections with the amygdala. It has recognized that the medial portion of the temporal pole (part of the perihinal cortex) has reciprocal projections to the amygdala (Herzog and Van Hoesen, 1976; Aggleton et al., 1980; Turner et al., 1980; Suzuki, 1996a).

These findings suggest that visual inputs are processed both in the visual cortex for object perception and in the amygdala for biological meanings. These two processes are performed in pararell in addition to a serial processing. The former depends on the tecto-thalamo-amygdala projections, and the latter depends on the cortical top-down projections via the inferotemporal or the posterior parietal association cortex (Fig. 26). The results of Experiment 2 and fear potentiation (Sasaki and Hanamoto, 2007) suggest that the top-down signals to the amygdala may play a role in modulation of the startle response and of emotion.

4.6. Physiological Studies in Humans: Synchronous Activity of Inferotemporal Cortex and Amygdala

Sabatinelli et al. (2005) reported correspondent functional imaging activity between amygdala and inferotemporal cortex during emotional picture viewing and suggested that the identified correspondence represents a structural covariation of affective meaning of the emotional contents. These data are consistent with a view that the cortical top-down pathway transmits visual signals from the inferotemporal cortex, including the perirhinal cortex, to the amygdala.

The perirhinal cortex in both monkeys and rats is composed of two areas (areas 35 and 36) (Suzuki, 1996b). In monkeys, perirhinal areas 35 and 36 form a band of cortex situated lateral to the full extent of the rhinal sulcus. On the ventral surface of the brain, the perirhinal cortex includes much of the inferotemporal gyrus (Suzuki, 1996b). Both the dorsal bank cortex (area 36) and the fundus of the rhinal sulcus (area 35) project to entorhinal cortex and amygdaloid nuclei (Shi and Cassell, 1999). The entorhinal cortex also has significant projections to the amygdala (McDonald and Mascagni, 1997).

4.7. Blindsight and Extrageniculate Visual Pathway

Some human patients with lesions to their primary visual cortex demonstrate residual visual capacity, without consious perception. The preserved ability to accurately respond to visual inputs has been demonstrated (Weiskrantz, 1996). The phenomenon is referred to blindsight. A possible mechanism for the blindsight has been proposed that a subcortical pathway can detect visual stimulus without the primary visual cortex. A patient is able to discriminate emotional facial expressions presented in his blind hemifield despite an extensive lesion of the corresponding striate cortex (Morris et al., 2001). One proposal is that this residual affective ability depends on a subcortical visual pathway comprising the superior colliculus, posterior thalamus (pulvinar) and amygdala (Morris et al., 1999; Morris et al., 2001; Pegna et al., 2005).

Recently, Goossens et al. (2007) examined the neural correlates of phobic fear by exposing spider phobic subjects to a visual presentation of spiders, using a functional imaging method. They found that spider phobics showed significantly increased activation in the amygdala and the pulvinar nucleus of the thalamus. These results support the involvement of an extrageniculostriate pathway in the process of phobic fear.

Pulvinar activation, as well as the amygdala activation has been observed while viewing fearful expressions (Morris et al., 1999). With brief presentations, a patient with complete unilateral loss of the pulvinar was incapable of recognizing fearful expressions in his contralesional field (Ward et al., 2007). They suggest that fear recognition is mediated by the human medial pulvinar and that the cortex in isolation from the entire pulvinar is incapable of recognizing fearful expressions.

From these findings the coliculo-pulvinar-amygdala pathway is involved in the recognition of an affective feature of an object. This view is further supported by data that dysfunction of the amygdala is critically related to some affectional disorders (Mayberg et al., 1999; Drevets, 2003).

4.8. Amygdala and the Affective Disorders

Functional connections between limbic structures and neocortex have long been considered critical to the evolution of emotional behaviors (James, 1884; Papez, 1937; MacLean, 1949; Rolls, 1990; Tucker et al., 1995). The limbic structures seem to be essentially included in affective, or mood disorders. Neuroimaging studies have identified neurophysiologic abnormalities in the amygdala, as well as the anatomically related areas of the prefrontal cortex, striatum, and thalamus in mood disorder (Drevets, 2000, 2003). Dysregulation of the interconnection of limbic-cortical pathways are hypothesized to play a role in the pathogenesis of the affective disorders (Mayberg, 1997; Mayberg et al., 1999). Sensory afferents via the thalamus to the amygdala thus provide a main source of the affection, mood, and emotion.

4.9. Amygdala Regulates the Prefrontal Cortical Activity

Amygdala modulates activity in the prefrontal cortex. The prefrontal cortical neurons reduce their spontaneous activity as a function of a degree of fear. And the prefrontal activity is negatively correlated with the activity of the amygdala (Garcia et al., 1999). They suggested that abnormal amygdala-induced modulation of prefrontal neuronal activity may be involved in certain forms of anxiety disorder. In consistent with this, altered activity in the amygdala and the prefrontal cortex have been reported in mood disorders. Abnormal elevations of resting cerebral blood flow and glucose metabolism in the amygdala have been reported in familial pure depressive disorder (Drevets et al., 1992; Drevets, 2000; Drevets, 2001). At the same time, reduction of activity in the prefrontal cortex in depressed subjects suffered from unipolar depression or in the depressed phase of bipolar disorder has been reported (Drevets, 2001). In contrast, subjects in the manic phase of bipolar disorder showed higher metabolism in the prefrontal cortex than control subjects (Drevets, 2001). These findings strongly suggest that amygdalar function is important for anxiety and fear responses and dysfunction of amygdala is critically involved in affective disorders.

4.10. Multimodal Processing for Object Recognition

The amygdala is in receipt of sensory information from many modalities. Direct projections from the medial geniculate body to the amygdala have been shown in rats and cats by using the retrograde axonal transport of horseradish peroxidase and fluorescent substances bisbenzimid and nuclear yellow (Ottersen and Ben-Ari, 1979; Maiskii et al., 1984; Doron and Ledoux, 1999; Russchen, 2004). The amygdala receives afferent projections also from the thalamic taste relay, and viscerosensory relay neurons (Turner and Herkenham, 1991).

Object recognition is based on sensory information derived from not a single specific modality but multimodal information about the object. Recent studies relating multisensory processing revealed that the recognition of an object is performed not as a result of processing in a single modality, but as a result of integration of various sensory perceptions of different modalities (Shimojo and Shams, 2001; Shams et al., 2004). Indeed, visual perception is altered by other sensory modalities (Shipley, 1964; Walker and Scott, 1981; Welch et al., 1986). Also, some neurons in the visual system show multimodal response characteristics, as well as amygdalar neurons (Schroeder et al., 2004; Rolls, 2004). From these findings it is suggested that the amygdala is involved in production of emotional responses based on multimodal sensory information.

All of these facts support the hypothesis that the physical features of a sensory signal are analyzed in the cortex, while the biological features (positive or negative; appetitive or aversive) and also psychological features (pleasant or unpleasant; fear, anxiety, or happiness) are analyzed mainly in the amygdala (Table 1). The visual signals to the amygdala are conveyed via three pathways; cortico-amygdala pathway through the perirhinal cortex, cortico-pulvinar-amygdala pathway, and the tecto-pulvinar-amygdala pathway. The former two pathways via the cortex are related to the conscious perception of an object and the subcortical pathway is involved in unconscious perception. Both pathways may contribute to amygdalar recognition of biological and psychological meanings of an incoming stimulus to produce emotional responses.

5. CONCLUSION

In this study the author proposed a new model for visual signal processing. It has been thought the visual signal is processed in the cortex for perception, and then the information is transferred to the limbic system for recognition. Here the author propose a dual processing model in which the visual signal is conveyed directly to the limbic system via a subcortical pathway, in addition to the cortical pathway. The dual processing circuits of the stimulus meanings provide a base for an explanation of differentiation or sprit of emotion and a logical mind, which is processed without and with consciousness, respectively.

ACKNOWLEDGMENTS

The author thank to Dr. Akiko Morimoto, Dr. Akira Nishio and Ms.Sumie Matsuura for substaintial help with RT studies. A part of this research was supported by the Ministry of Education, Culture, Sports, Science, and Technology, Grant-in-Aid for Scientific Research (C), No. 15500136, 2003.

REFERENCES

[1] Adam, J. J. and Van Veggel, L. M. (1991). Discrete finger response latencies in a simple reaction time task. *Perceptual and Motor Skills*, 73: 863-866.

[2] Adams, W. J. and Mamassian, P. (2004). The effects of task and saliency on latencies for colour and motion processing. *Proceedings, Biological Science*, 271: 139-146.

[3] Adolphs, A. (1999). The human amygdala and emotion. *Neuroscientist*, 5: 125-137.

[4] Agata, K. (2008). Planaria nervous system. *Scholarpedia*, 3: 5558.

[5] Agata, K., Soejima, Y., Kato K., Kobayashi C., Umesono Y. and Watanabe K. (1998). Structure of the planarian central nervous system (CNS) revealed by neuronal cell markers. *Zoological Science*, 15: 433-440.

[6] Aggleton, J. P., Burton, M. J., Passingham, R. E. (1980). Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). *Brain Research*, 190: 347-368.

[7] Albert, M. L., Reches, A. and Silverberg, R. J. (1975). Hemianopic colour blindness. *Journal of neurology, neurosurgery, and psychiatry*, 38: 546-549.

[8] Annett, M. and Annett, J. (1979). Individual differences in right and left reaction time. *British Journal of Psychology*, 70: 393-404.

[9] Aoki, R., Wake, H., Sasaki, H. and Agata, K. (2009). Recording and spectrum analysis of the planarian electroencephalogram. *Neuroscience*, 159: 908–914.

[10] Barton, J. J., Press, D. Z., Keenan, J. P. and O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, 58: 71-78.

[11] Berlucchi, G., Heron, W., Hyman, R., Rizzolatti, G. and Umilta, C. (1971). Simple reaction times of ipsilateral and contralateral hand to lateralized visual stimuli. *Brain*, 94: 419-430.

[12] Berry, L. H. (1990). Effects of hemispheric laterality on color-information processing. *Perceptual and Motor Skills*, 71: 987-993.

[13] Björk A. and Kugelberg E. (1953). The electrical activity of the muscles of the eye and eyelids in various positions and during movement. Electroencephalography and *Clinical Neurophysiology*, 5: 595-602.

[14] Blumenthal, T.D. (1996). Inhibition of the human startle response is affected by both prepulse intensity and eliciting stimulus intensity. *Biological Psychology*, 44: 85-104.

[15] Bour, L. J. , Aramideh, M. and Ongerboer De Visser, B. (2000). Neurophysiological aspects of eye and eyelid movements during blinking in humans. *Journal of Neurophysiology*, 83: 166-176.

[16] Boycott, B. B. and Waessle, H. (1974). The morphological types of ganglion cells of the domestic cat's retina. *The Journal of Physiology*, 240: 397-419.

[17] Brody, S. A., Dulawa, S. C., Conquet, F. and Geyer, M. A. (2004). Assessment of a prepulse inhibition deficit in a mutant mouse lacking mGlu5 receptors. *Molecular Psychiatry*, 9: 35-41.

[18] Bryden, M. P. *Laterality: Functional asymmetry in the intact brain*. New York: Academic Press; 1982.

[19] Büchel, C., Morris, J., Dolan, R. J. and Friston, K. J. (1998). Brain systems mediating aversive conditioning: an event-related fMRI study. *Neuron*, 20: 947-957.

[20] Caine, S. B., Geyer, M. A. and Swerdlow, N. R. (1995). Effects of D-sub-3/D-sub-2 dopamine receptor agonists and antagonists on prepulse inhibition of acoustic startle in the rat. *Neuropsychopharmacology*, 12: 139-145.

[21] Campeau, S. (1995). Involvement of the central nucleus and basolateral complex of the amygdala in fear conditioning measured with fear-potentiated startle in rats trained concurrently with auditory and visual conditioned stimuli. *Journal of Neuroscience*, 15: 2301-2311.

[22] Campeau, S. and Davis, M. (1995). Involvement of subcortical and cortical afferents to the lateral nucleus of the amygdala in fear conditioning measured with fear-potentiated startle in rats trained concurrently with auditory and visual conditioned stimuli. *Journal of Neuroscience*, 15: 2312-2327.

[23] Carlson, S. and Willott, J. F. (1996). The behavioral salience of tones as indicated by prepulse inhibition of the startle response: relationship to hearing loss and central neural plasticity in C57BL/6J mice. *Hearing Research*, 99: 168-175.

[24] Celebisoy, N., Varolgunes, N. and Akyurekli, O. (2000). Corneal reflex and blink reflex changes in thalamic hemorrhage. *Electromyography and clinical neurophysiology*, 40: 95-102.

[25] Christman, S. (1989). Perceptual characteristics in visual laterality research. *Brain and Cognition*, 11: 238-257.

[26] Christman, S. (1990). Effects of luminance and blur on hemispheric asymmetries in temporal integration. *Neuropsychologia*, 28: 361-374.

[27] Collewijn, H., Van der Steen, J. and Steinman, R. M. (1985). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of Neurophysiology*, 54: 11-|27.

[28] Conway, M. A., Turk, D. J., Miller, S. L., Logan, J., Nebes, R. D., Meltzer, C. C. and Becker, J. T. (1999). A positron emission tomography (PET) study of autobiographical memory retrieval. *Neuroimaging and Memory*, 7: 679-702.

[29] Corballis, P. M. (2003). Visuospatial processing and the right-hemisphere interpreter. *Brain and Cognition*, 53: 171-176.

[30] Corballis, P. M., Funnell, M. G. and Gazzaniga, M. S. (2002). Hemispheric asymmetries for simple visual judgments in the split brain. *Neuropsychology*, 40: 401-410.

[31] Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. and Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *Journal of Neuroscience*, 11: 2383-2402.

[32] Cruccu, G. , Agostino, R., Berardelli, A. and Manfredi, M. (1986). Excitability of the corneal reflex in man. *Neuroscience Letters*, 63: 320-324.

[33] Danilova, M. V. and Mollon, J. D. (2009). The symmetry of visual fields in chromatic discrimination. *Brain and Cognition*, 69: 39-46.

[34] Davidoff, J. (1976). Hemispheric sensitivity differences in the perception of colour. *The Quarterly Journal of Experimental Psychology*, 28: 87-394.

[35] Davis, M. (1992a). The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience*, 15: 353-376.

[36] Davis, M. The mammalian startle response. In: Eaton, R. C. (ed.). Neural mechanisms of startle behavior. London: Plenum; 1984, pp. 287-351.

[37] Davis, M. The role of amygdala in condiitoned fear. In: Aggleton, J. (ed.). *The amydgala: Neurobiological aspects of emotion, memory and mental dysfunction*. New York: Wiley-Liss; 1992b; pp. 255-305.

[38] De Valois, R. L. and De Valois, K. K. (1993). A multi-stage color model. *Vision Research*, 33:1053-1065.

[39] Doron, N. N. and Ledoux, J. E. (1999). Organization of projections to the lateral amygdala from auditory and visual areas of the thalamus in the rat. *Journal of Comparative Neurology*, 412: 383-409.

[40] Drevets, W. C. (2000). Neuroimaging studies of mood disorders. *Biological Psychiatry*, 48: 813-829.

[41] Drevets, W. C. (2001). Neuroimaging and neuropathological studies of depression: implications for the cognitive-emotional features of mood disorders. *Current Opinion in Neurobiology*, 11: 240-249.

[42] Drevets, W. C. (2003). Neuroimaging abnormalities in the amygdala in mood disorders. *Annals of the New York Academy of Sciences*, 985: 420-444.

[43] Drevets, W. C., Videen, T. O., Price, J. L., Preskorn, S. H., Carmichael, S. T. and Raichle, M. E. (1992). A functional anatomical study of unipolar depression. *Journal of Neuroscience*, 12: 3628-3641.

[44] Dunlap, W. P., Cortina, J. M., Vaslow, J. B. and Burke, M. J. (1996). Meta-analysis of experiments with matched groups or repeated measures designs. *Psychological Methods*, 1: 170-171.

[45] Ebert, U. and Ostwald, J. (1991). The mesencephalic locomotor region is activated during the auditory startle response of the unrestrained rat. *Brain Research*, 565: 209-217.

[46] Esteban, A. (1999). A neurophysiological approach to brainstem reflexes. Blink reflex. *Clinical Neurophysiology*, 29:7-38.

[47] Esteban, A., Traba, A. and Prieto, J. (2004). Eyelid movements in health and disease: the supranuclear impairment of the palpebral motility. *Clinical Neurophysiology*, 34: 3-15.

[48] Evinger, C., Bao, J., Powers, A. S., Kassem, I. S., Schicatano, E. J., Henriquez, V. M. and Peshori, K. R. (2002). Dry eye, blinking, and blepharospasm. *Movement Disorders,* 17: S75-S78.

[49] Evinger, C., Manning, K. A. and Sibony, P. A. (1991). Eyelid movements. Mechanisms and normal data. *Investigative Ophthalmology and Visual Science*, 32: 387-400.

[50] Evinger, C., Shaw, M. D., Peck, C. K., Manning, K. A. and Baker, K. (1984). Blinking and associated eye movements in human, guinea pigs and rabbits. *J. Neurophysiology*, 52: 323-339.

[51] Falls, W. A. and Davis, M. (1995). Lesions of the central nucleus of the amygdala block conditioned excitation, but not conditioned inhibition of fear as measured with the fear-potentiated startle effect. *Behavioral Neuroscience*, 109: 379-387.

[52] Fendt, M., Koch, M. and Schnitzler, H. U. (1994). Sensorimotor gating deficit after lesions of the superior colliculus. *Neuroreport*, 5: 1725-1728.

[53] Fendt, M., Liang, L. and Yeomans, J. S. (2001). Brain stem circuits mediating prepulse inhibition of the startle reflex. *Psychopharmacology*, 156: 216-224.

[54] Flaten, M. A. and Elden, A. (1999). Caffeine and prepulse inhibition of the acoustic startle reflex. *Psychopharmacology*, 147: 322-330.

[55] Foundas, A. L., Corey, D. M., Angeles, V., Bollich, A. M., Crabtree-Hartman, E. and Heilman, K. M. (2003). Atypical cerebral laterality in adults with persistent developmental stuttering. *Neurology*, 61: 1378-1385.

[56] Fukuda, Y. and Stone, J. (1974). Retinal distribution and central projections of Y-, X-, and W-cells of the cat's retina. *Neurophysiology*, 37: 749-772.

[57] Garcia, R., Vouimba, R. M., Baudry, M. and Thompson, R. F. (1999). The amygdala modulates prefrontal cortex activity relative to conditioned fear. *Nature*, 402: 294-296.

[58] Gazzaniga, M. S. and LeDoux, J. E. The integrated Mind. New York: Plenum; 1978.

[59] Gazzaniga, M. S., LeDoux, J. E. and Wilson, D. H. (1977). Language, praxis, and the right hemisphere: clues to some mechanisms of consciousness. *Neurology*, 27: 1144-1147.

[60] Goodale, M. A. and Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15: 20-25.

[61] Goossens, L., Schruers, K., Peeters, R., Griez, E. and Sunaert, S. (2007). Visual presentation of phobic stimuli: Amygdala activation via an extrageniculostriate pathway? *Psychiatry Research: Neuroimaging*, 155: 113-120.

[62] Goto, K., Ueki, A., Iso, H. and Morita, Y. (2002). Reduced prepulse inhibition in rats with entorhinal cortex lesions. Behavioural Brain Research, 134: 201-207.

[63] Graham, F. K. (1975). The more or less startling effects of weak prestimuli. *Psychophysiology*, 12: 238-248.

[64] Graybiel, A. M. (1972). Some extrageniculate visual pathways in the cat. *Investigative Ophthalmology and Visual Science*, 11: 322-332.

[65] Hannay, H. J. (1979). Asymmetry in reception and retention of colors. *Brain and Language*, 8: 191-201.

[66] Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P. and Grady, C. L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience*, 14: 6336-6353.

[67] Hayes, V. and Halpin, G. (1978). Reaction time of the fingers with responses measured on a typewriter keyboard. *Perceptual and Motor Skills*, 47: 863-867.

[68] Henriquez, V. M. and Evinger, C. (2007). The three-neuron corneal reflex circuit and modulation of second-order corneal responsive neurons. *Experimental Brain Research*, 179: 691-702.

[69] Herzog, A. G. and Van Hoesen, G. W. (1976). Temporal neocortical afferent connections to the amygdala in the rhesus monkey. *Brain Research*, 115: 57-69.

[70] Hitchcock, J. M. (1987). Fear-potentiated startle using an auditory conditioned stimulus: effect of lesions of the amygdala. *Physiology and Behavior*, 39: 403-408.

[71] Hoffman, H. S. and Ison, J .R. (1980). Reflex modification in the domain of startle: 1. Some empirical findings and their implications for how the nervous system processes sensory input. *Psychological Review*, 87: 175-189.

[72] Hoffman, H. S. and Searle, J. L. (1965). Acoustic variables in the modification of startle reaction in the rat*.* *J. Comp. Physiol. Psychol.* 60: 53-58.

[73] Hoffmann, D. C. and Donovan, H. (1994). D-sub-1 and D-sub-2 dopamine receptor antagonists reverse prepulse inhibition deficits in an animal model of schizophrenia. *Psychopharmacology*, 115: 447-453.

[74] Hoffmann, K. P. (1973). Conduction velocity in pathways from retina to superior colliculus in the cat: a correlation with receptive- field properties. *Journal of Neurophysiology*, 36: 409-424.

[75] Ison, J. R., Bowen, G. P. and O'Connor, K. (1991). Reflex modification produced by visual stimuli in the rat following functional decortication. *Psychobiology*, 19: 122-126.

[76] Jack, C. R. Jr., Twomey, C .K., Zinsmeister, A. R., Sharbrough, F. W., Petersen, R. C. and Cascino, G. D. (1989). Anterior temporal lobes and hippocampal formations: normative volumetric measurements from MR images in young adults. *Radiology*, 172: 549-554.

[77] James, W. (1884). What is an emotion? Mind, 9: 188-205.

[78] Jaskowski, P. (1982). Dependence of simple motor reaction time on luminance in various adaptation states. Acta Physiologica Polonica, 33:163-168.

[79] Kanwisher, N., McDermott, J. and Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17: 4302-4311.

[80] Khedr, E. M., Hamed, E., Said, A. and Basahi, J. (2002). Handedness and language cerebral lateralization. *European Journal of Applied Physiology*, 87: 469-473.

[81] Kimura, D. (1969). Spatial localization in left and right visual fields. *Canadian Journal of Psychology*, 23: 445-458.

[82] Klüver, H. and Bucy, P. C. (1939). Preliminary analysis of functions of the temporal lobe in monkeys. *Archives of Neurology and Psychiatry*, 42: 979-1000.

[83] Koch, M. (1999). The neurobiology of startle. *Progress in Neurobiology*, 59: 107-128.

[84] Kong, X. and Wilson, G. F. (1998). A new EOG-based eyeblink detection algorithm. *Behavior Research Methods, Instruments and Computers*, 30: 713-719.

[85] Krauter, E. E. (1987). Reflex modification by the human auditory startle blink by antecedent interruption of a visual stimulus. *Perceptual and motor skills*, 64: 727-738.

[86] LaBar, K. S., Gatenby, J. C., Gore, J. C., LeDoux, J. E. and Phelps, E. A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: a mixed-trial fMRI study. *Neuron*, 20: 937-945.

[87] Ladavas, E., Nicoletti, R., Umilta, C. and Rizzolatti, G. (1984). Right hemisphere interference during negative affect: a reaction time study. *Neuropsychologia*, 22: 479-485.

[88] Landis, C. and Hunt, W. The startle pattern. New York: Farrar and Rinehart; 1939.

[89] LeDoux, J. E., Wilson, D. H. and Gazzaniga, M. S. (1977). Manipulo-spatial aspects of cerebral lateralization: clues to the origin of lateralization. *Neuropsychologia*, 15: 743-750.

[90] Levy, J. (1969). Possible basis for the evolution of lateral specialization of the human brain. *Nature*, 224: 614-615.

[91] Linn, G. S. and Javitt, D. C. (2001). Phencyclidine (PCP)-induced deficits of prepulse inhibition in monkeys. *Neuroreport*, 12: 117-120.

[92] Lipp, O. V. and Siddle, D. A. T. (1998). The effects of prepulse-blink reflex trial repetition and prepulse change on blink reflex modification at short and long lead intervals. *Biological Psychology*, 47: 45-63.

[93] Lipp, O. V., Arnold, S. L., Siddle, D. A. T. and Dawson, M. E. (1994). The effect of repeated prepulse: Blink reflex trials on blink reflex modulation at short lead intervals. *Biological Psychology*, 38: 19-36.

[94] Lit, A., Young, R. H. and Shaffer, M. (1971). Simple time reaction as function of luminance for various wavelengths. *Perception and Psychophysics*, 10: 397-399.

[95] Livingstone, M. S. and Hibel, D. (1998). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240: 740-749.

[96] MacLean, P. D. (1949). Psychosomatic disease and the visceral brain: recent developments bearing on the Papez theory of emotion. *Psychosomatic Medicine*, 11: 338-353.

[97] MacLean, P.D. The triune brain, emotion, and scientific bias. In: Schmitt, F. O. (ed.). *The neurosciences: second study program*. New York: Rockefeller Univ. Press; 1970; pp. 336-349.

[98] Magladery, J. W. and Teasdall, R. D. (1961). Corneal reflexes: an electromyographic study in man. *Archives of Neurology*, 5: 269-274.

[99] Magnani, G., Mazzucchi, A. and Parma, M. (1984). Interhemispheric differences in same versus different judgments upon presentation of complex visual stimuli. *Neuropsychologia*, 22: 527-530.

[100] Maiskii, V. A., Gonchar, Yu. A. and Chepega, E. N. (1984). Neuronal populations in the posterior group of thalamic nuclei projecting to the amygdala and auditory cortex in cats. *Neurophysiology*, 16: 176-185.

[101] Malkani, S. and Rosen, J. B. (2001). N-Methyl-D-aspartate receptor antagonism blocks contextual fear conditioning and differentially regulates early growth response-1 messenger RNA expression in the amygdala: implications for a functional amygdaloid circuit of fear. *Neuroscience*, 102: 853-861.

[102] Malone, D. R. and Hannay, H. J. (1978). Hemispheric dominance and normal color memory. *Neuropsychologia*, 16: 51-59.

[103] Mayberg, H. S. (1997). Limbic-cortical dysregulation: a proposed model of depression. *Journal of Neuropsychiatry and Clinical Neurosciences*, 9: 471-481.

[104] Mayberg, H. S., Liotti, M., Brannan, K. S., McGinnis, S., Mahurin, R. K., Jerabek, P. A., Silva, J. A., Tekell, J. L., Martin, C. C., Lancaster, J. L. and Fox, P. T. (1999). Reciprocal limbic-cortical function and negative mood: Converging PET findings in depression and normal sadness. *American Journal of Psychiatry*, 156: 675-682.

[105] McDonald, A. J. and Mascagni, F. (1997). Projections of the lateral entorhinal cortex to the amygdala: a Phaseolus vulgaris leucoagglutinin study in the rat. *Neuroscience*, 77: 445-459.

[106] McDonald, A. J., Shammah-Lagnado, S. J., Shi, C. and Davis, M. (1999). Cortical afferents to the extended amygdala. *Annals of the New York Academy of Sciences*, 877: 309-338.

[107] McFie, J., Piercy, M., and Zangwill, O. (1950). Visual-spatial agnosia associated with lesions of the right cerebral hemisphere. *Brain*, 73: 167-190.

[108] McKeever, W. F. and Dixon, M. S. (1981). Right-hemisphere superiority for discriminating memorized from nonmemorized faces: affective imagery, sex, and perceived emotionally effects. *Brain and Language*, 12: 246-260.

[109] Miwa, H., Nohara, C., Hotta, M., Shimo, Y. and Amemiya, K. (1998). Somatosensory-evoked blink response: investigation of the physiological mechanisms. *Brain*, 121: 281-291.

[110] Mooney, R. D., Fish, S. E. and Rhoades, R. W. (1984). Anatomical and functional organization of pathway from superior colliculus to lateral posterior nucleus in hamster. *Journal of Neurophysiology*, 51: 407-431.

[111] Morris, J. S., DeGelder, B., Weiskrantz, L. and Dolan, R. J. (2001). Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*, 124: 1241-1252.

[112] Morris, J. S., Öhman, A. and Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences*, 96: 1680-1685.

[113] Mukuno, K., Aoki, S., Ishikawa, S., Tachibana, S., Harada, H., Hozumi, G. and Saito, E. (1983). Three types of blink reflex evoked by supraorbital nerve, light flash and corneal stimulations. *Japanese Journal of Ophthalmology*, 27: 261-270.

[114] Nagata, T. and Hayashi, Y. (1979). Innervation by W-type retinal ganglion cells of superior colliculus neurons projecting to pulvinar nuclei in cats. *Experientia*, 35: 336-338.

[115] Newton, I. (1672). *Opticks: or a treatise of the reflections inflections and colours of light*. New York: Dover Publications; 1952.

[116] Nicholls, J. G., Martin, A.R. and Wallace, B. G. From neuron to brain (third edition) Massachusetts: Sinauer; 1992.

[117] Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia*, 9: 97-113.

[118] Ongerboer de Visser, B.W. (1980). The corneal reflex: electrophysiological and anatomical data in man. *Progress in Neurobiology*, 15: 71-83.

[119] Ottersen, O. P. and Ben-Ari, Y. (1979). Afferent connections to the amygdaloid complex of the rat and cat. I. Projections from the thalamus. *The Journal of Comparative Neurology*, 187: 401-424.

[120] Papez, J. W. (1937). A proposed mechanism of emotion. *Archives of Neurology and Psychiatry*, 38: 725-743.

[121] Patel, A. D., Gibson, E., Ratner, J., Besson, M. and Holcomb, P. J. (1998). Processing syntactic relations in language and music: an event-related potential study. *Journal of Cognitive Neuroscience*, 10: 717-733.

[122] Pavlov, I. P. *Lectures on conditioned reflexes: twenty-five years of objective study of the higher nervous activity (behaviour) of animals*. (Translated from the Russian by Gantt, W. H.), London: M. Lawrence; 1928.

[123] Pearce, J. M. (2008). Observations on the blink reflex. *European Neurology*, 59: 221-223.

[124] Pegna, A. J., Khateb, A., Lazeyras, F. and Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nature Neuroscience*, 8: 24-25.

[125] Pennal, B. E. (1977). Human cerebral asymmetry in color discrimination. *Neuropsychologia*, 15: 563-568.

[126] Perry, V. H. (1980). A tectocortical visual pathway in the rat. Neuroscience, 5: 915-927.

[127] Poffenberger, A. T. (1912). Reaction time to retinal stimulation with special reference to the time lost in conduction through nerve centres. *Archives of Psychology*, 23: 1-73.

[128] Pujol, J., Deus, J., Losilla, J.M. and Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology*, 52: 1038-1043.

[129] Quednow, B. B., Kühn, K. U., Beckmann, K., Westheide, J., Maier, W. and Wagner, M. (2006). Attenuation of the prepulse inhibition of the acoustic startle response within and between sessions. *Biological Psychology*, 71: 256-263.

[130] Ralph, R. J., Varty, G. B., Kelly, M. A., Wang, Y. M., Caron, M. G., Rubinstein, M., Grandy, D. K., Low, M. J. and Geyer, M. A. (1999). The dopamine D2, but not D3 or D4, receptor subtype is essential for the disruption of prepulse inhibition produced by amphetamine in mice. *Journal of Neuroscience*, 19: 4627-4633.

[131] Ramachandran, V. S. and Blakeslee, S. Phantoms in the brain: Probing the mysteries of the human mind. New York: Morrow; 1998.

[132] Reijmers, L. G. and Peeters, B. W. (1994). Effects of acoustic prepulses on the startle reflex in rats: a parametric analysis. *Brain Research*, 661: 174-180.

[133] Rescorla, R. A. and Wagner, A. R. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: Black, A. H. and Prokasy, W. F. (eds.). *Classical conditioning II. Current research and theory*. New York: Appleton-Century-Crofts; 1972; pp. 64-99.

[134] Rodieck, R. W., Binmoeller, K. F. and Dineen, J. (1985). Parasol and midget ganglion cells of the human retina. *The Journal of Comparative Neurology*, 233: 115-132.

[135] Rodieck, R. W. The First Steps in Seeing. Massachusetts: Sinauer; 1998.

[136] Rolls, E. T. (1990). A theory of emotion, and its application to understanding the neural basis of emotion. *Cognition and Emotion*, 4: 161-190.

[137] Rolls, E. T. Multisensory neuronal convergence of taste, somatosensory, visual, olfactory, and auditory inputs. In: Calvert, G. A., Spence, C. and Stein, B. E. (eds.). *The handbook of multisensory processes*. London: Bradford Books (MIT Press); 2004; pp. 311-331.

[138] Rolls, E. T. *The brain and emotion*. New York: Oxford University Press; 1999.

[139] Rossi, B, Vista, M., Farnetani, W., Gabrielli, L., Vignocchi, G., Bianchi, F., Berton, F. and Francesconi, W. (1995). Modulation of electrically elicited blink reflex components by visual and acoustic prestimuli in man. *International Journal of Psychophysiology*, 20: 177-187.

[140] Rozenzweig, M. R., Leiman, A. L. and Breedlove, S. M. *Biological Psychology*. Massachusetts: Sinauer; 1999.

[141] Russchen, F. T. (2004). Amygdalopetal projections in the cat. II. Subcortical afferent connections. A study with retrograde tracing techniques. *The Journal of Comparative Neurology,* 207: 157-176.

[142] Sabatinelli, D., Bradley, M. M., Fitzsimmons, J. R. and Lang, P. J. (2005). Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. *Neuroimage*, 24: 1265-1270.

[143] Sander, D., Grafman, J. and Zalla, T. (2003). The human amygdala: an evolved system for relevance detection. *Reviews in the Neurosciences*, 14: 303-316.

[144] Sasaki, H. and Hanamoto, A. (2007). Shock sensitization and fear potentiation of auditory startle response in hamsters. *Perceptual and Motor Skills*, 105: 862-871.

[145] Sasaki, H. and Yoshii, N. (1984). Conditioned responses in the visual cortex of dogs. I. During wakefulness. Electroencephalography and Clinical Neurophysiology, 58: 438-447.

[146] Sasaki, H., Inoue, T., Iso, H., Fukuda, Y and Hayashi, Y. (1993). Light-dark discrimination after sciatic nerve transplantation to the sectioned optic nerve in adult hamsters. *Vision Research*, 33: 877-880.

[147] Sasaki, H., Iso, H., Coffey, P., Inoue, T. and Fukuda, Y. (1988). Prepulse facilitation of auditory startle response in hamsters. *Neuroscience Letters*, 248: 117-120.

[148] Sasaki, H., Morimoto, A., Nishio, A. and Matsuura, S. (2007). Right hemisphere specialization for color detection. *Brain and Cognition*, 64: 282–289.

[149] Sasaki, H., Nagata, T. and Inoue, T. Functional role of the extrageniculostriate system in visual perception. In: Nilsson, I. L., Lindberg, W. V. (eds.). *Visual perception: New research.* New York: Nova Science Publishers; 2008; pp. 49-89.

[150] Sato, W. and Aoki, S. (2006). Right hemispheric dominance in processing of unconscious negative emotion. *Brain and Cognition*, 62: 261-266.

[151] Schmidt, R. A. and Lee, T. *Motor control and learning: A behavioral emphasis*. Champaign: Human Kinetics; 1998.

[152] Schmidtke, K. and Buttner-Ennever, J. A. (1992). Nervous control of eyelid function: a review of clinical, experimental and pathological data. *Brain*, 115: 227-247.

[153] Schneider, G. E. (1969). Two visual systems, *Science*, 163: 895-902.

[154] Schroeder, C. E. and Foxe, J. J. Multisensory convergence in early cortical processing. In: Calvert, G. A., Spence, C. and Stein, B. E. (eds.). *The handbook of multisensory processes*. London: Bradford Books (MIT Press); 2004; pp. 295-309.

[155] Scotti, G. and Spinnler, H. (1970). Color imperception in unilateral hemisphere-damaged patients. *Journal of Neurology, Neurosurgery, and Psychiatry*, 33: 22-28.

[156] Sergent, J. (1982). Influence of luminance on hemispheric processing. *Bulletin of the Psychonomic Society*, 20: 221-223.

[157] Sergent, J., Ohta, S. and MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, 115: 15-36.

[158] Shams, L., Kamitani, Y. and Shimojo, S. Modulations of visual perception by sound. In: Calvert, G. A., Spence, C. and Stein, B. E. (eds.). *The Handbook of Multisensory Processes*. London: MIT Press; 2004.

[159] Shapley, R. and Perry, V. H. (1986). Cat and monkey retinal ganglion cells and their visual functional roles. *Trends in Neurosciences*, 10: 229-235.

[160] Shi, C. and Cassell, M. D. (1999). Perirhinal cortex projections to the amygdaloid complex and hippocampal formation in the rat. *Journal of Comparative Neurology*, 406: 299-328.

[161] Shi, C. and Davis, M. (2001). Visual pathways involved in fear conditioning measured with fear-potentiated startle: behavioral and anatomic studies. *Journal of Neuroscience*, 21: 9844- 9855.

[162] Shimojo, S. and Shams, L. (2001). Sensory modalities are not separate modalities: plasticity and interactions. *Current Opinion in Neurobiology*, 11: 505-509.

[163] Shipley, T. (1964). Auditory flutter-driving of visual flicker. *Science*, 145:1328-1330.

[164] Sincich, L.C. and Horton, J.C. (2005). The circuitry of V1 and V2: Integration of color, form, and notion. *Annual Review of Neuroscience*, 28: 303-326.

[165] Smit, A. E., Buisseret, P., Buisseret-Delmas, C., de Zeeuw, C. I., Vander- Werf, F. and Zerari-Mailly, F.(2006). Reticulo-collicular and spino-collicular projections involved in eye and eyelid movements during the blink reflex. *Neuroscience Research*, 56: 363-371.

[166] Smit, A. E., Zerari-Mailly, F., Buisseret, P., Buisseret-Delmas, C. and Vander- Werf, F. (2005). Reticulo-collicular projections: a neuronal tracing study in the rat. *Neuroscience Letters*, 380: 276-279.

[167] Smith, S. D. and Bulman-Fleming, M. B. (2004). A hemispheric asymmetry for the unconscious perception of emotion. *Brain and Cognition*, 55: 452-457.

[168] Smith, S. D., Tays, W. J., Dixon, M. J. and Bulman-Fleming, M. B. (2002). The right hemisphere as an anomaly detector: evidence from visual perception. *Brain and Cognition*, 48: 574-579.

[169] Sperry, R. (1982). Some effects of disconnecting the cerebral hemispheres. *Science*, 217: 1223-1227.

[170] Springer, J, A,, Binder, J. R., Hammeke, T. A., Swanson, S. J., Frost, J. A., Bellgowan, P. S., Brewer, C. C., Perry, H. M., Morris, G. L. and Mueller, W. M. (1999). Language dominance in neurologically normal and epilepsy subjects: a functional MRI study. *Brain*, 122: 2033-2046.

[171] Stern, J. A. and Dunham, D. N. The ocular system. In: Cacioppo, J. T. and Tassinary, L. G. (eds.). *Principles of psychophysiology: Physical, social, and inferential elements*. New York: Cambridge University Press; 1990; pp. 513–553.

[172] Stevenson, W. and Gratton, A. (2004). Role of basolateral amygdala dopamine in modulating prepulse inhibition and latent inhibition in the rat. *Psychopharmacology*, 176: 139-145.

[173] Sutherland, N. S. and Mackintosh, N. J. *Mechanisms of animal discrimination learning*. London: Academic Press; 1971.

[174] Suzuki, W. A. (1996a). Neuroanatomy of the monkey entorhlnal, perirhinal and parahlppocampal cortices: organization of corticcrl inputs and interconnections with amygdala and strlatum. *Seminars in Neuroscience*, 8: 3-12.

[175] Suzuki, W. A. (1996b). The anatomy, physiology and functions of the perirhinal cortex. *Current Opinion in Neurobiology*, 6: 179-186.

[176] Swerdlow, N. R., Braff, D. L., Taaid, N. and Geyer, M. A. (1994). Assessing the validity of an animal model of sensorimotor gating defieits in schizophrenie patients. *Archives of General Psychiatry*, 51: 139-154.

[177] Swerdlow, N. R., Mansbach, R .S., Geyer, M. A., Pulvirenti, L., Koob, G. F. and Braff, D. L. (1990). Amphetamine disruption of prepulse inhibition of acoustic startle is reversed by depletion of mesolimbic dopamine. *Psychopharmacology*, 100: 413-416.

[178] Swerdlow, N. R., Paulsen, J., Braff, D. L., Butters, N., Geyer, M. A. and Swenson, M. R. (1995). Impaired prepulse inhibition of acoustic and tactile startle response in patients with Huntington's disease. *Journal of Neurology, Neurosurgery and Psychiatry*, 58: 192-200.

[179] Szabo, C. A., Xiong, J., Lancaster, J. L., Rainey, L. and Fox, P. (2001). Amygdalar and hippocampal volumetry in control participants: differences regarding handedness. *American Journal of Neuroradiology*, 22: 1342-1345.

[180] Tucker, D. M., Luu, P. and Pribram, K. H. (1995). Social and emotional self-regulation. *Annals of the New York Academy of Sciences*, 769: 213-239.

[181] Turk, D. J., Heatherton, T. F., Kelley, W. M., Funnell, M. G., Gazzaniga, M. S. and Macrae, C. N. (2002). Mike or me? Self-recognition in a split-brain patient. *Nature Neuroscience*, 5: 841-842.

[182] Turner, B. H. and Herkenham, M. (1991). Thalamoamygdaloid projections in the rat: A test of the amygdala's role in sensory processing. *The Journal of Comparative Neurology*, 313: 295 -325.

[183] Turner, B. H., Mishkin. M. and Knapp, M. (1980). Organization of the amygdalopetal projections from modality-specific cortical association areas in the monkey. *The Journal of Comparative Neurology*, 191: 515-543.

[184] Ungerleider, L. G. and Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, 1994, 4:157-l65.

[185] Ungerleider, L. G. and Miskin, M. Two cortical visual systems. In: Ingle, D. J. , Goodale, M.A. and Mansfield, R. J. W. (eds.). *Analysis of Visual Behavior*. Cambridge: The MIT Press; 1982; pp. 549-586.

[186] Ungerleider, L. G., Courtney, S. M. and Haxby, J. V. (1998). A neural system for human visual working memory. *Proceedings of the National Academy of Sciences*, 95: 883-890.

[187] Valls-Solé, J., Valldeoriola, F., Molinuevo, J. L., Cossu, G. and Nobbe, F. (1999). Prepulse modulation of the startle reaction and the blink reflex in normal human subjects. *Experimental Brain Research*, 129: 49-56.

[188] VanderWerf, F., Reits, D., Smit, A. E. and Metselaar, M. (2007). Blink recovery in patients with Bell's palsy: A neurophysiological and behavioral longitudinal study. *Investigative Ophthalmology and Visual Science*, 48: 203-213.

[189] Veltman, A. and Gaillard, A. W. K. (1996). Physiological indices of workload in a simulated flight task. *Biological Psychology*, 42: 323-342.

[190] Walker, J. T. and Scott, K. J. (1981). Auditory-visual conflicts in the perceived duration of lights, tones, and gaps. *Journal of Experimental Psychology. Human Perception and Performance*, 7: 1327-1339.

[191] Wana, F-J. and Swerdlow, N. R. (1996). The basolateral amygdala regulates sensorimotor gating of acoustic startle in the rat. *Neuroscience*, 76: 715-724.

[192] Ward, R., Calder, A. J., Parker, M. and Arend, I. (2007). Emotion recognition following human pulvinar damage. Neuropsychologia, 45: 1973-1978.

[193] Weiskrantz, L. (1996). Blindsight revisited. *Current Opinion in Neurobiology*, 6: 215-220.

[194] Welch, R. B., Duttenhurt, L. D. and Warren, D. H. (1986). Contributions of audition and vision to temporal rate perception. *Perception and Psychophysics*, 39: 294-300.

[195] Whalen, P. J. and Kapp, B. S. (1991) Contributions of the amygdaloid central nucleus to the modulation of the nictitating membrane reflex in the rabbit. *Behavioral Neuroscience*, 105:141-153.

[196] Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F. and Mattingley, J.B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *The Journal of Neuroscience*, 24: 2898-2904.

[197] Zald, D. H. (2003). The human amygdala and the emotional evaluation sensory stimuli. *Brain Research Reviews*, 41: 88-123.

[198] Zangwill, O. Handedness and dominance. In: Money, J. (ed.). *Reading Disabilities*. Baltimore: Johns Hopkins Univ. Press; 1962.

[199] Zeki, S., Watson, J. P. G., Lueck, C. J., Friston, K., Kennard, C. and Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, 11: 641-649.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 51-88

Chapter 2

COLOR: ONTOLOGICAL STATUS AND EPISTEMIC ROLE

Anna Storozhuk
Fellow in Philosophy at the Institute of Philosophy and Law, Novosibirsk, Russia
Tutor at Novosibirsk State University, Russia

ABSTRACT

There are two basic approaches to studying color: one of them considers the issue of the physical reasons of color, the other investigates color perception. According to the first, color is not an objective physical entity; the second approach has many experimental evidences of color influence on human organism, for example, changes of the emotional condition, blood pressure, accuracy of perception, etc. The considered question can be formulated as follows: how color, being a sign without a referent, can make a real impact on the organism? A working hypothesis is that color is a non-conventional objective sign. This hypothesis will be subjected to critical analysis from the point of view of psychology of development in order to ascertain whether the sign properties of color are innate or are formed by the influence of culture. Another topic is a role of color in the world cognition. This question was usually considered from the point of view of direct influence on the increase of the visual recognition accuracy. We will investigate a question of indirect influence of color by means of pre-setting of the nervous system to perception; this is possible thanks to the system character of perception.

INTRODUCTION

Traditionally, the problem of color realism includes the discussion of the capability of color to be a reason of visual experience of a certain type. The problem is often formulated in the form ‘what does it mean to be colored?’, and the possible answers to this question appeal to color perception. However, philosophers avoid discussing the very process of color action on the organism, considering perception to be a simple non-problematic source of knowledge about the world. At the same time, raising the question concerning the ways of color action allows reformulating the issue of the color and reality relations.

The main purpose of this article is to discuss precisely the mechanisms of the color perception processes and the ways of color action on the organism, during which the subject experiences the sense of reality and has a cognitive experience. Clarification of the mechanism of appearance of the subjective color experience, which is a result of influence on the organism of electro-magnetic waves carrying certain energy, allows bringing to light the usually missed peculiarities of the mind-body problem. Based on the data on the ways of color action on the organism, there will be discussed the following questions: 'why does color make the perception more realistic?' and 'how does color influence the cognition process?'.

In the first part there are considered the physical properties of color discovered by Newton and interaction of various colors. It is studied then how can color, being a characteristic of electromagnetic wave and not being a property of objects, exert, nevertheless, its influence on the organism. The main attention is given to non-uniqueness of such influence. For example, a thin ray of white color, moving along the eye retina, will produce different color sensations. Besides, the action of color changes the sensitivity of other sense organs and of twilight vision. The following issues will be discussed: how do the color-sensing elements of the eye interact? How does color perception influence other sensor capabilities? What is the mechanism of transferring such influence? In this part I am using the data obtained by Russian physiologists whose work, as far as I know, has been rarely quoted. Nevertheless, the facts of mutual influence of various sensations have been known for a long time and are still being investigated by physiologists. At the same time, philosophers have been paying almost no attention to them. In the second part, we try to find the reason of philosophical inattentiveness to the adaptive changes of the sensor apparatus sensitivity. This consideration takes us to the Antique philosophy, in which there originated an orientation to identify the thought and being and then study the conceptions about the world in order to obtain knowledge. I call this orientation the principle of the being and thinking identity and show that it is the reason of so longstanding domination of the passive mirror paradigm of perception with consideration of experience as a separated isolated reaction of the organism to a singled-out irritant. These two suppositions about experience allow providing an isomorphism of cognition and existence; however, they have led philosophy into a dead-end. The views of philosophers on perception are full of myths and color perception is a good example to demonstrate irrelevancy of our conceptions about the process of acquiring experience.

I contrast the conception that our cognition is a result of separate atomic contacts with the world with *the principle of empirical holism*, in which there is postulated continuity of sensations and their complex influence on the organism. Then, from the point of view of empirical holism, there are given answers to the critical arguments against the logical empiricism and there are suggested new ways of resolving the difficulties of the passive-mirror conception: how does the sum of sensations form the bodies? How is the perception of space possible? How does color, not being an object, exert influence on the organism?

In the third part, it is shown that the influence of color on the organism can be explained only by taking into account continuity of sensations and their complex character. There is considered, from the point of view of empirical holism, the question of how does color give a greater realism to the image. Several possible mechanisms of such action are indicated, from an additional excitation of nervous system produced by colors to amplification of the organism reactions through influencing the emotional sphere. Finally, there are discussed the epistemological consequences of the perception continuity, which are illustrated by concrete examples of color influence on the organism.

1. THE PHYSICAL PROPERTIES OF COLOR AND ITS INFLUENCE ON THE ORGANISM

1.1. Newton on the Properties of Light and Color

To get an idea about the physical nature of color, let us turn to the history of optics. Isaac Newton was the first to explain the nature of color. He did it while solving a technical problem of improving telescopes. Observation through lenses was accompanied by chromatic aberration: the edges of the objects visible in the telescope were surrounded by a colored fringe degrading the picture. To find out the reason of its appearance and of the fuzziness introduced into the observation of the objects through glasses, Newton studied the mechanism of appearance of colors in the experiments which lasted more than 10 years. There existed three explanations of the nature of color at that time. The first one was due to Aristotle and connected the effect of color appearance with the boundaries of objects; Hooke presumed that color is caused by various modes of oscillation of the ether medium; whereas other philosophers believed that color is born out of shadow and light mixing. According to Newton, all these viewpoints had the same mistake of assuming that colors are not inherent in light from the beginning but acquired in reflection and refraction and generated by theses processes themselves. In particular, concerning the observation of prism’s decomposition of white light into its spectra it was presumed that the colors are an effect introduced by the prism itself. However, Newton could not accept these ideas, since color effects were manifested also without bodies: in rainbow, prisms, glasses, and liquids. He demonstrated that colors are contained in white light itself, they are inherent in it, not just appearing in reflections and refractions. To verify this, Newton decomposed first a light ray with the help of a prism and then recomposed the rays using a lens and a second prism. In both cases there was obtained the same white light as before the decomposition, which means that the prismatic colors do not disappear while forming whiteness but only mix together. Decomposition of white light into its spectra is possible due to the fact that the rays with different wavelengths have different refraction coefficients. Therefore, the bodies lighted by the composite light, seem to be fuzzy and colored; whereas the bodies lighted by homogeneous light seem distinct and are colored the same way as they are if you look at them simply by naked eyes.

> DEFIN. VII ‘The Light whose Rays are all alike Refrangible, I call Simple, Homogeneal and Similar; and that whose Rays are some more Refrangible than others, I call Compound, Heterogeneal and Dissimilar.
>
> DEFIN. VIII The Colours of Homogeneal Lights, I call Primary, Homogeneal and Simple, and those of Heterogeneal Lights, Heterogeneal and Compound’[1]

---

[1] Newton 1979 p. 4.

If we make the colors, obtained by decomposition, pass through a second prism, then the colored ray does not decompose further; i.e. this color is ‘pure’ or ‘simple’ because it contains the rays with one and the same wavelength. It also gave witness to the fact that the colors are not an effect of refraction in the prism but a property of the rays. Newton came to a conclusion that the prism serves just to separate the rays already present in the original light. At the same time, Newton understood that color arises as a result of interaction between the light radiation and our sensuous ability; the rays do not have colorings on their own.

Newton, following Descartes, supposed light to be corpuscles; but explained differently the reason of color sensation. Newton considered the speed of the particles to be the cause of our experiences of color, while Descartes thought it had to do with their rate of rotation.[2]

Later, when instead of Newton’s corpuscular optics, Ch. Huygens, T. Young, and O. Fresnel developed wave optics, Descartes’ explanation of the color sensation became more accepted and colors started to be explained by the differences in wavelength.

> The sensation of different colors depends on the different frequency of vibrations excited by light in the retina… Cause a sensation of light by beating and dashing against the bottom of the eye, something after the manner that vibrations in the air cause a sensation of sound by beating against the organs of hearing. Now, the most free and natural application of this hypothesis to the solution of phenomena I take to be this that the agitated parts of bodies, according to their several sizes, figures, and motions, do excite vibrations in the ether of various depths or bignesses, which, being promiscuously propagated through that medium to our eyes, effect in us a sensation of light of a white color; but if by any means those of unequal bignesses be separated from one another, the largest beget a sensation of a red color; the least, or shortest, of a deep violet, and the intermediate ones of intermediate colors.[3]

The explanation, given to the physical nature of color as wavelength, is basic nowadays. However, the subjective experience of color does not coincide with its objective characteristics as an electromagnetic wave of given energy. The perception of color may depend both on physical conditions (brightness, intensity, wavelength) and psychological readiness to perceive it. Although the color that we see depends on the characteristics of the rays coming to eyes, the connection between the color impression and physical composition of the stimulant is not simple. The rays, being different by composition, may cause absolutely identical observations of color. For example, white color can be obtained by mixing various pairs of complementary colors, the monochromatic yellow cannot be told apart from the mixture of red and green rays.

Besides, one and the same stimulant may give different sensations of color. For example, if a narrow white colored ray gets to various segments of the eye’s retina, then, depending on the position of the ray, its color will change from red in the central part of the eye and through orange and yellow to blue and violet spot in the ray’s center on the periphery of the eye.

Non-uniqueness of the correspondence between the light stimulant and reaction to it does not allow giving an unambiguous definition of color and requires taking into account a wide range of phenomena such as general picture of the excitation of the color-sensitive apparatuses and their interaction.

---

[2] Harré 1981.

[3] Young 1859 pp. 51-52.

1.2. Interaction of the Color-Sensing Elements of the Eye

A general picture of activation of the color-sensing apparatuses is given by the tristimulus theory, which presumes the presence of red-green- and blue-sensing cone cells in the eye retina. Color perception is connected with the fact that the absorbed photons stimulate decomposition of various pigments reacting in the cone cells due to incoming light. The perception of other colors is a result of their interaction; however, a number of experiments bear witness to the phenomena that the perceptions of monochromatic light and of the corresponding mixture of colors are not identical.

For example, according to the tristimulus theory, the yellow color perception depends on the excitation of the green- and red-sensing apparatuses of our color vision and is not independent. However, a number of observations show relative independence of yellow color from the excitation by green and red. For instance, after irritation of the eye by monochromatic yellow, its sensitivity to perception of blue color increases; whereas, after irritation by a mixture of red and green, it does not.[4] Another effect is connected with the fact that the boundaries of the peripheral vision’s domain for yellow color are wider than for green. Hartridge (1947) demonstrated that the presence of a yellow spot in the vision field increases the sensitivity of color resolution for the irritants of small angular size. The presence of red and green spots yielded no change in the visibility threshold of the control color spot.

Non-uniqueness of the reaction manifests also in non-equal time of reaction to various color irritants. Some colors excite faster the reacting apparatus of the retina’s rod cells, others affect the slowly reacting cone cells; the difference of the sensation time for rod and cone cells results in the difference of perception of brightness. Therefore, for two colors of the same brightness but different hue the rate of the sensation appearance is different.[5]

Piéron (1945) discovered that the rate of the blue color perception is minimal, whereas the perception of red and green colors has the maximal rate. The rate of sensation appearance was increasing for the red and green irritant differently and varied depending on adaptation since green color wearies the eye less. Different rate of the color sensations arising and developing leads to some interesting phenomena. For example, a disc with black and white sectors, which has been put into rotation, will be perceived as reddish, while the color distribution will depend on the rotation velocity. This is the result of the fact that the red rays, being components of the white color reflected from the white sectors, are perceived faster than the blue ones. A time difference arises also in the process of attenuation of after-images of different colors, the red excitation attenuating the fastest of all. If we compare the yellow and white irritation in the darkness conditions, then it will turn out that the subsequent image of the yellow irritation fades away faster, which serves as an argument for the introduction of yellow lights in cars.[6] Finally, the inhibiting influence of the cone-cell apparatus on the rod-cell one is widely known.

---

[4] Schwartz 1946 vol. 3.

[5] Piéron 1945.

[6] Kravkov 1950 p. 345.

The lighting of the central pit of the retina by red, blue and green colors results in diminishing excitability of the peripheral vision to a significantly greater degree than the lighting by the mixed white light.[7]

1.3. The Color Perception and the Mutual Interaction of Various Systems of the Organism

Colors exhibit a complex influence on the organism, which is not limited to the action on the visual apparatus but they excite or inhibit the abilities of perceiving the signals from other sense organs and also the thinking processes. There is also a backward influence when the irritations of other afferent systems may lead to the change in the color perception.

The question about the afferent systems interaction has been studied for a long time. For example, the first mentioning of this effect is due to Urbantschisch (1888), who asked the test persons to look at colored spots from such distance that the colors could not be identified. With the tuning-fork sound, the previously undistinguishable colors would become clearly visible. V. V. Lazarev (1904) demonstrated the dependence of the perceived sound volume on the illumination. He would, by turns, illuminate and darken a screen in front of the audience; and those present would hear distinctly that during the darkening of the screen the pitch-fork sound became quieter than on the light. Although the early researchers had established the facts of mutual influence of various afferent systems, they neither discovered regularities in the reactions nor indicated possible mechanisms of mutual interrelation of various afferent systems. The question concerning interrelation of the stimuli of various modalities was considered more specifically by the academician L.F. Orbeli (1935), whose collaborates had conducted many experiments trying to uncover such influence, in particular, regarding the action of color on the organism.

Depending on the color of the irritant acting on the eye, there occur some changes in the condition of both the eyes and the organism as a whole. Consider specific examples. Zaretskaya (1941) discovered that lighting one eye by green results in decreasing the intraocular pressure in the other eye, which amount to 80 percent from the initial level after 20 minutes after the exposition’s beginning. Lighting the eye by red color of the same brightness increases the intraocular pressure in the eye being studied. She discovered also that under the adaptation to green the blind spot decreases; under the adaptation to red, on the contrary, grows.

The general physiological condition noticeably influences color vision. Hypoxia significantly changes the thresholds of color vision, almost without any influence on the twilight one. The oxygen shortage, corresponding to the height of 5000 meters, leads to increasing sensitivity to red and yellow, diminishing the sensitivity to blue and green.[8]

The experiments by O. A. Dobryakova (1948) showed that general stimulation of the central nervous system, for example, an intense intellectual work, increases the sensitivity not only to the visual irritants but also to the acoustic, osmatic, and gustative ones.

---

[7] Lebedinskii, Pressman, Fadeeva 1948 pp. 104-111.

[8] Mkrtycheva L. I., Samsonova V. G. 1948.

The color-perceiving apparatus is connected also with the auditory one. For example, L. A. Schwartz (1949) demonstrated that adaptation of eyes to green color increases the auditory sensitivity; whereas, to red color, diminishes.

Kravkov (1934) investigated the changes of sensitivity of color vision in its dependence on the character of the sound and showed that, with sounds, the sensitivity to green and blue increases, whereas to red and orange decreases in proportion to sound's volume. In his laboratory, there were discovered analogous effects for the boundaries of color field: the boundaries of green and blue fields are getting wider with sounds, whereas of orange one, narrower.

Later, Kravkov observed that "in the conditions of loud noise produced by the aircraft engine, light sensitivity of twilight vision dropped down to 20 percent of its level in the quiet conditions before the start of auditory irritation".[9] Semenovskaya demonstrated that, after the cessation of sound, light sensitivity of the peripheral vision increases above the norm. The same effect is produced by an easy muscular work. Besides, Semenovskaya (1933) showed that lighting the eye by red light increases the sensitivity of twilight vision, whereas loud noise decreases it.

There were investigated also the influences of osmatic and gustative irritations on vision. For example, L. I. Seletskaya (1941) established that under the influence of rosemary smell the boundaries of the vision field for green are getting wider, whereas for red, conversely, they get narrower; and under the influence of indole smell there was observed a reverse narrowing of the vision field boundaries for green and widening, for red.

The research by Dobryakova (1944) of the gustative sensitivity showed that the sugar taste increases the color sensitivity to the region of blue-green rays and decreases it to the orange-red ones. Some changes in color vision arise also under the presence of stimuli from the proprioceptive apparatus. Schwartz (1946) established the influence of the proprioceptive irritants: with the head thrown back, the sensitivity to green color of 520 mm perceivably decreases, reaching after 90 minutes the 25 percent of the initial value; whereas, the sensitivity to orange-red somewhat increases. The muscular working capacity increases under green illumination and drops under red one.

The above mentioned studies show that a single perception influences the functioning of many other system of the organism. As applied to color, numerous experiments showed that under the influence of non-direct irritants (sounds, smells, chemical substances) there is observed a significant change of color perception of green-blue and orange-red rays, which are situated nearer to the center of the perceivable range; whereas, for the boundary rays of the spectrum − red and violet − it remains unchanged.

> For example, we saw that the auditory irritants increase the sensitivity of the dark-adapted eye in relation to orange-red rays; illumination of eyes make the sounds we hear louder; the tactile irritation of the hand by a weak electric current diminishes the auditory sensitivity; the hearing thresholds may change under the influence of osmatic sensations; illumination of eyes is favorable for the tactile sensitivity.[10]

---

[9] Kravkov 1948 p. 17.

[10] Ibid p. 110.

Single perceptions change the sensitivity of all sense organs, which indicates that the organism functions as a united, integral system. Under the irritation of one of sense organs, changes of the sensitivity in other sense organs sometimes take place after some time and develop during several minutes; and the effect from the irritant action is accompanied by a long aftereffect. At times, a secondary sensor irritant would give start to the sensitivity changing lasting more than half-hour and reaching maximum at the 20th minute and then the process would recede.

Schwartz (1948) proposed a hypothesis that the character of the irritant's influence is connected to the emotional condition, which accompanies the action of the irritant. To check her idea, she studied the influence of pleasant and disagreeable accords (consonance and dissonance) on the color perception and found that not only the action of sound but also the recollection about it produce very similar effects (see the table below reproduced from Schwartz, p. 317).

Influence of the recollection about the irritant on the subsequent sensitivity of color vision.

Secondary irritant	Color	Time of the aftereffect, minutes			
		1	10	20	30
Consonance (major third)	Red	130	134	134	113
	Yellow	131	157	158	135
	Green	64	60	61	68
	Blue	63	62	65	75
Dissonance (minor second)	Red	70	66	63	79
	Yellow	71	65	62	73
	Green	153	186	199	173
	Blue	124	187	150	129
Recollection of the consonance	Red	126	183	139	120
	Green	69	62	60	69
Recollection of the dissonance	Red	64	68	65	75
	Green	140	159	179	123

(The background is taken as 100 percent, the irritant action was during 2 min.)

In order to establish whether it is the emotional mindset that plays the role, not the action of the auditory irritant, she conducted another series of experiments, where the test persons were asked to recollect a joyful or sad event which played a significant role in their personal life. The results also confirmed the connection between the pleasant feelings and increasing sensitivity to red color, as well as between the unpleasant ones and increasing sensitivity to green color.

Summing up the discussion on mutual influences of various systems of the organism, we should indicate common features in the processes of the color sensitivity reaction to secondary irritants. The common in the action of various irritants on the organism is the character of changes taking place in the vegetative nervous system. Such irritants as sound, the smell of bergamot oil, camphor, rosemary, a sweet taste, slight thermal irritation activate the sympathetic branch of the nervous system; whereas, the indole smell and the thrown-back position of the head stimulate the parasympathetic branch.

The vegetative system has a central character and the vegetative shifts are one of the ways of influencing color vision. Let us consider in more detail the possible mechanisms of mutual interrelation of sense organs.

1.4. The Mechanisms of Mutual Influence of Sense Organs

The question about the mechanism of influencing was studied in detail by S. V. Kravkov; and in the sequel I will keep to his classification of the mutual influence factors.

Ephaptic Connections

Excitation of a certain nervous fiber is able to influence the condition of the adjacent nerves. Such way is called the influence through touch and was confirmed by juxtaposition of the encephalograms taken from the neighboring nerves at the moment of excitation of one of them and in the period of rest. Besides the direct excitation of the close-by nerves, the excited fiber may influence the irritation thresholds; i.e., the excitability of the nearby nerves.[11]

Irradiation Effect. The Rule of Leveling and Exaggeration

The influence of secondary irritant may manifest as an increase of sensitivity to some types of signals or decrease of sensitivity to some others. For example, sounds increase the vision acuity in distinguishing dark objects in front of a light background and diminish the ability to distinguish light object on a dark background. To explain such facts it was necessary to acknowledge non-uniformity of distribution of the additional excitation: it 'comes in a larger degree where there is already sufficient excitation and in a smaller degree to the less excited segments of our visual apparatus'.[12] This regularity is close to the dominant principle formulated by Ukhtomskii: 'the leading locus of excitation … accumulates in itself the excitation from the distant'.[13]

Connections between Centers

There are a large number of associating fibers between various segments of the cerebral cortex which may both stimulate and inhibit activity of the centers connected with them. For example, color vision exerts the inhibiting influence on the peripheral twilight vision by lowering sensitivity of the rod cells. In the experiments, where the test person was suggested, under hypnosis, the presence of irritations, there was demonstrated that the change of sensitivity depends in a greater degree on the processes in the nervous centers, not in the nerves.

The Role of the Vegetative Nervous System

The vegetative nervous system influences the functional changing of all the excitable tissues including the sense organs. L.A. Orbeli demonstrated that the vegetative nervous

---

[11] Katz, Schmidt 1940.

[12] My translation from Russian: Kravkov 1948 p. 110. In original: "в большей степени притекает туда, где уже имеется значительное возбуждение, и в меньшей мере добавляется к слабо возбужденным участкам нашего зрительного аппарата".

[13] Ukhtomskii 1925 p. 60.

system plays an important role in regulating functional systems of the organism. Since all the sense nerves pass through hypothalamus where the vegetative centers are located, irritation of any receptor may cause, besides a specific sensation, some changes throughout the entire organism: the heart rate increase, the change of blood pressure or breathing frequency and so on. The changes of the vegetative system have an extensive character, touching the entire organism or its large segments; therefore, the vegetative system is one of the most important ways through which some sense organs can influence others. For example, the influence of the green- and blue-sensing apparatuses of vision is connected with the sympathetic nervous system; whereas, the orange-red influence the parasympathetic one. Correspondingly, any influences on the corresponding system change the color sensitivity; for example, throwing back of the head increases sensitivity to red color and decreases, to green.

Sensor Conditioned Reflexes

The associative connections increase the sensations being expected or even generate them. For instance, a sight of an unlit cigarette may create illusion of the tobacco smell.

The Changing of Physiological Readiness of the Organism to Perception

Under the influence of irritation of one sense organ, there may change a condition which determines the readiness of perception of another sense organ. For example, sharp sound causes pupils narrowing which results in changing the conditions of light getting to the light-sensitive elements of the retina. The changes of the sensitivity thresholds of a sense organ under the influence of secondary irritations can be put into the same class.

Distinguishing the above mechanisms is a theoretical abstraction. In reality there always take place all the mentioned mutual influences, so that it is impossible to draw exact borders. ‘In such cases, there usually takes place restructuring of the adaptation reactions, which may create unfavorable conditions for those irritants which are not in the focus of attention at the given moment’.[14]

It should be indicated that each second our body receives hundreds of irritations coming both from interoception, muscular-articular sense, vestibular system and so on, and from exteroceptors. In particular, there was experimentally established the influence of unheard sounds and invisible light irritants. Taking into account that ‘our sensations may … change significantly depending on the action of secondary irritants to the subject, so weak on their own that they cannot produce any sensations’,[15] perception should be considered integrally, as a systemic process causing the global changes in the organism; not as an isolated separate act. All that was said above on the character of color action on the organism and mutual influence of various sensor systems on each other requires revising our conceptions concerning perception as a simple fixation of experience’s data. Activity of perception has lately become a widely discussed topic; however, in what follows I will discuss the problems

---

[14] My translation from Russian: Kravkov 1948 p. 88. In original: “В подобных случаях обычно происходит перестройка приспособительных реакций, могущая создать неблагоприятные условия для тех из раздражителей, которые не находятся в данный момент в фокусе внимания”.

[15] My translation from Russian: Kravkov 1948 p. 110. In original: “наши ощущения могут… заметным образом меняться в зависимости от действия на субъекта побочных раздражителей, настолько слабых самих по себе, что сами они каких-либо ощущений не вызывают”.

connected with another myth about perception: thinking about experience as an isolated atomic fact. Experience should be considered not as isolated acts of vision and hearing, but as a continuous process of mutually interrelated sensations. From my point of view, all misconceptions related to experience and, therefore, the cognition processes in general, have a common source which will be discussed next.

2. THE SOURCE OF THE MYTHS ABOUT EXPERIENCE: THE PRINCIPLE OF THE BEING AND THINKING IDENTITY

The topic of this section concerns discussion of the general foundations of our epistemological preferences; thus, it is somewhat abstract and, nolens volens, will take us away from our discussion of color, though they provide a nice example of inadequacy of our notions about experience. Probably, the reader has already noticed that the physiological research on color action on the organism, whose results were mentioned above, is rather old. In fact, the question of integration of sense organs was raised and experimentally studied already in the end of the 19th century and, by the middle of the 20th century, significant factual material had been accumulated. However, the physiologists' results had not been grasped and taken into account by philosophers, who are still considering experience as photography, as a simple objective source of knowledge about the world. The goal of this section is to uncover the reasons of such inertia of philosophical thinking.

In my opinion, the main source of the philosophical myths about experience is an orientation, formed in antiquity, toward studying thinking as the main source of knowledge about the world. This orientation was first formulated by Parmenides, according to whom, to think and to be is one and the same. I will refer to this orientation as *the principle of the being and thinking identity*. This principle was used implicitly, is still being applied, and has been of bad service: due to it, philosophy deviated from studying nature, having substituted it by studying the thoughts about nature. The goal of a brief review below is to familiarize the reader with the history of this principle.

1.1. The History of the Principle of the Being and Thinking Identity

Parmenides

The goal of Parmenides was to solve the problems resulted from Heraclitus' dynamics of nature. One of those problems was the problem of existence, because in order to exist the becoming should each moment arise from non-being and disappear into non-being. The second problem was the cognitive problem, because if we are to cognize the constantly changing world, then knowledge is impossible. To resolve this issues, Parmenides distinguishes a way of truth and a way of opinion; the former being a way of thinking, the second, of sensual cognition.

Both the possibility of cognition of the true existence and the existence of this true existence is derived from thinking. 'The one [way] that it is and that it is not possible not to be'.[16] It is because any really thinking object cannot not to exist, at least in thinking or as a thought; therefore, what is thought exists. Then, Parmenides makes a conclusion:

> For thought and being are the same. (B 3)
>
> *Thinking and the thought that it is are the same; for you will not find thought apart from what is, in relation to which it is uttered.* (B 8.)[17]

The identity of thinking and being allowed Parmenides moving away from dynamism and fluidity of things and substantiating the existence of the world and its cognizability; however, this principle put an end to natural philosophy. Since that time, studying thinking and studying language had become the main task of philosophy.

Plato

Plato considered 'Ideas' or 'Forms' to be the source of existence and cognition, while ascribing the properties of fluidity and non-being to matter which in conjunction with Ideas becomes the source of ordinary things. Since knowledge was connected with Ideas, Plato assigned a great importance to searching the definitions of the thing. 'To know that … F –, one must be able to say what the F, or Fness, is'.[18] The definition of knowledge according to Plato implicitly presupposes the identity of being and thinking, since expressibility of things in language became the criterion of knowing things. The supposition 'to know is to be able to say' forms a research orientation, having been perfected by his pupil Aristotle, of looking for a true definition in order to cognize the essence of the thing.

Aristotle

Since a definition of a thing requires indicating essential features, Aristotle developed an apparatus of language analysis with the purpose of searching for essence. In order to cognize the essence of a thing or what it is, it was necessary to assign it to a certain sort and class. Such a classification procedure was carried out by the analysis of notions. Aristotle is merited with the development of the foundations of logic; and one important contribution to the problem of relation between thinking and existence was his rule: 'existence is not a predicate'. This means that existence cannot be the subject of a logical proof. The method of Aristotle had been used during many centuries by the scholastics up to appearance of Early modern philosophy.

Descartes

Descartes, the founder of the Early modern philosophy, directly connected being with thinking, considering '*cogito ergo sum*' trustworthy. Let someone doubt his existence, but then there is, at least, the doubt. Then Descartes assigns this act of doubt to himself; it follows from this that I am a doubting thing, and hence 'I think therefore I am'. Certainly, the proof of Descartes is erroneous; the impossibility of correct proof follows from Aristotle's result. Let us demonstrate that this proof is neither necessary nor sufficient.

---

[16] Curd 2004 p. 58-59.

[17] Ibid. pp. 34-36.

[18] Dancy 2004 p. 36.

Necessity

Imagine you have the following dream: you see a person in contemplation, who would say to you, “I think therefore I am”.

You object, “Dear sir, you do not exist. You are only my dream”.

He would respond, “I doubted too that I was, but decided that since I doubted I existed”.

You continue to insist: “you with your doubts are only being dreamt by me, but you do not exist, don’t you understand?”

He says, “I have thought about it too that I might be mistaken, but since I am mistaken than I am”.

An imaginary dialogue can be continued ad infinitum, but since the presence of an act of thinking is accompanied by assigning a subject to the process of thinking, the dispute is unresolvable. With confidence, we can only affirm the presence of a certain thinking act: doubt, mistake and so on.

Sufficiency

The fact that the presence of thinking is not sufficient to confirm one’s own existence can be demonstrated by referring to medical practice dealing with the depersonalization-derealization syndrome. The basic forms of depersonalization may concern either the alienation of the outside world, or the alienation of one’s own body, or the alienation of one’s own self. The patient feels that his sensations and/or actions are detached from him, moved away, are not his own, are lost. At that, the person continues to think and be aware of himself, though in an alienated fashion. Thus, the presence of consciousness is not sufficient for the belief in one’s own existence. There are described in the clinical practice such cases when the person consider his thoughts to be not his; the patients may complain that their feelings are separated, are alien to them, are not their own or lost; or experience a sensation that their thoughts or movements belong to someone else or they feel themselves as playing on stage[19]. It is not at all so that the entire reality is experienced by the sufferer as imposed from outside, set up by somebody. No, part of his feelings would be perceived by the person as his own. Nevertheless, the presence of thinking does not guarantee the feeling of existence, since depersonalization is accompanied sometimes by the feeling of derealization, unlikeliness of surroundings, by lost of belief in the existence of one’s own self.

While reasoning about thinking and existence, Descartes set a problem, developed not only by philosophy but also psychology and other cognitive sciences. The mind-body problem was one of the basic problems of Early modern philosophy, and to solve it Leibnitz proposed a conception of pre-established harmony.

Leibnitz

The conception of pre-established harmony required coordination of the particles-monades which were the elements of the universe. Their nature was physical-psychic, they possessed both physical and psychic (perception and memory) properties. To realize the psycho-physical dualism, a possibility of interaction between such different substances was necessary. To provide such possibility, Leibnitz performed a certain mixing of the notions of material (physical) and logical causality.

---

[19] The description of the symptom and the examples see: Simeon Abugel 2006; Sadock 2008 p. 296.

Rational arguments draw their validity in the non-contradiction law and those, whose negation would lead to contradiction considered to be true. In distinction from logical, the metaphysical statements do not possess such necessity, and to endow the latter with the validity of the former, there was performed ascribing to the logical necessity the possibility of providing the ontological status of things. As an example, we can quote the following aphorisms by Leibnitz:

> 31. Our reasonings are grounded upon two great principles, that of contradiction, in virtue of which we judge false that which involves a contradiction, and true that which is opposed or contradictory to the false.
>
> 32. And that of sufficient reason, in virtue of which we hold that there can be no fact *real or existing, no statement true, unless therebe a sufficient reason,* why it should be so and not otherwise, although these reasons usually cannot be known by us.[20]

As the quoted excerpts show, being *or existence* and the logical property of *absence of contradiction* are considered to be essentially equivalent with respect to causality relations. Mixing the notions of the logical and physical causality is a necessary condition of application of the principle of the being and thinking identity; this mixing provides the possibility of application of the principle both in ontology and cognitive theory, because it allows moving from the domain of physical entities to logical statements and backwards. The pre-established harmony of Leibnitz were put in the foundation of symbolism, according to which only names may symbolize objects and only statements may symbolize facts.

Wittgenstein

The analytic tradition implicitly used the given principle to construct a logically flawless language by way of elimination of polysemanticity. To provide the possibility of juxtaposition of the world and language, the world was assigned the property of atomicity, discreteness, which is clearly seen from the following aphorism by L. Wittgenstein: '1.1 The world is the totality of facts, not of things', where ontology provides the opportunity to juxtapose one atomic sentence with one fact in order to produce the sought for isomorphism of language and the world. Wittgenstein's picture theory of representation presupposes a correspondence of the structure of the world to the logical structure of a sentence.

> 4.12 Propositions can represent the whole of reality, but they cannot represent what they must have in common with reality in order to be able to represent it — logical form. In order to be able to represent logical form, we should have to be able to station ourselves outside the world.
>
> 4.121. Propositions cannot represent logical form: it is mirrored in them. What finds its reflection in language, language cannot represent. What expresses itself in language, we cannot express by means of language. Propositions show the logical form of reality. They display it.

Thus, establishing the possibility of one-to-one transition from language to what is in the world solves the problems of gaining knowledge about the world through language and ensures validity of propositions (since the world is mirrored in them). The advantage of the

---

[20] Leibniz 2008 p. 196.

established possibility of one-to-one transition from language to reality consists of providing the possibility of obtaining knowledge about the world through analysis of language. Thus, the problem of realism is reduced to the problem of truthfulness and meaningfulness of sentences. However, for Wittgenstein's *picture theory* of language, the names of non-existing objects and the names of non-objects, the names of colors in particular, pose a problem.

> One cannot say of a name — for example, the name of a simple color R — that it is the name of a color. Or that it means such-and-such color. For one would be using the formal concepts of name and color in order to do so. Objects can only be named. Propositions can only say *how* things are, describe the contingent states of affairs in which objects are concatenated.[21]

The *picture theory* is based on implicit usage of the principle of the being and thinking identity and considers experience to be a means of unambiguous translation of the state of affairs into language. To provide such translation, experience must be a simple reflection of the world; to be a source of atomic propositions, experience must be a pure problem-free source of knowledge about the world. Besides, following the tradition of logical atomism, Wittgenstein ascribes the discreteness property to experience, so that each proposition would correspond to one isolated fact only. Such discretization of experience became a source of troubles for both realism and the semantics of color.

Modern Analytic Tradition

In the analytic tradition, a large attention has been paid to the color realism problem, and, hence, to the definition of the notion of color (identity of the being and existence!). The question 'what does it mean to be red (colored)' has been discussed from the position of semantics. Usually, the definitions of red implicitly presuppose a reference to the sensual experience. 'A perceptible object is red iff it looks red in standard circumstances'.[22]

Such definition, containing a biconditional term 'red' in both sides, makes us think about vicious circle. The given quotation rather provides us with a definition of standard circumstances, not a definition of red. Because of that, the initial definitions were made more complex; however, a more sophisticated version, whose development was undertaken to avoid the vicious circle, also contained a reference to sensation.

> (RED'3) Y is red' iff Y is a sensation of a phenomenal type Y such that (a), (under standard conditions and in the absence of beliefs to the effect that experiences are not to be trusted) having a sensation of type Y disposes an English-speaking subject to hold 'x is red' true iff x is the cause of y and (b) objects classified as 'red' by English-speaking subjects are disposed to cause sensations of type Y (under standard conditions and in a given subject).[23]

This definition is made more complex by the reference to a phenomenal type, which is an attempt to introduce a division on classes, characteristic for language, into the sphere of the objects of experience. This trick is similar to Russell's theory of types, which divides sets into types in order to avoid the set-theoretical paradoxes. As a whole, such classification is an

---

[21] Hacker 2001 p. 147.

[22] Peacocke 1984 p. 365.

[23] Glüer 2007 p.124.

attempt to fix the way of perceiving the objects in changing conditions; i.e., one more example of ascribing static character to perception, which quite fits the paradigm of the being and thinking identity. From the point of view of passive paradigm, the optimal situation would be the absence of any changes to provide stability in color perception. Such definitions of red should be considered from the point of view of their necessity and sufficiency. To do that, we consider several examples.

1) Necessity

One should "hold 'x is red' true iff x is the cause of y and (b) objects classified as 'red' by English-speaking subjects are disposed to cause sensations of type Y (under standard conditions and in a given subject)". However, nobody would classify as 'red' a signal perceived not by vision but, for example, by the skin surface in standard conditions. Red gives a sensation of warmth, not of red color, if it is sensed by the skin not by eyes. This example illustrates a general statement, known as Müller's doctrine of specific nerve energies. The law of specific nerve energies was first proposed in 1826 by J. Müller who defined perception according to pathway by which the sensory information is carried. The origin of the sensation does not determine the type of sensation. For example, pressing on the eye, action of electric current or chemical irritant all elicit the sensations of flashes of light.

> The same cause, such as electricity, can simultaneously affect all sensory organs, since they are all sensitive to it; and yet, every sensory nerve reacts to it differently; one nerve perceives it as light, another hears its sound, another one smells it; another tastes the electricity, and another one feels it as pain and shock… Sensation is not the conduction of a quality or state of external bodies to consciousness, but the conduction of a quality or state of our nerves to consciousness, excited by an external cause.[24]

2) Sufficiency

Let *x* be Mars. In this case, the English-speaking subject would hold '*x* to be red'. However, is it really that Mars is perceived as red? Are there many philosophers that can locate this planet on the starry sky? It looks like an ordinary star, being less bright than Jupiter or Venus. It shines like other stars; its color is almost as white as of the distant stars. If you look closely and very attentively, you can perceive a slight yellowish tincture. Mars does

---

[24] Müller 1844. s. 667. Translated by Edwin Clarke and Charles Donald O'Malley. The original text: „Sind die Nerven bloss Leiter für die Eindrücke des Lichtes, der Tonschwingung, der Riechstoffe wie kommt es, dass derjenige Nerve, welcher die Riechstoffe riecht nur für diese Art von Eindrucken ist, für andere nicht, und dass ein anderer Nerve die Riechstoffe nicht riechen kann; dass dor Nerve, welcher die Lichtmaterie oder die Oscillationen derselben empfindet, die Oscillationen der schallleitenden Körper nicht empfindet, der Gehörnerve für das Licht, der Geschmacknerve für die unempfindlich ist, der Gefühlsnerve die Schwingungen Körper nicht als Ton, sondern als Gefühl von Erbitterungen. Diese Betrachtungen haben die Physiologen genöthigt, einzelnen Sinnesnerven eine specifische Empfänglichkeit für Eindrücke

not look red. From the point of view of color realism, we should not consider the observation conditions to be normal. However, a look to the night sky is a quite ordinary observation, though Mars shines with a color different from the one that is seen on the photo of its surface made by a powerful telescope. Therefore, we cannot conclude that Mars ‘causes sensations of type Y’ and that ‘the object x is classified as ‘red’ by English-speaking subjects’.

Concluding the historic excursus on the principle of the being and thinking identity, I would emphasize that this principle is in the foundation of the tradition of investigating thinking instead of existence. Thanks to it, philosophers’ activity today is devoted to clarifying the notions and, to a great extent, has turned into the debate about words. Philosophers have received many times the indications of the falsity of this principle. For example, Ch. Fillmor (1968) and G. Lakoff (1965) have established, during the development of semantics and syntax, some discrepancies between the structures of consciousness and the outward structures of language.

The history of science abounds in the proofs of this principle’s falsity, in particular, the theory of atomic structure of matter, according to which the matter of the atom is concentrated in its center, which contradicts the manifested palpable solidity of the things. Another example is quantum mechanics with its discreteness and imaginary numbers, which so clearly contradicts the common notions about the continuity of processes and their being of real type! The world is arranged differently in comparison to our usual way of perceiving it, whereas our sense organs provide us only with an approximation sufficient for existence in a rather narrow range of conditions.

However, why is it so that philosophy continues to follow the orientation to study language, not the world? The reasons of inertia of the philosophical thinking lie not only in the antiquity of the linguistic tradition but also in the conveniences it provides. First of all, there is postulated the existence of the outside world or objective reality which is considered to be primary and a source of sensations. Secondly, cognizability of the world is presumed through the representational context, reality being the reason of sensation. Both physicalism and representationalism, presuming 'transparency' of perceptual experience, have the 'research aims to identify the material referents of phenomenal concepts’.[25] Finally, the identity of being and thinking ensures the cognition’s adequacy.

Thus, the passive paradigm provides an automatic resolution of the basic question of ontology and epistemology. However, the traditional picture theory, together with conveniences, has got some problems which are difficult to resolve within the framework of this conception. Let us mention several of them:

- how are the two-dimensional retinal images transformed into three-dimensional bodies;
- how is the knowledge possible about something outside of the vision field, for example,the back side of the Moon;
- how is the perception of (empty) space possible;
- how does a sum of sensations form the bodies;
- what is the ontological status of color – a quality which is not an object.

---

zuzuschreiben, vermöge welcher sie nur Leiter gewisse Qualitäten, nicht aber für andere sein sollten“.

[25] Papineau 2003 p. 207.

Besides the problems of clarification of some issues, there are critical arguments, many of them addressing too simplified understanding of experience. Slashing criticism of the passive conception had finally led to the situation when the rationalist tradition was left practically without a cognition theory, and experience as a method of obtaining scientific knowledge was discredited.

2.2. Critical Arguments against Experience

The positivists thought that there exists pure experience, expressed by the 'protocol sentences', on whose basis the scientific facts are formulated. Facts are reliable objective evidences, confirming hypotheses. Experience may confirm or refute a hypothesis and, on the basis of experience's data, the decision on falsity or truthfulness of any statement is to be made. However, there have been voiced a number of critical arguments against experience, which undermined the trust to experience as an 'objective independent evidence'. Let us consider in more detail the criticism of the empirical foundations of the scientific method.

> Underdetermination of theories by evidence (W. V. Quine).
>
> W. V. Quine (1969) indicated that the sensual data do not determine the scientific theories. It means that one and the same collection of facts may be explained from the point of view of various theories. Since the facts confirm more than one theory, they cannot be brought in as the grounds of preferring one theory to another; that is, cannot be engaged as independent evidences.[26]

2) Historical Development of the Scientific Fact (L. Fleck)

In the year of 1935, there was published a book by Ludwig Fleck, in which he considered the history of development of the medical conceptions about deceases. He demonstrated that the perception of data, description of the decease, and its diagnostics depends, in a decisive manner, on the conceptions being dominant in the society. It means that the fact is not invariant and objective evidence, but is a subject of historical development. Correspondingly, truthfulness or falsity of the evidence cannot be absolute but is determined by the context and style of thinking within which it was stated: 'Concerning other proto-ideas, such as the Greek pre-idea of the atom or that of the elements, we are also unable to decide whether they are right or wrong if they are taken out of their chronological context, because they correspond to a different thought collective and a different thought style'.[27] Thus, Fleck points out that fact cannot be independent objective evidence and cannot be considered as a reliable foundation of scientific knowledge.

---

[26] Quine 1969 pp. 26-68.

[27] Fleck 1981 p. 25.

3) Theoretical Ladenness of Observations (P. Duhem, N. R. Hanson, T. Kun, P. Feyerabend)

The question of ladenness of observations was first raised by P. Duhem in his 1905 book ‘The Aim and Structure of Physical Theory’. Describing the physical experiment, he indicated that obtaining the data of the experiment can be subdivided on two parts. The first part is observation; and to observe it suffices to be attentive and have a possibility to perceive. The second part of experiment consists of interpretation of observations which requires the knowledge of many physical theories and the skills of applying them. ‘A physical experiment is not simply the observation of a group of facts but also the translation of these facts into a symbolic language with the aid of rules borrowed from physical theories’.[28]

Duhem connects theoretical ladenness only with the theoretical interpretation of observations, assuming that the observation itself neither depend on the observer nor requires the knowledge of the theory. A stronger claim was made by Hanson (1958) in his ‘Patterns of Discovery’.

Norwood Russell Hanson started the book by considering the following example: two microbiologists are looking at *Amoeba* in a microscope; and, having been asked what they saw, one of them replies that he saw the nuclear, mitochondria, cytoplasm and other cell structure, while the other says that he saw the organs of movement and eating. The discrepancy between the answers is caused by the fact that the first considers amoeba to be a cell, whereas the second, an animal. Is this difference just a consequence of different interpretation of what they saw? Hanson claims that the difference here is much deeper: the microbiologists really see different things.

How is it possible to see different things while observing the same object? The physicist and the Eskimo child, while looking at a roentgen tube, have the same visual data; but the ways of their visual cognition are different, therefore one of them does not perceive the same thing through vision as the other. Observation is not just the presence of a visual experience but also a way, through which this visual experience is acquired. Hanson claims that vision contains more than just sensual data; and the difference of the sensual experience is caused by no means by different interpretations of the seen: vision takes place *before* any interpretation. Theoretical ladenness is a necessary condition of observation, because we tend to see what we expect to see.

The philosophical significance of the thesis of theoretical ladenness is that observation cannot be used for verification of the theory, since it is ‘infected’ with theoretical assumption and, therefore, there arises the danger of a vicious circle: we compare not the theory with the observations but the theory with the theory. Hence, observation cannot be an objective source of data about the world, since not only the interpretation of observation but the perception itself depends on the theoretical context.

---

[28] Duhem 1954 p. 156.

4) Impossibility to Draw a Line between Theory and Experience (G. Maxwell)

The positivists thought that there exists a distinct boundary between the observable and non-observable; moreover, it was considered that the observable was that that can be observed directly, by naked eye. However, in modern science, observation is becoming more and more indirect. When the instruments were less sophisticated, it was considered that they just amplify the sense organs. That which can be viewed in a binocular, can be also viewed by the eyes, if you come close enough. With such understanding, the usage of instruments in observation cannot be a source of problems. However, sophistication of the observation equipment has lead to the situation when many scientific observations can hardly be called ‘direct’. There are objects, such as electron, which can be detected only with the help of special devices.

The empiricism dogma about the existence of a distinct boundary between the observable and non-observable was criticized in a Grover Maxwell’s (1962) article. The main thesis of Maxwell is that there is no clear-cut boundary between the observable and theoretical. Maxwell begins his argument with a remark that such expressions as ‘theoretical entities’ and ‘dichotomy of the theoretical and observable’ are examples of erroneous categories. Terms and conceptions are theoretical, whereas entities can be observable or non-observable. Two questions follow from this distinction: is it possible to split our language into theoretical and non-theoretical parts and can we classify objects on observable and non-observable?

Maxwell gives negative answers to both of these questions. While compiling experimental reports, we use such words as ‘mass’, ‘impulse’ and must conclude that our language is laden with theory. Besides, our ‘theoretical’ knowledge significantly influences our perception. Suppose we show a tennis ball to a Stone Age man. He would not see it being a tennis ball, because to perceive a tennis ball one needs a conception of playing tennis. Thus, our language is substantially laden with theory.

Maxwell also rejects the possibility of subdivision of objects to observable and non-observable, because observability is most connected with the level of the technology development and the power of the instruments used for observation. Therefore, there exists a continuous sequence of the vision processes: vision through air, through a window, through a binocular, through an optic microscope, and through an electronic microscope. Thus, we cannot draw a clear line between the observable and non-observable: while genes were considered to be theoretical objects prior to invention of the electronic microscope, now we can see them in a microscope. Thus, the notion of observability does not presume that the given object can be viewed here and now. The object can be temporarily non-observable for various reasons, but it may become observable under different, more favorable circumstances. Observability is a principal possibility of being seen; thus, *x* is observable if the conditions exist such that if we put *x* there we will observe it.[29]

To sum up, Maxwell demonstrated that we cannot use the notion of observability as a ground to state that no theoretical objects exist. Maxwell’s argument is directed, for the most part, against resolution of the question about the ontological status of objects. Contrary to the positivists who considered real only that is observable, Maxwell insists that we must believe

---

[29] Maxwell 1962 p.16.

in reality of directly non-observable objects, because observability of an object, postulated by the theory, depends more on the level of technology development than on its nature.

The source of the passive paradigm's reliability – the hypothesis of an isomorphism between the objective reality and its reflection in consciousness – has ultimately led to relativism. Also, though some of the problems of ontology and cognition theory had received natural solutions, there appeared also some problems whose resolution required different conceptions about experience.

2.3. The Myths about Experience: Passivity and Discreteness of Perception

It was necessary for the tradition, which assumed an isomorphism of world and thinking, to formulate such conceptions about experience that one-to-one correspondence would be guaranteed. A passive paradigm, where perception is considered as a direct reflection of the world, was quite convenient for that purpose. Within the framework of the passive paradigm, the main question of philosophy − 'to identify the material referents of phenomenal concepts' − presupposed that a state of mind is caused by our experience (for instance, experience of color), and experience is represented in mind by 'qualia'.[30]

a) philosophical myths about experience: passivity of perception

In the end of the XX century, there was appearing more and more often another understanding of experience; the conceptions of passive reflection of reality were substituted by the understanding of experience as active, according to which observation includes motor activity. It was established that perception is impossible without movements; the necessity of motor impulses was experimentally discovered even for hearing – which apparatus is hidden deep inside a bone and, therefore, lacks its own movements.

The paradigm change took place under the influence of criticism; moreover, the main critical arguments put forth against experience were the direct consequences of the perception activity. *Activity of perception* includes searching, gathering, processing and ordering the information coming from the sense organs. Let us show that the above-mentioned criticism is a direct corollary of the perception activity.

The Thesis of Underdeterminacy as a Corollary of Perception Activity

Activity of perception, expressed as *searching* the information relevant for the observer, points to underdeterminacy of the data perception. Since perception is an active search of the information which the subject expects to find and which corresponds to his/her current interests and needs, one and the same situation will be perceived differently by the observer at different moments of time. On a higher level, this selectiveness of search leads to underdeterminacy of the theory by data.

---

[30] Shoemaker 2003 p. 253-255.

Historical Development of the Scientific Fact as a Corollary of the Perception Activity

Since activity of perception includes *gathering* of the relevant information, which corresponds to observer's expectations, this results in selecting the confirming examples. Each piece of experimental evidence will be interpreted according to the point of view, which the researcher subscribes to. Therefore, the fact possesses cultural relativity; the process of observation and formulation of its result turn out to be dependent on the dominating conceptions. Correspondingly, the change of the world outlook places the accents differently and requires reformulation of the evidence; so the scientific fact is not 'reliable' non-problematic evidence objectively showing the state of affairs in the world. It is a 'subject of historic development'; and both its interpretation and the perception itself depend, in particular, on the views and the world outlook accepted in the society.

Theoretical Ladenness of Observations as a Corollary of the Perception Activity

Sorting the obtained information is performed on the initial stages of perception and includes categorization: first, a rough one (visual image, sound, perception), then a notional one, which according to J. S. Bruner (1974) differs only by the degree of specification, not by nature. Thus, perception always turns out to be notionally laden; and any 'pure' perception is plainly impossible. The categorization process makes perception meaningful, which is confirmed by the examples of 'conceptual blindness' described by the eye surgeons.

A person is describing his first visual experience after the cataract removal:

> He heard a voice coming from in front of him and to one side: he turned to the source of the sound and saw a 'blur'. He realized that this must be a face. Upon careful questioning, he seemed to think that he would not have known that this is a face if he had not previously heard the voice and known that voices came from faces.[31]

A man without visual experience 'sees' only the chaos of colored spots, not understanding what is in front of him. This example shows a direct dependence of the real-time perception on the ability of categorization; i.e., the dependence of vision on theoretical interpretation.

Impossibility of Drawing a Boundary between Theory and Experience as a Corollary of the Perception Activity

Processing information includes interpretation and understanding of the perceived. On this stage, important roles are played by the prior experience, intentions, needs and many other factors, which are difficult to control, due to which the descriptions of one and the same

---

[31] Gregory Jean 1963 p. 366.

situation by different observers are different. Therefore, observation turns out to be so connected with theoretical expectations and axiological orientations that it is impossible to draw a clear line between objective vision and subjective orientations.

b) philosophical myths about experience: discreteness of perception

The tradition of considering experience as atomic and perception as a single act of receiving a signal of a certain sensor modality takes its origin in the necessity to adjust the conception of experience to the structure of language: a separate word must signify a separate object and a separate statement, a simple isolated fact. Such correspondence makes the understanding of experience compatible with the passive mirror paradigm. The formed tradition to consider experience as a succession of isolated discrete acts provides us with too simplified a picture. Beginning from the logical atomism and up to the first half of the XX-th century, the language was considered as a collection of separate sentences. Experience was also considered as a single isolated fact which can be expressed in the form of protocol or basic sentence.

It should be said in defense of the picture theory that there are physiological premises to treat perception as discrete. In part, such understanding is connected with our possibility of movement, which allows us to constantly change the vision field and constantly perceive something new. The organization of nervous system is such that it reacts more actively on new stimuli, rapidly lowering its activity in habituation. Accordingly, the first impression is the strongest and brightest; and it is this impression that is being referred to while talking about the observation of a fact or a state of affairs expressed by a separate sentence.

Another premise is the ability of vision to single out the objects from the background. A sophisticated complex of sensations coming, for example, from a cup is combined with the traces of the previous experience, as well as with the current goal orientations and thus form an image which we are used to denote by one word – ‘cup’. The process of perception of the cup is caused by formation of a complicated sensations complex. The permanent flow of sensations of different kinds is such that no sensation is exactly identical to any other, which is possible due to constant movement of eyes.

> There are three types of eye movements that may be made when tracking visual stimulus… Reflexive saccadic eye movements occur in response to the sudden on set of a peripheral stimulus… Voluntary saccadic eye movements occur under voluntary or planned control… Smooth pursuit eye movements represent a third type of eye movements used in tracking visual stimuli.[32]

The eye’s fovea changes its position ones in every 150-200 ms. The saccadic eye movements have the capacity to accelerate up to 1000 degrees/second.[33] The saccadic eye movements are very rapid and occur every 100-200 ms. The average saccade takes only 25-30 ms**.** Taking the day as 12 hours and the duration of every new phase of visual sensation to be 200 ms each, we get that only vision would provide us with more than 216,000 sensations per day. Hearing, skin and osmesis give no less sensations; and there are even more

---

[32] Nelson 2001 p.329.

[33] Erickson 2007 p. 58.

sensations from the muscle movements. And all this numerous psychic acts connect with each other every second and thus form sophisticated complexes of sensations, which we perceive as objects or surfaces, spatial extension or the rays of light.

As it was indicated earlier, it is impossible to explain how the person perceives the bodies while considering experience to be a discrete collection of sensations. However, as the logical atomism afterward gave place to theoretical holism in the form of the Duhem−Quine thesis,[34] also for experience the idea of independence of isolated perceptions must give way to a conception taking into account the experience continuity, the mutual influence of sense organs and the role of perceived information in creation of general tuning of the organism. Therefore, I am formulating

The Principle of Empirical Holism

Perception is a continuous in time process of action on the body of a sophisticated complex of irritants of various modality, which exert influence on the entire organism and its motor activity, whose excitation action on the sense organs we experience as sensation due to fixation of our attention on a part of the jointly acting stimuli being a small portion of the complete set of irritants.

On the mind-body language, this principle means that not only the informational component of the perceived signal should be taken into account but the influence of the signals on the condition of the body, since it is the latter that determines our ability to perceive. The body is a necessary mediator between the physical signal and its mental image. The body determines, to a large extent, which ones of the dozens of thousands of sensations acting on the organism each minute are worth of our attention and the action of which should be inhibited. For the philosopher, the body is the dwelling place of the enigma of the mind − brain relations and already because of this it requires attention. For this reason, the next paragraph will be devoted to the influence of the color perception on the body and the discussion of the question how the body can be a source of belief in existence. Let us consider first how the empirical holism principle may be used to overcome the traditional difficulties of the picture theory.

2.4. The Difficulties of the Picture Theory from the Point of View of the Empirical Holism Principle

how does the sum of sensations form bodies;

The jointly acting irritants are responsible for objectivity of our vision; it is precisely thanks to the complex character of perception that we see not the chaos of colored spots but the objects. The mechanism of the sensations connection was clarified in the conditioned reflexes theory of I. P. Pavlov, who indicated that if two different irritations had appeared simultaneously for some time, then a little afterwards the appearance of one of them would

---

[34] Duhem (1954) wrote: “An experiment in physics can never condemn an isolated hypothesis but only a whole theoretical group”. p. 183.

induce recollection and reaction to the other. Studying the mechanisms of the conditioned reflexes imprinting, Pavlov noticed that the coinciding in time sensations – visual, acoustic, tactile, gustative, or osmatic – are connected by the brain in such way that the appearance of one of these sensations causes expectation of some other. In such fashion, a photo of a fragrant flower may create a smell sensation. After the sensations of different modalities are combined in an integral complex, the presentation of one of them evokes from memory the idea about the others and there arises an idea about the object. As a result, the constantly concomitant sensations are united into relatively stable entities, so that the action of one of them immediately evokes in memory the entire complex; and so we see the objects, not a bunch of colored spots. The vision on its own is not sufficient for perception of the world; the continuity of experience is necessary combined with the traces of the former experience. Connection of sensations is accompanied by formation of concepts based on the past experience related to manipulation with the given object or action in a given situation. To explain objectivity of vision, we need to consider not an isolated observation but experience in a wider context which includes interaction of the sense organs of various modality and integration with the past experience.

how are two-dimensional retinal images transformed into three-dimensional bodies;

> The skill of vision is formed in early age together with the sense of touch, trying tastes, and manipulations with objects providing the idea of the objects extensionality. A prerequisite for the extensionality perception is the sufficient development of the spatial conceptions which are formed, to a large degree, due to observer's activity. The lack of either motional or sensor experience prevents one from perceiving the things as three-dimensional. The effect of seeing the world as flat can be produced artificially; such experiment was described by J. Gibson (1950) who created for himself certain presetting of vision in order to perceive the room not as a room but as a picture. To differentiate between two modes of vision he introduced the notions of visible field and visible world.[35]

Perception of objects may change to perception of picture also in the conditions when the normal perception of space is disturbed. Such effect was described by G. M. Stratton (1896) in the experiment with wearing lenses that turn the image upside down and invert it from left to right.

> All images at first appeared to be inverted; the room and all in it seemed upside down. The hands when stretched out from below into the visual field seemed to enter from above. Yet although these images were clear an definite, they did not at first seem to be real things, like the things we see in normal vision, but they seemed to be misplaced, false, or illusory images between the observer and the objects or things themselves. For the memory-images brought over from normal vision still continued to be the standard and criterion of reality. The present perceptions were for some time translated involuntarily into the language of normal vision; the present visual perceptions were used simply as signs to determine how and where the object would appear if it could be seen with restored normal vision. Things were thus seen in one way and thought of in a far different way. This held true also of my body. For the parts of my body were felt to lie where they would have appeared had the instrument been

---

[35] Gibson 1950 p. 16.

> removed; they were seen to be in another position. But the older tactual and visual localization was still the real localization.[36]

how the knowledge about the things outside of the vision field is possible, for example, the knowledge about the back side of the Moon;

Since perception has a complex character, the synthesis of information of various modalities gives an integral idea about the objects. Suppose we have never seen the given tomato, but since we have many times before held various other fruits we know that this tomato possesses a back side though we do not see it. Since there is a possibility to turn the visible object or walk around them, the idea of three dimensions becomes an unalienable property of our thinking about the objects.

Various spatial positions of the lightened hemi-sphere of the Moon with respect to the observer on the Earth, which turn the Moon into Crescent, surely indicate three-dimensional character of this body and, extrapolating the experience we have, we may draw a conclusion about this celestial body.

Note that oftentimes quite abstract or even theoretical ideas get involved in the conceptions about the objects. This is indeed so, and the very setting of the question about the other side of the Moon was impossible while the influence of Aristotle's authority was strong and the Moon was viewed as a perfect celestial body fixed on a crystal sphere. Such question could be raised only after the works of Galileo, who established material integrity of the celestial and earthly worlds and this made possible the extrapolation of the experience obtained in the condition of Earth to the celestial bodies. From the positions of empirical holism, to see means to have knowledge of a certain kind; vision is an amalgam of sensations, accumulated experience, expectations and intentions of the observer, theoretical orientations and language.

how the perception of (empty) space is possible;

Space is a complex conceptual-sensor entity, an uttermost generalization of the sensor data of various modalities. The capability of such large-scale synthesis is formed for a person only by the age of 12-13 years provided he/she possesses a sufficiently diverse life experience. For example, the pygmies of Africa, spending most of their life in the jungle, are not able to correctly estimate the distances on the open terrain.

R. Held and A. Hein conducted an experiment with two kittens; one of them was harnessed into a little cart and moved on its own, while the other was sitting tied in the cart. The rest of time the kittens spent in darkness. As a result, the active kitten would see normally; whereas the spatial vision failed to be formed for the passive one. Thus, the sensor-motor experience is necessary to correctly form the space-related conceptions. An important role is played by the exercises in estimation the perspective and changing the distances and the angles of observation of the objects.

At the same time, the sensor apparatus is equipped with special receptors perceiving only the spatial characteristics. For example, the sense of touch gives information about the spatial position of the irritating action; the sense of hearing can localize the sound source in space

---

[36] Stratton 1896 pp. 613-614.

(binaural hearing); there are the cells in the retina that react on the movement in a certain direction and the cells whose excitation is caused only by presentation of lines of a precise inclination.

Moreover, perception is provided not only by the five, known already from the Antiquity, organs of sense. There is also proprioception and interoception, providing the brain with information about the spatial position of the body, velocities and accelerations experienced by each muscle, and about the body orientation in space with respect to the vertical direction. The movements of the observer give information about the spatial characteristics of the environment; and this information, provided the corresponding experience is present, generates the perception of space. As it was indicated in the beginning, the data of various sensor systems are the foundation of synthesis of the spatial conceptions which development is consummated only in the adolescent age.

The issue of color realism will be discussed in the next chapter.

Summing up this chapter, we should emphasize the necessity of taking into account the integrity of experience, since sensations (even ones we are not aware of) play an important role in the observer's presetting for perception. A practical significance of such presetting is huge; it provides the very possibility of observation and perception. 'In such cases there is usually takes place reorganization of the adaptive reactions, which may create unfavorable conditions for those irritants that are not in the focus of attention at the moment'.[37] The influence of presetting is a general property of perception in general: we are inclined to pay attention only to those details of the surroundings that may serve solving our problems, while we disregard all the rest. However, it is customary now to treat experience as a succession of isolated observations occurring independently from each other. I connect the supposition about the experience discreteness with the philosophical premise concerning an isomorphism of thinking and the world, which I call the principle of the being and thinking identity. To ensure one-to-one correspondence, experience must be simple reflection of the reality. And since thoughts are expressed in the language consisting of separate sentences, experience was ascribed discreteness allowing assigning a separate fact to a separate sentence.

The picture theory was criticized and had some unsolved problems. In this chapter there was formulated the empirical holism principle and, based on it, there were suggested possible solutions of the problems of passive conceptions and the answer to criticism was given.

3. COLOR REALISM AND OTHER PHILOSOPHICAL ISSUES OF THE MUTUAL INFLUENCE OF SENSE ORGANS

Why is it important for the philosopher to know about the mechanism of perception? Because this knowledge allows shedding new light on the main question of philosophy: the mind-body problem. Since perception is a process during which material signals are

---

[37] My translation from Russian: Kravkov 1948 p. 88. The original text is: "В подобных случаях обычно происходит перестройка приспособительных реакций, могущая создать неблагоприятные условия для тех из раздражителей, которые не находятся в данный момент в фокусе внимания".

transformed into mental images, its investigation allows considering the mind-body relations in a quite localized fashion. The problem is that mind and body have absolutely different properties. In the sphere of the brain the informational processes controlled by electric impulses are dominant. The body is controlled by the electric signals not directly but chemically when there come into the blood the substances which exert stimulating or inhibiting influence on the entire organism. The endocrine glands, which produce neurotransmitters and hormones, are the mediators in passing the information from the brain to the body. The action of the chemical agents is non-local; it covers sufficiently vast domains of the organism. The control of the hormone systems is executed by the subcortical structures of the brain, for example, hypophysis and reticular formation, which influence the general condition of the entire body including the brain.

Signals from the sense organs come first to the subcortical structures, where they are additionally processed. These signals proceed by two paths: specific or nonspecific somatosensory pathways. The first path goes through the thalamus core and serves for the prompt and precise transfer of signals from the sense organs of one modality. The activating influences, coming from the thalamus cores, affect only some limited regions of the cortex. The selective increase of activity of a small region of the cerebral cortex organizes the attention by activating, against the general background, the work of a small number of cortex cells. Usually, the neurons of exactly those sections of the cortex are activated that are engaged at the moment in the most important for the organism activity. This significantly fosters the realization of specific functions of the brain: perception and processing of the most needful signals, and execution of the top-priority motional acts.

The nonspecific afferent paths go through reticular formation, where there takes place the synthesis of information having come from various sense organs. The nonspecific system provides with information the nervous centers responsible for coordination of all the systems of the organism. The ascending influences from reticular formation are slower and cover the entire cortex in a diffusive fashion, causing a general change of its functional condition. The experiments on animals showed that irritation of the nonspecific system increases the general activity level, the level of attentiveness to external signals and improves their perception. The impulses of the nonspecific system play an important role in regulating functional condition of the cerebral cortex neurons. These impulses are especially amplified under the action of new irritations, preparing the organism ahead of time to reacting to an unexpected situation. This always takes place in the investigatory reactions and initial stages of development of a conditioned reflex. The regulation of sensitivity is carried out by the vegetative nervous system which changes its state under the irritants action.

Thus, an external signal never produces an exclusively specific effect manifested in the perception act. Irritation of any sense organ induces at least four responses in the organism: sensor reaction or sensation (under the over-threshold irritation), motor, emotional and vegetative reactions. Correspondingly, color also exerts a complex influence on the organism which allows talking not only about the epistemological role of color but also discussing the ontological issues.

3.1. Color and Realism: Continuity of Experience as a Source of Belief in Existence

Color brings about more realism in the TV film images. The display of colors in the illustrative pictures and on TV screen greatly increases their realism as well as the enjoyment.[38] One of the mechanisms of increasing the color realism is the formation of emotional mood. In such fashion, red color is associated with apprehension; green, with tranquility; blue induces the feeling of coolness and so on. One of biological functions of emotions is amplification of reactions; thus, by inducing emotions, color makes sensations and the experience of the feeling of reality more intense. 'Color is one of most powerful elements in our environment; it is typically the first thing, we notice when we enter a room'.[39]

The aim of this paragraph is to discuss the mechanism through which colors increase realism of the perceived. Talking about realism in general, let us quote that existence is not a predicate since the problem of existence cannot be the subject of a logical proof. Existence of a certain object or phenomenon is always a question of belief; and, in the sequel, we will discuss the sources of this belief. Since rational reasoning cannot be a source of belief in existence (and all the proofs of existence contain logical errors), we consider how the experience, being the second source of knowledge about the world, can provide us with such belief.

There are some data that the belief in one's own existence is supported by continuity of sensations. These data come from the neurological practice that deals with the people having no sensation of their own body, no proprioception. The person, who does not feel his own body, seems to himself empty, hulled, and non-existing. There are also the reverse cases when, after amputation, a person continues to feel the amputated body part as his own even months after the operation. Oliver Sacks (1985) describes a case of a sailor with an amputated finger; and it seemed to the patient that this finger was there on its place and it protruded to such an extent that he had to turn his head when he would bring the hands to his face.

The patients with amputated limbs keep experiencing the phantom pains in the lost body part sometimes for months and even years. Therefore, the presence of sensations is not a necessary condition of existence; neither, it must be said, it is a sufficient one; it is just a source of psychological conviction.[40]

Taking into account that the continuity of sensations ensures the belief in one's own existence, let us consider in an analogous fashion the issue of belief in the outside world. Let us note that, though each second the receptors of our organism generate hundreds of signals about the presence of sensations, this issue is not simple. First of all, there is important not only the presence of permanent sensations but a certain level of adaptation, because a breakdown or a change of readings in one of the sensor systems may result in the lost of the feeling of reality. For example, Professor George Stratton, who conducted experiments with the lenses turning the images upside down and inverting them, noted the feeling of the visible images being unreal.

---

[38] Padham Sonders 1978 p. 47.

[39] Venolia 1988 p. 57.

[40] Mitchell 1872 p. 318.

> The course of experience was something as follows: all images at first appeared to be inverted; the room and all in it seemed upside down. The hands when stretched out from below into the visual field seemed to enter from above. Yet although these images were clear an definite, they did not at first seem to be real things, like the things we see in normal vision, but they seemed to be misplaced, false, or illusory images between the observer and the objects or things themselves. For the memory-images brought over from normal vision still continued to be the standard and criterion of reality.[41]

After a certain period of time, the unreality feeling disappeared; and after several weeks, the visual apparatus adapted to such a degree that the things started to appear normal as they did before the inversion. After the lenses removal, the reverse adaptation proceeded must faster and was not accompanied with the feeling of unreality of the surroundings.

However, experiencing the feeling of unreality of the surrounding world may occur not only due to non-typical irritation of visual apparatus; an analogous effect may be caused by unusual influences to other sensor systems. For example, the Soviet pilots-cosmonauts, describing the action of weightlessness on the organism, note that a certain percentage of people are losing the feeling of events reality when they come to the weightlessness conditions. Some people are experiencing complete disorientation and self-identity loss. For example, one of the tested persons, observed by the doctor, experienced a motor excitation, cried and his face had an expression of horror. Afterwards, he described his condition as follows: 'I did not realize that the conditions of weightlessness had come. Suddenly, I had a sensation of rapid downward falling; and it seemed to me that everything around was breaking down, decomposing and flying to all sides. I was taken by a feeling of horror; and I did not understand what was happening around me'.[42] This example, showing the reaction of the organism to the lack of habitual irritation of vestibular apparatus, also illustrates the presence of mutual influences of sense organs.

Now, let us turn to the question of how does color contribute more realism to images. Certainly, colors are an extra source of sensations and already by that they increase the reality feeling. However, this is not their only action; there are some other ways through which colors influence the organism.

For example, Faber Birren in his book 'Selling with Color' mentions on the effect that colored lights had on blindfolded subjects. In this instance the subjects stood before the light with arms extended straight out in front. Under the influence of red light, the subjects' arms spread apart; under the influence of green light, the arms tended to come together. This is an instance where color has worked independently of vision.[43] Hence, the electromagnetic radiation of various wavelengths, whose reaction with the retina is perceived by us as the sensation of color, exerts a complex influence on the organism. As it was already said in the first part, color acts on the vegetative nervous system, accelerating or inhibiting the biochemical processes and so exerts either exciting or inhibiting influence.

---

[41] Stratton 1896 pp. 613-614.

[42] My translation from Russian in: Leonov, Lebedev 1966 p. 7. The original text is: "Я не понял, что наступило состояние невесомости. У меня внезапно возникло ощущение стремительного падения вниз, и мне показалось, что все вокруг рушится, разваливается и разлетается в стороны. Меня охватило чувство ужаса, и я не понимал, что вокруг меня происходит".

[43] Abbot 1947 p. 131.

> It has been noted that warm colors are more stimulating than cool colors. Muscular activity was measured under various lights and showed the following effects. Under ordinary light muscular activity registered 23 units, under blue light 24 units, under green 28, under yellow 30, under orange 35, and under red 42 units. Tests indicated that students made greater progress in arithmetic while working under a brilliant red light than they made when under ordinary illuminatia.[44]

Correspondingly, while discussing the functions of color vision, we must take into account the complex action of the signal on the organism, its role in the formation of emotions. Emotion is a very old acquisition of the organisms in the process of evolution. It is an integrated reaction which allows evaluating promptly the quality of the irritant: whether it is beneficial or harmful, whether one has to seek it or avoid it. An emotional reaction arises well in advance of the complete recognition of the image and the formation of the actions program. The biological role of emotions is that they are a mechanism of amplification of the reactions. Thanks to emotion, a slight negative irritation may induce a powerful response. Color, as one of the factors of influence on the vegetative nervous system, has a direct access to the emotional sphere and, thus, it amplifies emotions and increases the feeling of realism.

It must be recognized that brightness and color strongly affect the attitudes and reactions of the entire human organism. High brightness and strong color stimulation tend to excite the body to increase muscular tension, blood pressure, and respiration. On the other hand, dimness and suppression of color tend to relieve tension and to relax the autonomous nervous system. Brightness, therefore, is conducive to muscular activity, while softness of color is conducive to mental activity.[45]

Summing up, let us indicate the main mechanisms of color influence on the increase of the realism of the perceived. First of all, colors are an additional source of perceptions, the continuity of which ensures the feeling of reality. Color exerts an additional influence on the nervous system, either increasing or inhibiting its activity, even without participation of vision. A strong connection between color and the mechanism of emotions provides amplification of the organism reactions to color, which additionally influences the nervous system and increase the reality feeling. Besides, color participates in the formation of presetting of the organism to the perception of other signals. Let us consider further the cognitive functions of color.

3.2. The Color and Cognition

Our ability to distinguish colors turns out to be one of the cognitive capabilities, which makes our orientation in the world easier. From the point of view of empirical holism, we must consider not only the process of color perception but also the influence of the color action on the emotional sphere, motor and vegetative systems. The fist two ways of the color influence on the cognitive processes have been widely investigated and are known. ‘Color adds dimension to a world that visually would otherwise consist only of light and dark, form and motion. With color, we can better tell the time of day, the ripeness of fruit, the identities

---

[44] Ibid p. 129.

[45] Birren 1959 p. 94.

of various plants and animals, and our state of health'.[46] Colors help us distinguish the things out of the background and, thus, accelerate the orientation in the surroundings. For example, 'conjunctions of color and depth in a visual search task is faster than the detection of targets defined by a single attribute'.[47]

The importance of color vision in the 'primitive' society of hunters and gatherers was so high that there were much less people suffering from colorblindness among those tribes, because they were subjected to the natural selection. Still, the frequency of colorblindness is smaller in the less civilized countries. One in twelve Caucasian (8%), one in 20 Asian (5%), and one in 25 African (4%) males are so-called 'red-green' colorblind.[48]

In the modern society, the color vision plays a smaller role, and the percentages of the cases of 'red-green' colorblindness are approximately 8% among males and 0,5% among females, while three-fourth of the people with the defects of color vision have a diminished sensitivity only to one color. However, color is not a necessary means of the world cognition, though provides some extra advantages. That the capability of distinguishing colors is not a very significant cognitive means is witnessed by the fact that the people with the color vision defects sometimes do not suspect them until the anomalies are discovered with the help of simple laboratory tests. Since the person cannot know which colors are perceived by other people, the manifest confusion of colors is not so easy to reveal during an oral enquiry. A person with a defect of vision who confuses red and green colors can recognize the traffic lights by their brightness and position. Experience has taught him to call a darker color red and a lighter one, green; even if he does not see the real difference in hues.[49]

Less is known about the influence of color on the cognitive abilities through its action on the vegetative and motor systems; and we consider this issue in more detail. From the point of view of enactive approach, the cognitive function of color, realized through its action on the motor system, is that color forms expectations and reinforce them. In this context, expectation means readiness to perception which includes a necessary presetting of the sensor apparatus. The abilities of perception and movement had undergone a lengthy co-evolution; they intertwine so closely that movement without perception and perception without movements are both impossible. The very process of perception proceeds not as passive imprinting but as an active from beginning to end process.[50] On the basis of the planned program of actions, the central nervous system carries out presetting the excitability of all the engaged sensor and motor elements.[51] The anticipatory actions are possible on the basis of foresight, a plan of actions thanks to which there takes place extrapolation and correction; the anticipatory movements are connected with changing the neuromuscular tone. The muscular presetting plays a significant role in the acceleration of recognition of what is seen; and color plays an important role in creating such presetting. Color is a characteristic property of objects and fosters their rapid recognition; for example, the colors of the dandelion, lemon and chick are different; and the perception of the corresponding tint of yellow creates readiness to perceive the corresponding object. Thanks to the color vision, we orientate better in space, because

---

[46] Venolia 1988 p. 57.

[47] Christophe Guibal Dresp 2004 p. 32.

[48] Okabe http://jfly.iam.u-tokyo.ac.jp/color/

[49] Padham Sonders 1978. pp. 212-213.

[50] Bernstein 2004 p. 486-487.

[51] Ibid p. 473.

blue hues seem to come from farther things and warm hues, from closer ones. ‘Blue is driven forward by the white ground, red-orange also, and yellow stands out only slightly from the white’ [52] . The spatial conceptions are extremely important for organization of future movements aimed at solution of sensor or motor tasks.

Perception is subordinated to the purpose-oriented behavior of the subject: those impulses we do not care about are simply not being noticed. The goal orientation determines the criteria of selection of information, relevant for the problem solution or the goal achievement. In order to demonstrate the importance of prior setting for perception, we consider an example.

Example of Presetting Influence on the Possibility of Observation

Newton held to the hypothesis of the corpuscular nature of light, that is, light being a bunch of linearly moving particles. Prior to Newton’s works, the phenomena of interference and diffraction was investigated and described in detail by F.M. Grimaldi, R. Hooke, and Ch. Huygens. However, ‘Newton seems to have ignored or overlooked diffraction effects of the use of a small hole as image, though these had been noticed by his contemporaries’.[53] At the same time, he had a possibility to observe the manifestation of the light ray diffraction, when there take place deviations of the ray from linear path and enlargement of the shadow thrown by a small object. Nevertheless, Newton had not noticed the inner strips of light appearing due to diffraction in the object’s shadow. Augustin Fresnel wrote that it is difficult to understand how the light bending into the inner part of the shadow could have eluded such an experienced observer as Newton. Most probably, it happened because of Newton’s theoretical convictions, which, to a certain extant, closed his eyes on the significant events that made the standing of his principle weaker.

> The experiment of Grimaldi on the crested fringes within the shadow, together with several others of his observations equally important, has been left unnoticed by Newton. Those who are attached to the Newtonian theory of light, or to the hypothesis of modern opticians founded on views still less enlarged, would do well to endeavor to imagine anything like an explanation of these experiments derived from their own doctrines; and if they fail in the attempt, to refrain at least from idle declamation against a system which is founded on the accuracy of its application to all these facts, and to a thousand others of a similar nature.[54]

This example shows the importance of preliminary setting for the perception process. Changing the physical readiness to perception may create unfavorable conditions for those irritants which are not in the center of attention. When the readiness to perceive a phenomenon is absent, it may remain unnoticed; and this is especially true for low-observable effects.

Besides, color exerts an additional activating influence on the nervous system. Since all excitations from the sense organs go through the center that regulates the tuning of vegetative nervous system, the color influence may cause changes involving the entire organism. At that,

---

[52] Itten 1970 p. 78.

[53] Harre 1981 p. 184.

color, as a source of additional irritation of the sensor system, oftentimes exerts an activating influence; and this favorably affects the perception of signals of other modalities. According to the rule of concentration of additional activation in proportion to the existing excitation of nervous centers, there takes place stronger concentration of attention on the background of general activity. Since every second the organism is being bombarded by a huge number of external irritants the majority of which miss the consciousness, an additional influence of color may increase the effectiveness of perception in general. As an example of positive influence of color on increasing the perception capability, we may point to a method applied during the World War II when, before the night flights, the airplane pilots would spend several minutes in a room lighted by red color. Such training exerted an activating influence on twilight vision.

Summing up, let us indicate that the ways of the color influence the organism are manifold and are not limited to seeing the object as colored. The complex character of the color influence is manifested also in organization of general activity of the central nervous system, influence on muscular tone, formation of the readiness to perception, and emotional coloring of the events. In my opinion, the answer to the question ‘what does it mean to be colored?’, presupposing the discussion of ontological and epistemological aspects, must take into account the integral and complex character of perception.

CONCLUSION

For the color realism tradition, the constant change of the conditions of color perception and the adaptive changes of sensitivity connected with it pose a problem. From the standpoint of the linguistic tradition, it would be convenient if we perceived red always the same way. The question concerning the changes of color sensitivity was a source of predicaments and is not considered. It is being disguised in the ‘normal conditions’ expression. The understanding of normal conditions is rather wide and, due to its uncertainty, allows partly hiding the difficulty of solving the problem of color’s ontological status. The light of a certain wavelength under its action on the cone-cells apparatus of the eye gives rise to the sensation of color; thus, the color experience is physically caused. However, the knowledge of the physical nature of light does not give understanding of what is the vision of red; there is an explanatory gap here.

We have rejected the traditional way and discussed the mechanisms of changing the color vision sensitivity and the mutual influences of various sense organs. Understanding of perception as a continuous process and taking into account the complex character of the color action on the organism allows shedding light differently on some ontological and theoretical-cognitive questions. Under the action of external irritants on the organism, not only some mental states arise but there are taking place some changes of the condition and motor activity of the entire body which points out to closer connection between mind and body than the modern philosophy assumes. The body transforms physical signals, coming from the outside world, into mental images or a certain state of mind; and the mechanisms of such transformation require the attention of philosophy.

---

[54] Fresnel 1859 p. 73-74.

In combination with enactive approach, the empirical holism principle was applied to the solution of some problems and the response to the critique of empiricism. Some approaches were outlined to solution of ontological problems from the standpoint of experience's continuity. The applied approach requires further development both in breadth, for example, to explain the phenomenon of speech and symbolic function of language, and in depth, to clarify better the process of interaction of mind and brain. Clearly, the precipice, which the person feels as the difference between the object and its mental image, should be considered in the context of the cause-and-effect connections. Brain and body have different languages. Nervous system uses electric signals to pass the messages. Body speaks the language of chemistry; even such electromagnetic by its nature process as the action of light ray to the retina, undergoes, on its way to cerebral cortex, a chemical transformation causing decomposition of the light-sensitive compounds like rhodopsin. Chemical processes are closely connected with electrical ones, being different from the latter by the non-local character of action. Therefore, any signal, for example, color, becomes the source of not only a mental image but has a wide opportunities to influence the general condition of the organism, including changing the very possibility of perception.

The analytic tradition, which concentrates its efforts on studying thinking and language, is unable to take into account such influences and they turn out to be excluded from the vision field of philosophers. However, studying the perception mechanisms may offer some interesting perspectives for understanding of the mind and body relation. Color is a promising theme within the framework of studying cognitive processes with the purpose of building bridges across the explanatory gap.

REFERENCES

Abbot, A. G. (1947). *The color of life*. New York: McGraw-Hill.

Birren, F. (1959). Functional use of color. In: *Field Applied Paints and Coatings.* National Research Council (U.S.), National Research Council (U.S.). Building Research Institute, 93-96.

Bruner, J. S. (1974). *Beyond the Information Given: Studies in the Psychology of Knowing* Ed. J.M. Anglin London: Allen and Unwin.

Carol, V. (1988). *Healing Environments: Your guide to indoor well being.* Berkley: Celestial Arts.

Christophe, R. C., Guibal, J. & Dresp, G. B. (2004). Interaction of color and geometric cues in depth perception: When does ''red'' mean ''near''? *Psychological Research, 69*, 30–40.

Curd, P. (1998). *Legacy of Parmenides: Eleatic Monism and Later Presocratic Thought.* Parmenides Publishing Princeton University Press.

Dancy, R.M. (2004). *Plato's Introduction of Forms.* Cambridge: Cambridge University Press.

Dobryakova, O. A. (1944). Influence of gustative, temperature and auditory irritants on the critical frequency of blinking of mono-chromatic rays. *Problems of physiological optics*, 1944, vol. 2. Добрякова, О. А. (1944). Влияние вкусовых, температурных и слуховых раздражителей на критическую частоту мелькания монохроматических лучей. *Проблемы физиологической оптики, 2,* 42-53.

Dobryakova, O. A. (1948). On some possibilities of conditional-reflex changing the sensitivity of vision. *Problems of physiological optics*, *6*, 308-313. Добрякова, О. А.

(1948). О некоторых возможностях условно-рефлекторного изменения чувствительности зрения. *Проблемы физиологической оптики, 6,* 308-313.

Duhem, P. (1954). *The Aim and Structure of Physical Theory.* Princeton: Princeton University Press. (translated from the second edition published in 1914 by P. Wiener).

Erickson, G. B. (2007). *Sports Vision: Vision Care for the Enhancement of Sports Performance*. St. Louis: Butterworth Heinemann Elsevier.

Fillmore, Ch. J.: (1968). The Case for Case. In E. Bach, R. T. Harms (eds.), *Universals in Linguistic Theory* (1-88). New York: Holt, Rinehart and Winston.

Fleck, L. (1981). *Genesis and Development of a Scientific Fact.* Chicago: Univ. of Chicago Press. (F. Bradley, Trans.).

Fresnel, A. (1859). Memoir on the Diffraction of Light. In: H. Crew (ed.) *The Wave Theory of Light Memoirs by Huygens, Young and Fresnel.* (79-144) New York: Cincinnati: Chicago American Book Company.

Gibson, J. (1950). *The perception of visual world.* London - NY: Prentice-Hall.

Glüer, K. (2007). Colors without circles? *Erkenntnis*, *66*, 107–131.

Gregory, R. L., & Jean G. (1963). *Wallace Recovery from Early Blindness: A Case Study.* Cambridge: W. Heffer and Sons.

Hacker P.M.S. (2001). *Wittgenstein: connections and controversies*. Oxford: Clarendon Press.

Harré, R. (1981). *Great scientific experiments: Twenty experiments that changed our view of the world.* Oxford: Phaidon Press Ltd.

Hartridge, H. (1947). The visual perception of fine detail. *Philosophical Transactions of the Royal Society of London*, 232, 519–671.

Held, R., & Hein, A. (1963). Movement produced stimulation in the development of visually guided behavior. *Journal of Conparative and Physiological Psychology*, 56, 873-876.

Itten, J. (1970). *The Elements of Color: A Treatise on the Color System of Johannes Itten Based on His Book "The Art of Color".* B. Faber (ed.), Van H. Ernst (trans.). New York, Van Nostrand Reinhold.

Katz, B. & Schmitt, O. H. (1940). Electric interaction between two adjacent nerve fibres. *J. Physiol, 97 (4),* 471–488.

Kravkov, S. W. (1934). Changes of visual acuity in one eye under the influence of illumination of the other or of acoustic stimuli. *J. &per. Psychol.,* 17, 805-812.

Kravkov, S. W., & Semenovskaja, E. N., (1933). Steigerung der Lichtempfindlichkeit des Auges dutch vorangehende Lichtreize, *Arch. Ophth*., Leipsic.

Kravkov, S.W. (1941). Colour vision and the autonomic nervous system. *J. Opt. Soc. Amer.*, *31*, 335-337.

Lakoff, G. (1965). *On the nature of syntactic irregularity.* Cambridge, Mass.: Harvard University, Computation Laboratory.

Leibniz, G. W. 1898 (2008). *The monadology and other philosophical writings*. Translated with introduction and notes by Robert Latta. Oxford: Oxford University Press.

Maxwell, G. (1962). The Ontological status of theoretical entities. In H. Feigl and G. Maxwell (eds.) *Minnesota Studies in the Philosophy of Science*, Vol. III: Scientific Explanation, Space, & Time. (3-27). Minneapolis: University of Minnesota Press.

Mitchell, S. W. (1872). *Injuries of nerves and their consequences.* Philadelphia: J. B. Lippincott.

Mkrtycheva, L. I. & Samsonova, V. G. (1948). Change of the color sensation under the hypoxemia influence. *Problems of physiological optics, 3*, 120-129. Мкртычева, Л. И. & Самсонова, В. Г. (1948). Изменение цветоощущения при воздействии гипоксемии. *Проблемы физиологической оптики, 3*, 120-129.

Müller, J. (1840). *Handbuch der Physiologie des Menschen für Vorlesungen.* J. Hölscher (ed.). Trans. E. Clarke and C. D. O'Malley. http://www.experiencefestival.com/a/Johannes_Peter_Mller_-_Quote/id/5188063.

Nanson, N. R. (1958). *Patterns of Discovery: An inquiry into the conceptual foundation of science.* Cambridge: Cambridge University Press.

Nelson, C. A. (2001). *Handbook of Developmental Cognitive Neuroscience.* Cambridge: MIT Press.

Newton, I. (1979). *Opticks: Or, A Treatise of the Reflections, Refractions, Inflections & Colour of Light.* New York: Courier Dover Publications.

Noë A. (2004). *Action in Perception.* Cambridge, MA: The MIT Press.

Okabe, M. (2002). (modified on 2.15.2008, 9.24.2008). Color universal design (CUD) How to make figures and presentations that are friendly to Colorblind people –Jikei Medial School (Japan) http://jfly.iam.u-tokyo.ac.jp/color/

Padgham, C.A. & Saunders, J. E. (1975). *The Perception of light and colour.* London, G. Bell and Sons.

Papineau, D. (2003). Could there be a science of consciousness? *Philosophical Issues, 13*,205-220.

Peacocke, C. (1984). Colour concepts and colour experience. *Synthese, 58*, 365-381.

Piéron H. (1945). *La sensation, guide de vie.* Paris: Gallimard. Piéron H. (1952) The sensations: Their functions, processes, and mechanisms (M. H. Pirenne & B. C. Abbott, Trans.). New Haven, CT: Yale University Press.

Quine W. V. O. (1969). *Ontological Relativity and Other Essays.* New York: Columbia University Press.

Sacks, O. (1985). *The man who mistook his wife for a hat.* London: Duckworth.

Sadock, B. J (2008). *Kaplan and sadock`s concise textbook of clinical psychiatry.* Manufacturer: Lippincott.

Schwartz, L. A. (1946). On the phenomena of the color vision sensitization. *Problems of physiological optics*, *3,* 33—39. Шварц, Л. А. (1946). О явлениях сенсибилизации цветного зрения. *Проблемы физиологической оптики, 3,* 33—39.

Schwartz, L. A. (1948). Change of the color sensation in the emotional states of vision. *Problems of physiological optics*, *6*, 314-318. Шварц, Л. А. (1948). Изменение цветоощущения в эмоциональных состояниях. *Проблемы физиологической оптики, 6*, 314-318.

Schwartz, L. A. (1949). Influence of the colored illumination on the hearing sensitivity under various condition of the person. *Problems of physiological optics, 7,* 53-56. Шварц, Л. А. (1949). Влияние цветного освещения на чувствительность слуха при различных состояниях человека. *Проблемы физиологической оптики*, *7,* 53-56.

Okabe, M. (2002). (modified on 2.15.2008, 9.24.2008). Color universal design (CUD) How to make figures and presentations that are friendly to Colorblind people –Jikei Medial School (Japan) http://jfly.iam.u-tokyo.ac.jp/color/

Shoemaker, S. (2003). Content, character and color. *Philosophical Issues, 13(1),* 253-278.

Simeon, D. & Abugel, J. (2006). Feeling Unreal*: Depersonalization Disorder and the Loss of the Self.* NY: Oxford University Press.

Stratton, G. M. (1896) Some preliminary experiments on vision without inversion of the retinal image. *Psychological Review, 3(6),* 611-617.

Ukhtomskii, A. A. (1925). The dominant principle. *New in reflexology and physiology of nervous system* (60—66). Leningrad-Moscow. Ухтомский, А. А. (1925). Принцип доминанты. *Новое в рефлексологии и физиологии нервной системы.* (60—66). Л.-М.: Госиздат.

Young, T. (1859). On the theory of light and colors. In: H. Crew (Ed.) *The wave theory of light: memoirs by Huygens, Young And Fresnel.* (45-61) New York: Cincinnati: Chicago: American Book Company.

Zaretskaya Z. (1941). B. The action of the color secondary irritants on the intraocular pressure. *Problems of physiological optics*, *1*, 35-37. Зарецкая, З. Б. (1941). Действие цветных раздражителей на внутриглазное давление нормального и патологического глаза. *Проблемы физиологической оптики,.1*, 35-37.

Кравков, С. В. (1948). *Взаимодействие органов чувств*. М. -Л.: Изд-во АН СССР.

Кравков, С. В. (1950). *Глаз и его работа*. М. -Л.: Изд-во АН СССР.

Кравков, С. В. (1951). *Цветовое зрение* М.: Изд-во АН СССР.

Лебединский, А. В., Прессман, Я. М. & Фадеева, А.А. (1948). Новые данные о взаимодействии центра и периферии сетчатки. *Проблемы физиологической оптики*, *6*, 104-111.

Леонов А.А.& Лебедев В. И. (1966). Об отражении человеком пространства вне Земли. *Вопросы философии, 1*, 3-11.

Орбели, Л.А. (1935) *Лекции по физиологии нервной системы*. Ленинград: Биомедгиз.

Шеварева, В. К. (1950). Влияние цветного освещения на мускульно-двигательную работоспособность. *Проблемы физиологической оптики, 9,* 127—130.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 89-123

Chapter 3

THE BIOLOGICAL SIGNIFICANCE OF COLOUR PERCEPTION

Birgitta Dresp-Langley & Keith Langley [*]
Universite de Montpellier, Montpellier, France

ABSTRACT

There is no colour without light, nor is there colour perception without a sensory organ and a brain to process visual input. This chapter first reviews how the colour of objects is produced. Most commonly, this depends on so-called pigments, the molecular nature of which provokes strong absorption of part of the incident light falling on an object. Colour can also be produced by optical phenomena such as refraction, dispersion, interference or diffraction from ordered structures within objects. A wide variety of photonic microstructures are known in the living world and specific examples will be described in mammals, birds, fish and insects. Some of these structures reflect light in the near ultraviolet spectral region, particularly pertinent for certain birds, insects and fish which are sensitive to these wavelengths. A detailed account of a particularly elaborate structure present in the king penguin beak will be given to illustrate the extent to which evolutionary pressure leads to the elaboration of such structures to satisfy specific needs of birds or animals. Subsequently, the perception of colour in man and animals and its biological significance is dealt with. For man, this will include a discussion of the symbolic meaning of different colours. In many species, especially birds, the colours of plumage and parts of the skin have an important survival function. Such biological colourations may fulfil the role of ornaments that determine mate choice and reproduction of the species, or signal good health, allowing individuals to secure and maintain territorial dominance. Colour perception may also have an underlying survival function in man, but more complex explanations are needed to relate perception to such a function. The colour of an object in the visual field is known to determine the way in which humans perceive relations between objects and their background, particularly which objects appear nearer. This suggests that colour perception is important in processing information about the physical structure of the world. The colour red plays an important role in this process, since it drives mechanisms of visual selection which attract attention to, or away from, objects in the visual field. Psychophysical studies of colour

---

[*] e-mail: klangley@numericable.fr

perception in both animals and man help to understand these complex processes. Finally, colour perception in man may contribute either to rewarding psychological sensations of warmth, comfort and safety or to aversive sensations of coldness and discomfort, sensations which can strongly influence individuals in their daily social interactions.

What Is Colour?

Without light there is no colour and even when the level of incident light is too low, man cannot detect it. Only when incident light is sufficiently bright is it possible for man to process this visual input and distinguish different colours in his environment. Thus, colour is a percept resulting from a response of the brain to data received by the visual system. Objects emit light of various wavelengths and these can be detected and analyzed precisely by inanimate machines. Our brains, however process signals produced by wavelength mixtures, enabling us to perceive them as a phenomenon we call colour. The perception of colour by a living organism thus requires both a sensory organ receiving external signals and a brain to process these signals, to transform them into meaningful representations.

How then can colour be defined? Colour theories have attempted to clarify what we mean by colour, how colours can be ordered, related to each other, and transformed to become new colours. A dictionary may define colour generally, as the aspect of any object that may be described in terms of hue, lightness and saturation, but this tells us little about the true nature of colour. In Ancient Greece, Aristotle developed the first known theory of colour, considering that all colours were a mixture of white and black light. He postulated that the gods sent down colour from the heavens as celestial rays and identified four colours corresponding to the four elements, earth, wind, fire, and water, a view essentially unchanged for many centuries. It was not until the optical experiments performed by Sir Isaac Newton in the mid 1660s when, using a glass prism, he demonstrated for the first time that white light could be split up into all the colours of the rainbow extending from red through to violet, each "refracted" by different amounts (Fig. 1). He also demonstrated that white light could be recreated by combining these different spectral hues using a second prism. Newton first used the word "spectrum" for this array of colours and recognized that it constitutes a range of energies, of a continuous electromagnetic spectrum, differing by their wavelength. He chose to name seven different hues: red, orange, yellow, green, blue, indigo and violet (Fig. 1). Each time we see a rainbow, we observe Nature's own confirmation of Newton's experiment, with white light split up not by a glass prism but by countless numbers of rain droplets or ice crystals. While Newton realized that the light rays, or electromagnetic waves, of the spectrum were not, strictly speaking, coloured as such and that "coloured light" does not exist, he recognized these rays had the power to stir up specific sensations of colour, and that colour, like beauty, is "in the eye of the beholder". Typical values of the wavelength of different colours of the visible spectrum are given in table 1. Thus, red is defined as a colour, perceived by man, corresponding to a wavelength of ca 650-700 nm. The colour green corresponds to a wavelength of ca 550nm, and blue to ca 450nm. Several attempts to specify and classify colour further have been made since Newton's invention of the colour circle, which tried to simplify our understanding of how colours could be combined to produce others. Early theories of colour were pure speculation but, with more and more data available, it became eventually possible to explain more and more precisely how the brain processes colour.

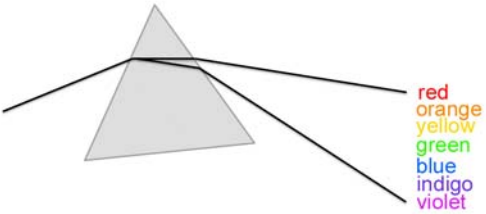


Figure 1. Schematic representation of Newton's prism experiment in which white light is split up into a spectrum of colours, when diffracted through a glass prism.

Table 1. Typical wavelength values of different colours in the visible spectrum.

Colour	Wavelength (nm)
Red (limit)	700
Red	650
Orange	600
Yellow	580
Green	550
Cyan	500
Blue	450
Violet (limit)	400

During the eighteenth century, it was shown that any colour could be obtained by mixing the right proportions of light of three wavelengths, provided they were far enough apart, a principle termed trichromacy. An important advance to explain trichromacy was made in 1801 by the English physician Thomas Young, who suggested that at each point in the retina there must exist at least three small, light-sensitive structures coding for the colours red, green, and violet. His theory was adopted and championed by Hermann von Helmholtz and came to be known as the Young-Helmholtz theory, but its basis was only confirmed by two independent research groups in the early 1960's (Brown and Wald, 1964; Marks, Dobelle and MacNichol Jr., 1964). This work examined microscopically the abilities of single cones to absorb light of different wavelengths. Three, and only three, different cone types were identified.

In the second half of the nineteenth century, the German physiologist Ewald Hering (1834-1918) devised a credible alternative theory of colour vision (Krech et al, 1982). He explained colour mixing by proposing the existence, in the eye, brain, or both, of three opponent processes, one for the red-green sensation, one for yellow-blue, and a third for black-white. He positioned the four primary colours (red, green, blue, and yellow) according to their polarity as poles of two perpendicular axes and suggested that intermediate colours were formed by additive mixing from the primary colours. The modern Swedish Natural Colour System (NCS) is based on this colour theory. In 1931 the CIE (Commission Internationale de l'Eclairage) established an international standard of colour measurement by creating the CIE chromaticity chart, which has the shape of a triangle proposed already in 1872 by the Scottish physicist James Maxwell. Red, green, and blue are the three primary components of light, the primary colours, at the corners, white is represented at the centre. Maxwell suggested that all known colours could be located within this triangle. Moving along its edges, red changes to orange, then to yellow, and finally to green; green changes to blue; blue changes to violet, to purple, and back to red. Moving from the edge towards the centre of the triangle, the brilliance of each primary colour is lost in a transition from full saturation at the edge to white at the centre. Maxwell established a system of analyzing any colour, which is identified by the geometric coordinates of any point within the triangle and defined by the quantities of the primary colour it contains, measured by the distance from each primary colour. This system, which was revised in 1964, is currently used to measure and quantify the colours produced on computer screens.

Colour, strictly speaking, refers to the spectral qualities of the light emitted or reflected from an object or living creature. It can thus be defined and measured precisely with spectrophotometers, which analyze the amount of energy present at each spectral wavelength. With such instruments daylight can be shown to be composed of a continuous range of colours corresponding to different wavelengths of unequal intensities, while tungsten light has a predominant red component and very little blue. The spectral reflectance of an artist’s pigment in general has a single broad peak the maximum wavelength of which corresponds to its so-called colour.

The term colour should, however, be distinguished from what we understand as biological colouration, which may be defined as the appearance of a living organism determined by the quality and quantity of light reflected by or emitted from its surface. The concept of biological colouration differs from that of colour since it depends on several other factors, including the relative location of coloured areas on the organism, the quality and intensity of light falling on it, the shape, posture and movement of the organism presenting the colouration and, of course, the visual capabilities of the organism looking at it. Since human vision is not the same as that of other animals, such as fish or birds, colour perception has to be viewed as a species specific process.

Biological Colourations in Living Organisms

There are three ways in which an organism may generate colouration: an organism may contain in its surface layers molecules referred to as pigments, which are molecules comprising specific chemical structures that endow them with the capacity of absorbing a proportion of incident light falling on them. Alternatively, colourations may be produced by particular physical structures close to the organism’s surface which interact with the incident light so that the reflected light is different. A third way in which an organism may generate colourations is by using chemical energy to produce endogenous light, which itself may be coloured. Each of these will be discussed in greater detail hereafter, with pertinent examples from nature and the animal world.

Pigment Based Colouration

The different groups of pigments found in the natural world impart widely different colours to plants and animals, varying from the brilliant colours of certain fungi and flowers, to the various browns, reds and greens of many organisms. Animal pigments are located in skin and skin derivatives, including hair in mammals, feathers in birds, scales in turtles and tortoises, cuticles and shells of many invertebrates. Pigment containing cells or chromatophores, which are derivatives of the neural crest, comprise melanophores, which contain black melanin pigments, erythrophores, which contain orange/red carotenoids and xanthophores, which contain yellow pteridines or xanthopteridines (Bagnara, 1966). A blue pigment containing chromatophore, the cyanophore, has recently been described (Fujii, 2000), but appears to be relatively rare. Mammals and birds, in contrast to cold-blooded animals, have melanocytes instead of melanophores. Some chromatophores contain vesicles containing more than a single pigment, such as pteridines and carotenoids for example, and the overall colouration generated then depends on their relative amounts (Matsumoto, 1965). Sudden changes in colouration in certain species may result from stress and/or changes in mood or temperature and thus be under hormonal or nervous control, or a combination of both. This may induce changes in size of chromatophores, migration of pigments within, or a reorientation of microstructures.

How do pigments within cells generate colourations? Since energy in a closed system is conserved and can be neither created nor destroyed, when a photon of light is absorbed by matter constituted of molecules, its energy is absorbed by the matter. It is then either converted into heat, or emitted in the form of a photon of light. The energy of such emitted photons is determined by the energy states permitted for the molecule in question, the difference between such states being explained by quantum theory. Complex organic molecules containing multiple double bonds with the resulting excess of orbiting electrons have the type of structures with vibrational or rotational energy, typical of pigments. The more complex the molecule, the more possibilities there are for different energy levels to exist, but even very simple molecules, like water, are subject to this phenomenon. When in the solid state, the bonds between hydrogen and oxygen are stronger, allowing adsorption at the red end of the spectrum thus producing the pale blue colour characteristic of bulk ice. Natural pigments are complex organic compounds which contain a “colour bearing” group or “chromophore”, often made up of a chain of atoms joined by alternating single and double bonds. If these chains are long enough, they can absorb in the visible spectrum and emit in the visible region.

Two broad classes of natural pigments can be distinguished on the basis of their chemical composition: those containing nitrogen and those lacking it. The most important non-nitrogenous pigments in animal colouration are the carotenoids. Others, such as the napthoquinones, anthraquinones and flavanoids, which like carotenoids are only synthesized in plants, do not contribute significantly to animal colouration. The most important nitrogenous pigments in animal colouration are the melanin polymers, which in contrast to carotenoids are synthesized by animals. Other pigments of this general class include the porphyrins (pyrole containing molecules) and their derivatives, which form the red or green compounds in blood, and the green chlorophylls of plants.

The carotenoids are constituted of long chain conjugated systems which can absorb violet or blue light, resulting in their yellow, orange or red appearance. Carotenoids contribute to the yellow, orange, and red colours of the skin, shell, or exoskeleton of aquatic and other animals. They are ubiquitous in living organisms and are the most widespread pigments found in nature, synthesized by bacteria, fungi, algae and many plants (Shahidi et al., 1998). They may be absorbed from these organisms to produce animal colouration. A typical example is the flamingo (Fig. 2), the characteristic pink colour of which is derived from the beta carotene in their diet of shrimps and blue-green algae, which is subsequently transported into the erythrophores (Bagnara, 1998). In captivity, flamingos are often given a diet supplemented with canthaxanthin, a ubiquitous carotenoid pigment first isolated in edible mushrooms and also found in green algae, bacteria, crustaceans, and certain fish. Canthaxanthin is also fed to farmed salmon to give them a more attractive pink colouration. Carotenoids are well documented in both feathers and bills of certain birds (McGraw and Nogare, 2004; Peters et al., 2004). Their quantity in the plumage of an individual is strongly influenced by diet and may thus reflect the bird's general condition (Price, 2006).

Figure 2. Pink flamingos with carotenoid based pink colouration of feathers and skin.

A second major group of animal pigments are the indoles, which comprise the melanins. They are present in the melanophores of lower animals and in the equivalent human cells, the melanocytes. These pigments, which include eumelanin, a complex molecule synthesized from tyrosine with dihydroxyindole-2-carboxylic acid and several pyrole rings and phaeomelanine, give rise to buff, red-brown, brown and black colourations in the feathers of birds, mammalian hair, eyes, and in the skin and scales of many fish species, amphibians and reptiles, in squid and octopus ink, and in various invertebrate tissues (Ito and Wakamatsu, 2003). These pigments are present in vesicles throughout melanocyte cytoplasm. Although nitrogenous pigments, such as melanins, are predominant in marine organisms, pigments belonging to all the major structural classes of natural products are also found (Bandaranayake, 2006). Colourations produced by melanins are affected by different levels of traces of copper, light hair containing less than dark hair, for example. Melanins, like carotenoids, are common in bird feathers, but melanin patterns in birds seem to be less affected by diet than carotenoids. The intensity of melanization after moult is affected by social interactions during the moult and by raising birds in humid conditions. Hormonal manipulations can have dramatic effects on both the kinds of melanin produced (eumelanin or phaeomelanin) and the patterns they form (Price, 2006). The melanin pigments in fish skin are dependent on breeding conditions (Seikai et al., 1987). It has recently been suggested that carotenoids may be a condition-dependent trait, whereas melanin-based colouration is not, a difference that may be highly relevant when studying the evolution of multiple mating preferences. The expression of these two traits may be regulated by different mechanisms (Senar et al., 2003).

A pigment, the chemical structure of which has only recently been elucidated (McGraw and Nogare, 2004), gives rise to the red colouration of parrot feathers, to which it owes its name, psittacofulvin (literally in Greek: parrot colour). The chemical structure of the group is based on long unsaturated carbon chains with an oxygen terminal. Unlike carotenoids, which are absorbed from food, these are synthezised by parrots, and apparently only by them, which means that the colour of parrot feathers does not depend on diet and will not fade when they lack carotenoids. The green colours of parrot feathers result from a combination of blue structural colours (see below) and a yellow pigment which could be related to the psittacofulvins.

Other pigments have important biological activities in certain organisms. Pteridines, which are molecules composed of fused pyrimidine and pyrazine rings containing a wide variety of substitutions, synthezised from guanosine triphosphate (GTP), are the red-yellow pigments of composite eyes of arthropods They were first discovered in butterfly wings (hence their name from Greek: pteron; wing). Other purine derivatives, present in leucophores, are not pigments, but form the white crystals producing the structural colourations (see below) of amphibians and lizards and cephalopods, also responsible for the whitish skin colourations on the undersides of many fish.

Another less common pigment of the quinine group, the naphthoquinones, which can be red, purple or green are present in shells of echinoids or sea urchins. The yellow or orange red flavonoids are present in plants but are rare in the animal kingdom, although a sub class has been found in the yellow wing colouration of some species of butterfly. Porphyrins represent an important class of pigments in the plant kingdom, although they are present in the skins or shells of invertebrates, forming the green chlorophyls of higher plants and the hemoglobins of animal blood.

Structure Based Colourations

Colour can be produced by any object purely in accordance with the laws of optical physics if they contain sub-microscopic, so-called photonic, structures that are able to modify incident white light, by either specifically absorbing or reinforcing certain of its component colours. This manipulation of incident light originates from the basic optical phenomena of thin-film interference, multilayer interference, and reflection or diffraction grating effects, (Dyck, 1976; Parker, 1998; Vukusic et al., 2001; Kinoshita and Yoshioka, 2005). Light scattering similar to that occurring in certain types of structural colours present in living organisms has been reproduced in purely artificial systems consisting of polystyrene microspheres (Guillaumée et al., 2008). Artificial grating structures can be fabricated with electron-beam lithography, which can produce iridescent blue colours by the same process as in the wings of certain butterflies. Nature has evolved an extraordinary diversity of highly specialized structures capable of reflecting different colours or ultraviolet light, UV, (Parker, 2000; Vukusic and Sambles, 2003), which have been well documented in insects, fish, butterflies, birds and plants. In such photonic structures, white light can be fractionated and thus modified by interference after reflection from successive ultra-thin layers, often producing iridescent effects where the perception of colour varies with viewing angle. The wavelength of the reflected light is governed by physical laws, such as Bragg's law, and depends on both the angle and the distance between the parallel successive reflective layers, a phenomenon termed coherent scattering. A different type of scattering, Rayleigh scattering, termed non coherent and similar to the effect first discovered by the British physicist Tyndall in the 19th century, is due to the preferential reflection of light of shorter wavelengths (blue) by finely dispersed particles in a material, while longer wavelengths (red and yellow) pass through. This is why the sky appears blue on a sunny day and for more than a century the blue colouration of living organisms was thought to be due to Rayleigh scattering, but many studies have since categorically refuted this interpretation. Raman was the first to question it (Raman, 1935), postulating that the colour was due to the interference of light, a study ignored until 1971 when Jan Dyck, a Danish scientist (Dyck, 1971) concluded that the blue and blue-green colours produced by the spongy structure of feather barbs were not due to Rayleigh scattering, but to the interference of light by backscattering from numerous hollow, randomly oriented keratin cylinders. In 1998 and 1999, Prum and co-workers (Prum, Torres , Williamson and Dyck , 1998; Prum , Torres , Williamson and Dyck, 1999) confirmed that feathers look blue because of differences in the distances travelled by light waves reflected off of each successive layer within the spongy keratinous layer in the barbs. Thus, in fishes, birds and mammals including humans, blue is almost always a structural colour based on coherent scattering, while in lower vertebrates, blue is produced from crystalline platelets termed schemochromes, which are constituted of guanine in iridophore cells. Their orientation determines the brightness and iridescence of the colour that is perceived (Taylor, 1969; Morrison, 1995). A rare exception to this was recently found in certain fish, the blue colour of which is due to a blue pigment of unknown chemical structure present in the vesicles of cyanophores (Fujii, 2000). The leucophore, a structural colour producing cell found in many fish species, have crystalline purine reflectors, which produce a dazzling white (Fujii, 2000). In amphibians, reptiles and birds, the scatter of blue wavelengths, together with the presence of yellow pigmentation, is fundamental for the expression of green colourations (Bagnara, Fernandez and Fujii, 2007; Fox, 1979). A detailed description of all the different types of structures capable of generating biologically relevant colourations found in the animal kingdom would go beyond the scope of this chapter. However, general examples will be referred to and a detailed account will be given of a particularly relevant, highly complex UV-reflecting structure, recently found in the King Penguin beak.

Considerable interest has been devoted to the structural colourations of butterfly wings and detailed information has been reported on the nature of these structures. All butterfly and moth scales and bristles are made of non-living insect cuticle, each produced from a single epithelial cell. Even though all cuticular patterns in insects have common basic elements, some are highly specialized, with stacks of thin-films, lattices, or other minute structures which interact with light to produce structural colours (Ghiradella, 1994). The numerous studies on the structural colourations of butterfly wings are now in general agreement that multilayer reflectors are commonly at their origin and these are recognised to produce the most intense structural colours (Parker, McPhedran, McKenzie, Botten and Nicorovici, 2001). Multilayer reflectors with similar optical properties are common in other insects and have even been found in fossils of an extinct species of beetle (Parker and McKenzie, 2003). Despite their anatomical diversity at the nanoscale level, all structurally coloured butterfly scales share a single fundamental physical colour production mechanism - coherent scattering (Prum, Quinn and Torres, 2006). The blue colour of the wings of the Morpho butterfly is generated by multilayer microstructures with as many as 24 layers (Wong et al., 2003 ; Kinoshita, Yoshioka and Kawagoe, 2002 ; Vértesy et al., 2006), often producing a marked iridescent effect (Vukusic et al., 2002). Some butterflies reflect ultraviolet light, a phenomenon often reserved to the male of the species which suggest a role in sexual communication (Ghiradella et al., 1972). Similar optical interference produces the bright green dorsal iridescence in species as diverse as insects (Vukusic, Wootton and Sambles, 2004) and molluscs (Brink, van der Berg and Botha, 2002).

Although structural colourations have been found in many different animal species, their biological significance has been investigated mainly in birds (for reviews see Auber, 1957; Dyck, 1976). Several physical mechanisms have been evoked, but avian plumage structural colour is now considered to result from coherent light scattering, either from a spongy keratin-air matrix (Prum et al., 1998) or from photonic crystals constituted of melanin rods within a keratin-air matrix (Zi et al., 2003). This contrasts with the structural skin colour, produced by coherent light scattering ordered collagen arrays in more than 2.5% of all avian species (Prum and Torres, 2003; 2004), and which can also produce UV reflectance in the facial skin of certain birds (Prum, Torres, Kovach, Williamson and Goodman, 1999). The display of the male Indian Peafowl (peacock) is remarkable enough to attract man, even though it has evolved this highly specialized visually striking colouration by evolutionary pressure only to attract peahens (Fig. 3). This bird's iridescent blue-green and green coloured plumage, which shimmers and changes with viewing angle as in many bird feathers, results from coherent scattering from periodic nanostructures made up of the melanin layers in the barbules. Different colours correspond to different distances between the periodic structures. Brown feathers are produced by a mixture of red and blue, produced by varying the lattice constant and the number of periods (Zi et al., 2003; Li et al., 2005). Some birds employ keratin fibres to produce structural colours, as in the green and purple barbules of pigeon feathers, Fig.4 (Yin et al., 2006). Structural colourations can, in addition, combine with pigment based colourations in bird feathers (Osorio and Ham, 2002; Shawkey and Hill, 2005).

Since most birds detect near-UV light and pigments emitting in the UV region are hitherto unknown, photonic structures reflecting in the UV range have aroused considerable interest in recent years, particularly with regard to their potential biological function (Finger and Burkhardt, 1994; Mougeot et al., 2006). Such structures were first discovered in avian plumage (Hausmann et al., 2003; Prum Torres, Williamson and Dyck 1999), but are also present in other avian tissues, including skin (Mougeot et al., 2005; Prum, Torres, Kovach, Williamson and Goodman, 1999; Prum and Torres, 2003), mouth tissue (Hunt et al., 2003) and comb tissue (Mougeot et al., 2005). The King Penguin beak provides a particularly interesting example of UV structural colour. This bird has several coloured ornaments including the carotenoid based yellow breast feathers, but only the beak horn, which is perceived by the human visual system as yellow-orange coloured, with a more or less pronounced pinkish-violet tint (Fig. 5), reflects as shown by reflectance spectrophotometry, in the near UV region (Fig. 6), with an average peak around 370nm. A second, broader peak typical of carotenoids is present in the yellow-orange-red region of the visible spectrum.

Figure 3. Peacock displaying its tail feathers, illustrating the complex colouration patterns that can be produced structurally.

Figure 4. Green and purple colouration of pigeon neck feathers, due principally to structural colour.

Figure 5. King Penguins in nuptial parades on the beach in Crozet island in the sub-Antarctic. Note the way in which they flaunt their beaks in face to face encounters with potential partners.

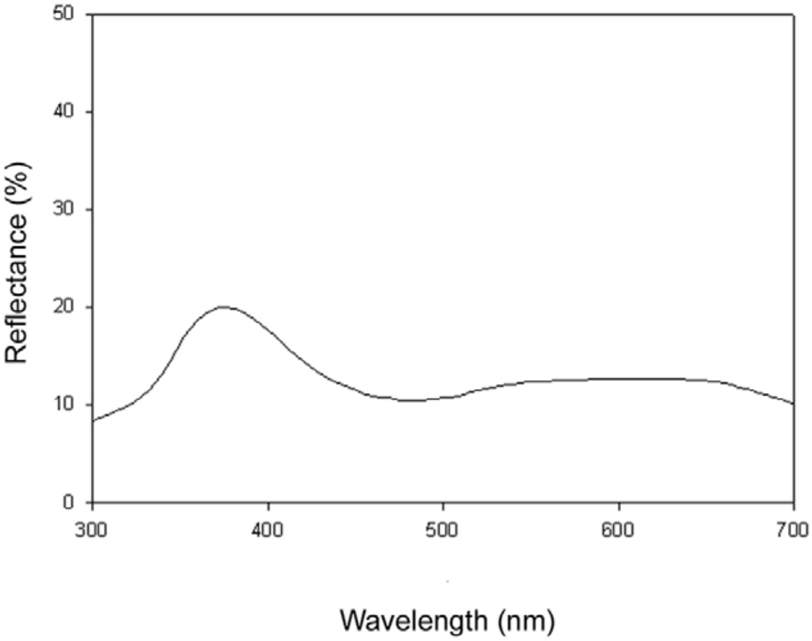


Figure 6. Reflectance spectrum from King Penguin beak horn, showing a pronounced peak around 370nm in the UV range and a broad peak due to carotenoids in the visible region.

We (Dresp and Langley, 2006) demonstrated that only structures situated within the upper region of the beak horn, comprising a corny layer (*stratum corneum*) of this specialized skin tissue, reflect UV. They consist of interconnected microstructures of a multiply folded membrane doublet that produces up to forty quasi-parallel layers in individual microstructures, formed from interdigitated cell plasma membranes of adjacent keratinocytes (Figs. 7, 8). Calculations using lattice dimensions measured by transmission electron microscopy accurately predicted the wavelength experimentally measured of the near ultraviolet reflectance from these multiple layered microstructures. These calculations were based on Bragg's law (Bragg and Bragg, 1915):

$$\theta_{\max} = n2d \sin\theta$$

where $\theta_{\max}$ is the peak wavelength of reflected light, n is the average refractive index of the tissue, d is the separation of the layers (lattice dimension) and θ the angle of incidence of the light (here 90°). As in all animals, the quality of the structural colour in a bird may reflect its individual hormonal status or health and, therefore, its intra-specific ability to compete and, therefore, to survive.

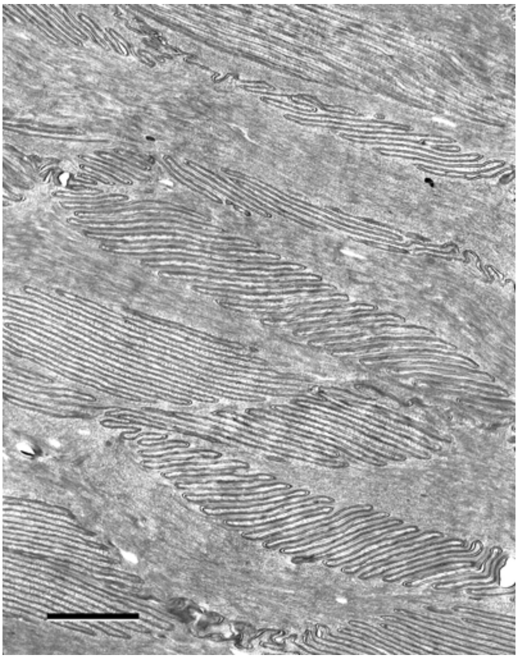


Figure 7. Low power transmission electron micrograph of the upper region of the King Penguin beak horn, which is filled with interconnected microstructures constituted of multiple layers of folded membranes, each of which is formed from a doublet. The microstructures vary in shape and size. Irregular bundles of intermediate filaments fill the space between microstructures. Scale bar 2.0 µm.

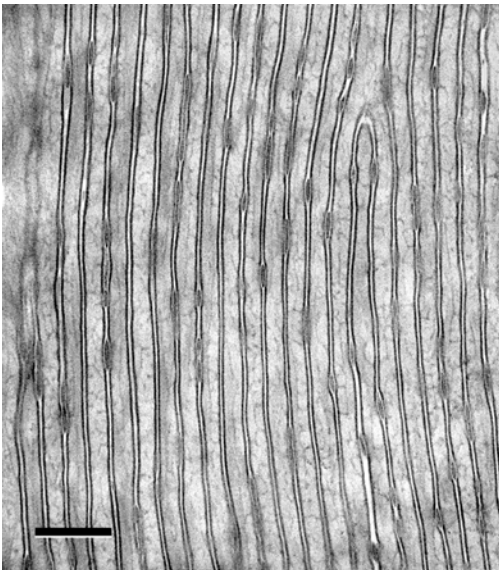


Figure 8. Higher magnification electron micrograph of part of a microstructure present in the upper region of the King Penguin beak horn, showing parallel reflecting multilayers composed of folded cell membranes compressed together. Note also that one of the folds is shorter than the others. Scale bar 0.5 µm.

Bioluminescence: Colourations from Light

Although we live in a world where the most important light source is the sun, man learned early to produce artificial sources of light, which enabled him to cope in the absence of natural light or under low lighting conditions. Light can also be produced endogenously by certain living organisms, through biochemical processes occurring in so-called photophores or light producing organs. This form of light production, known as bioluminescence, is more often present in organisms which live in low light habitats, such as deep water fishes or nocturnal species of insects. Bioluminescence is mainly a marine phenomenon not found in freshwater. On land, it is seen only in a few species of fungi and insects. There are no luminous flowering plants, birds, reptiles, amphibians or mammals. Bioluminescence is phylogenetically diverse, occurring in many different groups, including bacteria, fungi, dinoflagellates (algae) coelenterates (jellyfish), annelids (sea worms) molluscs (squid and clams), crustaceans (shrimps), insects (firefly), echinoderms (brittle stars) and many bony and cartilaginous fish (Herring, 1987). Bioluminescence is most prevalent at mid-ocean depths, where some daytime illumination penetrates and where bioluminescence may occur in over 95% of the individuals. Above and below mid-ocean depths, luminescence occurs in less than 10% of all individuals and species. Among the coastal species, less than 2% are bioluminescent.

Bioluminescence is a form of "cold light emission”, less than 20% of the light generating thermal radiation (Hastings, 1983). It is produced by the interaction of a group of substances known collectively as luciferins and the enzyme luciferase, which catalyzes its combination with oxygen to form an oxyluciferin in an electronically excited state, which quickly decays, emitting a photon as it does. Since bioluminescence has evolved independently many times, the genes and proteins involved are unrelated in the different groups of bioluminescent organisms. Thus, each uses its particular organism-specific luciferin and luciferase. Bioluminescence may produce blue, green, yellow, orange, or red light. Land-living organisms tend to produce yellow or green light, and marine organisms blue or green light. In the deep sea, most bioluminescence is blue, the wavelength of light transmitted best by ocean waters. This is no doubt linked to the fact that most marine organisms are sensitive to blue light. Most deep-sea animals can only see blue light, except a few fish, such as the black dragon fish, which appear sensitive to and produce both blue and red light. Because their red bioluminescence is not detected by most deep-sea animals, such fishes may use their red light for intra-specific communication and/or predation.

Non-marine bioluminescence is less widely distributed, but a wider variety in colourations is observed. Famed for their ability to emit light - the glow-worm was aptly described by Wordsworth as "the earth-born star" in his poem 'The Pilgrim's Dream' (*circa* 1820). Bioluminescent fire-flies, like the glow-worm, belong to the same Lampyridae family of beetles. Some bioluminescent organisms, such as certain fungi and bacteria, emit light continuously, while dinoflagellates, a group of marine algae, produce light only when disturbed.

Functional Anatomy of Colour Vision across the Species

Colour perception is a result of evolutionary pressure and the ability to see colour has evolved, to a greater or lesser extent, in many different species. To be able to distinguish certain colourations from others plays an important part in the processes which ensure survival. Such ability is determined by the anatomy and functional development of the visual system a given species is equipped with.

In the animal world, at least forty different types of visual systems exist, the simplest just able to tell light from dark while sophisticated ones can distinguish both shapes and colours, the most complex belonging to the mantis shrimp, a predatory crustacean living on the ocean floor. There is an enormous diversity in both retinal structure and visual neuronal mechanisms across the animal kingdom, with a corresponding diversity in the role of colour vision in animal's perception, behaviour, and interactions with the environment (Land and Nilsson, 2002). With regard to retinal anatomy, the vertebrate retina is "back to front" i.e. the photoreceptors are located behind a layer of neurons, as opposed to the cephalopod retina, in which the photoreceptors are located in front of the processing neurons, which means that cephalopods do not have a blind spot. However, the cephalopod retina is not an outgrowth of the brain, as in vertebrates, illustrating that vertebrate and cephalopod eyes have evolved separately.

Colour Vision in Non-Humans

At the start of the 20th century colour vision was thought to be exclusive to man. Now however it is well established that colour vision is widespread in non-human animals, although even among vertebrates, the ability to perceive colour and the spectral range detected varies widely, having evolved several times. Nevertheless, the precise colour perception capabilities of the majority of animal species are still not known, since behavioural or physiological tests for colour vision are not easy to perform. Human colour vision (see below) is made possible by the presence of three types of colour sensitive receptors, a lack of colour receptors (cones) sensitive to red, blue, or green light provoking deficiencies in colour vision or various kinds of colour blindness. In general terms for all living organisms, if organisms possess only a single retinal pigment then they will only "see" in monochrome and for even limited colour vision at least two types of cones are required. However the number of retinal pigments in animal species is not limited, as in man, to three. Using behavioural studies and spectrophotometric analysis of light absorbed by animal retina, it can be deduced that four exist in approximately thirty species of birds and five in certain butterflies and many more for sea organisms such as the mantis shrimp and the sea manta, a giant ray (Cronin , Caldwell and Marshall, 2001; Marshall, Cronin and Kleinlogel, 2007). While the human eye cannot detect all of the electromagnetic spectrum emitted by the sun, notable UV, which in any case is absorbed by the human cornea, lobsters, gold fish, trout, bees, tortoises, many bird species and rodents such as rats and mice can perceive in this region (Cuthill et al., 2000). At the other end of the spectrum, some species, such as snakes, perceive infra- red but these rays are captured by specialized heat sensitive organs and not by the retina.

Colour vision of non-primate mammals is still a question of on-going research, varying considerably between species and often dependant on the nocturnal or diurnal nature of the animal. Much research is currently devoted to elucidating the capacity of colour perception in many different animal species, but there remains a vast number for which little concrete data exist. While certain mammals, such as the shrew (in spite of having a reputation of poor sight) and certain squirrel species are considered to be trichromatic, in general non-primate mammals are considered to have relatively limited colour vision. The variation in colour vision results from the fact that the capacity to detect colour has evolved more than once, with gene duplication for visual opsin pigments (Bowmaker, 1998). In addition, probably because of their nocturnal ancestry, mammals have rod-dominated retinas and many lack cones with red sensitive pigment and therefore have poorer (only dichromatic) colour vision: some species lack cones completely, such as the guinea pig and are thus totally colour blind. Bulls, like many mammals and in spite of the importance of the colour red in bull-fights, are insensitive to this colour. Similarly, the cat is dichromate with one type of cone sensitive to blue indigo ca 450nm and another to yellow/green ca 556nm, thus incapable of perceiving red, as is also the case for the ferret (Calderone and Jacobs, 2003). Cats do however have more rods (the highly light sensitive receptors) and less cones, giving good night, albeit monochrome, vision. Behavioural studies performed in the 1970's suggested that rabbits have a rather limited capacity to distinguish certain wavelengths, although they can differentiate between green and blue. Horses also have only dichromatic vision detecting blue and green and the colours based on them, even though the equine eye is the largest of any land mammal (Carroll et al., 2001). This is sometimes taken into consideration when designing obstacles in horse jumping events. Horses do, however, have more rods than humans, in addition to twenty fold more rods than cones, giving them better night vision.

A different system has evolved in rats and mice which have excellent night vision, due to a higher number of rods than cones, but see poorly in colour although both are dichromatic. Both rat and mouse cones co-express two photopigments, one sensitive to wavelengths of ca 510nm and one to ca 360 nm i.e. UV. Their visual systems exploit differences in the spectral absorption properties among the cones, enabling them to make certain dichromatic colour discriminations, which is also the case for gerbils (Jacobs and Williams, 2007; Jacobs, Fenwick and Williams 2001; Jacobs, Williams and Fenwick, 2004; Jacobs and Deegan 2nd., 1994). Both diurnal rodents and rodents which live in almost lightless conditions have been found to have similar colour vision (Williams, Calderone and Jacobs, 2005; Jacobs et al., 2003).

Amongst mammals, primates represent exceptions with regard to colour perception. Sound data confirm the long held suspicion that colour vision in primates including humans, apes, and Old World monkeys is better developed than in other mammals: in spite of data lacking on many species, these are all considered to be trichromatic (Jacobs, 1993). Variations nevertheless exist (Jacobs, 1996; Jacobs and Deegan 2nd., 1999). Variations amongst New World monkeys are even greater, some species being trichromatic while others are only dichromatic (Jacobs and Williams, 2006). In addition, evidence predicts that all male New World monkeys are dichromats while, depending on their opsin gene array, individual females can be either dichromatic or trichromatic (Jacobs and Deegan 2nd., 2003; 2005; Rowe and Jacobs, 2004). Some nocturnal species appear to be monochromatic however (Jacobs 1996).

The situation for aquatic mammals is quite different. Many species, including dolphins and seals, and in particular mammals that live in deep water tend to have blue shifted vision compared to that of many terrestrial mammals and are monochromatic (Fasick et al., 1998).

This is considered to result from the absence of evolutionary pressure to maintain colour in the dark monochromatic oceanic environment (Newman and Robinson, 2005).

Of species studied so far, the best colour vision appears to be found in lower vertebrates such as certain birds, aquatic creatures, and certain insects including butterflies and honeybees. Birds vary according to species in their capacity to perceive colour. Diurnal birds tend to have increased ultraviolet sensitivity, with far more cones than rods and their cones are sometimes complex, while nocturnal species such as owls tend towards sensitivity in the infrared end of the spectrum with a relatively high proportion of rods and are colour-blind. The most acute avian vision is found in raptors, such as hawks and eagles that rely on their sight to spot prey from altitude. They are bifoviate, increasing the potential number of cones, some of which are double, a phenomenon also observed in fish, amphibians, and reptiles. An eagle has a larger retina than a human with five times more cones and its structure, like that of most birds, is more complex. Many birds have four types of cone making them potentially tetrachromats.

Fish appear to have quite well developed visual systems, comparable in some species to those of birds. Some have photoreceptors with peak sensitivities in the ultraviolet range. This may be because, like birds, they move about in a blue environment and need to contrast food sources or predators against a blue background. Teleostei, regrouping about 23,600 vertebrate species making up 95% of all known fish species, perceive red, yellow/green/blue, violet and UV up to 365nm. However, since sea water selectively absorbs longer wavelengths, i.e. red light, many fish living below 10 metres see “poorly” in the red region. Nevertheless many reef fish species living at this depth emit red fluorescence the origin of which are guanine crystals and do perceive this colour (Michiels et al., 2008).

Amphibians see fairly well in colour with a maximum day vision principally in yellow and at night in green. Colour vision in reptiles is also well developed with turtles able to distinguish between blue, green and orange and lizards between yellow, red, green and blue. Reptiles have genera that possess rods and four spectral classes of cone each representing one of the five visual pigment families, endowing these species with the potential for tetrachromatic colour vision (Bowmaker, 1998).

Many insects, including butterflies, flies and bees, have colour vision. Butterflies vary widely in their sensitivity to light, and are considered to have the widest visual range of any form of wildlife. The Chinese yellow swallowtail butterfly (Papilio xuthus) has a pentachromatic visual system, i.e., the eyes contain five different types of cones, sensitive to UV, violet, blue, green, and red wavelength peaks. In nature, these butterflies feed on nectar provided by flowers of various colours not only in direct sunlight, but also in shaded places and on cloudy days. The windmill butterfly (Atrophaneura alcinous) has a visual spectral range from at least 400 nm to 700 nm, while the Sara Longwing butterfly (Heliconius sara) has a range from 310nm to 650nm. Mosquitoes do not perceive yellow but do see purple, the reason for which traps emit blue to ultraviolet light which attracts the insects. Bees, have complex compound eyes, four visual cells in each ommatidium responding to yellow/green light (530 nm), two responding maximally to blue light (430 nm) and the remaining two responding best to ultraviolet light (340 nm), allowing the honeybee to distinguish colours (except red). However, an additional feature of bee vision is that they are dichroic, i.e. sensitive to polarized light, which would pose a problem in perceiving colour from waxy plant surfaces since this is partially linearly polarized. Bees and many other insects overcome this problem since the majority of their photoreceptors are twisted like a corkscrew which enables them to perceive the same colour in all directions (Wehner and Bernard, 1993).

Colour and the Human Visual System

Two major ancient Greek schools attempted to provide a primitive explanation of human vision. The first theory, championed by scholars like Euclid and Ptolemy and their followers, was the "emission theory" which considered that vision was “produced” when rays emanating from the eyes intercept objects. The second theory advocated by Aristotle, Galen and their followers, considered vision to result from something representative of the object entering the eyes. While it contains essential aspects of present day explanations, light did not play any role in this theory and it remained only a speculation lacking any experimental foundation. In 1021 Ibn al-Haytham (also known as Alhacen or Alhazen), the "father of optics", was the first to reconcile both schools of thought in his Book of Optics. He argued from extensive scientific experimentation that vision is due to light from objects entering the eye and was the first to suggest that visual perception occurs in the brain, rather than the eyes. He also pointed out that personal experience has an effect on what people see and how they see, i.e. that vision and perception are subjective. The anatomical studies of Leonardo da Vinci, 1452-1519, were the first to demonstrate the special optical qualities of the eye and he considerably advanced ideas on vision when he realized that there is a distinction between central (foveal) and peripheral vision.

Today we know that only part of the colour processing performed by the human visual system takes places within the photoreceptors themselves, or before the signals reach the higher levels of the brain (Cronin and Marshall, 2001). Anatomical, microscopical, physiological and biochemical data provide detailed explanations of how the visual system in humans permits information from the environment to be detected and processed. The first stage consists of forming of an image on a light-sensitive membrane, the retina, at the back of the eye, which is actually part of the brain serving as a transducer to convert patterns of light into neuronal signals. In the adult human eye the retina constitutes 72% of a 22 mm diameter sphere, with a 3 mm^2 area lacking photoreceptors where the optic nerve leaves the eye, often called "the blind spot". In contrast, lateral to this is the fovea, most sensitive to light, responsible for our sharp central vision. The photoreceptive cells of the retina, due to the presence of a photosensitive pigment, respond to photons of light by producing neural impulses, hyperpolarizing cell membranes and ultimately producing electrical signals in retinal ganglion cells. These are then processed in a hierarchical fashion by different parts of the brain, from the retina to the lateral geniculate nucleus, to the primary and secondary visual cortex of the brain to form a representation of the external environment in the brain. The retina contains two types of photoreceptors, rods and cones. The rods, responsible for our dark-adapted vision are more numerous, 75-150 million compared with the 7 million cones in man, employ a sensitive photopigment called rhodopsin, with a thousand fold more sensitivity to light than cones. Rods adapt slowly to low levels of light and their sensitivity peaks sharply in the blue, i.e. shorter wavelengths compared to daylight vision, accounting for the increased apparent brightness of green leaves in twilight. They are better motion sensors and since they predominate in the peripheral vision, this affords better vision of dimmer objects in peripheral vision. Visual acuity or visual resolution is, however, much better with the cones. Cones in man, divided into "red" cones (64%), "green" cones (32%), and "blue" cones (2%), provide the eye's colour sensitivity, making man trichromatic. The green and red cones are concentrated in a spot known as the macula, the centre of which contains densely packed cones and no rods. The "blue" cones have the highest sensitivity and are mostly found outside the fovea, leading to some distinctions in the eye's blue perception.

However, how colour may actually be perceived is, as the very early intuitions of Leonardo da Vinci and others suggested, most often determined by complex processes and interactions between brain structures well beyond the receptor level. While humans can name the colour they see, it is impossible to tell which colour a non-human animal actually perceives when it responds selectively to a given colouration in an experimental task, for example. This will most likely for always remain a mystery to humans. However, cleverly designed psychophysical studies have allowed a better understanding of how non-human animals react to colourations, and how such reactions may be linked to environmental pressures or constraints. Moreover, recent scientific studies have shown that colour perception in humans is also quite strongly influenced by the immediate visual environment or context as well as by cultural factors.

Comparative Psychophysics and the Biological Role of Colour Perception in Animals

Over a century ago workers such as J. Lubbock and K. von Frisch developed behavioural criteria establishing that non-human animals see colour. Many animals in most phyla have since then been shown to have colour vision. Colour is used for specific behaviours, such as phototaxis and object recognition, while other behaviours such as motion detection are not dependant on colour. Having established the existence of colour vision, research focussed on the question of how many spectral types of photoreceptors were involved. Recently, data on photoreceptor spectral sensitivities have been combined with behavioural experiments and physiological models to systematically study the next logical question: ‘what neural interactions underlie colour vision?’ Kelber, Vorobyev and Osorio (2003) give an overview of the methods used to study animal colour vision, and discuss how quantitative modelling can suggest how photoreceptor signals are combined and compared to permit the discrimination of biologically relevant stimuli.

Comparative psychophysics is able to address questions about how colour perception influences behaviour in the different species. Does a bull get enraged by the colour of a red cape or by its movements? Do colourations help bees to discriminate flowers which are plump with nectar from others? Do specific colourations help a cat detect prey more rapidly? What do animals see when they detect colour and do they actually perceive colour? While no one knows exactly what animals see or perceive, there are several aspects of these questions that can and indeed have been explored. Firstly, we need to know how their visual systems work from a physiological perspective and also the spectral sensitivities of the photopigments, which have been reviewed above. More important, however, is the question of how an animal’s brain processes colour signal input. Some researchers think that animals "understand" little of what they see, just as humans rarely "understand" abstract paintings. Although we know that visual abilities differ among animals, there is an important distinction between detecting light that illuminates the retina, and understanding what is actually “out there”.

Since animals cannot answer questions about the colours they perceive, scientists have had to develop experiments in which animals are trained to make selective behavioural choices on the basis of colour. If an animal's food is always placed under a red square instead of a green square, if both squares are otherwise identical from all points of view and re-positioned randomly over time, and if the animal still and consistently keeps looking under the red square when it is hungry, we may indeed conclude that it is capable of distinguishing what we perceive as red from what we perceive as green. Yet, what we know about colour perception in the animal kingdom pales in comparison to that what is yet to be discovered.

Thirty years ago virtually everything known about primate colour vision derived from psychophysical studies of normal and colour-defective humans and from physiological investigations of the visual system of the macaque monkey, the most popular human surrogate for this purpose. The years since have witnessed much progress toward the goal of understanding this remarkable feature of primate vision. Among many advances, investigations focussed on naturally occurring variations in colour vision in a wide range of nonhuman primate species have proved to be particularly valuable. Results from such studies (Jacobs, 2008) were central to expanding our understanding of the interrelationships between opsin genes, cone photopigments, neural organization, and colour processing. This work also generated valuable insights into the evolution of colour perception. Latanov, Leonova, Evtikhin, and Sokolov (1997) studied colour discrimination using an instrumental learning paradigm in monkeys (Macaque rhesus) and fish (Carpio cyprinus L). Confusion matrices composed of probabilities of instrumental responses were treated by factor analysis. The spherical structure of perceptual colour space revealed in both species was found to be similar to that in humans, corresponding to "red-green," "blue-yellow" and the neuronal channels signalling for "brightness" and "darkness".

The dance of the honeybee has been researched extensively, and we have a relatively good understanding of the colour vision of bees and related insects. Mosquitoes and flies have been studied because of their role in spreading diseases, and it has been shown that they are attracted or repelled by specific surface colours, and by specific coloured sources of light. Interestingly, the surface colours they prefer do not necessarily correlate with the light source colours that attract them. Studying colour perception in birds is also quite challenging. From observation, it is clear that different species are attracted to bird feeders of particular colours, and that changing the colour of ambient light can trigger early breeding, or alter fertility rates, by mimicking the change of seasons. It is as hard for us to imagine how birds perceive colour as it is for a colour blind person to imagine full colour vision: it is outside our experience. Some species which we see as having identical male and female plumage differ when seen in the ultraviolet range - a difference which the birds themselves perceive. Butterflies also perceive colourations and often identify each other quite easily using ultraviolet markings. The male and female little sulphur butterflies (*Eurema lisa*) differ only in the ultraviolet region, with males being strongly ultraviolet reflective and females not.

Over many millions of years, sea creatures have developed a range of light reflectance properties. One example is the large variation in the patterns and colours of fish inhabiting the world's coral reefs. Attempts to understand the significance of the colouration have been made, but all too often from the perspective of a human observer. A more ecological approach requires us to consider the visual system of those for whom the colours were intended, namely other sea life. A first step is to understand the sensitivity of reef fish themselves to colour. Physiological data has revealed wavelength-tuned photoreceptors in reef fish, and provided behavioural evidence for their application in colour discrimination. Using classical conditioning, freshly caught damselfish were trained to discriminate coloured patterns for a food reward (Siebeck, Wallis, and Litherland, 2008). Within 3-4 days of capture, the fish selected a target colour on over 75% of trials. Brightness of the distractor and target were systematically varied to confirm that the fish could discriminate stimuli on the basis of chromaticity alone. The study demonstrated that reef fish can learn to perform two-alternative discrimination tasks, and provided the first behavioural evidence that reef fish have colour vision. Fishes such as members of the billfish family also appear to perceive colourations. These highly visual predatory teleosts inhabit the open ocean. Little is known about their visual abilities in detail, but previous studies indicated that these fish were likely to be monochromats. However, there is evidence of two anatomically distinct cone types in billfish. The cells are arranged in a regular mosaic pattern of single and twin cones as in many fishes, and this arrangement suggests that the different cone types also show different spectral sensitivity, which is the basis for colour vision. First measurements using microspectrophotometry (MSP) revealed peak absorption of the rod pigment at 484 nm, indicating that MSP, despite technical difficulties, will be a decisive tool in demonstrating colour vision in these offshore fishes. When hunting, billfish such as the sailfish flash bright blue bars on their sides, which also reflect UV light at 350 nm as revealed by spectrophotometric measurements. Billfish lenses block light of wavelengths below 400 nm, presumably rendering the animal blind to the UV component of its own body colour. Interestingly, at least two billfish predatory species have lenses transmitting light in the UV waveband and are therefore likely to perceive a large fraction of the UV peak found in the blue bar of the sailfish (Fritsches, Partridge, Pettigrew and Marshall, 2000). Wavelength discrimination ability of the goldfish has also been investigated on the basis of a behavioural training technique in the UV spectral range (Fratzer, Dörr and Neumeyer, 1994). First, spectral sensitivity was determined for two fishes to adjust the monochromatic lights (between 334 and 450 nm) to equal subjective brightness. The results of the wavelength discrimination experiment showed that, independent of which wavelength the fish were trained on, the relative choice frequency reached values above 70% only at wavelengths longer than 410 nm. Wavelength discrimination between 344 and 404 nm was not possible. These observations cannot be explained on the basis of the cone sensitivity spectra. Instead, inhibitory interactions, which suppress the short wavelength flanks of the short-, mid-, and long-wavelength sensitive cone types in the UV range have to be proposed. Kitschmann and Neumeyer (2005) demonstrated that goldfish are able to categorize spectral colours after habituation to a specific training wavelength. Subsequently, Poralla and Neumeyer (2006) trained goldfish on more than one wavelength to prevent very accurate learning. In one experiment goldfish were trained on six adjacent wavelengths with equal numbers of rewards, and, thus, equal numbers of learning events. Generalization tests showed that some wavelengths were chosen more often than others, indicating that certain spectral ranges are either more attractive or more easily remembered than others. This is a characteristic of the "focal" colours or centres of colour categories in human colour perception and the findings in goldfish may thus be interpreted accordingly. There appear to be four categories in spectral ranges approximately coinciding with the maximal sensitivities of the four cone types, and three categories in-between. Experiments with two training colours have shown that there seems to be no direct transition between categories analogous to human "green" and "red", but that there is a colour analogous to human "yellow".

However, visual systems sensitive to colour are confronted with the fact that the external stimuli are ambiguous because they are subject to constant variations of luminance and spectral composition. Furthermore, the transmittance of the ocular media, the spectral sensitivity of visual pigments and the ratio of spectral cone types are also variable. This results in a situation where there is no fixed relationship between a stimulus and a colour percept. Colour constancy has been identified as a powerful mechanism to deal with this set of problems, but is active only in a short-term time range. Changes that cover longer periods of time require additional tuning mechanisms at the photoreceptor level or at post-receptor stages of chromatic processing. Wagner and Kröger (2005) used the trichromatic blue acara (Aequidens pulcher, Cichlidae) as a model system and studied retinal physiology and visually evoked behaviour after rearing fish for 1-2 years under various conditions, including near monochromatic lights (spectral deprivation) and two intensities of white light (controls). In general, long-term exposure to long wavelength light had lesser effects than light of middle and short wavelengths. Within the cone photoreceptors, spectral deprivation did not change the absorption characteristics of the visual pigments. By contrast, the outer segment length of middle and long-wave-sensitive cones was markedly increased in the blue rearing group. Furthermore, in the same group, a loss of 65% short-wave-sensitive cones was observed after 2 years. These changes were interpreted as manifestations of compensatory mechanisms aimed at restoring the balance between the chromatic channels. At the horizontal cellular level, the connectivity between short-wave-sensitive cones and the H2 cone horizontal cells were affected in the blue light group. Responses of H2 horizontal cells to light were also sensitive to spectral deprivation showing a shift of the neutral point towards short wavelengths in the blue rearing group. An intensity effect was found in the group reared in bright white light, where the neutral point was more towards longer wavelength than in the dim light group. Like changes in the cones, the reactions of horizontal cells to spectral deprivation in the long wave domain may be characterized as compensatory. The spectral sensitivity of the various experimental groups of blue acara in a visually evoked behaviour task revealed that changes in relative spectral sensitivity were too complex to be explained by a simple extrapolation of adaptive and compensatory processes in the outer retina. The inner retina, and/or the optic tectum appear to be involved here, reacting to changes of the spectral environment. Thus in summary, there appears to be considerable developmental plasticity in the colour vision system of the blue acara, where epigenetic adaptive processes at various levels of the visual system respond to the specific spectral composition of the surroundings and provide a powerful mechanism to ensure functional colour perception in different visual environments. Processes involving an active fine-tuning of photoreceptors and post-receptor processing of chromatic information during ontogenetic development are a general feature of all colour vision systems. These appear to establish a functional balance between the various chromatic channels. This is likely to be an essential condition for cognitive systems to extract relevant and stable information from unstable and changing environments. Comparisons of functionally important changes at the molecular level in model systems have identified key adaptations driving isolation and speciation. In cichlids, for example, the long wavelength-sensitive opsins appear to play a role in mate choice and variations in colourations of the males, within and among species. To test the hypothesis that the evolution of elaborate colourations in male guppies (*poecilia reticulata*) is also associated with opsin gene diversity, Ward et al. (2008) sequenced long wavelength-sensitive opsin genes in six species of this family and concluded that enhanced wavelength discrimination may be a possible consequence of opsin gene duplication and divergence. This might have been an evolutionary prerequisite for colour-based sexual selection and may have led to the extraordinary colourations now observed in male guppies and in many other species.

Many living organisms thus clearly appear to detect visual information relative to colour, and are able to perceive differences in colourations. How essential is it for their survival, and is its absence life threatening? Several generalities can be postulated: there exists a strong interdependence between the habitat and/or behaviour patterns of different species and their capacity to perceive colour. For example, flying birds require a comprehensive visual perception in three-dimensional space, while birds that live on seeds and fruits in the forest canopy need to differentiate between green and the colours of their chosen foods. Monkeys need to distinguish between orange fruits and green foliage to find food. Ultraviolet vision as possessed by the kestrel can offer a significant advantage in spotting the traces left by prey, such as urine and faeces. The spectral range of vision of bees and butterflies also extends into the ultraviolet, which could aid them in seeking nectar in flowers they pollinate which have specific ultraviolet patterns. Evolutionary forces have been operational in developing specific characteristics, including particular spectral sensitivities and specific colourations, so that species survive better in a highly competitive environment. Thus, biological colourations may have different functions, but they all represent a means of signalling to members of the same or other species. These functions may be divided into three broad categories: deceptive signalling or camouflage, advertising, and repulsive signalling.

Deceptive Signalling or Camouflage

Deceptive signalling comprises the capacity of organisms for camouflage. Homochromy, which does not necessarily involve changing colour, is a strategy which has evolved to escape predators and consists of attempting to appear the same colour as the immediate environment. It can be referred to as deceptive colouration, or camouflage. The larger sized species tend not to mimic the colourations of specific objects, but to blend in with the tones present in their environment, e.g. leopards with their dark spots melt into the brush. Other principles underlying camouflage have been described in addition to such background pattern matching, or *crypsis*. *Crypsis* is, in fact, not an optimal strategy of concealment because edge information remains fully available to a potential predator. Another strategy, called disruptive colouration, has long been assumed more effective. Disruptive colouration is a contrast effect where high contrast elements at edges mask the perception of shape despite the fact that edge elements may be independently visible. Spectrophotometric studies, combined with data on the perception of shape targets by non-human animals (e.g. Stevens et al., 2006), have provided evidence in support of the idea that disruptive colouration reduces the chances of bird predation of artificially created targets.

Smaller sized species, like fish, reptiles, and amphibians, such as those of tropical rain forests, are able to rapidly change their colourations in response to changes in their environment, having developed complex mechanisms that allow them to deceptively "disappear" by blending in with their surroundings. This is achieved on the basis of a redistribution of the pigments in their chromophores, thus changing their colour. In the most well known example of this type of deceptive signalling, the chameleon, different species can change colours to pink, blue, red, orange, green, black, brown, yellow and turquoise. Two cell types are present in the upper layer of their skin, containing yellow and red pigments respectively, above a layer of iridophores, which can reflect, blue light. A layer of melanophores influences the "lightness" of the reflected light. All these pigment cells can rapidly relocate their pigments and thereby alter the colouration of a chameleon almost instantly. Similar processes occur in other animals, including fish, and detailed molecular mechanisms of pigment redistribution have been studied in several animal species, especially fish (Logan et al., 2006), and cephalopods such as calamari, cuttlefish and octopi with bright colours (Cloney and Florey, 1968; Demski, 1992). Rapid colour change in many fish species can be provoked by osmotic changes in the chromatophores (Lythgoe and Shand, 1982), and the regulation mechanisms underlying such changes have been extensively studied (Glaw and Vences, 1994; Valverde et al., 1995; Rodionov et al., 1998; Kashina et al., 2002; Aspengren et al., 2003; Mäthger et al., 2003; Sugden et al., 2004; Snider et al., 2004; Logan et al., 2006).

Cuttlefish are particularly clever masters of disguise, rapidly changing colouration to blend with their backgrounds and thereby seemingly vanishing from the scene. Recent studies (Cuthill, 2007) have shown that cuttlefish also use this ability to rapidly change their colouration with exactly the opposite aim, breaking their camouflage to "stick out" in order to direct warning messages at specific predators which are particularly likely to be dissuaded by visual signals. This kind of strategic signalling then falls into the repulsive category, which will be discussed later. Indeed, animals change their colouration for various reasons and not always, as is often assumed, for camouflage. Far more frequently, such changes are a genuine mode of communication within and across species and include warning signals in response to stress, attractive signalling to find a mate (see the next section), and signalling illness or submission to predators (Stuart-Fox and Moussalli, 2008; Porras et al., 2003; Deacon et al., 2003; Fujii, 2000).

Another type of deceptive signalling is employed by some bioluminescent marine species, which employ this not to avoid being detected, but to lure prey. Thus the anglerfish use their bioluminescence to attract small animals to within striking distance. The cookiecutter shark uses bioluminescence essentially for camouflage. A small patch on its underbelly remains dark and appears like a small fish to large predators like tuna and mackerel, and when these fish try to catch what they perceive as a "small fish", they are captured by the shark. The marine plankton dinoflagellates display an interesting twist on this mechanism. When a predator of this plankton is sensed through motion in the water, the dinoflagellate luminesces and, in turn, attracts even larger predators, which then will consume the smaller would-be predator of the dinoflagellate. This kind of, somewhat risky, selective strategy of deceptive signalling, also called "bluffing", is used by predated animals of various species (Langridge, Broom, and Osorio, 2007).

Advertising and Mate Choice

Animals largely employ their colourations to advertise their presence, either to attract members of their own species or repel those of others. Both colour and ultraviolet reflectance play an important role in attempting to attract a sexual partner as well as communicating worthwhile information in mate choice. This is well documented in fish (Boulcott, Walton and Braithwaite, 2005 ; Rick and Bakker, 2008b ; Modarressie, Rick and Bakker, 2006; Sköld et al., 2008), where bioluminescence has also been shown to play a significant role (Herring, 2000). Fish, such as sticklebacks and Siamese fighting fish, also employ both visible colour and UV in territorial defence (Rick and Bakker, 2008a). Many fish can display dramatic colour changes during courtship displays related to the degree of sexual arousal of the male, which are produced in the short term by pigment redistribution within melanophores.

Many reports have emphasized the potential biological role of both UV reflectance and fluorescence in avian communication (Andersson and Amundsen, 1997; Hunt et al., 1999, 2001; Örnborg et al., 2002; Siitari et al., 2002; Pearn et al., 2003). Male individuals of various avian species exhibit conspicuous colours on their feathers which are the product of sexual selection driven by mating preferences (Andersson, 1994; Darwin, 1871) and the additional capacity of avian ornaments to reflect UV plays an important role during sexual displays (Hausmann et al., 2003; Hunt et al., 2001; Andersson and Amundsen, 1997; Bennett et al., 1997; Hausmann et al., 2003; Finger, Burkhardt and Dyck, 1992; Pearn, Bennett and Cuthill, 2003; Siitari et al., 2002; Parker, 1995).

The highly coloured ornaments of King Penguins (*Aptenodytes patagonicus*), notably the yellow/orange breast and auricular feathers and the two orange/pink UV reflecting beak horns on each side of the beak the have been suggested to be implicated in mate choice (Dresp et al., 2005). It is significant that during courtship displays King Penguins flaunt their beak ornaments when encountering potential partners (Fig. 5) in a way similar to the flamboyant display of peacocks when they rapidly shake their feathers to produce a shimmering iridescence colour show with the unique aim of attracting their mate. The fact that the horn is both ultraviolet and also orange-pink in colour increases the signal, as more than a single type of photoreceptor would be activated and its perception would also be heightened by a contrast effect since the tissue surrounding the horn is black. In addition, the multiplicity of microstructures with slightly different orientations producing the UV reflectance spreads both the wavelength and also the angle over which it is reflected, producing a more easily perceptible signal. This potential biological function is strengthened by the fact that such UV reflecting ornaments are absent in sexually immature juveniles (Fig. 9), supporting such a hypothesis (Jouventin et al., 2005; Massaro, Lloyd and Darby, 2003; Dresp, unpublished results). Colour, and particularly colour change, in nuptial behaviour is also widespread among fish and has been shown to be hormone dependent (Sköld et al., 2008).

Apart from the function of visually attracting potential mates with coloured ornaments, different colours can also communicate information on general fitness of individuals, in particular whether an individual is well nourished and healthy, although in females this is not always the case indicating that female ornamentation in certain species has evolved by direct sexual selection on females through male choice (Pärn, Lifjeld and Amundsen, 2005). This would thus provide additional criteria particularly for males in attracting female partners (McGraw et al., 2002). Pigment-based ornaments have repeatedly been shown to be condition dependent, even though carotenoid based and melanin-base pigments are regulated differently, (Senar, Figuerola and Domènech, 2003), but more recently structural coloration has also been demonstrated to be condition dependent (Johnsen et al., 2003). Signalling of condition criteria for mate choice has also been evoked in butterflies (Kemp and Rutowski, 2007).

Figure 9. Sexually immature King Penguins which lack the distinctive beak horn ornament.

Bioluminescent light emission is also important for communication during courtship to attract a mate, which has been well documented in insects. This is seen actively in both fireflies and glow-worms, whose abdomens flash periodically with species-specific temporal patterns to attract mates. Both sexes emit specific patterns in an apparent genuine communication for sexual attraction. After mating the female no longer emits light and lays her eggs. Coded bioluminescent signals for mating have also been well-documented in certain small crustaceans such as ostracods. While pheromones may be used for long-distance communication, bioluminescent is useful at close range to "home in" on the target.

Con-specific communication between individuals of the same species does not have to be sexual but can serve to simply recognise each other, as is the case for neon fish in the murky shallow waters of the Amazonian rain forest, but also for many fish species that form schools to give them a numerical advantage for survival. In-flight signalling of certain butterfly species has also been documented (Vukusic et al., 2002). In addition, certain fish species use their bioluminescence as a form of "night light” for navigation, but it can be used, in addition to the functions already discussed, for communication, with other members of the same species. Moreover, if this is red, communication is “private”, since few fish perceive red (Michiels et al., 2008).

Repulsive Signalling

As well as enhancing camouflage, improving communication and/or conferring reproductive advantage, body colours may also reflect behavioural strategies, notably those related to territorial defence. This may be to defend nests or spawning sites, but can be maintained throughout the year to defend a territory to ensure an adequate food supply, as is the case for reef fishes. This has been shown to be hormonally influenced (Korzan et al., 2008). When males defend territories they are usually bigger and more colourful than their female counterparts. Colour can also sometimes be a warning signal to animals dangerous or of the inedible quality of other organisms, red, black and yellow being commonly employed for this. The black and yellow colouration of bees and wasps represent typical examples. Some animals mimic such warning colours to avoid becoming the prey of others, as examples of selective strategic signalling including "bluffing", mentioned earlier, clearly show.

Additional Functions

The symbiotic relationship between flowers and butterflies and other pollinators such as bees has evolved so that flowers attract pollinators to feed on their nectar. Unique colourful and/or contrast visual cues, sometimes in the UV range, provide an important ploy used by flowering plants to attract potential pollinators, in the same way that gastronomic restaurants serve meals with visual appeal. The colour of flowers of the horse chestnut tree (*Aesculus hippocastanum*) can change from yellow to red when nectar is no longer produced, i.e. when there is no longer need for pollination: red is not perceived by pollinating bees although their compound eyes are trichromatic being able to see UV (Wakakuwa et al., 2005; Wakakuwa, Stavenga and Arikawa, 2007). Butterflies tend to avoid the colour green when feeding, but are attracted to it during egg laying, since the next generation of caterpillars requires a good source of food after hatching. The green photoreceptors are thus not used when foraging, but the others (blue and UV sensitive) are critical in reducing the time taken to find nourishment (Spaethe, Tautz and Chittka, 2001). Plants that do not depend on insect or bird pollination are unlikely to have showy or scented flowers. The ultraviolet patches on some butterflies are directionally iridescent, so that they appear to flicker in flight. This flickering is thought to have an important role in butterfly behaviour and communication.

Colour Perception in Man: Context Effects, Culture and Colour Symbolism

It is clear from the intensive research reviewed above that colour plays a major role in the processes which ensure survival, propagation, and every day behavioural patterns of a large number of non-human living organisms. Colour perception is, indeed, the result of a complex evolutionary process that has produced different colour vision systems in various species across the phylogenetic scale, as we have seen above.

How vital is colour perception for man? Is such ability a mere luxury that makes our lives more enjoyable, as some have suggested? Colour signalling is employed everywhere in the world around us, from traffic signals and red warning lights to the bright and colourful advertisements in shops, streets and on the television screen. Research on colour perception in humans tends to suggest that even in man, even though perhaps to a lesser extent than in non-humans, colour perception plays an undeniable functional role and allows humans to better cope with specific environmental constraints. Also, phenomenological observations and psychophysical data have shown that the way in which we perceive a given colour strongly depends on the immediate visual context the colour is embedded in.

Context Effects in Colour Perception

Colour perception strongly depends on the immediate visual context around the coloured object, its luminance, and its shape. The colour red of a red square, for example, with a constant chromaticity and luminance, is seen as a darker red when against a background with a brighter colour compared with when it is against a background with a darker colour (Fig 10). This well-known observation is called simultaneous colour contrast. Such colour contrast phenomena influence other perceptual processes, such as depth perception and relative impressions of "nearer" and "further away" objects in the visual field (Guibal and Dresp, 2005). The colour red appears to play a particularly important role in such colour based depth perception (see also earlier observations by Bugelski, 1967), and the brain mechanisms potentially underlying this have been linked to both colour stereopsis (Dengler and Nitschke, 1993) and neural interactions in area V4 of the primate visual system (Desimone and Schein, 1987). The functional implications of such a dependency between colour and impressions of near and far may be related to colour based perceptual mechanisms driving attention to detail (Yantis and Jonides, 1991). These may well be equivalent to colour specific perceptual mechanisms in non-human animals, which may help a species detect a prey or predator of a specific colour more rapidly, or may help it assess how far or near it is likely to be.

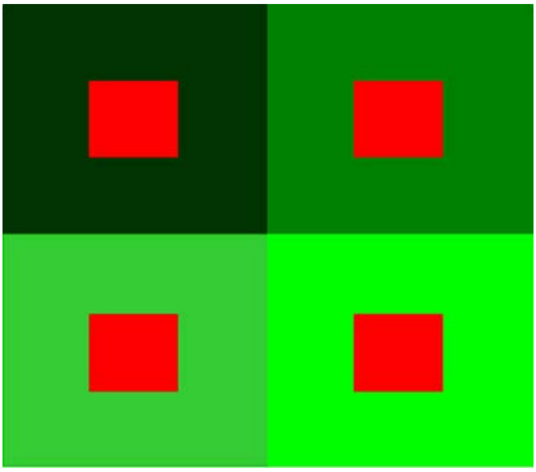


Figure 10. How a colour is perceived depends on the immediate visual context in which the colour is embedded. The red square on the dark green background shown on top here, for example, is perceived as a brighter than that on the light green background at the bottom. The luminance and chromaticity of all four red squares shown are strictly identical. This phenomenon, also known as subjective simultaneous colour contrast, is accompanied by other visual effects. For example, the red square on the lightest green background here seems nearer to the observer than the red square on the darkest green background.

Colour Perception and Cultural Differences

Colour perception plays an important psychological role in the daily life of human individuals. The importance of colour for humans definitely goes far beyond the "simpler" functions it ensures in non-human animals, such as helping individuals to seek and choose food, to look attractive to a potential mate, or to deceive or discourage a potential predator. In humans, colour information and perception has assumed a deeper and far more complex psychological significance. It has assumed a symbolic level and as such has become culture dependent in the sense that what “blue” may evoke in a European is not necessarily what it may evoke in a Chinese or a member of a remote African tribe. Research on colour cognition across cultures has generated substantial evidence for differences in colour cognition between language communities, including semi-nomadic African tribes, revealing a considerable diversity in the way different languages partition the physical continuum of colours visible to man. While some languages have been reported to use as few as two terms to describe all visible colours, others use up to twelve. Whatever the origin of these differences, it appears that even when two different languages have the same number of terms for similar points in colour space, there are significant differences in their cognitive organization as a function of culture and visual environments (Roberson et al., 2005). Cognitive organization or mapping of perceived events to metaphors, or terms of a given language may lead human individuals to contradict input from visual perception when judging the brightness of physical objects, for example (Meier et al., 2007). Emotions in particular seem to influence how the colours we perceive may be given a cognitive interpretation that is detached from visual perception as such. Thus, when making category judgements (Meier, Robinson, and Clore, 2004), people seem to have a tendency to assume, possibly unconsciously, that objects with bright colours are “good”, “uplifting”, and “forward”, whereas objects with darker colours are “bad”, “depressing”, and “obscure”.

Colour Symbolism and Emotions

In the most general terms, we tend to call colours “beautiful” or “ugly “, “warm” or “cold”, “gay” or “sad”, but we also go well beyond such categories. Colours may indeed evoke a variety of emotions, ranging from surprisingly strong to subtle and rather finely tuned. Red, the colour of blood often provokes an intense reaction, symbolising the passion and destruction indicated by it. It also often represents the forbidden, danger, even social revolt and, thus, courage. Pink, in contrast, symbolises noble emotions such as love, affection tenderness, femininity, babies and, more generally, harmony. Violet is associated in most cultures with spiritual peace, meditation and religious reflection and as such confers the notion of mystery. Purple, close to violet, adds a “noble” aspect to the latter and as such becomes the colour of kings and noblemen and social and spiritual power. Blue is the colour of the sky and stretches of water and thus suggests ideas of space and serenity. At the same time it provokes a sensation of cold. Green is found everywhere in Nature and symbolises life, freshness, vitality, health and optimism. It does not strongly stimulate the emotions and thus is a calming colour. Yellow is a luminous stimulating colour representing joy, but can provoke many different emotions. Orange, a colour close to that of flames induces a feeling of warmth (either physical or human). Brown, an essential colour of soil evokes honesty and as such feelings of comfort and stability. Black is a colour closely associated with night and therefore with death, bad luck, despair and sadness. Nevertheless in modern European society, black can also represent modernity, elegance and “chic”. Grey is a totally neutral colour symbolising equilibrium and confidence. White at the opposite extreme to black and devoid of sensuality is the icon of psychic and physical purity, of innocence and light.

The vast commerce devoted to colour schemes and decoration for our houses and apartments pays witness to how much we consider that colour, or the “right” choice of colour, is important to us. The colour of what we eat or drink contributes an essential aspect in whether we choose and enjoy a particular food or beverage. This is because we have built into our basic experiences the notion that a particular foodstuff has to be a particular colour for it to be edible, i.e. its colour will determine acceptance or rejection of it. This is taken into consideration in preparing food and making it appear more attractive. Thus the colour of salmon in a shop is the first characteristic noted by the consumer. Salmon can be, and often is, rendered pinker by adding carotenoids to food given to fish in fish farms (Shahidi, Metusalach, and Brown, 1998). Likewise margarine (from the Greek *margaron*, pearl white), invented in France in 1869 to replace butter, which was then scarce, is given a yellowish tint to suggest more pleasant sensations than those elicited by spreading white fat on our sandwiches.

Also, despite the fact that black has become the most fashionable colour to wear worldwide, man has not lost the desire to attract partners by colour. It is clear that man can invent many artificial, creative ways of using colour and resort to sophisticated colourful ornaments to attract others. The use of lip stick, make-up, or colourful sparkling jewellery or underwear by humans has such obvious parallels in the animal world that is almost bound to reflect the ultimate expression of the complex evolutionary process that has led to the emergence of colour perception.

REFERENCES

Andersson S and Amundsen T, 1997 Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond., B* 264: 15887-11591

Andersson M, 1994 *Sexual selection*. Princeton University Press, Princeton, New Jersey.

Arikawa K, 2003 "Spectral organization of the eye of a butterfly, Papilio". *J. Comp.* Phys. A 189, 791-800.

Aspengren S, Sköld HN, Quiroga G, Mårtensson L and Wallin M, 2003 Noradrenaline- and melatonin-mediated regulation of pigment aggregation in fish melanophores. *Pigment Cell Res*. 16:59–64

Auber L, 1957 The distribution of structural colors and unusual pigments in the Call Aves. *Ibis* 99: 463-476

Bagnara JT, Fernandez PJ, Fujii R, 2007 On the blue coloration of vertebrates. *Pigment Cell Res*. 20(1):14-26;

Bagnara JT, 1998 Comparative Anatomy and Physiology of Pigment Cells in Nonmammalian Tissues in The Pigmentary System: Physiology and Pathophysiology, Oxford University Press.

Bagnara JT. 1966 Cytology and cytophysiology of non-melanophore pigment cells. *Int Rev Cytol*. 20:173–205.

Bandaranayake WM. 2006 The nature and role of pigments of marine invertebrates. *Nat Prod Rep*. 23 (2):223-55

Bennett AT, Cuthill IC, Partridge JC and Lunau, K 1997 Ultraviolet plumage colors predict mate preferences in starlings. *Proc Natl Acad Sci U S A 94*: 8618-21

Boulcott PD, Walton K, Braithwaite VA. 2005 The role of ultraviolet wavelengths in the mate-choice decisions of female three-spined sticklebacks. *J Exp Biol*. 208 (Pt 8):1453-8.

Bowmaker JK. 1998 Evolution of colour vision in vertebrates. *Eye*. 12 (Pt 3b):541-7

Bragg WH and BraggWL 1915 X*-rays and crystal structure.* G.Bell, London.

Brink DJ, van der Berg NG, Botha AJ. 2002 Iridescent colors on seashells: an optical and structural investigation of Helcion pruinosus. *Appl Opt.* 41(4):717-22

Brown PK, Wald G. 1964 Visual pigments in single rods and cones of the human retina. Direct measurements reveal mechanisms of human night and color vision. *Science.* 144:45-52.

Bugelski, BR 1967 Traffic signals and depth perception. *Science*, 157, 1464-1485.

Calderone JB, Jacobs GH. 2003 Spectral properties and retinal distribution of ferret cones. *Vis Neurosci*. 20(1):11-7

Carroll J, Murphy CJ, Neitz M, Ver Hoeve JN, Neitz J 2001. "Photopigment basis for dichromatic color vision in the horse." *Journal of Vision*, 1(2):2, 80-87

Cloney RA. & Florey E. 1968 Ultrastructure of cephalopod chromatophore organs. Z Zellforsch Mikrosk Anat. 89:250–280;

Cronin T.W., Marshall, N.J. 1989 A retina with at least ten spectral types of photoreceptors in a mantis shrimp. *Nature* 339, 137 - 140.

Cronin TW, Caldwell RL, Marshall J. 2001 Sensory adaptation. Tunable colour vision in a mantis shrimp. *Nature* 411(6837):547-8;

Cronin TW, Marshall J. 2001 Parallel processing and image analysis in the eyes of mantis shrimps. *Biol Bull.* 200(2):177-83.

Cuthill IC, Partridge JC, Bennett ATD, Church SC, Hart NS, and Hunt S. 2000 Ultraviolet Vision in Birds. *Advances in the Study of Behavior*. 29: 159-214.

Cuthill, IC 2007 Animal behaviour: strategic signalling by cephalopods. *Current Biology*, 18, 1059-1060.

Darwin, 1871 The Descent of Man and Selection in Relation to Sex. Murray, London.

Deacon SW Serpinskaya AS, Vaughan PS, Lopez Fanarraga M, Vernos I, Vaughan KT, Gelfand VI. 2003 Dynactin is required for bidirectional organelle transport. *J Cell Biol* 160:297-301

Demski LS. 1992 Chromatophore systems in teleosts and cephalopods: a levels oriented analysis of convergent systems. *Brain Behav Evol.* 40:141-56.

Dengler, M, & Nitschke, W 1993 Color stereopsis: a model for depth reversals based on border contrast. *Perception & Psychophysics*, 53, 150-156.

Desimone, R, and Schein, SJ 1987 Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *Journal of Neurophysiology*, 57, 835-868

Dresp B, Jouventin P, Langley K. 2005 Ultraviolet reflecting photonic microstructures in the King Penguin beak. *Biol Lett.* 1(3):310-3.

Dresp B, Langley K. 2006 Fine structural dependence of ultraviolet reflections in the King Penguin beak horn. *Anat Rec A Discov Mol Cell Evol Biol.* 288(3):213-22.

Dyck J. 1971 Structure and Spectral Reflectance of Green and Blue Feathers of the Rose-Faced Lovebird (Agapornis Roseicollis). *Biol.Skrifter* Vol.18 no.2; 5-65

Dyck, 1976 Structural Colours. Proc.Int.Orn.Congr 16: 426-437

Fasick JI, Cronin TW, Hunt DM, Robinson PR. 1998 The visual pigments of the bottlenose dolphin (Tursiops truncatus). *Vis Neurosci.* 15(4):643-51.

Finger E and Burkhardt D, 1994 Biological aspects of bird coloration and avian colour vision including the ultraviolet range. *Vision Res* 34: 1509-1514

Finger, E., Burkhardt, D. & Dyck, J. 1992 Avian plumage colors: origin of UV reflection in a black parrot. *Naturwissenschaften* 79, 187-188.

Fox, DL 1979 Biochromy: the natural coloration of living things

Fratzer C, Dörr S, Neumeyer C. Wavelength discrimination of the goldfish in the ultraviolet spectral range. *Vision Res.* 1994 34(11):1515-20.

Fritsches KA, Partridge JC, Pettigrew JD, Marshall NJ. 2000 Colour vision in billfish. *Philos Trans R Soc Lond B Biol Sci.* 355(1401):1253-6.

Fujii R. 2000 The regulation of motile activity in fish chromatophores. *Pigment Cell Res.* 13:300-19.

Ghiradella H, Aneshansley D, Eisner T, Silberglied RE, Hinton HE. 1972 Ultraviolet Reflection of a Male Butterfly: Interference Color Caused by Thin-Layer Elaboration of Wing Scales. *Science*. 178(4066):1214-1217

Ghiradella H. 1994 Structure of butterfly scales: patterning in an insect cuticle. *Microsc Res Tech.* 27(5):429-38

Glaw, F, Vences, M 1994. A Field Guide to Amphibians and Reptiles of Madagascar 2nd edition. Köln: Verlag GBR

Guibal, CRC, & Dresp, B 2005 Interaction of color and geometric cues in depth perception: when does "red" mean "near"? *Psych Res*, 69, 30-40.

Guillaumée M, Liley M, Pugin R, Stanley RP. 2008 Scattering of light by a single layer of randomly packed dielectric microspheres giving color effects in transmission. *Opt Express.* 16(3):1440-7

Hastings J.W. 1983 Biological diversity, chemical mechanisms, and the evolutionary origins of bioluminescent systems. *J. Mol. Evol*. 19,309

Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. 2003 Ultraviolet signals in birds are special. *Proc. R. Soc. Lond.,* B 270, 61-67.

Herring PJ. 2000 Species abundance, sexual encounter and bioluminescent signalling in the deep sea. *Philos Trans R Soc Lond B Biol Sci*. 355(1401):1273-6.

Herring PJ. 1987 Systematic distribution of bioluminescence in living organisms. *J Biolumin Chemilumin.* (3):147-63

Hunt S, Cuthill IC, Bennett AT, Griffiths R (1999) Preferences for ultraviolet partners in the blue tit. *Anim. Behav* 58: 809-815

Hunt, S., Kilner, R.M., Langmore, N.E., Benett, A.T. 2003 Conspicuous, ultraviolet-rich mouth colours in begging chicks. *Proc R Soc Lond B Biol Sci. 270* Suppl 1:S25-8.

Hunt S, Cuthill IC, Bennett AT, Church SC, Partridge JC. 2001 Is the ultraviolet waveband a special communication channel in avian mate choice? *J Exp Biol*. 204(Pt 14):2499-507.

Ito S & Wakamatsu K. 2003 Quantitative analysis of eumelanin and pheomelanin in humans, mice, and other animals: a comparative review. *Pigment Cell Res.* 16:523-31

Jacobs GH, 1993 The distribution and nature of colour vision among the mammals. *Biol Rev Camb Philos Soc.* 1993 68(3):413-71.

Jacobs GH, Calderone JB, Fenwick JA, Krogh K, Williams GA. 2003 Visual adaptations in a diurnal rodent, Octodon degus. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol.* 189(5):347-61

Jacobs GH, Deegan JF 2nd. 1994 Sensitivity to ultraviolet light in the gerbil (Meriones unguiculatus): characteristics and mechanisms. *Vision Res*. 34(11):1433-41

Jacobs GH, Deegan JF 2nd. 1999 Uniformity of colour vision in Old World monkeys. *Proc Biol Sci.* ;266(1432):2023-8

Jacobs GH, Deegan JF 2nd. 2005 Polymorphic New World monkeys with more than three M/L cone types. *J Opt Soc Am A Opt Image Sci Vis.* 22(10):2072-80;

Jacobs GH, Deegan JF 2nd. 2003 Cone pigment variations in four genera of new world monkeys. *Vision Res*. 43(3):227-36;

Jacobs GH, Fenwick JA, Williams GA. 2001 Cone-based vision of rats for ultraviolet and visible lights. *J Exp Biol.* 204(Pt 14):2439-46;

Jacobs GH, Williams GA, Fenwick JA. 2004 Influence of cone pigment coexpression on spectral sensitivity and color vision in the mouse. *Vision Res.*44(14):1615-22.

Jacobs GH, Williams GA. 2007 Contributions of the mouse UV photopigment to the ERG and to vision. *Doc Ophthalmol.* 115(3):137-44;

Jacobs GH, Williams GA. 2006 L and M cone proportions in polymorphic New World monkeys. *Vis Neurosci.* 23(3-4):365-70).

Jacobs GH. 2008 Primate color vision: a comparative perspective. *Vis Neurosci.* Sep-Dec; 25(5-6):619-33.

Jacobs GH. Primate photopigments and primate color vision. *Proc Natl Acad Sci U S* A. 1996 93(2):577-81;

Johnsen A, Delhey K, Andersson S, Kempenaers B. 2003 Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proc Biol Sci.* 270(1521):1263-70

Jouventin, P., Nolan, P.M., Ornborg, J. and Dobson, F.S. 2005 Ultraviolet beak spots in king and emperor penguins. The Condor (in press).

Kashina AS, Semenova IV, Ivanov PA, Potekhina ES, Zaliapin I, Rodionov VI. 2002 Protein kinase A, which regulates intracellular transport, forms complexes with molecular motors on organelles. *Curr Biol.* 14:1877–81.

Kelber A , Vorobyev M and Osorio D. 2003 Animal colour vision – behavioural tests and physiological concepts. Biol. *Reviews of the Cambridge Philosophical Society*, 78:1:81-118.

Kemp DJ, Rutowski RL. 2007 Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. *Evolution.* 61(1):168-83

Kinoshita S, Yoshioka S, Kawagoe K. 2002 Mechanisms of structural colour in the Morpho butterfly: cooperation of regularity and irregularity in an iridescent scale. *Proc Biol Sci. 269*(1499):1417-21

Kinoshita S, Yoshioka S. 2005 Structural colors in nature: the role of regularity and irregularity in the structure. *Chemphyschem.* 6(8):1442-59

Korzan WJ, Robison RR, Zhao S, Fernald RD. 2008 Color change as a potential behavioral strategy. *Horm Behav*. 54(3):463-70.

Krech, D., Crutchfield, R.S., Livson, N., Wilson, W.A. Jr., Parducci, A. 1982 Elements of psychology (4th ed.). New York: Alfred A. Knopf. pp. 108-109

Langridge, KV, Broom, M, and Osorio, D 2007 Selective signalling by cuttlefish to predators. *Current Biology,* 18, 1044-1045

Land M.F. and Nilsson D.E. 2002, *Animal Eyes,* Oxford University Press

Latanov AV, Leonova AYu, Evtikhin DV, Sokolov EN. 1997 Comparative neurobiology of color vision in humans and animals. *Neurosci Behav Physiol.* 27(4):394-404.

Li Y, Lu Z, Yin H, Yu X, Liu X, Zi J. 2005 Structural origin of the brown color of barbules in male peacock tail feathers. *Phys Rev E Stat Nonlin Soft Matter Phys*. 72(1 Pt 1):010902).

Logan DW Burn SF and Jackson IJ, 2006 Regulation of pigmentation in zebrafish melanophores. *Pigment Cell Res*. 19:206-13

Lythgoe JN and Shand J. 1982 Changes in spectral reflexions from the iridophores of the neon tetra. *J Physiol.*

Marks WB, Dobelle WH, MacNichol EF Jr. 1964 Visual pigments of single primate cones. *Science.* 143:1181-3.

Marshall J, Cronin TW, Kleinlogel S. 2007 Stomatopod eye structure and function: a review. *Arthropod Struct Dev.* 36(4):420-48

Massaro, M., Lloyd, S. D. & Darby, J. Y. 2003 Carotenoid-derived ornements reflect parental quality in male and female yellow-eyed penguins Megadyptes antipodes. *Behav. Ecol. Sociobiol.* 55, 169-175.

Mäthger LM, Land MF, Siebeck UE, Marshall NJ. 2003 Rapid colour changes in multilayer reflecting stripes in the paradise whiptail, Pentapodus paradiseus. *J Exp Biol.* 206(Pt 20):3607-13;

Matsumoto J. 1965 Studies on fine structure and cytochemical properties of erythrophores in swordtail, Xiphophorus helleri. *J Cell Biol.* 27:493–504.

McGraw KJ and Nogare MC, 2004 Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots. *Comp*. Biochem. Physiol. B Biochem. *Mol. Biol 138:* 229-33

McGraw KJ, Mackillop EA, Dale J, Hauber ME. 2002 Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J Exp Biol. 205*(Pt 23):3747-55.

Meier BP, Robinson MD, Clore GL 2004 Why good guys wear white. *Psychol Sci 15:* 82-87.

Meier BP, Robinson MD, Crawford LE and Ahlvers WJ 2007 When light and dark thoughts become light and dark responses: affect biases brightness judgements. *Emotion* 7: 366-376.

Michiels NK, Anthes N, Hart NS, Herler J, Meixner AJ, Schleifenbaum F, Schulte G, Siebeck UE, Sprenger D, Wucherer MF. 2008 Red fluorescence in reef fish: a novel signalling mechanism? *BMC Ecol.* 8:16

Modarressie R, Rick IP, Bakker TC. UV matters in shoaling decisions. *Proc Biol Sci.* 2006 273(1588):849-54.

Morrison RL. A transmission electron microscopic (TEM) method for determining structural colors reflected by lizard iridophores. Pigment Cell Res. 1995 8(1):28-36.

Mougeot Mougeot F and Arroyo BE. 2006 Ultraviolet reflectance by the cere of raptors. *Biol Lett.* 2(2):173-6.

Mougeot, F., Redpath, S.M. and Leckie, F. 2005 Ultra-violet reflectance of male and female red grouse, Lagopus lagopus scoticus: sexual ornaments reflects nematode parasite intensity. *J. Avian Biol*. 36, 203–209,

Newman LA, Robinson PR. 2005 Cone visual pigments of aquatic mammals. *Vis Neurosci.* 22(6):873-9

Örnborg J, Andersson S, Griffiths R, Sheldon BC (2002) Seasonal changes in an ultraviolet structural colour signal in blue tits, *Parus caeruleus. Behav. J. Linn. Soc* 76: 237-245

Osorio D and Ham AD. 2002 Spectral reflectance and directional properties of structural coloration in bird plumage. *J Exp Biol.* 205(Pt 14):2017-27.

Parker AR 2000 515 million years of structural colour. *J.Opt. A: Pure Appl*. Opt 2: R15-R28

Parker AR and McKenzie DR. 2003 The cause of 50 million-year-old colour. *Proc Biol Sci.* 270 Suppl 2:S151-3

Parker AR, 1998 The diversity and implications of animal structural colours. *J Exp Biol.* 201(Pt 16):2343-7.

Parker AR, 1995 Discovery of functional iridescence and its coevolution with eyes in the phylogeny of Ostracoda (Crustacea). Proc. Roy. Soc. Lond. B 262: 349-355

Parker AR, McPhedran RC, McKenzie DR, Botten LC and Nicorovici NA, 2001 Photonic engineering. Aphrodite's iridescence. Nature 409: 36-7

Pearn SM, Bennett AT and Cuthill IC, 2003 Proc. Roy. Soc. Lond. B 270: 859-65

Peters A, Denk AG, Delhey K and Kempenaers B, 2004 Carotenoid-based bill colour as an indicator of immunocompetence and sperm performance in male mallards. J. Evol. Biol 17: 1111-20

Poralla J and Neumeyer C, 2006 Generalization and categorization of spectral colors in goldfish. II. Experiments with two and six training wavelengths. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol.* 192 (5):469-79

Porras MG De Loof A, Breuer M and Aréchiga H, 2003 Corazonin promotes tegumentary pigment migration in the crayfish Procambarus clarkii. *Peptides*. 24:1581–9

Price TD, 2006 Phenotypic plasticity, sexual selection and the evolution of colour patterns. *J Exp Biol.* 209(Pt 12):2368-76.

Prum R.O., Torres R.H., Williamson S. and Dyck J, 1998 Coherent Light Scattering by Blue Feather Barbs. *Nature* 396, 28-29;

Prum RO, Quinn T and Torres RH, 2006 Anatomically diverse butterfly scales all produce structural colours by coherent scattering. *J Exp Biol.* 209 (Pt 4):748-65

Prum RO and Torres R. 2003 Structural colouration of avian skin: convergent evolution of coherently scattering dermal collagen arrays. *J Exp Biol.* 206 (Pt 14):2409-29.

Prum RO and Torres RH. 2004 Structural colouration of mammalian skin: convergent evolution of coherently scattering dermal collagen arrays. *J Exp Biol.* 207 (Pt 12):2157-72.

Prum RO, Torres RH, Kovach C, Williamson S, Goodman SM, 1999 Coherent light scattering by nanostructured collagen arrays in the caruncles of the malagasy asities (Eurylaimidae: aves) *J. Exp. Biol* 202: 3507-3522

Prum RO, Torres RH, Williamson S and Dyck J 1999 Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. *Proc. Roy. Soc.* Lond. B 266: 13-22

Raman CV. 1935 The Origin of the Colours in the Plumage of Birds Proc. *Indian Acad. Sci. Sect.*A, 1-7.

Rick IP, Bakker TC. 2008a Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (Gasterosteus aculeatus). *Naturwissenschaften.* 95(7):631-8.

Rick IP, Bakker TC. 2008b Color signaling in conspicuous red sticklebacks: do ultraviolet signals surpass others? *BMC Evol Biol.* 8:189.

Roberson D, Davidoff J, Davies IRL, and Shapiro LR 2005 Color categories: Evidence for the cultural relativity hypothesis. *Cog Psych* 50:378-411.

Rodionov VI, Hope AJ, Svitkina TM, Borisy GG, 1998 Functional coordination of microtubule-based and actin-based motility in melanophores. *Curr Biol.* 8:165-8;

Rowe MP and Jacobs GH. 2004 Cone pigment polymorphism in New World monkeys: are all pigments created equal? *Vis. Neurosci*. 21(3):217-22

Seikai T, Matsumoto J, Shimozaki M, Oikawa A, Akiyama T. 1987 An association of melanophores appearing at metamorphosis as vehicles of asymmetric skin color formation with pigment anomalies developed under hatchery conditions in the Japanese flounder, Paralichthys olivaceus. *Pigment Cell Res.*1(3):143-51

Senar JC, Figuerola J and Domènech J. 2003 Plumage coloration and nutritional condition in the great tit Parus major: the roles of carotenoids and melanins differ. *Naturwissenschaften*. 90(5):234-7.

Shahidi F, Metusalach and Brown JA. 1998 Carotenoid pigments in seafoods and aquaculture. *Crit Rev Food Sci Nutr*. 38(1):1-67

Shawkey MD and Hill GE. 2005 Carotenoids need structural colours to shine. *Biol Lett.* Jun 22;1(2):121-4

Siebeck UE, Wallis GM and Litherland L. 2008 Colour vision in coral reef fish*.* *J Exp Biol.* Feb;211(Pt 3):354-60.

Siitari H, Honhavaara J, Huhta E, Viitala J, 2002 Ultraviolet reflection and female mate choice in the pied flycatcher Ficedula hypoleuca. *Anim. Behav.* 63: 97-102.

Sköld HN, Amundsen T, Svensson PA, Mayer I, Bjelvenmark J, Forsgren E. 2008 Hormonal regulation of female nuptial coloration in a fish. *Horm Behav.* 54(4):549-56.

Snider J Lin F, Zahedi N, Rodionov V, Yu CC, Gross SP. 2004 Intracellular actin-based transport: how far you go depends on how often you switch. *Proc Natl Acad Sci USA*. 101:13204-9

Spaethe J, Tautz J, Chittka L. 2001 Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc Natl Acad Sci U S A* 98(7):3898-903.

Stevens, M, Cuthill, IC, Alejandro Pàrraga, C, and Troscianko, T 2006 The effectiveness of disruptive coloration as a concealment strategy. *Prog Brain Res*, 155, 49-64.

Stuart-Fox, D. and Moussalli, A. 2008 Selection for social signaling drives the evolution of chameleon colour change. *Public Library of Science Biology,* 6, 25.

Sugden D Davidson K, Hough KA, Teh MT. 2004 Melatonin, melatonin receptors and melanophores: a moving story. *Pigment Cell Res*. 17:454-60

Taylor JD. 1969 The effects of intermedin on the ultrastructure of amphibian iridophores. *Gen Comp Endocrinol*. 12:405-16.

Valverde P, Healy E, Jackson I, Rees JL, Thody AJ 1995 Variants of the melanocyte-stimulating hormone receptor gene are associated with red hair and fair skin in humans. *Nat. Genet.* 11:328-30.

Vértesy Z, Bálint Z, Kertész K, Vigneron JP, Lousse V, Biró LP. 2006 Wing scale microstructures and nanostructures in butterflies--natural photonic crystals. *J Microsc*. 224(Pt 1):108-10.

Vukusic P and Sambles JR 2003 Photonic structures in biology. *Nature* 424: 852-855

Vukusic P, Sambles JR, Lawrence CR, Wootton RJ (2001) Structural colour. Now you see it - now you don't. *Nature* 410: 36.

Vukusic P, Sambles JR, Lawrence CR, Wootton RJ. 2002 Limited-view iridescence in the butterfly Ancyluris meliboeus. *Proc Biol Sci*. 269(1486):7-14.

Vukusic P, Wootton RJ, Sambles JR. 2004 Remarkable iridescence in the hindwings of the damselfly Neurobasis chinensis chinensis (Linnaeus) (Zygoptera: Calopterygidae). *Proc Biol Sci.* 271(1539):595-601.

Wakakuwa M, Kurasawa M, Giurfa M and Arikawa K. 2005 Spectral heterogeneity of honeybee ommatidia. *Naturwissenschaften*. 92(10):464-7.

Wakakuwa M, Stavenga DG and Arikawa K. 2007 Spectral organization of ommatidia in flower-visiting insects. *Photochem Photobiol*. 83(1):27-34.

Ward Ward MN, Churcher AM, Dick KJ, Laver CR, Owens GL, Polack MD, Ward PR, Breden F, Taylor JS. 2008 The molecular basis of color vision in colorful fish: four long wave-sensitive (LWS) opsins in guppies (Poecilia reticulata) are defined by amino acid substitutions at key functional sites. *BMC Evol Biol.* 8:210.

Wehner R and Bernard GD. 1993 Photoreceptor twist: a solution to the false-color problem. *Proc Natl Acad Sci U S A*. 90(9):4132-5.

Williams GA, Calderone JB and Jacobs GH. 2005 Photoreceptors and photopigments in a subterranean rodent, the pocket gopher (Thomomys bottae). *J Comp Physiol A Neuroethol Sens Neural Behav Physiol*. 191(2):125-34.

Wong TH, Gupta MC, Robins B, Levendusky TL. 2003 Color generation in butterfly wings and fabrication of such structures. *Opt Lett. 28*(23):2342-4.

Yin H, Shi L, Sha J, Li Y, Qin Y, Dong B, Meyer S, Liu X, Zhao L, Zi J. 2006 Iridescence in the neck feathers of domestic pigeons. *Phys Rev E Stat Nonlin Soft Matter Phys.* 74(5 Pt 1):051916).

Zi J, Yu X, Li Y, Hu X, Xu C, Wang X, Liu X, Fu R. 2003 Coloration strategies in peacock feathers. *Proc Natl Acad Sci U S A*. 100(22):12576--8

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 125-160

Chapter 4

INDIVIDUAL DIFFERENCES IN COLOUR VISION

M.I. Suero, P.J. Pardo, A.L. Pérez
Dept. of Physics, Avda. de Elvas s/n, Badajoz, University of Extremadura, Spain

ABSTRACT

Since the formulation of the Young-Helmholtz chromatic theory in the 19th century, it has generally been accepted that human colour vision is trivariant, i.e., it is possible to match any colour stimulus by mixing three primary stimuli in appropriate proportions. This resulted in the definition by the International Commission on Illumination in 1931 of the standard colorimetric observer for fields of 2° only three years after the definition of the standard photometric observer known as the V_λ luminous efficiency curve.Much progress has been made in the knowledge of colour vision since then, in such fields as physics, physiology, genetics, biochemistry, neuroscience, and psychology. That is why it is perhaps the time to raise our level of exigency a step when it comes to characterizing a chromatic observer. The question we should ask ourselves is not whether that figure of the standard colorimetric observer represents the average of the population, because this can indeed be done with successive corrections. Rather it is whether there exist very large individual differences in the perception of colour, and if so how these differences manifest themselves. This is of course apart from observers characterized as defective.In this chapter, we review the state-of-the-art in this field, and present our own latest research results concerning this question.

1. INTRODUCTION

Colour is defined by the International Commission on Illumination (CIE) as the attribute of visual perception by which an observer can distinguish differences between two fields of the same size, shape, and texture that may be due to differences in the spectral composition of the electromagnetic radiation related to the observation. This is called psychophysical colour to clearly indicate that it is the response of sensory perception to radiant stimuli, thus emphasizing its bipolar nature. This dual nature was often denied by scientists of one of the two disciplines to which its name alludes – physics and psychology.

The first specific theory of colour vision was enunciated by Thomas Young in 1801. It included physical and physiological terms, and was based on the impossibility of there existing in the retina an infinity of particles that could vibrate in resonance with each possible undulation associated with light. It had to be assumed that the number of types of these particles is finite, corresponding to the three main colours – red, yellow, and blue. Each sensitive filament of the nerve could be divided into three portions, one sensitive to red, another to yellow, and a third to blue [1]. This theory is known as the Three Receptor or Trichromatic Theory. Because of its clear limitations, it was not widely accepted. It was Helmholtz who later developed Young's ideas in his 1896 *Handbuch der Physiologischen Optik* [2], in the second volume of which he wrote:

> "The eye is equipped with three different sets of nerve fibres. Stimulation of the first excites the sensation of red, stimulation of the second excites the sensation of green, and stimulation of the third excites the sensation of violet.
>
> "Homogeneous light excites these three types of fibres in various degrees depending on their wavelength. But this does not mean that every colour of the spectrum does not stimulate the three types of fibres, some weakly and others strongly. On the contrary, to explain a series of phenomena it is necessary to assume that this is precisely what occurs."

At the end of the nineteenth century, a German physiologist, Ewald Hering [3], developed a theory of colour vision based on the subjective appearance of colours rather than on physical experiments. The trichromatic theory was inadequate to explain the appearance of colours. It could not reasonably explain why red and green lights are perceived as yellow when mixed, or why this yellow mixed with blue produces a perfect white [4]. Most defenders of the trichromatic theory were physicists who, at that time, disdained consideration of the appearance of colour as being of little scientific interest. Hering, however, asked himself why we never perceive a reddish green or a greenish red, but we do perceive greenish blues, etc. Hering speculated that the answer could lie in a process of opponent colours. He suggested that the visual system might be capable of generating signals of two opposing types depending on the wavelength. This idea was not favourably received by either physicists or physiologists. More than half a century had to pass until several experiments supported Hering's *Opponent Process Theory* of colours.

The trichromatic theory and the opponent process theory of colours competed with each other for some time, until the conflict was resolved in around 1920 when the physiologist G.E. Müller [5] and the physicist Edwin Schrödinger [6] developed the *Zone Theory* to show that the previous two theories were not really incompatible. According to the zone theory, trichromatic separation of the type proposed by Young-Helmholtz occurs initially in one zone, followed by the opponent colour process of the Hering type in another zone. The zone theory postulates three stages of processing:

1. An initial photochemical stage.
2. An intermediate chemical stage.
3. A final stage corresponding to the excitation of the fibres of the optic nerve.

Both Hering's opponent process theory of colour and Müller's zone theory were entirely qualitative in their formulation. This resulted in prolonging the dominance of the trichromatic theory as being the only one that was backed up by quantitative data, in particular, by those from the Colour-Matching Functions (CMF) proposed by the CIE in 1931.

It was not until 1949 that Judd [7], on the basis of the ideas outlined by Müller, put forward an empirically verifiable quantitative formulation reflecting the initial ideas of the zone theory. In this formulation, Judd used the colour matching functions for normal trichromats as well as those for deuteranopes and protanopes. He also took into account the achromatic stimuli perceived by the different types of dichromats, and the spectral location of the stimulus that generates the single yellow. The mathematical validity of Judd's formulation of the zone theory of Müller is unquestionable, but it is far from providing a physiological correspondence for each of its terms [8].

Three types of cones were postulated, each containing a different type of photopigment with its own absorption spectrum. The spectral response functions of each cone can be expressed as linear combinations of the CIE's 1931 colour matching functions for trichromat observers:

$$\begin{aligned} \bar{p}_1(\lambda) &= 3.1956\cdot\bar{x}(\lambda)+2.4478\cdot\bar{y}(\lambda)-0.6434\cdot\bar{z}(\lambda) \\ \bar{p}_2(\lambda) &= -2.5455\cdot\bar{x}(\lambda)+7.0492\cdot\bar{y}(\lambda)+0.4963\cdot\bar{z}(\lambda) \\ \bar{p}_3(\lambda) &= \qquad\qquad\qquad\qquad\qquad\qquad 5.0000\cdot\bar{z}(\lambda) \end{aligned} \tag{1}$$

where $p_1(\lambda)$, $p_2(\lambda)$, $p_3(\lambda)$ are the spectral response functions of the three types of cone.

In the second stage of zone theory, the responses of the cones are combined to give a signal that opposes a yellowish red stimulus yR to a bluish green stimulus bG:

$$\alpha_1(\lambda)=\bar{p}_1(\lambda)-\bar{p}_2(\lambda) \tag{2}$$

A greenish yellow stimulus gY is also opposed to a reddish blue stimulus rB:

$$\alpha_2(\lambda)=0.0151\bar{p}_1(\lambda)-0.3849\bar{p}_2(\lambda)-0.4000\bar{p}_3(\lambda) \tag{3}$$

Finally, Judd postulated six neural signals carrying the sensations of white, black, red, green, yellow, and blue. The signals that provide chromatic sensations are generated through two opponent processes:

$$\begin{aligned} \beta_1(\lambda) &= \alpha_1(\lambda)-0.6265\alpha_2(\lambda) \\ \beta_2(\lambda) &= \alpha_2(\lambda)+0.1622\alpha_1(\lambda) \end{aligned} \tag{4}$$

where β_1 is a red-green type signal, and β_2 is a blue-yellow type signal.

The signal which gives the achromatic sensation is obtained primarily through the signals emerging from the first process level together with minor contributions of signals from the second process level:

$$\beta_3(\lambda) = 0.0075\overline{p}_1(\lambda) + 0.1912\overline{p}_2(\lambda) + \\ 0.0013\overline{p}_3(\lambda) + 0.0810\alpha_1(\lambda) + 0.0024\alpha_2(\lambda) \tag{5}$$

Similarly, before the physiological confirmation of the existence of opponent processes, in 1955 Hurvich & Jameson [9] provided Hering's theory of opponent processes with the quantitative basis that allowed it to be directly compared with the mixture function supported trichromatic theory. In Hurvich & Jameson's initial formulation of the opponent process theory, the chromatic response functions represent the differential effect of light on four substances B, G, Y, and R, whose spectral sensitivities are expressed as linear combinations of the mixture functions.

By assumption, the chromatic and achromatic response curves can be derived from these sensitivity curves, and expressed as linear combinations of the standard observer colour matching functions [8]:

$$\begin{aligned} y(\lambda) - b(\lambda) &= k_1\left[-0.0039\overline{x}_\lambda + 0.3998\overline{y}_\lambda - 0.3999\overline{z}_\lambda\right] \\ r(\lambda) - g(\lambda) &= k_2\left[1.0065\overline{x}_\lambda - 1.0006\overline{y}_\lambda - 0.0051\overline{z}_\lambda\right] \\ w(\lambda) - bk(\lambda) &= (k_3 - k_4)\left[0.0078\overline{x}_\lambda + 40.0042\overline{y}_\lambda + 0.0018\overline{z}_\lambda\right] \end{aligned} \tag{6}$$

To corroborate this theory, it was necessary to determine the spectral sensitivity of the human visual system. The response of a linear system to any stimulus can be determined if one knows its response to spectral stimuli of constant energy, or if one determines the energy of spectral stimuli that give rise to the same response [10]. The response to constant energy spectral stimuli is a function of the wavelength which is known as the spectral sensitivity. The inverse of the energy of spectral stimuli that give rise to the same response is also a function of wavelength and is known as the action-spectrum. When the system is linear, the spectral sensitivity and the action-spectrum are proportional, and both curves carry the same information. In the particular case of human vision, since one wishes to characterize the response without damaging the system, it is not possible to measure the spectral sensitivity of its components directly. Instead one opts for characterizing by means of the action-spectrum of the light-sensitive elements of the human retina – the cones and rods – obtaining their fundamental response curve.

Because the laws of colorimetry are a reflection of the physiological processes underlying colour matching, the properties on which colorimetry is based such as trivariance and linearity can be attributed to these processes. Thus, trivariance or trichromacy implies the existence of three independent physiological mechanisms that have different sensitivities in different parts of the visual spectrum, and linearity implies that each of these mechanisms performs a linear operation on the spectral distribution of luminous stimuli [11]. These three mechanisms do not necessarily have to be three kinds of receptors. It is only necessary that they are three independent physiological responses, each sensitive to a different part of the spectrum. Nonetheless, a three-receptor based theory has been widely accepted since it seems the most straightforward way to explain trichromatism.

Physiological knowledge of the human visual system has confirmed the existence of three types of cones responsible for colour vision. The spectral sensitivity of these three types of photoreceptor can be derived from colour matching data. This is of great importance both theoretically and practically. The fact that makes it possible to derive the fundamentals from colour matching data is the linearity of the matching process. This linearity is a consequence of how light interacts with the pigment in the photoreceptor. While the processes that occur during the interaction of light quanta with the photosensitive pigments are complicated to describe, the final outcome is fairly easy to explain through the principle of univariance established by Rushton [12] in 1972 for rhodopsin, the photopigment of the rods, but which can be extrapolated to the cones:

> "Any pair of light quanta that are equally absorbed by the photopigments will be equally perceived through the receptors."

Let S(λ) be the fraction of incident quanta of wavelength λ which are captured effectively in the photoreceptor, thus defining the photoreceptor's spectral sensitivity function. If Q(λ) is the spectral distribution of quanta of a luminous stimulus Q, the quantity

$$S = \int S(\lambda)Q(\lambda)d\lambda \tag{7}$$

is the total effective stimulus. Given three classes of receptors with three spectral sensitivity functions $S_1(\lambda)$, $S_2(\lambda)$, $S_3(\lambda)$, the three quantities

$$\int S_1(\lambda)Q(\lambda)d\lambda \quad \int S_2(\lambda)Q(\lambda)d\lambda \quad \int S_3(\lambda)Q(\lambda)d\lambda \tag{8}$$

are the respective physiological tristimulus values produced by stimulus Q in these three photoreceptors.

It is trivial to demonstrate that the physiological tristimulus values are formally equivalent to the colorimetric tristimulus values: if two lights P and Q cause the same physiological tristimulus then they are indistinguishable.

Suppose we are measuring the colour matching functions of a normal trichromat observer, and we have chosen as the R, G, and B primaries three monochromatic lights of equal quantum flux. When the viewer is presented with a stimulus consisting of one unit of primary R, this stimulus will produce an effective capture of S_{1R}, S_{2R}, S_{3R} quanta in the three receptors. If instead of one unit of flux of primary R, we present the observer with $\bar{r}$ units, the corresponding tristimulus will be $\bar{r}S_{1R}$, $\bar{r}S_{2R}$, $\bar{r}S_{3R}$. The case is similar for the G and B primaries. The corresponding physiological tristimuli can be written as:

$$\begin{matrix} \bar{r}S_{1R} & \bar{r}S_{2R} & \bar{r}S_{3R} \\ \bar{g}S_{1G} & \bar{g}S_{2G} & \bar{g}S_{3G} \\ \bar{b}S_{1B} & \bar{b}S_{2B} & \bar{b}S_{3B} \end{matrix} \tag{9}$$

Since the principle of univariance is satisfied, the mixture of quantities $\bar{r}$, $\bar{g}$, $\bar{b}$ of the primaries R, G, and B will be equivalent in receptor S_1 to a single stimulus of value:

$$S_1 = \bar{r}S_{1R} + \bar{g}S_{1G} + \bar{b}S_{1B} \tag{10}$$

and analogously in the other two receptors.

If we ask an observer to match monochromatic stimuli u(λ) of constant quantum flux based on these primaries, we shall be able to express the result by means of the expression:

$$u(\lambda) = \bar{r}(\lambda)R + \bar{g}(\lambda)G + \bar{b}(\lambda)B \tag{11}$$

where $\bar{r}(\lambda), \bar{g}(\lambda), \bar{b}(\lambda)$ will be the colour matching functions of this observer.

Since each monochromatic stimulus u(λ) will produce an effective stimulus $S_1(\lambda)$ in photoreceptor S_1, the equation of the match of the corresponding physiological tristimuli over the entire spectrum can be written as:

$$S_1(\lambda) = S_{1R}\bar{r}(\lambda) + S_{1G}\bar{g}(\lambda) + S_{1B}\bar{b}(\lambda) \tag{12}$$

Because $S_1(\lambda)$ represents the spectral sensitivity function of receptor S_1, the above equation states that the fundamental $S_1(\lambda)$ is a linear combination of the colour matching functions $r(\lambda)$, $g(\lambda)$, and $b(\lambda)$, with the argument being generalizable to receptors S_2 and S_3:

$$\begin{pmatrix} S_1(\lambda) \\ S_2(\lambda) \\ S_3(\lambda) \end{pmatrix} = \begin{pmatrix} S_{1R} & S_{1G} & S_{1B} \\ S_{2R} & S_{2G} & S_{2B} \\ S_{3R} & S_{3G} & S_{3B} \end{pmatrix} \cdot \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} \tag{13}$$

The above matrix equation states that the fundamentals of colour vision are linear combinations of the CMFs [11]. If one could determine the matrix $S_{1R}...S_{3B}$, the fundamentals of any observer could be determined by means of his or her colorimetric matches.

One method of determining the coefficients of this matrix, used by most scientists because of its simplicity, is to make use of the fact that there exist observers called dichromats. These do not require the mixture of three primary stimuli to match foveally any chromatic stimulus, but just two. Such observers seem to have a reduced form of normal colour vision.

In the eyes of a normal observer, the dichromat confuses a series of colours. Maxwell [13] in 1857 was the first to note that the colours which each type of dichromat confuses (which really are the metameric colours for that type of dichromat) lie on a straight line when their chromaticity coordinates are plotted on a trichromatic chromaticity diagram. Maxwell concluded from this observation that these dichromats had a reduced form of a normal observer's colour perception.

For each of the three types of dichromats that exist – protanope, deuteranope, and tritanope – two colour matching functions are sufficient to specify their colour matching. Moreover, the dichromat matching functions must be linear combinations of the colour matching functions of normal observers. For example, in the (X,Y,Z) system, the two colour matching functions of the protanope observer can be written as follows [14]:

$$\begin{aligned} p_1(\lambda) &= p_{11}\bar{x}(\lambda) + p_{12}\bar{y}(\lambda) + p_{13}\bar{z}(\lambda) \\ p_2(\lambda) &= p_{21}\bar{x}(\lambda) + p_{22}\bar{y}(\lambda) + p_{23}\bar{z}(\lambda) \end{aligned} \tag{14}$$

In terms of the tristimulus values for normal observers X, Y, Z, the dichromat bistimulus values are defined by the following two planes:

$$\begin{aligned} P_1 &= p_{11}X + p_{12}Y + p_{13}Z \\ P_2 &= p_{21}X + p_{22}Y + p_{23}Z \end{aligned} \tag{15}$$

so that all colours which generate the same bistimuli must satisfy the above equation. Furthermore, any other colour with bistimuli $P_1'=kP_1$, $P_2'=kP_2$, will have the same chromaticity coordinates as the initial stimulus.

In normal trichromatic space, the intersections of the plane X+Y+Z=1 representing the chromaticity diagram with the planes of constant dichromat chromaticity coordinates are straight lines called lines of confusion. These lines meet in the point of confusion (X_{pc}, Y_{pc}, Z_{pc}), and satisfy the condition:

$$\begin{aligned} X_{pc} + Y_{pc} + Z_{pc} &= 1 \\ p_{11}X_{pc} + p_{12}Y_{pc} + p_{13}Z_{pc} &= 0 \\ p_{21}X_{pc} + p_{22}Y_{pc} + p_{23}Z_{pc} &= 0 \end{aligned} \tag{16}$$

It can be shown that the primaries (L,M,S) used to construct a photoreceptor based colour space are the points of confusion of the three types of dichromat – protanopes, deuteranopes, and tritanopes – under the assumption that dichromatism is based on the absence one of the three types of receptor cones. This is known as the *König hypothesis [*15].

If the König hypothesis is accepted, the expression for the normal colour vision fundamentals can be derived from the colour matching functions of normal observers and the situation of the three points of confusion $P\ (X_{cp}, Y_{cp}, Z_{cp})$, $D\ (X_{cd}, Y_{cd}, Z_{cd})$, and $T\ (X_{ct}, Y_{ct}, Z_{ct})$ in the trichromatic space (X,Y,Z).

To derive the above transformation, one considers the dichromat matching functions to be linear combinations of the trichromat colour matching functions. For example, for a protanope:

$$\begin{pmatrix} \bar{p}_1(\lambda) \\ \bar{p}_2(\lambda) \end{pmatrix} = \begin{pmatrix} p_{11} & p_{12} & p_{13} \\ p_{21} & p_{22} & p_{23} \end{pmatrix} \cdot \begin{pmatrix} \bar{x}(\lambda) \\ \bar{y}(\lambda) \\ \bar{z}(\lambda) \end{pmatrix} \tag{17}$$

The normal observer colour matching functions can be written as linear combinations of the fundamentals:

$$\begin{pmatrix} \bar{x}(\lambda) \\ \bar{y}(\lambda) \\ \bar{z}(\lambda) \end{pmatrix} = \begin{pmatrix} n_{11} & n_{12} & n_{13} \\ n_{21} & n_{22} & n_{23} \\ n_{31} & n_{32} & n_{33} \end{pmatrix} \cdot \begin{pmatrix} S_1(\lambda) \\ S_2(\lambda) \\ S_3(\lambda) \end{pmatrix} \tag{18}$$

Substituting this expression into the previous one, one has the dichromat colour matching functions expressed in terms of the fundamentals:

$$\begin{aligned} \bar{p}_1(\lambda) &= (p_{11}n_{11} + p_{12}n_{21} + p_{13}n_{31})S_1(\lambda) + \ldots \\ \bar{p}_2(\lambda) &= (p_{21}n_{11} + p_{22}n_{21} + p_{23}n_{31})S_1(\lambda) + \ldots \end{aligned} \tag{19}$$

Now from the König hypothesis, if the fundamental absent in the protanope is S$_1$, the corresponding coefficients in the above equation must be zero:

$$\begin{aligned} p_{11}n_{11} + p_{12}n_{21} + p_{13}n_{31} &= 0 \\ p_{21}n_{11} + p_{22}n_{21} + p_{23}n_{31} &= 0 \end{aligned} \tag{20}$$

The above condition is satisfied by taking the coefficients $n_{11} = C_1 Xc_P$, $n_{21} = C_1 Yc_P$, and $n_{31} = C_1 Zc_P$, where C_1 is an arbitrary constant. The argument is analogous for deuteranopes and tritanopes.

This model of reduced colour vision for the case of dichromats can be used for the detection and classification of colour vision deficiencies by isomeric mixing [16] instead of the traditional metameric matching employed in anomaloscopes.

Finally, the equation that defines the basic transformation between the tristimulus XYZ values and the fundamentals with the current LMS notation is as follows:

$$\begin{pmatrix} X \\ Y \\ Z \end{pmatrix} = \begin{pmatrix} X_{cp} & X_{cd} & X_{ct} \\ Y_{cp} & Y_{cd} & Y_{ct} \\ Z_{cp} & Z_{cd} & Z_{ct} \end{pmatrix} \cdot \begin{pmatrix} L \\ M \\ S \end{pmatrix} \tag{21}$$

where (X_{cp} , Y_{cp} , Z_{cp}) , (X_{cd} , Y_{cd} , Z_{cd}) , (X_{ct} , Y_{ct} , Z_{ct}) are the components of the points of confusion of protanopes, deuteranopes, and tritanopes.

If the chromaticity coordinates of these points are known, and given that the coordinates and components are proportional, the equation can be written as:

$$\begin{pmatrix} X \\ Y \\ Z \end{pmatrix} = \begin{pmatrix} x_{cp} & x_{cd} & x_{ct} \\ y_{cp} & y_{cd} & y_{ct} \\ z_{cp} & z_{cd} & z_{ct} \end{pmatrix} \cdot \begin{pmatrix} k_{cp} & 0 & 0 \\ 0 & k_{cd} & 0 \\ 0 & 0 & k_{ct} \end{pmatrix} \cdot \begin{pmatrix} L \\ M \\ S \end{pmatrix} \tag{22}$$

where k_{cp} , k_{cd} , k_{ct} are arbitrary scaling constants.

If one wants to express the values of the responses of the cones to a stimulus expressed in terms of its tristimulus values, one has the following expression:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} k'_{cp} & 0 & 0 \\ 0 & k'_{cd} & 0 \\ 0 & 0 & k'_{ct} \end{pmatrix} \cdot \begin{pmatrix} x_{cp} & x_{cd} & x_{ct} \\ y_{cp} & y_{cd} & y_{ct} \\ z_{cp} & z_{cd} & z_{ct} \end{pmatrix}^{-1} \cdot \begin{pmatrix} X \\ Y \\ Z \end{pmatrix} \qquad (23)$$

where the coefficients k'_{cp}, k'_{cd}, k'_{ct} are the inverses of the coefficients k_{cp}, k_{cd}, k_{ct}.

Once the coordinates of the points of confusion and the scaling factors have been chosen, the correspondence between the tristimulus values and the LMS values is established.

If the above equation is particularized to the case of an equal-energy spectrum, taking the XYZ tristimulus values to be the CMFs $\bar{x}_\lambda$, $\bar{y}_\lambda$, $\bar{z}_\lambda$, one obtains:

$$\begin{pmatrix} S_L(\lambda) \\ S_M(\lambda) \\ S_S(\lambda) \end{pmatrix} = \begin{pmatrix} k'_{cp} & 0 & 0 \\ 0 & k'_{cd} & 0 \\ 0 & 0 & k'_{ct} \end{pmatrix} \cdot \begin{pmatrix} x_{cp} & x_{cd} & x_{ct} \\ y_{cp} & y_{cd} & y_{ct} \\ z_{cp} & z_{cd} & z_{ct} \end{pmatrix}^{-1} \cdot \begin{pmatrix} \bar{x}(\lambda) \\ \bar{y}(\lambda) \\ \bar{z}(\lambda) \end{pmatrix} \qquad (24)$$

$S_L(\lambda)$, $S_M(\lambda)$, $S_S(\lambda)$ are the spectral sensitivities of the L, M, and S mechanisms, respectively. These values are the König-type fundamentals.

2. COMPARATIVE STUDY OF THE FUNDAMENTALS

Towards the end of the twentieth century, many authors derived their own cone fundamental response curves. In this section, we shall review the most important, trying to highlight the distinguishing particularities of each, and ending with a comparative study.

We shall begin chronologically in 1971, when Vos & Walraven [17] derived their fundamentals by equating the luminance Y to the sum of the output signals L, M, and S. I.e., the sum of the spectral sensitivities of the fundamentals is equal to the spectral sensitivity curve V_λ:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} 0.15516 & 0.54308 & -0.03702 \\ -0.15516 & 0.45692 & 0.02969 \\ 0 & 0 & 0.00732 \end{pmatrix} \begin{pmatrix} X' \\ Y' \\ Z' \end{pmatrix} \qquad (25)$$

where X', Y', Z' are the tristimulus values obtained using the CMFs modified by Judd in 1951 [18].

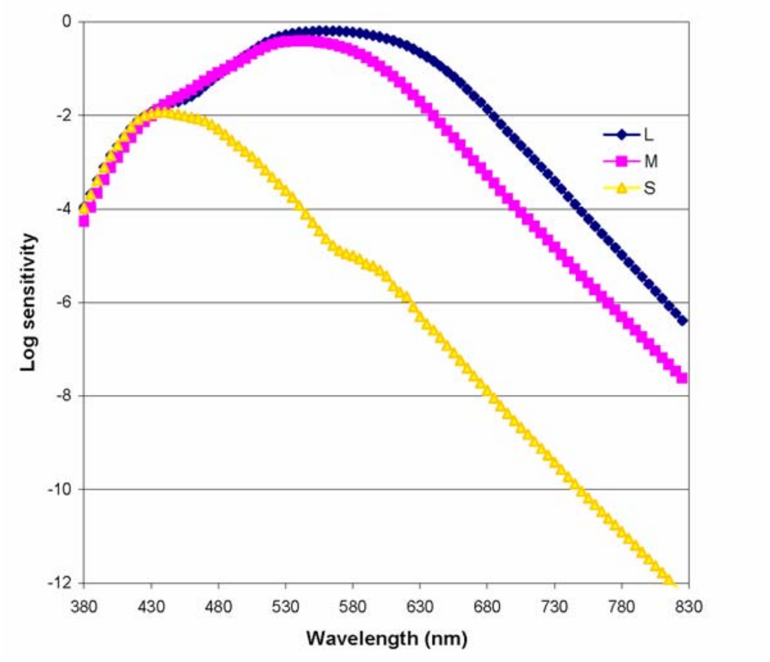


Figure 1. Vos-Walraven fundamentals on a logarithmic scale.

In 1975, Smith & Pokorny [19] imposed the boundary condition Y = L + M on their fundamentals, i.e., $V_\lambda = S_L(\lambda) + S_M(\lambda)$, leaving the S cone scaling condition open. The scaling condition related to the luminance implies that:

$$SL(570)-2SM(570)=0 \tag{26}$$

From this condition, the Smith-Pokorny fundamentals are given by the following general expression:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} 0.15514 & 0.54312 & -0.03286 \\ -0.15514 & 0.45684 & 0.03286 \\ 0 & 0 & a_{33} \end{pmatrix} \begin{pmatrix} X' \\ Y' \\ Z' \end{pmatrix} \tag{27}$$

The S cone scaling condition may be taken to obey different criteria, so that which choice is made has led to different fundamentals. For instance, in 1982, Wyszecki & Stiles [14] derived their own fundamentals taking those of Smith-Pokorny and applying the scaling condition:

$$S_L(475.5)+S_M(475.5)= 16\ S_S(475.5) \tag{28}$$

This scaling condition is not arbitrary. It is based on the invariant blue and yellow hues observed at 475.5 and 570 nm respectively by Walraven in 1961 [20]. Applying this condition yields the following fundamentals:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} 0.15514 & 0.54312 & -0.03286 \\ -0.15514 & 0.45684 & 0.03286 \\ 0 & 0 & 0.00801 \end{pmatrix} \begin{pmatrix} X' \\ Y' \\ Z' \end{pmatrix} \tag{29}$$

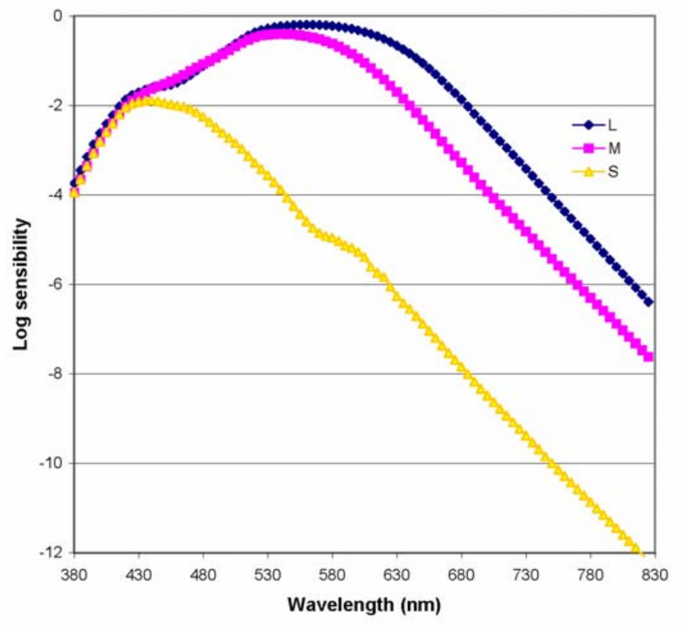


Figure 2. Wyszecki-Stiles fundamentals (1982).

Similarly, in 1979 MacLeod & Boynton [21] derived their fundamentals by applying the following S cone scaling condition:

$$S_L(400)+S_M(400)= S_S(400) \tag{30}$$

resulting in the fundamentals

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} 0.15514 & 0.54312 & -0.03286 \\ -0.15514 & 0.45684 & 0.03286 \\ 0 & 0 & 0.01608 \end{pmatrix} \begin{pmatrix} X' \\ Y' \\ Z' \end{pmatrix} \tag{31}$$

Analogously, the scaling condition could have been taken to be:

$$S_L(498)+S_M(498)= S_S(498) \tag{32}$$

yielding the fundamentals associated with the Boynton space:

$$\begin{pmatrix} L \\ M \\ S \end{pmatrix} = \begin{pmatrix} 0.15514 & 0.54312 & -0.03286 \\ -0.15514 & 0.45684 & 0.03286 \\ 0 & 0 & 1.0066 \end{pmatrix} \begin{pmatrix} X' \\ Y' \\ Z' \end{pmatrix} \tag{33}$$

In 1990, Estevez, Vos & Walraven [22] derived their cone fundamentals from the colour matching functions of Stiles & Burch of 1955 [23], using the following expression:

$$\begin{pmatrix} S_L(\lambda) \\ S_M(\lambda) \\ S_S(\lambda) \end{pmatrix} = \begin{pmatrix} 0.3551190 & 1.21996 & 0.0720867 \\ 0.0680884 & 1.76564 & 0.144688 \\ 0.00118981 & 0.0345747 & 1.55540 \end{pmatrix} \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} \tag{34}$$

These functions are given in normalized energy units according to the ratio L:M:S = 0.68:0.34:0.02.

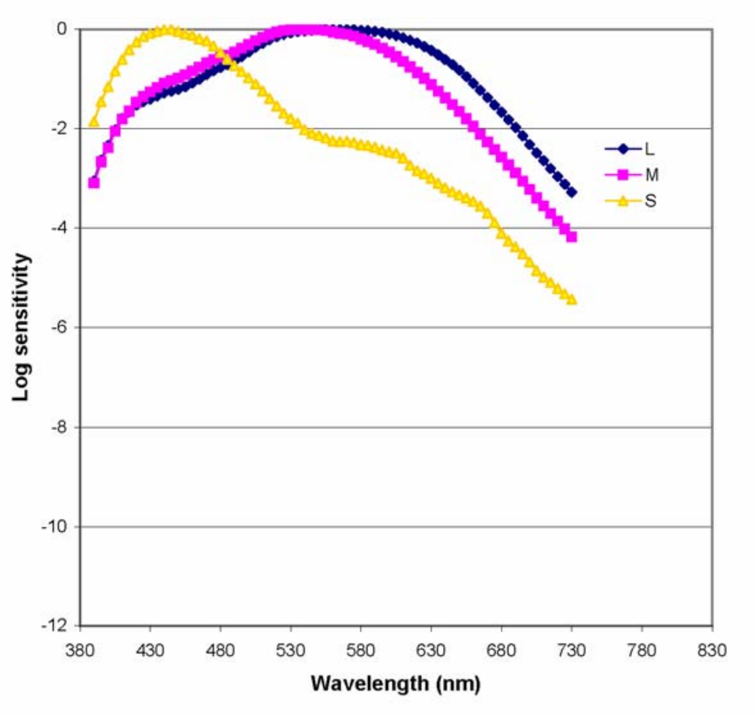


Figure 3. The Estevez-Vos-Walraven fundamentals.

Similarly, in 1993 Stockman, MacLeod, & Johnson [24] developed their 2° cone fundamentals on the basis of the colour matching functions of Stiles & Burch of 1955 for fields of 2° [23]:

$$\begin{pmatrix} S_L(\lambda) \\ S_M(\lambda) \\ S_S(\lambda) \end{pmatrix} = \begin{pmatrix} 0.214808 & 0.751035 & 0.045156 \\ 0.022882 & 0.940534 & 0.076827 \\ 0 & 0.016500 & 0.999989 \end{pmatrix} \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} \tag{35}$$

Summing the functions $S_L(\lambda)$ and $S_M(\lambda)$ with respective weights of 0.68273 and 0.53235 gives a good approximation to the modified CIE spectral sensitivity curve $V_M(\lambda)$ [25]. The above expression was scaled so that, in energy units, the maximum spectral sensitivity of each cone is unity.

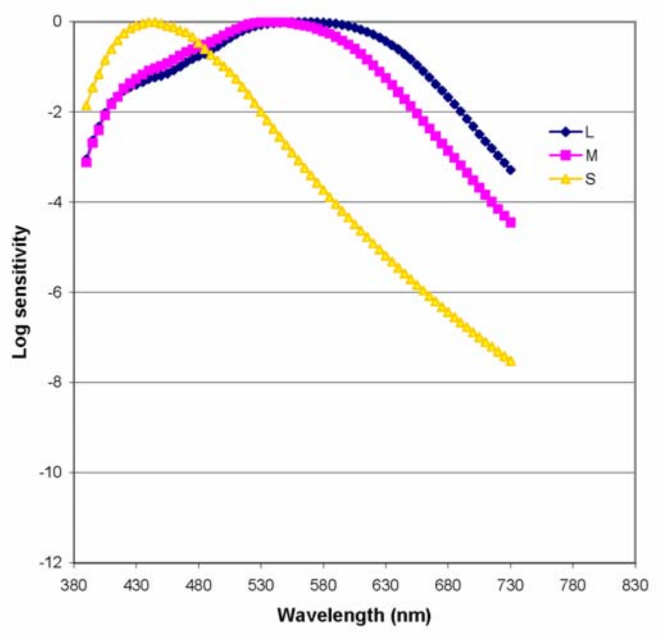


Figure 4. The Stockman-MacLeod-Johnson fundamentals.

Finally, in 2000 Stockman & Sharpe [26] derived their cone fundamentals on the basis of the colour matching functions of Stiles & Burch of 1955 for fields of 10° [23] adjusted to 2°.

The final expression for their fundamentals is the following:

$$\begin{pmatrix} S_L(\lambda) \\ S_M(\lambda) \\ S_S(\lambda) \end{pmatrix} = \begin{pmatrix} 2.846201 & 11.092490 & 1 \\ 0.168926 & 8.265895 & 1 \\ 0 & 0.010600 & 1 \end{pmatrix} \begin{pmatrix} \bar{r}(\lambda) \\ \bar{g}(\lambda) \\ \bar{b}(\lambda) \end{pmatrix} \tag{36}$$

This expression again was scaled so that the maximum spectral sensitivity of each cone is unity.

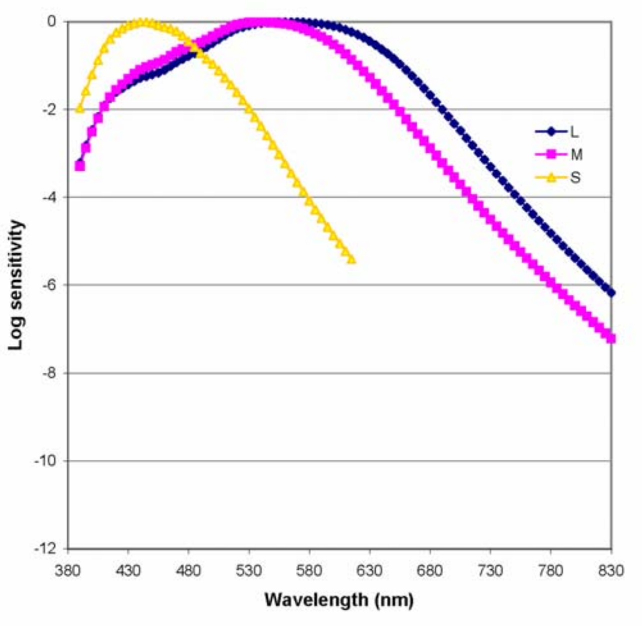


Figure 5. The Stockman-Sharpe fundamentals.

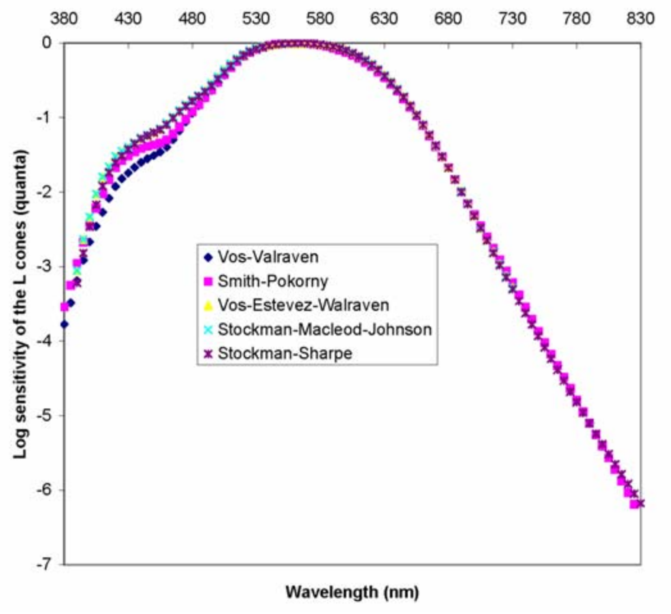


Figure 6. Comparison of rescaled L fundamental curves.

The diversity of fundamentals described above may give rise to doubt about which triad of fundamental curves is the most appropriate, and how to know which offers the greatest guarantee in a laboratory implementation. Doubt could also arise as to the population they are able to represent according to which population formed the subjects of the psychophysical experiments on which they were constructed. So as to allow a more reliable evaluation of the goodness of the different fundamentals, each type of fundamental was compared separately, rescaling them so that they all have their maximum logarithm at zero.

Figure 6, for example, shows the L fundamentals proposed by the different authors, re-scaled to all have their maxima at zero.

One appreciates a major degree of overlap among all the authors' fundamental response curves. Only for short wavelengths are there small variations.

Figure 7 shows the M fundamentals proposed by the different authors, re-scaled to all have their maxima at zero.

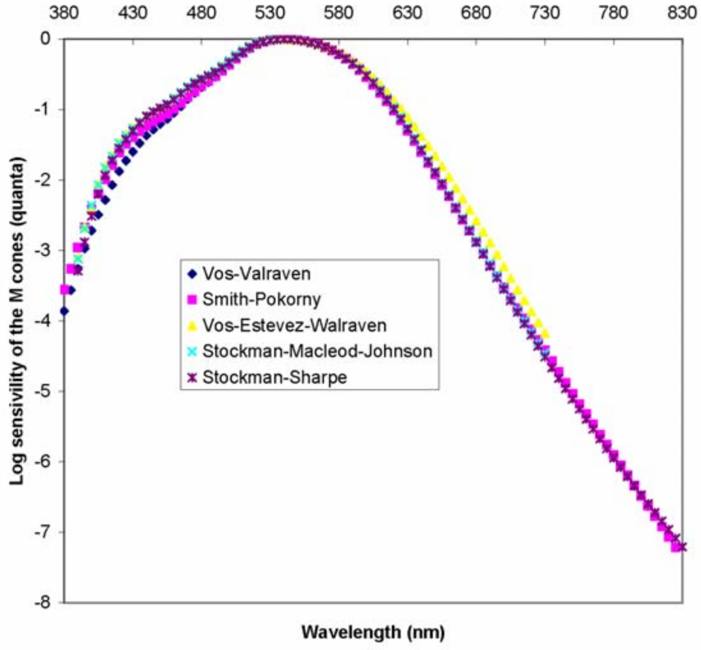


Figure 7. Comparison of the rescaled M fundamental curves.

Again one appreciates an almost total overlap among the fundamental response curves proposed by the different authors.

Figure 8 shows the S fundamentals proposed by the different authors, re-scaled to all have their maxima at zero.

One observes that for short wavelengths there is great agreement among the curves of the different authors, but that there are major variations from 530 nm onwards. However, given that for these longer wavelengths the response of the S cones is much smaller (two logarithmic units), these differences have relatively little influence.

All this might lead one to believe that the question of characterizing the human visual system by obtaining the fundamental response curves has now been solved, and that given the small differences between the fundamentals proposed by the various authors, these fundamentals represent very reliably most of the population. Nonetheless, one must not overlook the fact that most fundamentals were constructed on the basis of one of only two data sets – the colour matching functions modified by Judd in 1951 [18] or those defined by Stiles & Burch in 1955 [23]. This must unavoidably contribute to a lesser divergence of data.

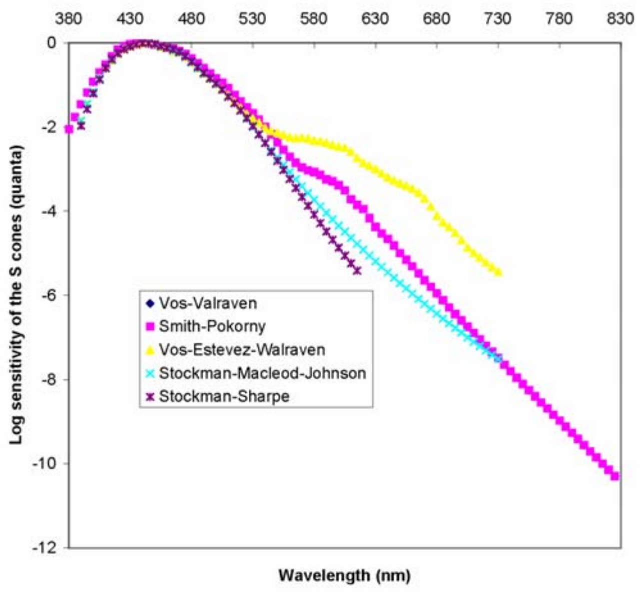


Figure 8. Comparison of the rescaled S fundamental curves.

The question that remains open is: Do these fundamentals represent the colour perception of the entire "normal" population. Or, in other words: To what extent do each of us perceive colour differently from other human beings?

3. DIFFERENCES BETWEEN MEN AND WOMEN

There have been many experiments that have shown differences in colour perception between individuals classified as normal observers. These differences in sensitivity to chromatic stimuli are due to variations that occur in several physiological factors such as the optical density of intraocular media [27] the long (L-) to medium (M-) wavelength sensitive cone photopigment [28], the cone ratio [29], etc.

Genetic research has shown that colour vision is a sex-linked trait, because the genes encoding the L- and M-cone photopigments are located in small arrays on the q arm of the X-chromosome [30]. Genotypes involving more than three photopigment opsin variants are common [31] and these commonly occurring genetic polymorphisms produce variations in the spectral tuning of the expressed photopigments due to amino acid substitutions at a specific location on the opsin gene [32].

A stochastic event determines which type of photopigment gene is actually expressed [33-34], and there is the possibility of an individual expressing more that three retinal photopigments [35-36]. The complexities of the hybrids and anomalies that are involved will not be dealt with here. Due to the intricacies of gene expression mechanisms, people who possess the genetic code for the three usual photopigments may or may not express them all in their retinas. Even in the simplest case of observers who have only three genes encoding the L-, M- and S- photopigments, there are two spectral subtypes of L-cone pigments that are classified as normal. They are generated by an amino acid dimorphism at position 180 of the

X-chromosome gene that encodes this type of photopigment. Serine *vs* alanine at this position makes a difference of 4 to 7 nm in the spectral peak of the encoded photopigment [37] (Sharpe et al. [38] give a detailed review of this topic in particular, and of the genetics of colour vision in general.)

In the case of men, who have only a single copy of the X chromosome, normally only one type of L cone and one type of M cone are expressed in the retina. Of the two types of L-pigment accepted as normal, approximately half of all men have the L_A type (43.7%) expressed in their retina and the other half have the L_S type (56.3%) [38].

In the case of women, who have two copies of the X chromosome, in early stages of embryo development each cell inactivates at random one of the copies [39] so that approximately half of the embryo's cells inactivate the copy from the mother and the other half the copy from the father. The result is that there are three population subtypes of women: about half of all women may express both L-pigments in their retina (heterozygotic), and the other half is split between expressing just one or the other L-pigment (homozygotic) [40].

Previous research proposed that such genetic heterozygosity may have perceptual consequences in individuals who actually express all four types of photopigment genes, because each gene type produces different retinal photopigment sensitivities, in effect yielding a four-cone-class retinal phenotype and a possible tetrachromacy. [41-48] However, such psychophysical variations are still a matter of dispute because there have been many studies that have failed to find significant differences between the two population groups [49-50].

Two forms of tetrachromacy should be distinguishable according to the level to which the four signals remain independent. There is first the possibility that there are four types of cone photopigment but only three independent post-receptoral channels. This has been referred to as weak tetrachromacy by Jordan and Mollon [36]. The second possibility is that the four cones in the retina have access at the level of the cortex to four independent transformations of these signals. Jordan and Mollon refer to this possibility as strong tetrachromacy.

With the weak tetrachromacy hypothesis, if 50% of women who have both pigments behave like the average of the women who have only one photopigment, L_A or L_S, the average of all women must match the average of all men. But if this is not so, the differences in the expression of retinal L cones between men and women could give rise to sex differences in the perception of colour, so that they would have to be considered as different population groups. Testing the validity of this hypothesis was also an objective of this chapter.

When a trichromat observer is asked to judge the validity of a colour match in which two juxtaposed chromatic hemifields are presented, the observer evaluates unconsciously the equality of the colour attributes of the two hemifields – luminosity, hue, and saturation. If the colour stimuli that are presented are not subject to temporal or inductive effects that influence the two hemifields differently, the perceived attributes are directly related to the effective capture of photons by the photopigments of the three types of cone – L, M, and S – that are found in the retina of a trichromat.

For each of these three types of cone, this effective capture can be expressed in terms of the visible radiation reaching the eye, and of the response of each type of cone. For example, for the L cones:

$$L = \int_{vis} P_{\lambda} \bar{l}_{\lambda} d\lambda \tag{37}$$

where P_{λ} is the spectral radiance at the observer's eye, and $\bar{l}_{\lambda}$ is the fundamental L-cone response curve. The calculations for the M and S cones are analogous.

If the observer is presented with a spectral yellow stimulus matched by the mixture in appropriate proportions of a spectral red and a spectral green stimulus, most information on the correct matching of the two halves of the visual field is carried by the L and M cones. Because the spectral stimuli used have the same narrow bandwidth, we can express the colour matching of the two hemifields in terms of the colorimetric equations for the L and M cones:

$$\begin{aligned} \bar{l}_r P_r + \bar{l}_g P_g &= \bar{l}_y P_y \\ \bar{m}_r P_r + \bar{m}_g P_g &= \bar{m}_y P_y \end{aligned} \tag{38}$$

where i=y,r,g refer to the stimuli, $\bar{l}_i$ and $\bar{m}_i$ are the L and M cone response fundamental curve values for the quasi-monochromatic stimuli red, green, and yellow, and P_i are the radiances of these three stimuli.

For a male observer, whose retina has cones with only one type of L-pigment, one can express the previous equation in the following terms:

$$\begin{aligned} \bar{l}_{a\,r} P_r + \bar{l}_{a\,g} P_g &= \bar{l}_{a\,y} P_y \\ \bar{m}_r P_r + \bar{m}_g P_g &= \bar{m}_y P_y \end{aligned} \tag{39a}$$

$$\begin{aligned} \bar{l}_{s\,r} P_r + \bar{l}_{s\,g} P_g &= \bar{l}_{s\,y} P_y \\ \bar{m}_r P_r + \bar{m}_g P_g &= \bar{m}_y P_y \end{aligned} \tag{39b}$$

depending on whether the allele is alanine (39a) or serine (39b). From Eqs. (39a) and (39b) we can obtain the P_r/P_g and P_y/P_g ratios of the radiances of the red, green, and yellow stimuli used in the matching, which is the experimental parameter usually measured in this type of test.

For a female observer belonging to the 50% of women who can have both types of L photopigments in their retinas in approximately the same proportion, one has (assuming that there is random inactivation of the X chromosome for genes that encode normal photopigments):

$$\begin{aligned} \left(\frac{\bar{l}_a + \bar{l}_s}{2}\right)_r P_r + \left(\frac{\bar{l}_a + \bar{l}_s}{2}\right)_g P_g &= \left(\frac{\bar{l}_a + \bar{l}_s}{2}\right)_y P_y \\ \bar{m}_r P_r + \bar{m}_g P_g &= \bar{m}_y P_y \end{aligned} \tag{40}$$

This expression corresponds to Jordan & Mollon's weak tetrachromacy hypothesis mentioned above. From it, one can obtain the ratio of the radiances in the mixture of red and green spectral stimuli used to match a yellow spectral stimulus by a female observer whose retina has both L-cone photopigments. The question is whether this radiance ratio is equal to the average of the ratios used by a group of male observers 43.7% of whom have LA-type pigment and 56.3% the LS-type pigment.

Knowing the spectral intraocular lens [51] and macular pigment [52] optical densities, the template [26] of the photopigment optical densities for the L and M cones, and taking the usual values [53] for the wavelengths of the maximum photopigment optical densities (λ_{max}) for the L_S, L_A, and M pigments – 563.2 nm, 554.2 nm, and 530.8 nm, respectively – one can estimate the cone response fundamental curve values for Eqs. (39) and (40). The P_r/P_g ratio can then be derived in both cases. The estimated difference between the average man and the average woman using this procedure is about 4.5%. The initial hypothesis thus remains open.

One way to confirm or reject this initial hypothesis is to determine experimentally the radiance ratio used by the average male observer and by the average female observer. Other workers have studied how variations corresponding to the presence of different types of photopigment in the human retina affect Rayleigh matching. The experimental method used was very similar to standard Rayleigh matching [54]. In this, the observer may adjust the proportion of 670 nm and 545 nm primary lights in the mixture field to match the 589 nm light in the reference field. The observer may also adjust the luminance of the 589 nm field to achieve the exact match. In this present work, we introduced slight modifications that make it advisable not to use the term Rayleigh matching for our procedure. In particular, the observers were allowed to change the luminances of the 546 nm and 671 nm stimuli, but not the 589 nm stimulus which was fixed at 21 cd/m^2. Fixing the luminance of the reference stimulus reduces the number of variables in Eqs. (38) and (39) by converting one of them into a known constant.

A. STIMULUS GENERATING *SYSTEM*

The colour generating system was a new visual colorimeter recently constructed by the authors [55] by recycling an old fluorescence spectrophotometer with two monochromators. An optical system was designed that allows the fusion of two visual stimuli coming from the two monochromators of the spectrofluorimeter. Each of these stimuli has a wavelength and bandwidth control.

B. PSYCHOPHYSICAL *TEST*

The psychophysical test had to be simple and fast enough to present no problems when done by subjects with no prior experience in psychophysical testing. This would allow us to enlarge the size of the observer sample, which is usually small in this type of experiment. With these premises, we opted for metameric matching of a spectral stimulus to a mixture of another two spectral stimuli, presented in a 2° circular field divided vertically into equal halves by a fine separating line (Figure 9).

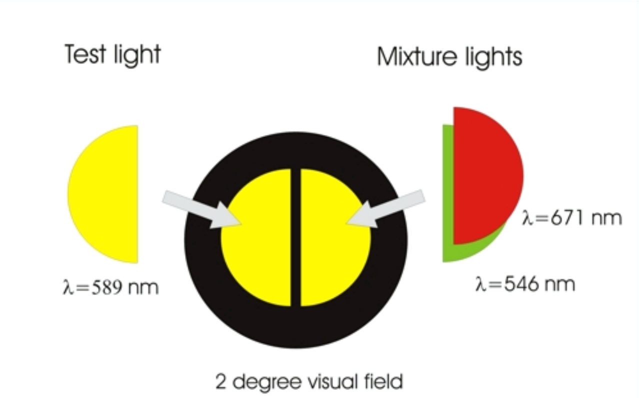


Figure 9. Metameric matching of spectral stimuli.

In the right half of the field, the observer is presented with a yellow stimulus of 589 nm from an external monochromator (H20-VIS, Jobin-Ivon), and in the right half with red and green stimuli of 671 and 546 nm from the two internal holographic diffraction gratings of the visual colorimeter. The bandwidth of the three monochromatic stimuli was 10 nm. The stimuli are presented for more than 30 seconds in each exposure to ensure a stable level of photopigment bleaching. The luminance of the yellow stimulus is kept constant at 21 cd/m^2. The luminance of the stimuli in the right half is regulated independently by adjusting the voltages of the power supplies to each lamp. This was done using the aforementioned digital power supplies and chromatic characterization system. The experiment was carried out in a dark room. Each observer adapted to the darkness for several minutes before beginning to match the stimuli. The stimuli were matched in hue and luminosity using a stepping method in which the observer was asked to express judgements on the relative hue and luminosity of the two halves of the field.

C. SAMPLE

The subjects were chosen randomly from teaching and administration staff and students of the Science Faculty, and from passers-by who were on the university campus. Initially, 65 people – 32 men and 33 women – were selected. Of these, two were rejected on the basis of a prior personal interview – a woman suffering the first stages of cataracts, and a man who had recently received medication that made his participation inadvisable. The remaining 63 were between 18 and 55 years old. The mean age of both populations was very similar – 31.5 years the men, 28.0 years the women (29.7 years for the overall sample), although in this experiment the age was not an important factor since the spectral stimuli used are far from the visible zone which is affected by the preretinal absorption as an individual ages [27].

The observers participated in the test with their vision compensated by eyeglasses or contact lenses when necessary, and having previously passed the Ishihara 38 plates edition and Farnsworth D-15 colour vision tests. The aim of the psychophysical test was simply to study the possible differences between the average male observer and the average female observer, without attempting to identify the various subgroups within the two populations which would have required a larger number of observers.

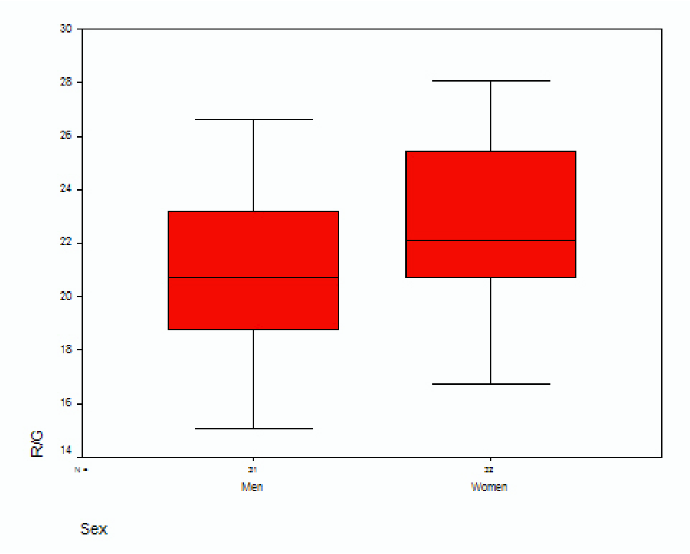


Figure 10. Box plot of the experimental results for the male and the female populations.

The results of the experiment were analyzed using statistical software (SPSS 11.5, SPSS Inc.), with the principal variable being the ratio between the radiance of the red and the green stimuli (R/G) in each observer's match. Figure 10 shows a box plot of the experimental results for the male and the female populations. The mean, the standard deviation, and the standard error of the mean were calculated for the total population and for the two groups (men and women) into which we divided the sample (Table1).

Table 1. R/G ratio (mean and standard error) by groups, and the statistical test results.

		R/G ratio		Anova				Kruskal -Wallis
Groups		*mean*	*std error*		*Sum of sqrs.*	*Mean square*	*Sigma*	*Sigma*
Sex	Men	20.99	0.53	Between grps.	0.038	0.038	0.034	0.049
	Women	22.60	0.54	Within grps.	0.492	0.008		
Total		21.81	0.39	Total	0.529			

° Statistically significant at a confidence level of 95%.

The mean ratios $\overline{R/G}$ between the radiances of the red and green stimuli for the total group of observers and for the two subgroups into which they could be divided by sex were different, the difference between men and women being about 7%. The women subjects used on average more red light in the mixture that the men under the same conditions. This difference of 7% between the average male observer and the average female observer is higher than the theoretical difference of 4.5% calculated previously. A theoretical difference of 7% can be obtained using the values $\lambda_{max} = 564$ nm in the case of the L_S-type photopigment and $\lambda_{max} = 553$ nm in the case of the L_A-type photopigment, but the question is whether or not this difference in the $\overline{R/G}$ ratio between the average male observer and the average female observer is statistically significant.

The inter-group and intra-group variances were studied using a parametric test (ANOVA) and a non-parametric test (Kruskal-Wallis). The null hypothesis was the absence of differences between groups split by sex, and therefore the recognition that the potential 50% of the female population whose retinas have both types of L-cone photopigments present behaviour that is equiparable to the average of the two populations whose retinas have potentially only one or the other type of photopigment. The ANOVA test needs to check three prerequisites – randomness, normality, and homoskedasticity of the sample – before being applied, but it is robust enough for use with samples like these that are theoretically bimodal and trimodal. We also performed the Kruskal-Wallis non-parametric test. The result of the two tests was the same (Table 1): the differences between men and women recorded in the ratios of the red/green mixture were indeed statistically significant ($P<0.05$), the null hypothesis could be rejected, and the alternative hypothesis that the two groups could be treated as distinct populations could be accepted.

4. DIFFERENCES IN THE MODEL OF COLOUR VISION

In the previous section, we saw that there exist significant differences in colour perception between different groups of observers in their Rayleigh metameric matches. It remains to be seen whether these differences are general, or just apparent in matching tests. To test this idea, a psychophysical experiment was devised based on obtaining each observer's isobrightness curve.

The CIE in 1978 in its publication No. 41 [56] called attention to the difference between the luminous efficiency function V_λ and the data obtained from direct heterochromatic luminosity matches, with the efficiency of the latter being greater than that of the former at both ends of the visible spectrum. This highlighted the need to obtain a luminous efficiency curve that would provide the luminosity perceived by an observer in response to a monochromatic stimulus (isobrightness curve).

In 1981, a luminous efficiency curve of this type was obtained for a 2° field, based on the data of 19 observers. Finally, in 1985, more data were added for the function corresponding to a 2° field, corresponding to a population of 63 observers between 18 and 50 years in age, and a photopic light level of between 50 and 500 trolands. The result is shown in Fig. 11 together with the 1924 CIE luminous efficiency curved as amended in 1951 by Judd [18] and in 1978 by Vos [25].

To obtain this curve, monochromatic stimuli were used displayed on a bipartite field in which one of the hemifields acted as reference and the other was matched by the observer. The data from which this curve was constructed were obtained by different researchers whose methods may have differed. For instance, for the field of observation, some used a white reference hemifield while others used a spectral stimulus of a particular wavelength. The time of exposure to the stimuli also varied from worker to worker, from 0.004 seconds to an unlimited time.

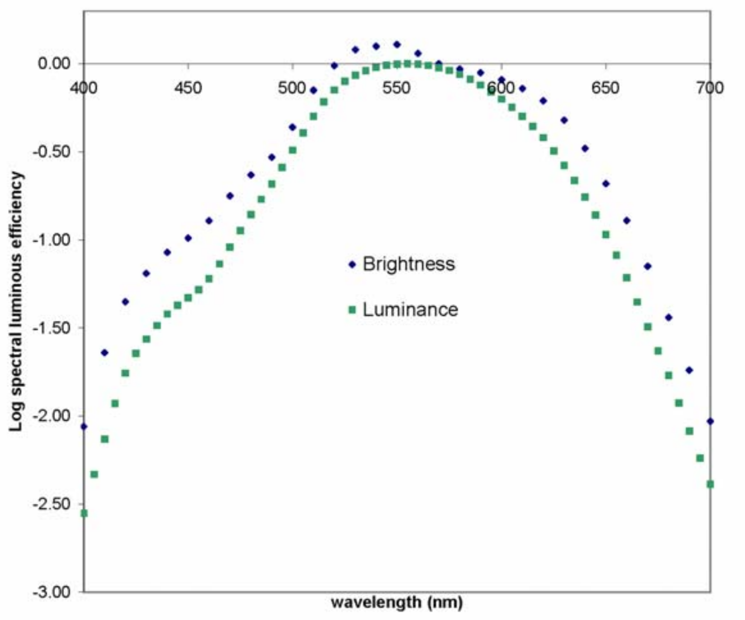


Figure 11. Isoluminance vs. Isobrightness curve.

The principal drawback of this brightness efficiency curve is that it should not be used with light sources of a compound spectrum since the additivity law is not satisfied. It can, however, provide us with information on each individual's underlying colour vision model, as we shall see below.

To perform the experiment, the aim was to attempt to simulate observing conditions similar to those of everyday life. To this end, we introduced a surrounding adaptive field of white with luminance 10 cd/m², which ensures the adaptation of the visual system to the photopic level and minimizes the effects of auto-adaptation to the test stimulus itself. The exposure time was unlimited. Luminosity matches were made after some seconds of exposure to ensure a stable level of photopigment bleaching.

Since this experiment had a twofold objective – obtaining a luminosity efficiency curve and using those data to study the colour vision models – the L, M, and S values were recorded together with the luminance of spectral stimuli over a large part of the visible spectrum (400–700 nm) whose common characteristic is that the observer perceives them with the same luminosity as the surrounding field. In particular, the matching performed was heterochromatic by direct comparison. To this end, the observer was asked, starting from a spectral stimulus of 570 nm, to fix its luminance level so that it was perceived to have the same luminosity as the adaptive field. This was done for the two plates of the visual field. Then the wavelength of the spectral stimulus of each plate began to be varied alternately in steps of 5 nm.

To facilitate the observer's evaluation of the luminosity, he or she was told to use both referents – the luminosity of the achromatic stimulus of the surrounding field, and the luminosity of the adjacent plate – but priority was given to the surrounding field.

This test was performed with three observers in sessions of about an hour, until completing a total of five sessions per observer each performed on different days. Observer 1 was a 25 year old man without previous experience in the topic. Observer 2 was a 29 year old woman also without previous experience. Observer 3 was a 40 year old woman with experience in tasks of evaluating chromatic stimuli.

Below are the luminous efficiency curves together with the LMS tristimulus curves obtained from the experimental data for these three observers.

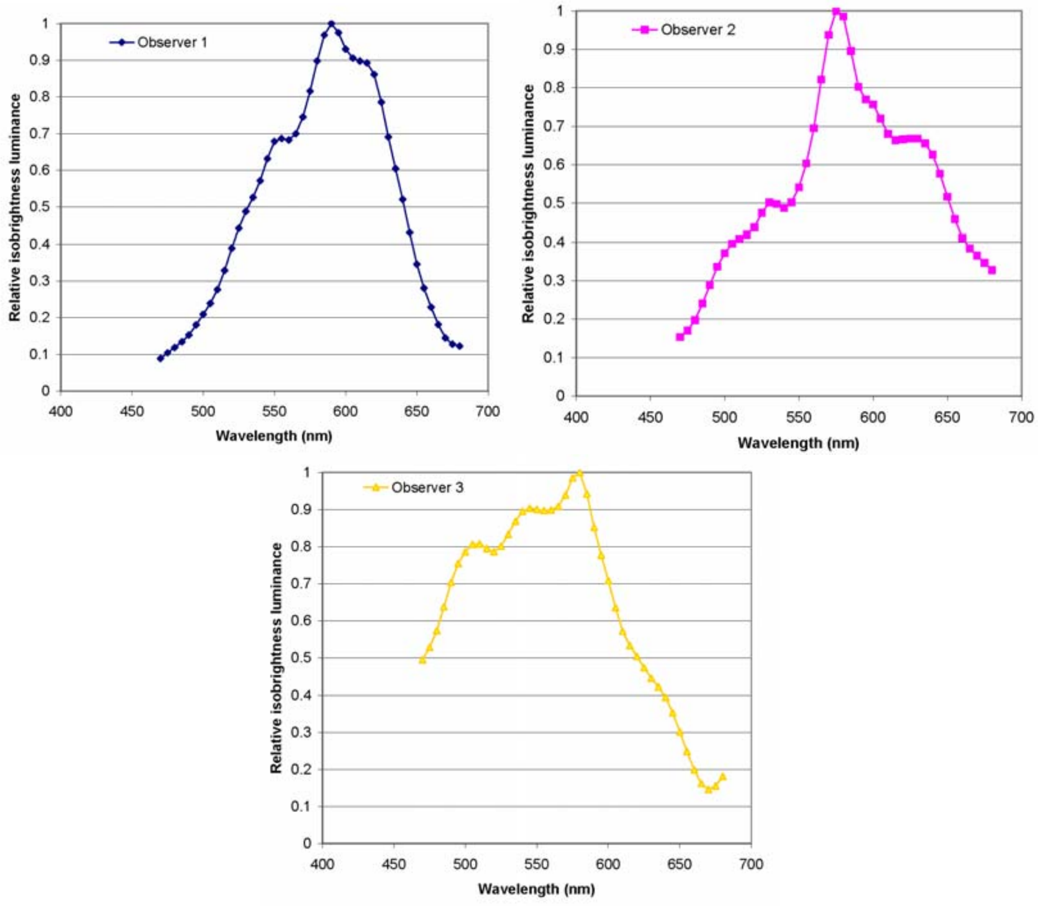


Figure 12. Luminance curve which gives the same luminosity as the white reference for the three observers.

For the three observers, the luminance curve which gives the same luminosity as the white reference appears in figure 12. In these three curves, one observes a very pronounced absolute maximum at around 580 nm, and a second lower local maximum at longer wavelengths.

To continue with the analysis of the results of this experiment, we will now consider the LMS tristimulus values obtained for each match of brightness. For the three observers, the L values are shown in fig. 13. The plot of the M value curves for the three observers appear in fig 14, and finally, we complete the data obtained from this experiment with the curves of the S values, which are shown in the figure 15 for the three observers.

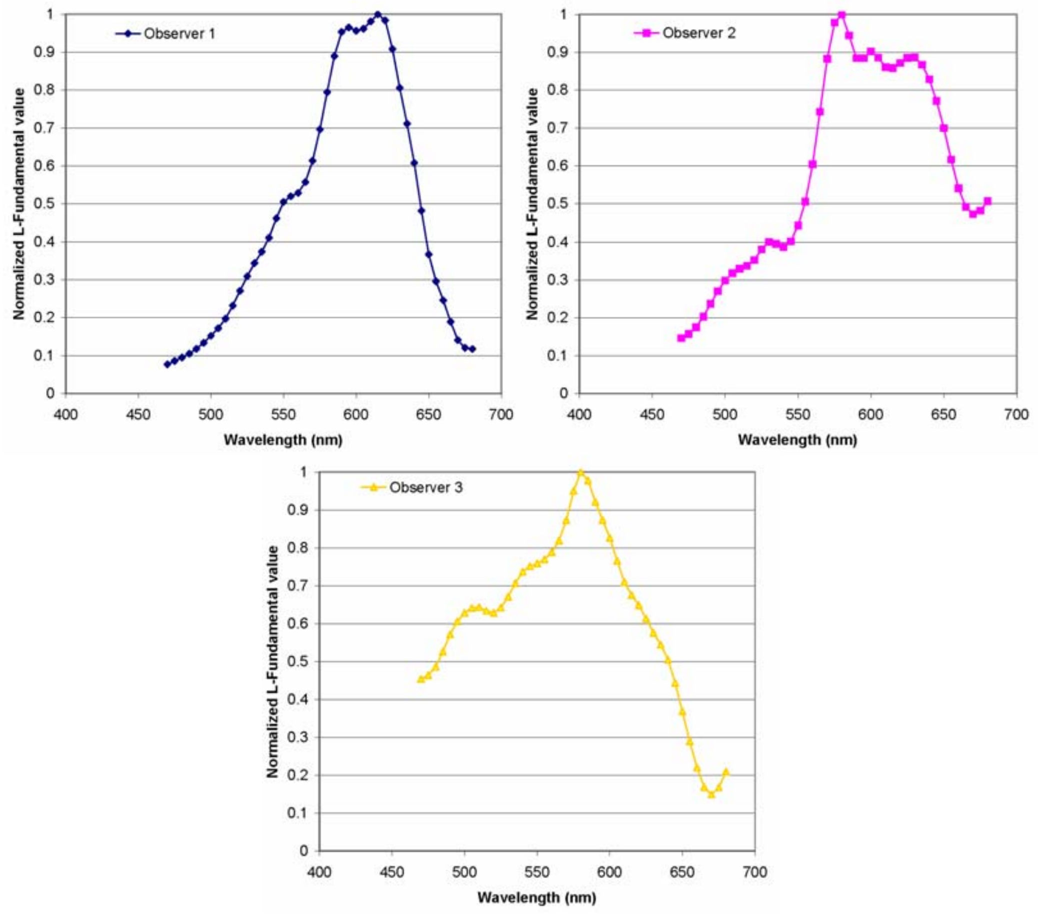


Figure 13. Normalized L-Fundamental values of stimuli which gives the same brightness as the white reference for the three observers.

In this graphical analysis of the results, there stand out the differences between the three observers. *A priori*, this would indicate major differences in their colour vision. The plots were displayed normalized so that each observer's absolute maximum was of value unity. In order to determine the magnitude of these differences in the intensity of the peaks, we must refer to the un-normalized data. One observes in this data that there is agreement between LMS values of Observers 1 and 2 over the entire range of values of the visible spectrum studied. This is not the case, however, for Observer 3, for whom the short wavelength LMS values are much higher than for Observers 1 and 2. This difference declines with increasing wavelength, but for the zone of the spectrum corresponding to wavelengths near 470 nm the differences reach about four times the L and M values obtained for Observers 1 and 2, and even a factor of six for the S values.

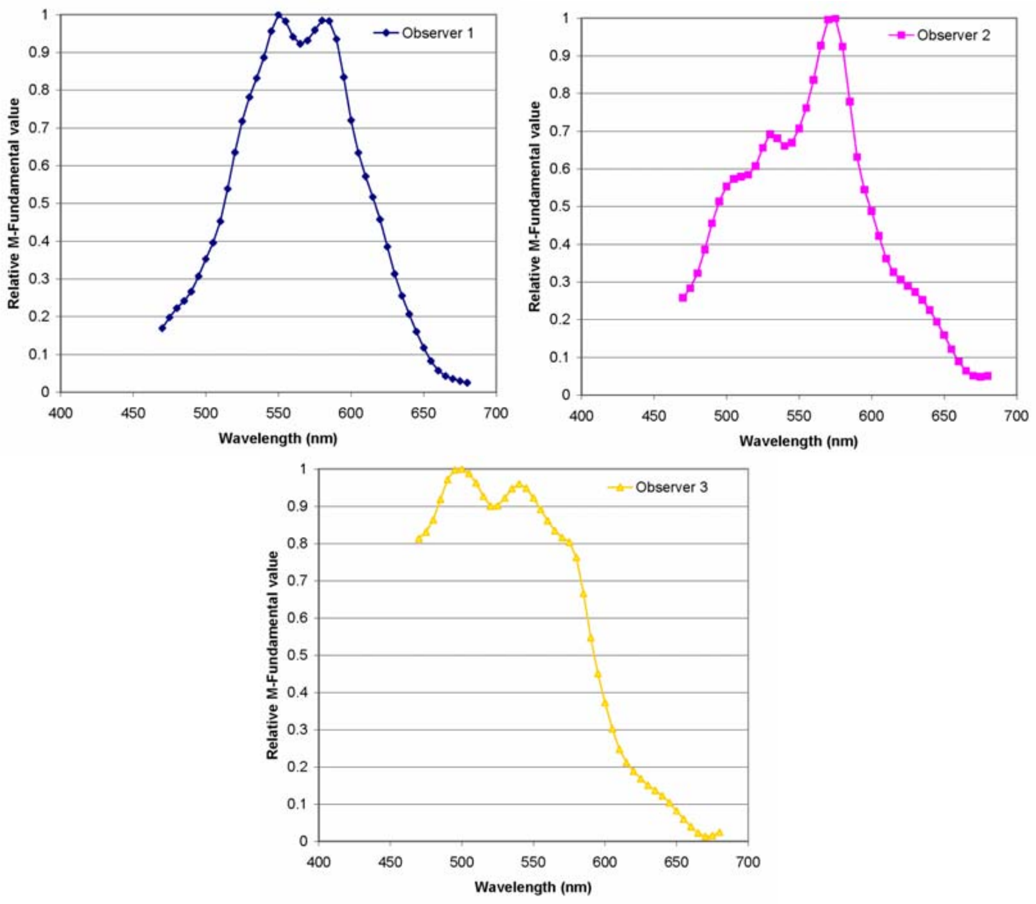


Figure 14. Normalized M-Fundamental values of stimuli which gives the same brightness as the white reference for the three observers.

That Observer 3's LMS values were higher, especially for short wavelengths, indicates that this observer's visual system requires more light in that part of the spectrum than the other two observers (the LMS units are the number of photons effectively captured per second, per m^2, and per steradian in each type of cone). This type of behaviour could be the result of either a yellowing of the intraocular media which filter the radiation incident on the eye, especially in zone close to the ultraviolet, or a high optical density of the macular pigment (Fig. 16).

It is known that there is great variation in yellowing of the lens, expressed as the optical density of the intraocular lenses, together with the optical density of the macular pigment in the population [57] and in the same individual over the course of his or her life [58]. Figure 16 shows the spectral variation of the optical density due to the macular pigment and the intraocular lenses, and the sum of the two used by Stockman & Sharpe [26]:

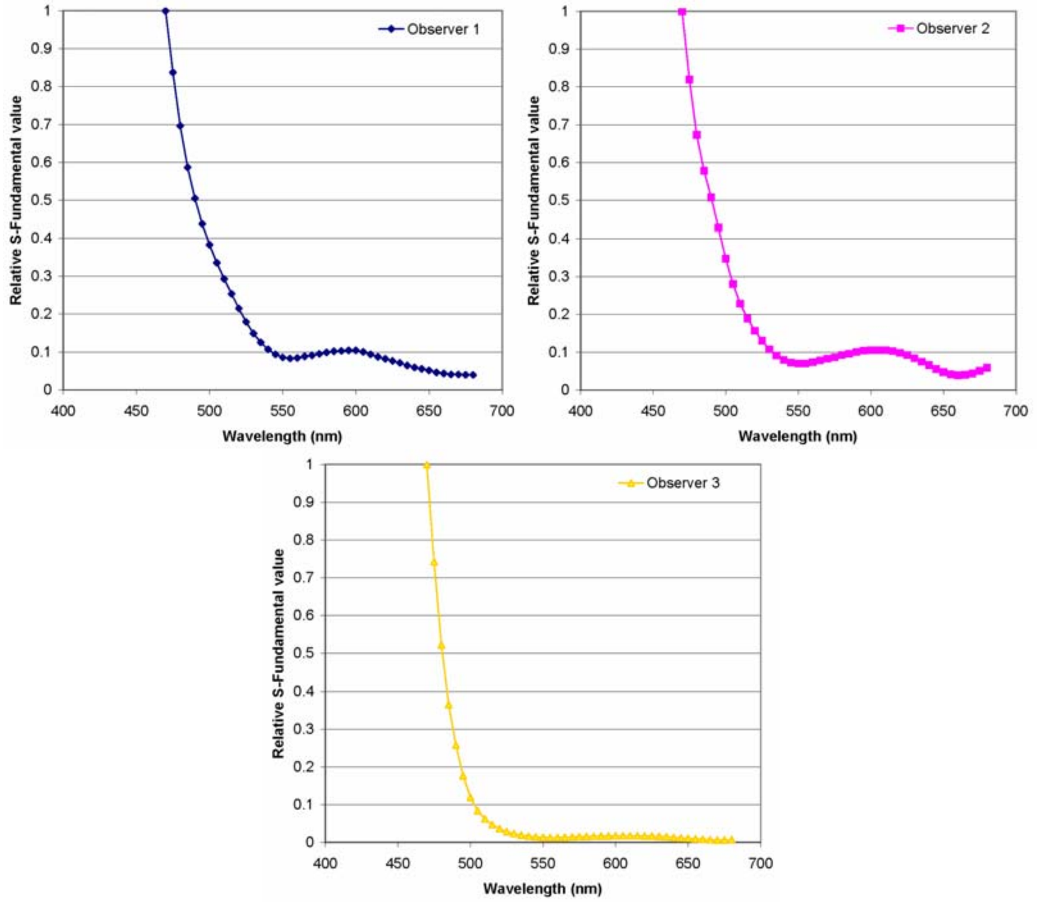


Figure 15. Normalized S-Fundamental values of stimuli which gives the same brightness as the white reference for the three observers.

On this last point, since the fundamental response curves reflect the different densities of the intraocular media (lenses and macular pigment), and this optical density is known in the case of Stockman & Sharpe's fundamentals, we can try to disentangle this information, and obtain the optical density of the photopigments of each type of cone. Based on the fundamentals of Stockman & Sharpe and the optical densities of the lenses and macular pigment that they also obtained (Fig. 16), one can extract the information corresponding to the photopigment response curves. Plotting them on a logarithmic scale of wavelengths, and shifting the curves so that they all have their maxima at the same point, one obtains the curves shown in Fig. 17:

It is clear that, once the contribution of the intraocular media has been discounted, and the response of the three cones has been rescaled and shifted on the logarithmic scale of wavelength so that all their maxima coincide, the three types of photopigment have essentially the same behaviour in their response curves.

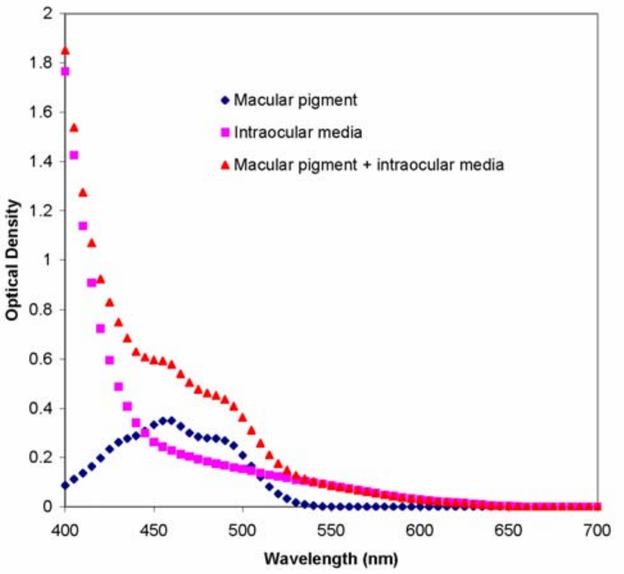


Figure 16. Optical density of intraocular media.

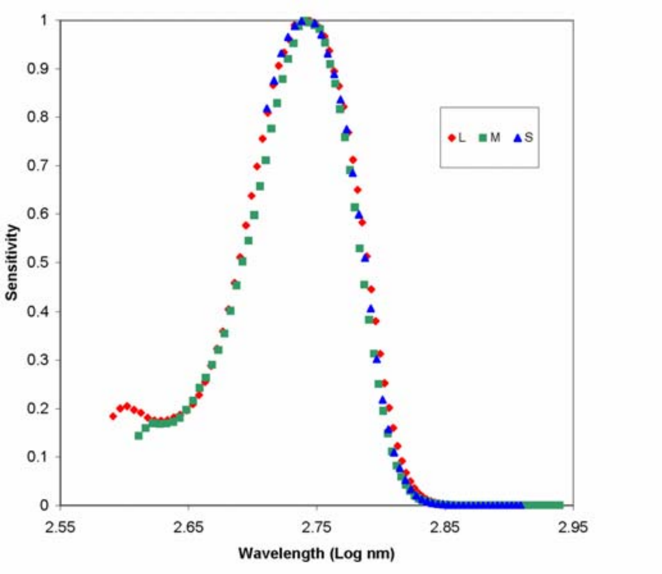


Figure 17. Optical density of photopigments normalized and centred in a Log scale.

This figure shows that the spectral sensitivity curve of the photopigment found in each type of cone is the same except for the scaling conditions. With these facts as a basis, we can approach the task of generating fundamental response curves for each observer, using for this purpose the intraocular lens and macular pigment optical densities and the wavelengths of maximum sensitivity of each of the three types of cone.

In 1991, the CIE set up the technical committee TC 1-36 with the following Terms of Reference: "Establish a fundamental chromaticity diagram of which the coordinates correspond to physiologically significant axes". In 2006, this TC published a report [59] with estimates of cone fundamentals for the normal observer, ranging in viewing angle from 1° to 10°. The report starts with the choice of the 10° CMFs of Stiles & Burch (1959). Then, following the ideas put forward by Stockman & Sharpe [26], by application of König's hypothesis, and using the most recent data on the spectral sensitivity functions of dichromats, this is followed by the derivation of the spectral sensitivity functions of the long-wave sensitive (L-), medium-wave sensitive (M-) and short-wave sensitive (S-) cones, measured in the corneal plane for a 10° viewing field – the so called "cone fundamentals".

Next, by correcting these functions for the absorption of the ocular media and the macular pigment, and taking into account the optical densities of the cone visual pigments, all for a 10° viewing field, the low density absorbance functions of these pigments were derived. Using these low density absorbance functions one can derive from the absorption of the ocular media and the macula, and taking into account the densities of the visual pigments for a 2° viewing field, the 2° cone fundamentals. Using the same procedure one can derive cone fundamentals for every viewing angle between 1° and 10°. Effects of age can also be incorporated by application of the relationship of the absorption of the lens as a function of age [60].

In our experiment, Observer 3 was significantly older than the other two observers, and the difference in the observed LMS values was particularly acute for those obtained from the S fundamental. Recall that the LMS values were obtained using the fundamentals of Stockman & Sharpe, and that these fundamentals were obtained using average values of the macular pigment and intraocular media optical densities. Assuming that the large difference in the LMS values of Observer 3 relative to the other two observers was due to a greater optical density of the intraocular lenses, and modifying the fundamentals of Stockman & Sharpe to take this into account, one obtains new LMS values for Observer 3, as shown in the following curves.

The normalized curve of L, M & S values obtained after correcting the fundamentals of Stockman & Sharpe for the optical density of the intraocular media is presented in the figure 18.

As can be seen in the above figures, applying this correction leads to the LMS curves of Observer 3 having many more similarities with the same curves of Observers 1 and 2 than before.

Before continuing with the data analysis, we must first reflect on the nature of those data. The psychophysical experiment gave some points of perception space of different hues and saturation, but the same luminosity as the surrounding achromatic referent. This makes the variation in the data as one moves along the spectrum to be mainly in hue, then in saturation, and finally in luminance, since the test was at equal luminosity.

Principal component analysis [61] seeks linear combinations of the variables comprising the data set that account for as much of the variability in the data as possible. It is an appropriate technique when the original variables are strongly correlated, as in the present case. When this is so, much of the information contained in the data set overlaps among several variables, thus hindering its identification. Principal component analysis constructs a new set of uncorrelated variables to avoid repetition of the information.

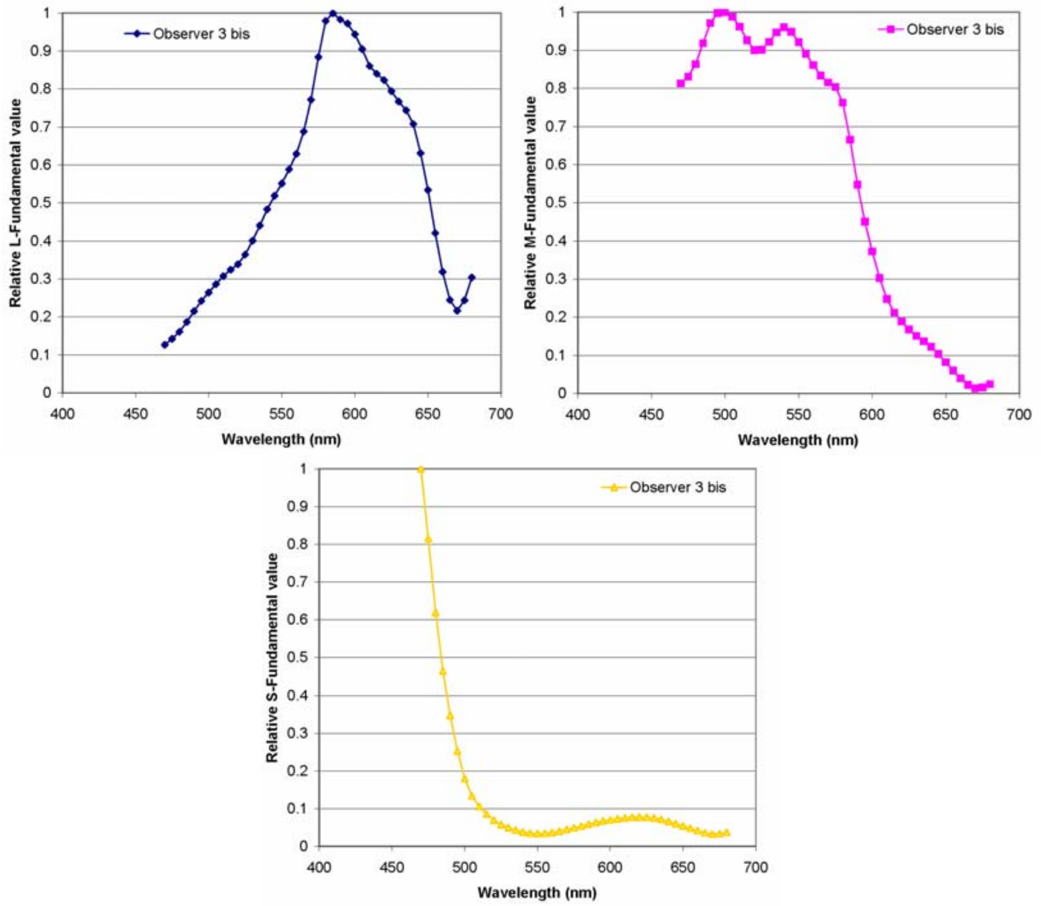


Figure 18. Normalized L,M,S- Fundamental rebuilt values for observer 3

The first principal component is the linear combination which accounts for as much of the variability as possible. The second is the linear combination uncorrelated with the first principal component that accounts for as much of the remaining variability as possible. The third is the linear combination uncorrelated with the first two principal components that accounts for as much of the remaining variability as possible, and so on.

Another interesting point is the possibility of working with other new variables which are rotations of the original variables and better explain the variability of the data. It has to be borne in mind that the principal components depend on the scaling of the original variables so that, for the data resulting from the principal component analysis to be valid, one must maintain the scaling conditions. Although this statistical tool was designed to eliminate variables with little influence on the event under study, in the present case we shall apply it to the data obtained in our experiment for the three observers in order to obtain a linear combination of the LMS components that reveals the underlying colour vision model.

There was a question as to whether the data should be subjected to a principal component analysis or to a common (principal) factor analysis. This latter is applied assuming that not all the variance can be explained by the variables involved in the study, so that there is always a reduction in the number of dimensions of the resulting space. In the present case, there were no reasons that would allow us to make this assumption, so that we opted for principal component analysis.

Before beginning with the principal component analysis, it is advisable to standardize the data, especially if the starting variables represent values of a different nature. In the present case, although the nature of the data is the same since they indicate the effective capture of photons in the three types of cone, their behaviour is very different for each type of cone. We therefore proceeded to standardize the data making the mean of each variable 0 and the variance 1.

There are several ways of performing a principal component analysis according to whether the basis is the correlation matrix or the covariance matrix, and according to the normalization applied to the results. In our case, we used the correlation matrix and the Hotelling normalization [62]. This gives equal importance to all three initial LMS variables assuming that each has a variance of 1 and the total variance of the system is 3. Also, the resulting components are scaled such that each retains the proportion of the observed variance while maintaining the variance of 3 for the complete system.

Some workers, including Boynton et al. [63] and Hunt [64], consider that wavelengths shorter than 442 nm or longer than 613 nm do not provide optimal chromatic stimuli since in these regions of the visible spectrum the rate of change of hue with wavelength falls rapidly. This variation in the scaling of the hue *versus* wavelength may affect the method used in the previous analysis, since the experimental data on which it was based surpassed the upper limit of 613 nm, reaching 680 nm. This was not the case, however, for the other end of the spectrum, because the experimental data were obtained only down to 470 nm. Performing the principal component analysis on the experimental data only in the range 470–615 nm, we obtained the results described in tables 2-4.

Table 2. Total variance explained for Observer 1.

Component	Initial eigenvalues			Sums of the squares of the saturations		
	Total	% Variance	Cumulative %	Total	% Variance	Cumulative %
1	2.280	75.992	75.992	2.280	75.992	75.992
2	0.548	18.283	94.275	0.548	18.283	94.275
3	0.172	5.725	100.000	0.172	5.725	100.000

Extraction method: Principal component analysis

Table 3. Total variance explained for Observer 2.

Component	Initial eigenvalues			Sums of the squares of the saturations		
	Total	% Variance	Cumulative %	Total	% Variance	Cumulative %
1	2.183	72.751	72.751	2.183	72.751	72.751
2	0.548	18.253	91.003	0.548	18.253	91.003
3	0.270	8.997	100.000	0.270	8.997	100.000

Extraction method: Principal component analysis

In tables 2-4, Component 1 accounts for more thant 70% of the total variance. Component 2 accounts for 18% of the variance, and Component 3 accounts for the remaining 6-10% for the three observers.

Table 4. Total variance explained for Observer 3.

Component	Initial eigenvalues			Sums of the squares of the saturations		
	Total	% Variance	Cumulative %	Total	% Variance	Cumulative %
1	2.156	71.878	71.878	2.156	71.878	71.878
2	0.542	18.057	89.935	0.542	18.057	89.935
3	0.302	10.065	100.000	0.302	10.065	100.000

Extraction method: Principal component analysis

In the component matrix (Table 5), it could be seen for the three observers that Component 1 accounts for the contributions of L and M, from which is subtracted the variable S. This coincides with the usual treatment of the channel D in neural models. Component 2 has the form of an opponent channel of type T, with the contribution of the variable M being subtracted from that of the variable L, and an almost negligible contribution of the variable S. Component 3 is a sum of contributions of the three variables L, M, and S with small weights, and may correspond to variations in the achromatic channel A in the determination of the isobrightness curve.

It should be emphasized that Components 2 and 3, which resemble channels T and A, respectively, arose solely from the statistical treatment applied to the experimental data.

Table 5. Component matrix for Observer 1.

	Ob1's components			Ob2's components			Ob3's components		
	1	2	3	1	2	3	1	2	3
L	0.827	0.534	0.176	0.821	0.525	0.226	0.803	0.570	0.176
M	0.837	-0.513	0.191	0.822	-0.522	0.228	0.839	-0.459	0.293
S	-0.946	0.013	0.323	-0.913	0.002	0.408	-0.899	0.080	0.430

4. CONCLUSION

The statistical results of the previous section show an underlying structure of the experimental data that is common to all three observers, and coincident with the channels into which neural models of colour vision are usually divided.

The first component reflects the behaviour of a blue/yellow or type D channel in Guth's terminology, in all cases accounting for over 70% of the variance. The second component corresponds to the behaviour of a red/green or type T channel, accounting for 18% of the variance for the three observers. Finally, the third component would correspond to the behaviour of a luminance or achromatic channel accounting for the remainder of the variance, but with certain differences.

These differences bring out the particularities of each observer's colour perception, not only in the physical but also in the perceptive aspect, since this last experiment included a correction for the differences in the optical density of the macular pigment and lenses.

The principal component analysis yielded completely uncorrelated linear combinations of the original variables, which explained 100% of the initial variance in a three-dimensional vector space. Independently of the normalization applied to the principal components which indicates their different weights in the total variance, these principal components indicate the directions in the three-dimensional vector space into which the original variance is mapped. Expressing these components by means of the angles corresponding to their direction cosines is a way of representing them that is independent of the particular weight that they each have in accounting for the total variance.

Thus, for Component 1 or channel D, for Component 2 or channel T and, for Component 3 or channel A one has the angles expressed in the tables 6-8.

Table 6. Direction angles of Principal Component 1.

Component 1	θ_L	θ_M	θ_S
Observer 1	56.79	56.34	128.79
Observer 2	56.24	56.20	128.17
Observer 3	56.85	55.15	127.75

Table 7. Direction angles of Principal Component 2.

Component 2	θ_L	θ_M	θ_S
Observer 1	43.83	133.87	88.99
Observer 2	44.83	134.84	89.84
Observer 3	39.26	128.57	83.76

Table 8. Direction angles of Principal Component 3.

Component 2	θ_L	θ_M	θ_S
Observer 1	64.89	62.58	38.85
Observer 2	64.22	63.97	38.26
Observer 3	71.32	57.78	38.51

This allows one to better appreciate the consistency of the results for Component 1 (channel D) between all three observers, and the small variations, especially for Observer 3, in Component 2 (channel T) and in Component 3 (channel A).

Therefore, the next step in colorimetry should be to provide coverage for all these individual differences [65] which also have great importance for the preservation of metameric matches in digital devices (LCDs, printers, etc.) [66]. To attain this goal, it is essential to develop a straightforward chromatic characterization of observers so that these colorimetric transformations can subsequently be implemented in digital devices. The authors' group has been working on this topic for several years, and is currently carrying out a research project entitled "*Intelligent System for the Chromatic Characterization of Observers*" which is hoped soon to yield relevant results.

ACKNOWLEDGMENTS

Thanks are due to Prof. Françoise Viénot of the Natural History Museum of Paris and to the Department of Optics of the University of Granada, and in particular to Prof. Enrique Hita

Villaverde for his constant support. This work was supported by the Spanish Ministry of Science and Innovation through the Plan Nacional de Investigación Científica, Desarrollo e Innovación Tecnológica (I+D+I) and the FEDER program of the European Union, grant FIS2006-06110 and by the Consejería de Economía, Comercio e Innovación of the Junta de Extremadura.

REFERENCES

[1] MacAdam, D.L. *Sources of color science*; M.I.T. Press: Cambridge, 1970.
[2] Helmholtz, H. v. *Handbuch der Physiologischen Optik*; 2nd ed.; Voss: Hamburg, 1896.
[3] Hering, E. *Zur lehre vom Lichtsinne*; Carl Gerold's Sohn: Viena, 1878.
[4] Romero, J.; García, J. A.; García-Beltrán, A. *Curso introductoria a la Óptica Fisiológica*; Ed. Comares: Granada, 1996.
[5] Müller, G.E., *Darstellung und Erklärung der verschieden Typen der Farbemblindheit*; Vandenhock y Ruprecht: Göttingen, 1924.
[6] Schrödinger, E. *Annalen der Physik und CEIME* 1920, 63, 481-520.
[7] Judd, D.B. *J. Res. Nat. Bur.* 1949, 42, 1.
[8] García J.A. *Determinación experimental de diferencias de color: normalización colorimétrica y modelos de visión*; Universidad de Granada: Ph.D. Tesis, 1990.
[9] Hurvich, L. M.; Jameson, D. *Outline of a Theory of the light sense*; Harvard University Press: Cambridge, 1964.
[10] Capilla P.; Artigas, J. M.; Pujol, J.; Luque, M. J.; Malo, J.; Martínez-Verdú, F. *Fundamentos de Colorimetría*; Ed. Universidad de Valencia: Valencia, 2002.
[11] Estevez, O. *On the fundamental data-base of normal and dichromatic color vision*; Universidad de Amsterdan: Ph.D. Tesis, 1979.
[12] Rushton, W.A.H. in *Handbook of Sensory Physiology*; Springer-Berlag: NY, 1972; Vol. VII/1, pp. 364-394.
[13] Maxwell, J.C. *Trans. Roy. Soc. Edinburgh* 1857, 21, 275.
[14] Wyszecki, G.; Stiles, W. S.; *Color Science: Concepts and methods, quantitative data and formulae*; Second edition; John Wiley & Sons: New York, 1982.
[15] König, A. *Gesammelte Abhandlungen*; Barth-Verlag: Leipzig, 1903.
[16] Pardo, P.J.; Pérez, A.L.; Suero M.I. *Displays* 2001, 22, 165-168.
[17] Vos, J.J., Walraven, P.L. *Vision Res.* 1971, 11, 799-818.
[18] Judd, D. B. in *Proceedings of the Twelfth Session of the CIE, Stockholm*; Bureau Central de la CIE: Paris, 1951; Vol. 1, pp. 11.
[19] Smith, V.C., Pokorny, J. *Vision Res.* 1975, 15, 161-71.
[20] Walraven, P. L. *J. Opt. Soc. Am.* 1961, 51, 1113–6
[21] MacLeod, D.I.A.; Boynton, R. M. *J. Opt. Soc. Am.* 1979, 69 1183–6
[22] Vos, J. J.; Estévez, O.; Walraven, P. L. *Vision Res.* 1990, 30, 936-943.
[23] Stiles, W. S.; Burch, J. M. Optica Acta 1955, 2, 168-181.
[24] Stockman, A.; MacLeod, D.I.; Johnson, N.E. *J. Opt. Soc. Am. A* 1993, 10, 491-521.
[25] Vos, J.J. *Color Res. Appl.* 1978, 3, 125-128.
[26] Stockman, A.; Sharpe, L.T. *Vision Res* 2000, ***40,*** 1711-1737.
[27] Webster, M.A.; MacLeod, D.I.A. *J. Opt. Soc. Am. A.* 1988, 5, 1722-1735.

[28] Stockman, A.; Sharpe, L.T. Vision Res. 1999, 38, 3193-3206.

[29] Brainard, D.H.; Roorda, A.; Yamauchi, Y.; Calderone, J.B.; Metha, A.; Neitz, M.; Neitz, J.; Williams D.R.; Jacobs,G.H. *J. Opt. Soc. Am. A* 2000, 17, 607-614.

[30] Nathans, J.; Thomas, D.; Hogness, D. S. *Sci.* 1986, 232, 193-202.

[31] Neitz, J.; Jacobs, G.H. *Nat.* 1986, 323, 623-625.

[32] Deeb, S.S.; Motulsky, A.G. *Beh. Gen.* 1996, 26, 195-206.

[33] Hayashi, T.; Motulsky, A.G.,; Deeb, S.S. *Nat. Gen.* 1999, 22, 90-93.

[34] Hayashi, T.; Yamaguchi, T.; Kitahara, K.; Sharpe, L.T.; Jägle, H.; Yamade, S. et al. *Color Res. Appl.* 2001, 26, S79-S83.

[35] Nagy, A.L.; MacLeod, D.I.A.; Heyneman, N.E.; Eisner, A. *J. Opt. Soc. Am. A* 1981, 71, 719-722.

[36] Jordan, G.; Mollon, J.D. *Vision Res.* 1993, 33, 1495-1508.

[37] Neitz, M.; Neitz, J.; Jacobs, G.H. *Sci.* 1991 252, 971–974.

[38] Sharpe, L.T.; Stockman, A.; Jägle, H.; Nathans, J. in *Color Vision: From genes to perception*; K.R. Gegenfurtner & L.T. Sharpe, Eds.; Cambridge Univ. Press: Cambridge, 1999; pp. 14.

[39] Lyon M.F. *Acta Paediatr. Suppl.* 2002, 439, 107-112.

[40] Neitz, M.; Kraft, T. W.; Neitz, J. *Vision Res.* 1998, 38, 3221-3225.

[41] Jameson, K.A.; Bimler, D.; Wasserman, L.M.; in *Progress in Colour Studies 2: Cognition*; Pitchford, N.J. & Biggam, C.P. Eds; John Benjamins Publishing Co: Amsterdam, 2006.

[42] Jameson, K.A.; Highnote, S; Wasserman, L.M. *Psych Bull. Rev.* 2001, 8, 244-261.

[43] Bimler, D.L.; Kirkland, J.; Jameson, K.A. *Color Res. Appl.* 2004, 29, 128-134.

[44] Sayim, B.; Jameson, K.A.; Alvarado, N.; Szeszel, M.K. *J. Cog. Cult.* 2005, 5, 427-486.

[45] Jakab, Z.; Wenzel, K. *Perception* 2004, 33, S64.

[46] Winderickx, J. D.; Lindsey, T.; Sanocki, E.; Teller,D.Y.; Motulsky, A.G.; Deeb, S.S. *Nat.* 1992, 356, 431 - 433.

[47] Sanocki, E.; Lindsey, D.T.; Winderickx, J.; Teller, D.Y.; Deeb, S.S.; Motulsky, A.G. *Vision Res.* 1993, 33, 2139-2152.

[48] Sanocki, E.; Shevell, S.K.; Winderickx, *J. Vision Res.* 1994, 34, 377-382.

[49] Melgosa, M,; Rivas, M.J.; Hita, E.; Viénot, F. *Color Res. Appl.* 2000, 25, 356-367.

[50] Webster, M.A.; Miyahara, E.; Malkoc, G.; Raker, V.E. *J. Opt. Soc. Am. A* 2000, 17, 1545-1555.

[51] Stockman, A.; Sharpe, L.T.; Fach, C.C. *Vision Res.* 1999, 39, 2901-2927.

[52] Bone, R.A.; Landrum, J. T.; Cains, A. *Vision Res.* 1992, 32, 105-110.

[53] Dartnall, H.J.A.; Bowmaker, J.K.; Mollon, J.D. *Proc. Roy. Soc. Lon.* 1983;B220:115-130.

[54] Working-Group-41. Procedures for Testing Color Vision, NAS-NRC Committee on Vision. In Washington: DC National Academy Press, 1981.

[55] Pardo, P.J.; Pérez, A.L.; Suero, M.I. *Rev. Sci. Instr.* 2004, 75, 42-45.

[56] CIE 41, *Light as a true visual quality: principles of measurement*; Bureau central de la CIE: Paris, 1978.

[57] Hammond, Jr.B.R.; Nanez, J.E.; Fair, C.; Snodderly, D.M. *Ophthal. Physiol. Opt.* 2000, 20, 381–386.

[58] Lerman, S. *Radiant energy and the eye*; Macmillan Publishing Co.: New York, 1980.

[59] CIE 170-1, *Fundamental Chromaticity Diagram with Physiologically Significant Axes Part I* ; Bureau central de la CIE: Paris, 2006.
[60] Vienot, F.; Serreault, L.; Pardo, P.J. *Vis. Neurosci.* 2006, 23, 419-427.
[61] Jolliffe, I. T., *Principal component analysis*; Springer-Verlag: New York, 1986.
[62] Hotelling, H. *J. Educ. Psychol.* 1933, 24, 417-441, 498-520.
[63] Boynton, R.M.; Gordon, J. *J. Opt. Soc. Am.* 1965, 55, 78–86.
[64] Hunt, R.W.G. *Color. Res. Appl.* 1989, 14, 235–239.
[65] Pardo, P.J.; Perez, A.L.; Suero, M.I. *Color Res. Appl.* 2007, 32, 433-439.
[66] Oicherman, B.; Luo, M.R.; Rigg, B.; Robertson, A.R. *Color Res. Appl.* 2008, 33, 346-359.

In: Color Perception: Physiology, Processes and Analysis
Editors: D. Skusevich, P. Matikas, pp. 161-183
ISBN: 978-1-60876-077-0

Chapter 5

COLOR-SENSITIVE NEURONS IN THE VISUAL CORTEX: AN INTERACTIVE VIEW OF THE VISUAL SYSTEM

Maria C. Romero,[1] Ana F. Vicente,[1] Maria A. Bermudez[1] and Francisco Gonzalez[1,2]
[1]Department of Physiology, School of Medicine, University of Santiago de Compostela, Santiago de Compostela, Spain
[2]Service of Ophthalmology, Complejo Hospitalario Universitario de Santiago de Compostela, Santiago de Compostela, Spain

ABSTRACT

Classically, different physical attributes of the visual stimulus were thought to be solved in parallel by interdependent neuronal populations conveying information from the retina to the parietal and temporal cortical areas. According to this assumption, while neurons in the dorsal areas of the visual system were mainly related to the analysis of motion and spatial information, those located at the more ventral positions were mostly associated to shape and color processing. However, although this functional segregation between visual areas has been supported for several decades, there is also strong experimental evidence suggesting an alternative task-driven view of the visual system. According to this more recent perspective, neuronal responses in cortical visual areas can be simultaneously dependent on more than one single visual attribute. As far as color perception plays a central role in visual recognition, it could be assumed that color-sensitive neurons would be also involved in the analysis of some other critical visual attributes. In agreement with this idea, it has been shown that V1 double opponent cells respond to edges defined not only by chromatic and luminance differences, but also by the orientation of their receptive fields. Furthermore, results from many electrophysiological and neuroimaging studies have also demonstrated that color-sensitive neurons in V2 and V3, modulate their responses depending on diverse physical attributes of the stimulus such as the stimulus direction, orientation, luminance and shape, revealing the simultaneous contribution of magno- and parvocellular inputs from the Lateral Geniculate Nucleus (LGN) at different levels of the visual system. At higher visual areas, several authors have reported the existence of multi-sensitive neurons.

Middle Temporal (MT) neurons, in the dorsal stream, are sensitive to motion spots defined by single or combined changes in texture and color. In the ventral stream, responses to both, color and orientation have been described in V4 and the inferotemporal cortex. Additionally, results from several studies blocking the magno- and parvocellular projections from the LGN to V4 have shown that these two channels can simultaneously contribute to neuronal responses at this level of processing. All these data evidence that even sharply-color-tuned neurons can show color-related responses modulated by many other visual attributes.

1. INTRODUCTION

Over the past few decades, the functional role of many cortical regions has been elucidated. Thus, the specific role of these regions was labeled according to the new findings from different approaches and methods. Following such a multidisciplinary perspective, sensory and cognitive processes were thought to be achieved by a number of neuronal populations working in parallel, each solving one specific component of the analysis. It has been suggested that the information about color, shape, depth and motion is processed in many cortical regions, mainly organized into two independent cortical pathways: the dorsal and ventral streams of the visual system (Ungerleider & Mishkin, 1982; Haxby et al., 1992, 1994, 2000; Ungerleider & Haxby, 1994; Courtney et al., 1996; Ungerleider et al., 1998). According to this assumption, the occipitotemporal cortex would be composed of separate functionally discrete regions, processing visual complex stimuli (Ishai et al., 1999; Haxby et al., 2000; Nystrom et al., 2000), such as faces or other biologically relevant stimuli (Sergent et al., 1992; Haxby et al., 1994, 1996; Clark et al., 1996; Courtney et al., 1996; Sams et al., 1997; Ungerleider et al., 1998). The functional distribution of these visual areas gave rise to the ‘segregation’ hypothesis. From this hypothesis, object perception implies the analysis of different physical attributes such as color, shape or motion, all developed by different neuronal populations. Thus, while neurons in the ventral stream would code information about color and shape, neurons in the dorsal stream would be more involved in motion and spatial processing (Desimone et al., 1985; Goodale & Milner, 1992; Kiper et al., 1997).

Although this idea was classically supported for many decades (Ungerleider & Mishkin, 1982; Mishkin et al., 1983), the whole theory was nevertheless against the basic requirements for a complex visual processing. Whenever the observer fixates a particular object, its visual system must combine, at least, the color- and shape-related information in it to allow higher perceptual mechanisms. As possible combinations between attributes become infinite when we consider the entire visual world, the idea of independent cells specialized in all different combinations seems unlikely. Instead, numerous evidences strongly support the idea of a neuronal cooperation at different stages of the visual system. Named as the *binding problem*, the idea of how our brain can combine multiple bits of information arriving from separated brain areas to build up a single coherent percept remains under debate.

Since the 1980s, several authors have tried to explain the binding problem (Julesz, 1986; Treisman, 1986). In general, it was accepted that different visual properties could be encoded in different *feature maps* during a preattentive stage of perception. Later on, attention would work as a filter, selecting and linking these specific features by both, increasing the salience of the attended stimulus, and reducing the perceived surrounding field (Reynolds & Desimone, 1999).

From an alternative approach, other authors (Optican & Richmond, 1987; Gray, 1999; Singer, 1999) have focused their studies on the temporal aspects of this problem. Their data suggest that neural oscillations and synchronous signals are present in the brain, and that neurons can use these signals to strengthen their synaptic communications. This interactive system could explain the communication occurred between nearby neurons, but also between those separated by several cortical columns, or even areas, in the visual cortex (Eckhorn et al., 1988; Gray & Singer, 1989). According to this perspective, cells located at different areas can show coherence in their responses to specific stimuli, favouring a comprehensive perception of the visual object.

Whatever the particular mechanism is involved in this task, visual information must be integrated at some level to allow a complete processing, and cooperative strategies between the neuronal populations are required. One of the most prolific approaches to the study of neuronal cooperation in the visual system comes from the analysis of color perception.

2. COLOR PROCESSING IN THE PRIMATE BRAIN—GENERAL OVERVIEW

Generally speaking, human- and non human-primate color decoding systems follow similar anatomical distributions (Sereno et al., 1995), showing high functional homology in both, the eye, and early visual stages (DeValois et al., 1974). Although from the primary visual cortex (V1) this homology decreases (Heywood et al., 1991; Zeki et al., 1991; Rizzo et al., 1993; McKeefry & Zeki, 1997; Beauchamp et al., 1999; Zeki et al., 1998), the parallelism is still evident, and therefore neurophysiological studies in monkeys have provided a powerful tool to understand the processes involved in human color perception.

Primate color vision starts in the retinal color-tuned photoreceptors, named as cones, which spatial density peaks in the fovea, declining rapidly towards the periphery. Cones with spectral sensitivities to long (red-type) and half wavelengths (green-type) are shared by most mammals (Mollon, 1989), but only primates show an additional third type of cones, sensitive to short wavelengths (blue-type) (Dartnall et al., 1983; Nathans et al., 1986). A linear model in which cell responses are proportional to the sum (rectified sum for complex cells) of these three types of cones can describe quite well the chromatic properties of cells in the Lateral Geniculate Nucleus (LGN) and the visual cortex (Derrington et al., 1984). The color opponent centre-surround structure found in the receptive field (RF) of LGN neurons filters the information that will be send to cortical structures, projecting chromatic information through low-pass channels, and luminance information through spatial band-pass channels (De Valois et al., 1977; Derrington et al., 1984).

Most of the studies in both, humans and apes have been traditionally consistent with the idea that the color processing is concentrated in ventral occipitotemporal areas. Thus, the analysis of patients with brain injury at this level have shown that deficits in color perception can be mainly associated with lesions in the ventral cortex (Meadows, 1974; Zeki, 1990), although different cortical areas have been equally involved. Studies in patients with cerebral achromatopsia suggested that the occipitotemporal cortex, together with the fusiform and lingual gyri, and the Inferotemporal cortex (IT) can be crucial structures for color processing (Damasio et al., 1980; Zeki, 1990; Beauchamp et al., 2000; Girkin & Miller, 2001).

Against this classical idea, some authors have reported that the activation of selective color-related neurons is not exclusive of the ventral stream. Several dorsal areas (Corbetta et al., 1991) including the superior parietal lobule (Gulyás & Roland, 1994; Claeys et al., 2004), and higher cortical areas as the frontal cortex (Mckeefry & Zeki, 1997) are also involved in color processing. These observations are strongly supported by recent results obtained from different methodological approaches. Indeed, clear arguments against the 'segregation hypothesis' for color processing have been increasingly found in the past decades leading to revise the classical functional distribution between the ventral and the dorsal visual streams. A wider connectivity network providing ventro-dorsal feedback has been already proved to exist at different stages of the visual system. As a result, the idea that ventral and dorsal streams can solve different but simultaneous aspects of color processing, is gaining more popularity.

2.1. Evidences For and Against the Segregation Hypothesis

Traditionally, it was thought that the parallel parvo- (P) and magnocellular (M) pathways remained segregated beyond the cortical level supporting the idea of an independent analysis of color and motion in the visual system. These first studies showed that, in an early stage of processing, the LGN contain clusters of color-sensitive cells responding to diffuse colored lights, and clearly distributed in separate anatomical and functional layers (De Valois, 1965; Wiesel & Hubel, 1966; De Valois & Pease, 1971; De Valois et al., 1977; Derrington et al., 1984; Lennie et al., 1990, Reid & Shapley, 1992). The outer layers of the LGN (3-6) are composed of small cells (Parvo; P) which receive inputs from all three cone types, transmitting suitable chromatic information (Ingling & Martinez, 1983; Ingling & Tsou, 1988; Schiller & Logothetis, 1990; DeValois & DeValois, 1993). The inner layers (1-2), composed of larger cells (Magno; M), receive input from red and green cones but not from the blue type, and therefore they are consider to carry color-blind information (Schiller & Logothetis, 1990).

Direct inputs from the LGN to blob and stripe regions, in V1 and V2 carry color information to the cortex (Livingstone & Hubel, 1988; Shipp & Zeki, 2002). In the blobs, color tuning is organized in clusters of cells (Daw, 1968, 1984; Hubel, 1988), especially prominent in the superficial layers 2 and 3. These color sensitive cells, called double-opponent cells have concentrically organized RFs, and receive direct inputs from the parvocellular layers of the LGN (Livingstone & Hubel, 1984, 1987, 1988; Michael, 1987 a-c, 1985; Casagrande & Norton, 1991; LeVay & Nelson, 1991), projecting in turn to V2 (Figure 1). Due to the special properties of the RFs of these neurons, it is thought that they can cover the whole range of chromaticities and luminances (Vautin & Dow, 1985; Boynton & Olson, 1990; Yoshioka & Dow, 1996; Yoshioka et al., 1996), showing band-pass spatial frequency tuning for chromatic gratings (Livingstone & Hubel, 1984; Thorell et al., 1984; Lennie et al., 1990; Hubel & Livingstone, 1987; Johnson et al., 2001). Together with these cells, a second type of V1 neurons, showing direct inheritance from simple opponent cells in the LGN have been described, at least, in the blind spot area at the striate cortex (Komatsu et al., 2000). These cells are thought to be necessary for completing the filling-in process responsible for uniform color perception (Walls, 1954; Gerrits et al., 1966; Yarbus, 1967; Pessoa et al., 1998). In the interblob and stripe regions, cells show orientation selectivity, receiving their main input from the magnocellular layers of the LGN (Livingstone & Hubel, 1984, 1988; De Yoe & Van Essen, 1985; Hubel & Livingstone, 1987; LeVay & Nelson, 1991).

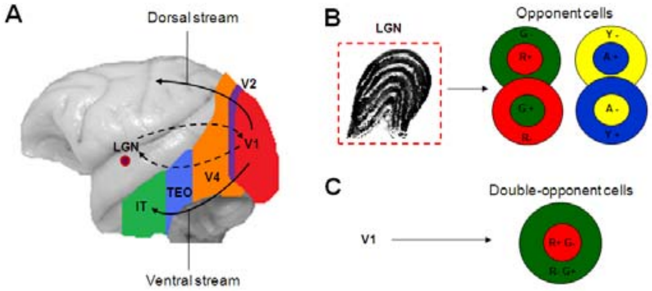


Figure 1. A. View of color-sensitive areas in the ventral stream of the macaque brain. B. RF structure showing a classical *opponent cell* in the LGN. These cells can adopt four different arrangements depending on their selectivity to a specific wavelength of light (yellow-blue and red-green opponent organization). According to the center-surround special configuration of their RFs, LGN cells respond to spots of particular color surrounding by their opponent wavelengths. Although primates do not have any yellow receptor, cells with excitatory input from simultaneously red and green cones are sensitive to yellow. C. RF structure of a *double-opponent cell*, clustered in blobs, in layer 4 of V1. Double-opponent cells have higher and more complex RFs than simple opponent cells, responding ideally to heterochromatic gratings of the appropriate spatial frequency, but also to chromatic modulation of a spatially uniform field. Based on their particular structure, these cells respond to center-surround differences in wavelength, showing selectivity for a particular stimulus size.

The idea of color and motion segregation at early visual areas was first described by Margaret Livingstone and David Hubel (1982, 1983, 1987), who identified the anatomical connections between blobs and stripes in areas V1 and V2 of the monkey. Based on their anatomical observations, these authors defended the functional segregation between the P and M pathways in both, V1 and V2. According to their model, the M pathway projects from the magnocellular layers of the LGN to the striate cortex, first to layer 4Cα and then to layer 4B, which in turn send direct and indirect projections (via stripes) to the Middle Temporal area (MT), and from there to the Posterior Parietal Cortex (PPC) (Merigan & Maunsell, 1993; Merigan et al., 1997) (Figure 2). In parallel, cells in the parvocellular layers of the LGN project to layer 4Cβ of V1, reaching the blobs and the interblobs, which directly project to respectively, the thin stripes and the interstripe regions in V2. These thin stripes and interstripe areas finally project to several and discrete subregions in V4, and from there to the IT cortex (Merigan & Maunsell, 1993). Thus, although the segregation of the visual signal was mainly considered in the earlier visual areas, the functional and anatomical independence of P and M pathways at higher processing areas has also been proposed, extending to the PPC and IT (Girkin & Miller, 2001).

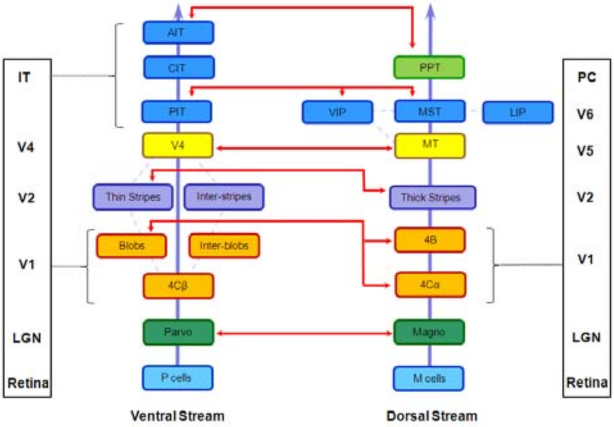


Figure 2. Modified from Merigan & Maunsell (1993). Functional organization of the ventral and dorsal streams in the primate visual system. The dashed lines represent solid projections within the same cortical area. Against the segregation hypothesis, interactions between ventral and dorsal structures have been already described. Red thick arrows indicate this map of connections, supporting the idea of a multistage ventro-dorsal communication in the visual system.

Following this traditional approach, many authors have supported the segregation hypothesis in the visual system (De Yoe & Van Essen, 1988; Martin, 1988; Desimone & Ungerleider, 1989; Felleman & Van Essen, 1991; Kaas & Garraghty, 1991). However, numerous anatomical and neurophysiological observations have already suggested the possible interdependence of ventral and dorsal routes at different stages of the visual pathway.

2.1.1. Early Visual Areas

As previously mentioned, first studies in the LGN and early cortical visual areas proposed the independence of separate color- and broad-band-orientation-sensitive regions mainly in, areas 2 and 3 of 4Cβ (V1) (Livingstone & Hubel, 1984, 1988; De Yoe & Van Essen, 1985; Hubel & Livingstone, 1987; Shipp & Zeki, 1985, 2002). These regions showed abundance of chromatically opponent units, in such a way that 70 % of neurons with non-oriented RFs presented this functional structure (Livingstone & Hubel, 1984; Ts'o & Gilbert, 1988). However, selective stainings and inactivations at different levels of the P and M pathways in the LGN, have shown that parvo- and magnocellular signals are effectively interconnected in this area (Malpeli et al., 1981; Lachica et al., 1992; Nealey & Maunsell, 1994). If such interdependence between signals exists, cells in this structure and their main input receptors should be sensitive to different combinations of visual parameters. Indeed, numerous evidences have been found supporting this idea.

In macaques, Leventhal and colleagues (1995) have shown that stimulus color, direction and orientation varied continuously among V1 cells, in such a way that non discrete selective regions can be described in this area (see also Blasdel & Fitzpatrick, 1984). According to these authors, the proportion of color-sensitive cells in V1 could be higher than the classically accepted, and their activity would be both, direction and orientation biases. From the same perspective, Zipser and colleagues (1994) have also reported color, orientation and depth coding signals in most V1 cells, and DeBruyn and collaborators (1993) found shape sensitivity in cells within and outside the CO-rich regions in bush babies.

Taken together, all these evidences provide strong arguments against the classical segregation model in the primary visual cortex (Livingstone & Hubel, 1988). From this perspective, color, shape and motion responses can be simultaneously observed in most neurons from, at least, layers 2, 3, 4 and 6 of V1, varying among cells (Leventhal et al., 1995).

In area V2, the functional segregation was also shown to be originally overestimated (Livingstone & Hubel, 1988). Neurons selective for color, shape and motion were found between the stripes (Peterhans & von der Heydt, 1993; Gegenfurtner et al., 1996). Supporting this idea, intrinsic anatomic connections have been described between cytochrome oxidase compartments in V2 (Levitt et al., 1994), suggesting that classical clusters cannot explain the RF properties observed in these neurons (Kiper et al., 1994).

One of the most complete studies showing the intercommunication between P and M pathways in early visual areas was recently developed by Friedman and colleagues (2003). These authors recorded the activity of individual neurons in V1 and V2 in the macaque monkey by flashing optimally oriented colored bars into their RFs. With this procedure, they found that color-selective cells responded to both, surfaces and edges showing orientation bias. Several authors had previously reported that color selective cells were higher concentrated in the fovea and less frequent at increasing eccentricities, while orientation selective cells would follow the opposite trend (Zeki, 1983a; Livingstone & Hubel, 1984). Contrarily to this hypothesis, Friedman's group found that V1 and V2 neurons showed a lack of correlation between color selectivity and their ability to signal edges (Friedman et al., 2003).

Studies one step further in this field have finally lead to suggest that color estimation in V1 and V2 can be extracted from orientation specific signals (Zhou et al., 2000; Friedman et al., 2003; von der Heydt et al., 2003). The fact that many oriented cells in these areas are selective for edge polarity could support this hypothesis (Gerrits & Vendrik, 1970; Land & McCann, 1971; Poggio et al., 1975; Michael, 1978a; Thorell et al. 1984; Cohen & Grossberg, 1984; Livingstone & Hubel, 1984; Conway, 2001; Johnson et al., 2001) although more and most specific studies would be necessary to prove it.

2.1.2. Higher Visual Areas

As we have seen, authors re-examining the visual segregation in areas V1 and V2 have showed clear results supporting an interactive communication between P and M pathways. In higher visual areas, the situation is quite similar. In V3, Gegenfurtner and colleagues (1997) have observed interaction between color and motion processing. Similarly, in area V4, the Superior Temporal Sulcus (STS) or MT, where segregation between color and motion was classically accepted (Zeki, 1974; Baker et al., 1981; Van Essen et al., 1981; Maunsell & Van Essen, 1983; Albright, 1984; Maunsell et al., 1990), several authors have already started to suggest their possible interaction (Felleman & Van Essen, 1991; Martin, 1992). Ferrera and colleagues (1992, 1994) have selectively blocked the parvo- and magnocellular layers of the LGN, and analyzed the effect in higher cortical areas. Their observations suggest that magnocellular inactivations only reduce responses in the dorsal stream (MT; Maunsell et al., 1990), whereas neuronal responses in the ventral stream (V4) can be reduced by blocking the activity of either the parvocellular or magnocellular layers in the LGN. In other words, while the dorsal pathway seems to primarily receive input from magnocellular layers, the ventral pathway accepts both, parvo- and magnocellular input.

As the final destination in the ventral visual stream, the IT cortex receives parvo- and magnocellular signals. Accordingly, this area has been traditionally involved in color, shape, disparity and texture complex analyses (Cowey & Gross, 1970; Gross et al., 1972; Schwartz et al., 1983; Ptito & Zatorre, 1988; Ptito et al., 1991; Tanaka et al., 1991; Komatsu et al., 1992; Zeki, 1993; Sáry et al., 1995; Buckley et al., 1997; Takechi et al., 1997; Howard et al., 1998; Zeki & Marini, 1998; Huxlin et al., 2000; Uka et al., 2000; Tanaka et al., 2001), all they necessary elements for object recognition. However, although IT cells are widely sensitive, many of them are only selective for one visual parameter, and the strength of their response varies for different factorial combinations (Komatsu & Ideura, 1993). Thus, while significant activation of the IT cortex occurs during complex visual analyses (Howard et al., 1998; Zeki and Marini, 1998; Barrett et al., 2001), the activity for simpler processing is less prominent (Corbetta et al., 1991; Gulyás et al., 1994, 1998). By significantly increasing its activity, this structure projects more efficiently to some other integrative areas, such as the fusiform gyrus or the Prefrontal Cortex (PFC), activating the neural network for object recognition and analysis (Haxby et al., 1991, 2000; Sergent et al., 1992; Köhler et al., 1995; Sams et al., 1997; Ishai et al., 1999; Nystrom et al., 2000; Barrett et al., 2001).

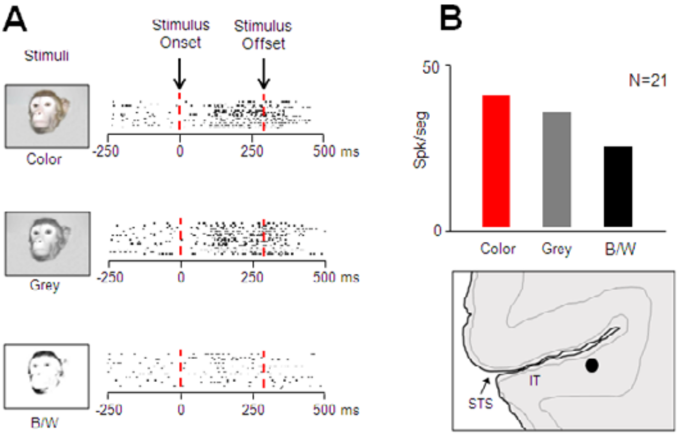


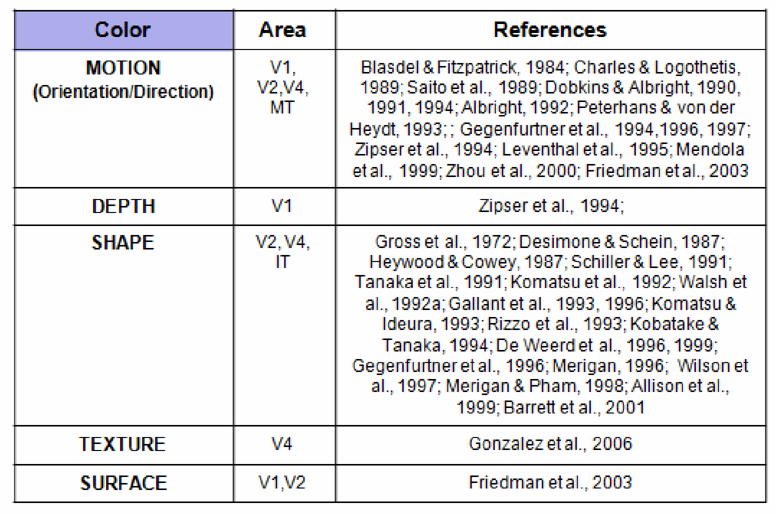
Figure 3. A. Rasters showing cell responses to three different representations of the same stimulus are plotted. The red dashed lines represent the stimulus onset and offset. According to these rasters, cells were significantly more sensitive to images when color or grey stimuli were presented, decreasing their activity for binary images. These results suggested that surface information contained in grey but not B/W images, was mainly responsible for this activity. However, subtle differences were also observed when responses to grey and color images were compared. Thus, the simultaneous presentation of surface and color increased the firing rate of the cells. B. Histogram showing the same trend for a population of 21 cells. It is clear that these cells reached their maximal firing rates when complex color stimuli were presented. A schematic section of the inferotemporal cortex, where this cell was recorded (black dot), is shown. STS: Supero Temporal Sulcus. IT: Inferotemporal cortex.

As an example of the multi-selectivity observed in IT cells, figure 3 shows the results obtained in a preliminary study developed by Gonzalez and collaborators. In this study, cell responses were recorded in the IT cortex of a macaque monkey while fixating complex face stimuli. By showing a comprehensive set of images, the stimulus eliciting the best cell response was identified and then presented in three different versions, color, grayscale and black-and-white (B/W).

Resulting from the earlier connections between the P and M pathways, dorsal structures show also mixed sensitivity to different visual attributes. One clear example comes from MT neurons. It has been described that direction-sensitive neurons in this area modulate their responses depending on color although they do not show isolated color responses (Charles & Logothetis, 1989; Saito et al., 1989; Dobkins & Albright, 1990, 1991, 1994; Albright, 1992; Gegenfurtner et al., 1994).

The following table summarizes the main studies showing combined responses for color and some other visual attributes at different stages along the visual pathway.

Table 1. Mixed responses to color and other visual attributes in human and monkey studies. Information about the specific areas considered is included, showing the intercommunication observed all along different visual stages.



Color	Area	References
MOTION (Orientation/Direction)	V1, V2,V4, MT	Blasdel & Fitzpatrick, 1984; Charles & Logothetis, 1989; Saito et al., 1989; Dobkins & Albright, 1990, 1991, 1994; Albright, 1992; Peterhans & von der Heydt, 1993; ; Gegenfurtner et al., 1994,1996, 1997; Zipser et al., 1994; Leventhal et al., 1995; Mendola et al., 1999; Zhou et al., 2000; Friedman et al., 2003
DEPTH	V1	Zipser et al., 1994;
SHAPE	V2, V4, IT	Gross et al., 1972; Desimone & Schein, 1987; Heywood & Cowey, 1987; Schiller & Lee, 1991; Tanaka et al., 1991; Komatsu et al., 1992; Walsh et al., 1992a; Gallant et al., 1993, 1996; Komatsu & Ideura, 1993; Rizzo et al., 1993; Kobatake & Tanaka, 1994; De Weerd et al., 1996, 1999; Gegenfurtner et al., 1996; Merigan, 1996; Wilson et al., 1997; Merigan & Pham, 1998; Allison et al., 1999; Barrett et al., 2001
TEXTURE	V4	Gonzalez et al., 2006
SURFACE	V1,V2	Friedman et al., 2003

2.2. Evidences For and Against a Specialized Color Centre in the Primate

Most of classical studies in color processing suggested the existence of a color centre in the primate brain. Such a critical area, involved in high chromatic analyses, was located in V4, and subdivided into two main regions, an anterior one, called V4α, and a posterior one, simply named V4, and localized at the posterior fusiform circumvolution (Zeki & Bartels, 1999). However, the exact location of this area seems to vary for every subject, extending from the collateral sulcus, at the fusiform circumvolution, to the lingual gyrus (Beauchamp et al., 1999).

Area V4 performs higher level color analyses, including the comparison of wavelength differences with surrounding objects (Lueck et al., 1989; Zeki et al., 1991; Zeki & Marini, 1998). It has been suggested that the role played by this structure would not be related with simple color processing, but more to color and shape interactive analyses of objects (Heywood & Cowey, 1987; Schiller & Lee, 1991; Walsh et al., 1992a; Merigan, 1996;

Merigan & Pham, 1998; De Weerd et al., 1996, 1999; Barrett et al., 2001). Furthermore, area V4 is an important region for visual attention, as attentional modulation appears to improve the spatial selectivity in this area (Moran & Desimone, 1985; Haenny et al., 1987; Maunsell et al., 1991; Motter, 1994; McAdams & Maunsell, 1999) and its selective lesion disrupt performance in attentionally demanding visual searching tasks (Schiller and Lee, 1991; Schiller, 1995; De Weerd et al., 1999).

In the macaque, V4 is one of the largest visual areas, occupying about 10% of the visual cortex and 5% of the neocortex (Felleman & Van Essen, 1991). Situated as an intermediate structure in the ventral visual stream (Ungerleider & Mishkin, 1982), this area receives direct inputs from V2, and projects primarily to the posterior IT cortex (area TEO) (Felleman & Van Essen, 1991). Neurophysiological studies have shown that macaque area V4 contains a high proportion of color selective cells (Schein & Desimone, 1990; Zeki, 1975, 1983b). As the complex analyses developed by these cells largely exceed the chromatic processing observed in earlier visual areas, V4 has been suggested to play an important role in color constancy (Zeki, 1980; Zeki et al., 1999). However, pure achromatopsia can be derived from different lesions at several visual structures (Cowey & Heywood, 1995; Heywood et al., 1995; Hadjikhani et al., 1998; Heywood & Cowey, 1998), and therefore, simple damage in V4 is not enough to explain the whole deficit (Kölmel, 1988; McKeefry & Zeki, 1997).

In humans, whereas ventral V4 (V4v) has been localized next to VP (V3v) (Sereno et al., 1995; De Yoe et al., 1996), its dorsal subdivision (V4d) has not been yet clearly identified, contributing to maintain the current debate on the functional equivalence between human and non-human primate area V4 (Tootell & Hadjikhani, 2001). To solve the homology problem, Zeki and colleagues (1991) proposed the fusiform and the lingual gyri in the human cortex as the equivalent areas to V4 in the monkey brain. Later on, this group suggested the posterior fusiform gyrus as a more precise location for human V4 (McKeefry & Zeki, 1997). In agreement with this idea, functional Magnetic Resonance Imaging (fMRI) studies have shown that patients with cerebral achromatopsia often present damage at this structure, together with, in some particular cases, specific damage of the lingual gyrus and the basal temporal cortex (Meadows, 1974; Green & Lessell, 1977; Lapresle et al., 1977; Damasio et al., 1980; Damasio & Frank, 1992; Allison et al., 1993; Lee et al., 2000; Girkin & Miller, 2001). The simultaneous lesion of these three structures is common in subjects affected by visual hallucinations and prosopagnosia (Damasio et al., 1982; Lee et al., 2000).

Similarly, selective lesions of the fusiform gyrus may affect face and object recognition as well as color perception (Puce et al., 1996; Kanwisher et al., 1997; Girkin & Miller, 2001). A small face-selective area has been described in the right lateral middle fusiform gyrus, (Halgren et al., 1999; Haxby et al., 1999; Rossion et al., 2000, 2003), in homology to the IT cortex (Tootell et al., 2003).

The reported data highlight the relevance of V4 and the fusiform gyrus in color processing. However, the observed color sensitivity of cells at different cortical stages has opened a debate about the existence of a possible color centre in the primate brain. In a recent study, Gonzalez and collaborators (2006) showed that the neuronal activity evoked in the human fusiform gyrus is strongly dependent on the stimulated hemifield (Gonzalez et al., 2006). This hemifield dependence indicates the early activation of this structure, suggesting that higher cortical areas can be required to combine the information from both visual hemifields. This new evidence supports the idea of a multistaged cortical system for color processing (Zeki & Marini, 1998). In agreement with this idea, it has been shown that color categorization can still occur after V4 ablation in the macaque (Walsh et al., 1992b). Additionally, lesion studies in patients with posterior cerebral infarcts demonstrated that color discrimination can be independent of color memory, reinforcing the assumption of multiple areas involved in color perception (Schoppig et al., 1999). From the same perspective, several authors found a left-dominant but mainly bilateral multistage activation of color-related areas in the human brain (Zeki et al., 1991; Corbetta et al., 1991; Howard et al., 1998; Zeki & Marini, 1998; Beauchamp et al., 1999; Barrett et al., 2001). These authors indicated that different visual areas could be selectively recruited for different chromatic analyses depending on the specific requirements of the task.

Finally, as in earlier chromatic visual areas, cells in V4 and the fusiform gyrus respond to complex combinations of visual parameters. Several neurophysiological studies in human and non-human primates have demonstrated that these cells are not only sensitive to color, but also to some other properties of the stimulus, such as the stimulus orientation (Mendola et al., 1999), and shape (Desimone & Schein, 1987; Gallant et al., 1993, 1996; Rizzo et al., 1993; Kobatake & Tanaka, 1994; Wilson et al., 1997; Allison et al., 1999; James et al., 1999; Pasupathy & Connor, 1999). In humans, Gonzalez and colleagues (2006) have found combined responses to color and texture in the fusiform gyrus. In their study, functional evoked potentials were recorded from subdural electrodes implanted in a patient suffering from occipital epilepsy. During simple fixation, dynamic squares of colorful dots were presented to the patient in both, left and right visual hemifields (contra- and ipsilaterally to the affected hemisphere). Following this procedure fusiform activation was found after dynamic-textured squares but not solid squares (Figure 4).

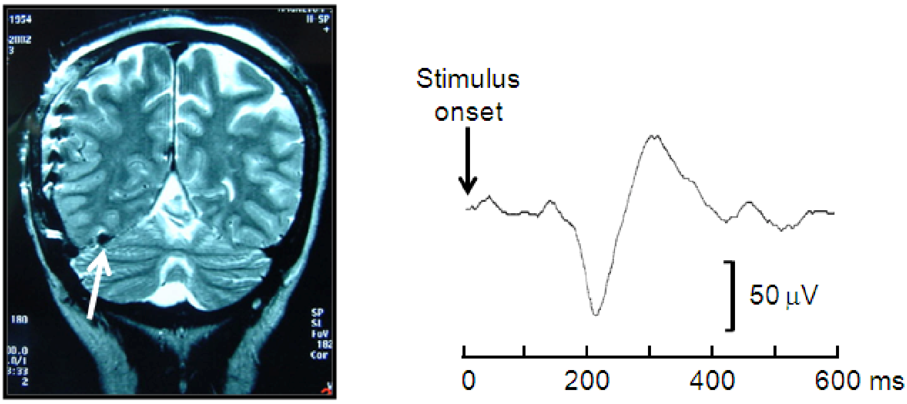


Figure 4. Visual evoked responses recorded in the right fusiform gyrus of a patient suffering from occipital epilepsy (bipolar recording; BOT strip). The stimuli used consisted of solid figures and textured squares composed by dynamic random dots, all surrounded by a dark background. Only texture-related images evoked responses in the fusiform gyrus while no activation was observed for the solid stimuli. The thick line on the abscissa indicates the time the stimulus was on. On the left side, lateral and coronal views of the brain are shown, signaling the exact location of the electrode arrays implanted.

CONCLUSION

Taken together, the reported data suggest that the segregation hypothesis for color processing could have been overestimated. The different experimental procedures and techniques required in visual neurophysiological studies, and the interest for developing regular and simple rules which could help to understand the visual function, could partially explain the possible bias.

One big source of variability could be related to the different stimuli considered in the experiments. Studies comparing simple and meaningful pattern processing have reported the activation of less and more posterior areas in both occipital and temporal lobes than those activated by complex patterns (Baker et al., 1996; Corbetta et al., 1991, 1993; Fink et al., 1997; Gulyás et al., 1994; Nobre et al., 1997). To explore this phenomenon, Zeki and Marini (1998) analyzed the possible interaction between color and stimulus patterns. In their study, several Mondrian-like scenes and pictures of natural objects dressed in natural and unnatural colors were presented to subjects during an fMRI session. The activity profiles obtained showed that although all types of stimuli activated the ventral pathway, the activity produced by natural coloured objects reached more anterior regions at the fusiform gyrus, the hippocampus and the ventrolateral frontal cortex. Unnatural colored objects, by contrast, activated the dorsolateral frontal cortex. Based on their observations, these authors have suggested that complex chromatic analyses involved in color-object definition, color memory and learning exceed the ventral areas, requiring the simultaneous activation of higher structures.

Some other studies have been more focused on the nature of the stimulus. Leventhal et al. (1995) found that color-sensitive cells in layers 2 and 3 of 4Cβ (V1) showed higher orientation-sensitivity when tested with high spatial frequency gratings, while moving bars produced lower responses. In agreement with this idea, it has been found that most cortical cells show less sensitivity to orientation when tested with sinusoidal gratings of relatively low spatial frequencies (Hammond & Pomfret, 1990; Thompson et al., 1994). Since most early studies in V1 used bars but not sinusoidal gratings as stimulus, a possible underestimation of orientation tuning in color-sensitive cells could have been produced.

Overall, we have reported here solid arguments enough to conclude that the segregation hypothesis, at least as it was originally conceived, should be now reviewed and reinterpreted. The fact that many cortical areas work together to achieve complex perceptual goals, reflects the idea of a global brain, combining the efficiency of multiple processing stages to optimize its resources. A direct effect of this model is, of course, an economical view of the brain function, as the strength of the interaction would allow a more powerful and fast communication between areas. As color processing is one of the most studied sensory phenomena, its review provides valuable information to analyze the segregation problem. However, the latest results obtained in visual neuroscience predict that similar data can already be described for some other visual attributes. The challenging task for a near future will be to integrate all this knowledge for a better understanding of the visual function.

ACKNOWLEDGMENTS

This work was partially supported by grants and BFU2007-61034, CONSOLIDER-INGENIO 2010 from the Spanish Ministerio de Educacion y Ciencia, FEDER, and Rede Galega de Nanomedicina.

REFERENCES

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106-1130.

Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science*, *255*, 1141-1143.

Allison, T., Begleiter, A., McCarthy, G., Roessler, E., Nobre, A. C., & Spencer, D. D. (1993). Electrophysiological studies of color processing in human visual cortex. *Electroencephalography and Clinical Neurophysiology*, *88*, 343-355.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex*, *9*, 415-430.

Baker, S. C., Frith, C. D, Frackowiak, R. S. J., & Dolan, R. J. (1996). Active representation of shape and spatial location in man. *Cerebral Cortex*, *6*, 612-619.

Baker, J. F., Petersen, S. E., Newsome, W. T., & Allman, J. M. (1981). Visual response properties of neurons in four extrastriate visual areas of the owl monkey (Aotus trivirgatus): A quantitative comparison of medial, dorsomedial, dorsolateral and middle temporal areas. *Journal of Neurophysiology*, *45*, 397-416.

Barrett, N. A., Large, M. M., Smith, G. L., Michie, P. T., Karayanidis, F., Kavanagh, D. J., Fawdry R, Henderson, D., & O'Sullivan, B. T. (2001). Human Cortical Processing of Colour and Pattern. *Human Brain Mapping*, *13*, 213-225.

Beauchamp, M. S., Haxby, J. V, Jennings, J. E., & DeYoe, E.A. (1999). An fMRI version of the Farnsworth-Munsell 100-hue test reveals multiple color-selective areas in human ventral occipitotemporal cortex. *Cerebral Cortex*, *9*, 257-263.

Beauchamp, M. S., Haxby, J. V., Rosen, A. C. & DeYoe, E. A. A. (2000). MRI functional case study of acquired cerebral dyschromatopsia. *Neuropsychologia*, *38*, 1170-1179.

Blasdel, G. G., & Fitzpatrick, D. (1984). Physiological organization of Layer 4 in macaque striate cortex. *The Journal of Neuroscience*, *4*, 880-895.

Boynton, R. M., & Olson, C. X. (1990). Salience of chromatic basic color terms confirmed by 3 measures. *Vision Research*, *30*, 1311-1317.

Buckley, M. J., Gaffan, D., & Murray, E. A. (1997). Functional double dissociation between two inferior temporal cortical areas: perirhinal cortex versus middle temporal gyrus. *Journal of Neurophysiology*, *77*, 587-598.

Casagrande, V. A., & Norton, T. T. (1991). Lateral geniculate nucleus: a review of its physiology and function. In: Leventhal, A. G. (Ed.), *The neural basis of visual function* (pp.41-84). London: Macmillan.

Charles, E. C., Logothetis, N. K. (1989). The responses of middle temporal (MT) neurons to isoluminant stimuli. *Investigative Ophthalmology & Visual Science*, *30*, 427.

Claeys, K. G., Dupont, P., Cornette, L., Sunaert, S., Van Hecke, P., De Schutter, E., & Orban, G.A. (2004). Color discrimination involves ventral and dorsal stream visual areas. *Cerebral Cortex*, *14*, 803-822.

Clark, V. P., Keil, K., Maisog, J. M., Courtney, S., Ungerleider, L. G., & Haxby, J. V. (1996). Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography. *Neuroimage 4*, 1-15.

Cohen, M. A., & Grossberg, S. (1984). Neural dynamics of brightness perception: features, boundaries, diffusion, and resonance. *Perception & Psychophysics*, *36*, 428-456.

Conway, B. R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). *The Journal of Neuroscience*, *21*, 2768-2783.

Corbetta, M., Miezin, F., Dobmeyer, S., Shulman, G., & Peterson, S. (1991). Selective and divided attention during visual discriminations of shape, colour and speed: functional anatomy by positron emission tomography. *The Journal of Neuroscience*, *11*, 2383-2402.

Corbetta, M., Miezin, F., Shulman, G., & Petersen, S. (1993). A PET study of visuospatial attention. *The Journal of Neuroscience*, *13*, 1202-1226.

Courtney, S. M., Ungerleider, L. G., Kil, K. & Haxby, J.V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, *6*, 39-49.

Cowey, A., & Gross, C. G. (1970). Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. *Experimental Brain Research*, *11*, 128-144.

Cowey, A., & Heywood, C. A. (1995). There's more to colour than meets the eye. *Behavioural Brain Research*, *71*, 89-100.

Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: Anatomic basis and behavioural mechanisms. *Neurology*, *32*, 331-341.

Damasio, H., & Frank, R. (1992). Three-dimensional in vivo mapping of brain lesions in humans. *Archives of Neurology*, *49*, 137-143.

Damasio, A., Yamada, T., Damasio, H., Corbett, J., & McKee, J. (1980). Central achromatopsia: Behavioural, anatomic, and physiologic aspects. *Neurology*, *30*, 1064-1071.

Dartnall, H. J., Bowmaker, J. K., & Mollon J. D. (1983). Human visual pigments: Microspectrophotometric results from the eyes of seven persons. *Proceedings of the Royal Society of London (Series B)*, *220*, 115-130.

Daw, N. W. (1968). Color-coded ganglion cells in the goldfish retina: Extension of their receptive fields by means of new stimuli. *The Journal of Physiology*, *197*, 567-592.

Daw, N. W. (1984). The psychology and physiology of colour vision. *Trends in Neurosciences*, *7*, 330-335.

DeBruyn, E. J., Casagrande, V. A., Beck, P. D. & Bonds, A. B. (1993). Visual resolution and sensitivity of single cells in the primary visual cortex (V1) of a nocturnal primate (bush baby): Correlations with cortical layers and cytochrome oxidase patterns. *Journal of Neurophysiology*, *69*, 3-18.

Derrington, A. M., Krauskopf J., & Lennie P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *The Journal of Physiology*, *357*, 241- 265.

Desimone, R., & Schein, S. J. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *Journal of Neurophysiology*, *57*, 835-868.

Desimone, R., Schein, S. J., Moran, J. & Ungerleider, L. G. (1985). Contour, color and shape analysis beyond the striate cortex. *Vision Research*, *25*, 441-452.

Desimone, R., & Ungerleider, L. G. (1989). Neural mechanisms of visual processing in monkeys. In: Boiler F. & Grafman J. (Eds.), *Handbook of Neuropsychology* (12, pp. 267-299). New York: Elsevier.

DeValois, R. L. (1965). Analysis and coding of color vision in the primate visual system. *Cold Spring Harbor Symposia on Quantitative Biology*, *30*, 567-579.

DeValois, R. L., & DeValois, K. K. (1993). A multi-stage color model. *Vision Research, 33*, 1053-1065.

DeValois, R. L., Morgan, H., & Snodderly, D. M. (1974). Psychophysical studies of monkey vision III. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision Research, 14*, 75-81.

DeValois, R. L. & Pease, P. L. (1971). Contours and contrast: responses of macaque lateral geniculate cells to color and luminance figures. *Science*, *171*, 694-696.

DeValois, R. L., Snodderly, D. M. Jr., Yund, E. W., & Hepler, N. K. (1977) Responses of macaque lateral geniculate cells to luminance and color figures. *Sensory Processes*, *1*, 244-259.

De Weerd, P., Desimone, R., & Ungerleider, L. G. (1996). Cue-dependent deficits in grating orientation discrimination after V4 lesions in macaques. *Visual Neuroscience*, *13*, 529-538.

De Weerd, P., Peralta, M. R., Desimone, R., & Ungerleider L. G. (1999). Loss of attentional stimulus selection after extrastriate cortical lesions in macaques. *Nature Neuroscience*, *2*, 753-758.

De Yoe, E. A., Carman, G. J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D., & Neitz J. (1996). Mapping striate cortex and extrastriate visual areas in human cerebral cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 2382-2386.

De Yoe, E. A., & Van Essen, D. C. (1985). Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature*, *317*, 58-61.

De Yoe, E. A., & Van Essen, D. C. (1988), Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences*, *11*, 219-226.

Dobkins, K. R., & Albright, T. D. (1990). Color facilitates motion correspondence in visual area MT. *Abstracts - Society for Neuroscience*, *16*, 1220.

Dobkins, K. R., & Albright, T. D. (1991). The use of color- and luminance-defined edges for motion correspondence. *Abstracts - Society for Neuroscience*, *17*, 524.

Dobkins, K. R., & Albright, T. D. (1994). What happens if it changes color when it moves?: the nature of chromatic input to macaque visual area MT. *The Journal of Neuroscience*, *14*, 4854-4870.

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: A mechanism of feature linking in the visual cortex? *Biological Cybernetics*, *60*, 121-130.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1-47.

Ferrera, V. P., Nealey, T. A., & Maunsell, J. H. R. (1992). Mixed parvocellular and magnocellular geniculate signals in visual area V4. *Nature*, *358*, 756-758.

Ferrera, V. P., Nealey, T. A., & Maunsell, J. H. R. (1994). Responses in macaque visual area V4 following inactivation of the parvocellular and magnocellular LGN pathways. *The Journal of Neuroscience*, *14*, 2080-2088.

Fink, G. R., Dolan, R. J., Halligan, P. W., Marshall, J. C., & Frith, C. D. (1997). Space-based and object-based visual attention: shared and specific neural domains. *Brain*, *120*, 2013-2028.

Friedman, H. S., Zhou, H., & von der Heydt, R. (2003). The coding of uniform colour figures in monkey visual cortex. *The Journal of Physiology*, *548*, 593-613.

Gallant, J. L., Braun, J., & Van Essen, D. C. (1993). Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. *Science*, *259*, 100-103.

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., & Van Essen, D. C. (1996) Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *Journal of Neurophysiology*, *76*, 2718-2739.

Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M., Carandini, M., Zaidi, Q., & Movshon, J. A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience*, *11*, 455-466.

Gegenfurtner, K. R., Kiper, D. C. & Fenstemaker, S. B. (1996). Processing of color, form, and motion in macaque area V2. *Visual Neuroscience*, *13*, 161-172.

Gegenfurtner, K. R., Kiper, D. C., & Levitt, J. B. (1997). Functional properties of neurons in macaque area V3. *Journal of Neurophysiology*, *77*, 1906-1923.

Gerrits, H. J. M., de Haan, B. & Vendrik, A. J. H. (1966). Experiments with retinal stabilized images. Relations between the observations and neural data. *Vision Research*, *6*, 427-440.

Gerrits, H. J. M., & Vendrik, A. J. H. (1970). Simultaneous contrast, fillingin process and information processing in man's visual system. *Experimental Brain Research*, *11*, 411-430.

Girkin, C. A., & Miller, N. R. (2001). Central disorders of vision in humans. *Survey of Ophthalmology*, *45*, 379-405.

Gonzalez, F., Relova, J. L., Prieto, A., Peleteiro, M., & Romero, M. C. (2006). Hemifield dependence of responses to colour in human fusiform gyrus. *Vision Research*, *46*, 2499-2504.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20-25.

Gray, C. (1999). The temporal correlation hypothesis of visual feature integration: Still alive and well. *Neuron*, *24*, 31-47.

Gray, C., & Singer, W. (1989). Stimulus specific neuronal oscillations in orientation columns of cat visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *86*, 1698-1702.

Green, G. J., & Lessell, S. (1977). Acquired cerebral dyschromatopsia. *Archives of Ophthalmology*, *95*, 121-128.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of cells in inferotemporal cortex of the macaque. Journal of Neurophysiology, *35*, 96-111.

Gulyás, B., Cowey, A., Heywood, C. A., Popplewell, D., & Roland, P. E. (1998). Visual form discrimination from texture cues: a PET study. *Human Brain Mapping*, *6*, 115-127.

Gulyás, B., Heywood, C. A., Popplewell, D., Cowey, A., & Roland, P. E. (1994). Visual form discrimination from color or motion cues: functional anatomy by positron emission tomography. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 9965-9969.

Gulyás, B., & Roland, P.E. (1994). Processing and analysis of form, colour and binocular disparity in the human brain: functional anatomy by positron emission tomography. *The European Journal of Neuroscience*, *6*, 1811-1828.

Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. H. (1998). Retinotopy and color sensitivity in human visual cortical area V8. *Nature Neuroscience*, *1*, 235-247.

Haenny, P. E., Maunsell, J. H. R., & Schiller, P. H. (1987). State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. *Experimental Brain Research*, *69*, 245-259.

Halgren, E., Dale, A. M., Sereno, M. I., Tootel, R. B. H., Marinkovic, K., & Rosen, B. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping*, *7*, 29-37.

Hammond, P., & Pomfret, C. J. D. (1990). Influence of spatial frequency on tuning and bias for orientation and direction in the cat's striate cortex. *Vision Research*, *30*, 359-369.

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L., Mishkin, M., & Carson, R. E. (1992). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *88*, 1621-1625.

Haxby, J. V., Grady, C., Ungerleider, L., & Horwitz, B. (1991). Mapping the functional neuroanatomy of the intact human brain with brain work imaging. *Neuropsychologia*, *29*, 539 -555.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *The Journal of Neuroscience*, *14*, 6336-6353.

Haxby, J. V., Petit, L., Ungerleider, L. G., & Courtney, S. M. (2000). Distinguishing the functional roles of multiple regions in distributed neural systems for visual working memory. *Neuroimage*, *11*, 380-391.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189-199.

Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C.L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 922-927.

Heywood, C. A., & Cowey, A. (1987). On the role of cortical area V4 in the discrimination of hue and pattern in macaque monkeys. *The Journal of Neuroscience*, *7*, 2601-2617.

Heywood, C. A., & Cowey, A. (1998). With color in mind. *Nature Neuroscience*, *1*, 171-173.

Heywood, C. A., Cowey, A., & Newcombe, F. (1991). Chromatic discrimination in a cortically color blind observer. *The European Journal of Neuroscience*, *3*, 802-812.

Heywood, C. A., Gaffan, D., & Cowey, A. (1995). Cerebral achromatopsia in monkeys. *The European Journal of Neuroscience, 7*, 1064-1073.

Howard, R. J., ffytche, D. H., Barnes, J., McKeefry, D., Ha, Y., Woodruff, P.W., Bullmore, E.T., Simmons, A., Williams, S. C. R., David, A. S., & Brammer, M. (1998). The functional anatomy of imagining and perceiving colour. *Neuroreport*, *9*, 1019-1023.

Hubel, D. H. (1988). *Eye, Brain, and Vision*. New York: Scientific American Library.

Hubel, D. H., & Livingstone, M.S. (1987). Segregation of form, color, and stereopsis in primate area 18. *The Journal of Neuroscience*, *7*, 3378-34 15.

Huxlin, K. R., Saunders, R. C., Marchionini, D., Pham, H. A., & Merigan, W. H. (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cerebral Cortex, 10*, 671-683.

Ingling, C. R. Jr., & Martinez, E. (1983). The spatiochromatic signal of the R-G channel. In: Mollon, J. D., & Sharpe, L. T. (Eds.), *Colour Vision* (pp. 433-444). London: Academic Press.

Ingling, C. R. Jr., & Tsou, B. H. (1988). Spectral sensitivity for flicker and acuity criteria. *Journal of the Optical Society of America*, *5*, 1374-1378.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 9379-9384.

James, T. W., Wilkinson, F., Wilson, H. R., Gati, J. S., Menon, R. S., & Goodale, M. A. (1999). fMRI activation of fusiform face and object areas by concentric and radial gratings. *Investigative Ophthalmology & Visual Science*, *40*, S819.

Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience*, *4*, 409-416.

Julesz, B. (1986). Stereoscopic vision. *Vision Research*, *26*, 1601-1612.

Kaas, J. H., & Garraghty, P. E. (1991). Hierarchical, parallel, and serial arrangements of sensory cortical areas: connection patterns and functional aspects. *Current Biology*,*1*, 248-251.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*, 4302-4311.

Kiper, D. C., Fenstemaker, S. B., & Gegenfurtner, K. R. (1997). Chromatic properties of neurons in macaque area V2. *Visual Neuroscience*, *14*, 10610-1072.

Kiper, D. C., Gegenfurtner, K. R., & Fenstemaker, S. B. (1994). Representation of color in macaque V2. *Abtracts - Association for Research in Vision and Opthalmology*, *35*, 1972.

Kobatake, E., & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology*, *71*, 856-867.

Köhler, S., Kapur, S., Moscovitch, M., Winocur, G., & Houle, S. (1995). Dissociation of pathways for object and spatial vision: a PET study in humans. *Neuroreport*, *6*, 1865-1868.

Kölmel, H. W. (1988). Pure homonymous hemiachromatopsia: findings with neuro-opthalmologic examination and imaging procedures. *European Archives of Psychiatry and Neurological Sciences*, *237*, 237-243.

Komatsu, H., & Ideura, Y. (1993). Relationships between color, shape, and pattern selectivities of neurons in the inferior temporal cortex of the monkey. *Journal of Neurophysiology*, *70*, 677-694.

Komatsu, H., Ideura, Y., Kaji, S., & Yamane, S. (1992). Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. *The Journal of Neuroscience*, *12*, 408-424.

Komatsu, H., Kinoshita, M., & Murakami, I. (2000). Neural responses in the retinotopic representation of the blind spot in the macaque V1 to stimuli for perceptual filling-in. *The Journal of Neuroscience*, *20*, 9310-9319.

Lachica, E. A., Beck, P. D., & Casagrande, V. A. (1992). Parallel pathways in macaque monkey striate cortex: anatomically defined columns in layer III. *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 3566-3570.

Land, E. H., & McCann, J. J. (1971). Lightness and retinex theory. *Journal of the Optical Society of America*, *61*, 1-11.

Lapresle, J., Metreau, R., & Annabi, A. (1977). Transient achromatopsia in vertebrobasilar insufficiency. *Journal of Neurology*, *215*, 155-158.

Lee, H. W., Hong, S. B., Seo, D. W., Tae, W. S., & Hong, S. C. (2000). Mapping of functional organization in human visual cortex. *Neurology*, *54*, 849-854.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *The Journal of Neuroscience*, *10*, 649-669.

LeVay, S., & Nelson, S. B. (1991). Columnar organization of the visual cortex. In: Leventhal A.G. (Ed.), *Vision and visual dysfunction. The neural basis of visual function* (4, 266-315). London: Macmillan.

Leventhal, A. G., Thompson, K. G., Liu, D., Zhou, Y., & Ault, S. J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3 and 4 of monkey striate cortex. *The Journal of Neuroscience*, *15*, 1808-1818.

Levitt, J. B., Kiper, D. C., & Movshon, J. A. (1994). Receptive fields and functional architecture of macaque V2. *Journal of Neurophysiology*, *71*, 2517-2542.

Livingstone, M. S., & Hubel, D. H. (1982). Thalamic inputs to cytochrome oxidase-rich regions in monkey visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *79*, 6098-6101.

Livingstone, M. S., & Hubel, D. H. (1983). Specificity of cortico-cortical connections in monkey visual system. *Nature*, *304*, 531-534.

Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *The Journal of Neuroscience*, *4*, 309-356.

Livingstone, M. S., & Hubel, D. H. (1987). Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey. *The Journal of Neuroscience*, *7*, 3371-3377.

Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement and depth: anatomy, physiology, and perception. *Science*, 240, 740-749.

Lueck, C. J., Zeki, S., Friston, K. J., Deiber, O. J., Cope, P., Cunningham, V. J., Lammertsma, A. A., Kennard, C., Frackowiak, R. S. J. (1989). The colour centre in the cerebral cortex of man. *Nature*, *340*, 386-389.

Malpeli, J. G., Schiller, P. H., & Colby, C. L. (1981). Response properties of single cells in monkey striate cortex during reversible inactivation of individual lateral geniculate laminae. *Journal of Neurophysiology*, *46*, 1102-1119.

Martin, K. A .C. (1988). From enzymes to visual perception: a bridge too far? *Trends in Neurosciences, 11*, 380-387.

Martin, K. A. C. (1992) Parallel pathways converge. *Current Biology*, *2*, 555-557.

Maunsell, J. H., Nealey, T. A., & DePriest, D. D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *The Journal of Neuroscience*, *10*, 3323-3334.

Maunsell, J. H., Sclar, H., Nealey, T. A., & DePriest, D. D. (1991). Extraretinal representations in area V4 in the macaque monkey. *Visual Neuroscience*, *7*, 561-573.

Maunsell, J. H., & Van Essen, D. C. (1983). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *The Journal of Neuroscience*, *3*, 2563-2586.

McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron* , *23*, 765-773.

McKeefry, D. J., & Zeki, S. (1997). The position and topography of the human color centre as revealed by functional magnetic resonance imaging. *Brain*, *120*, 2229-2242.

Meadows, J. C. (1974). The anatomical basis of prosopagnosia, *Journal of Neurology, Neurosurgery, and Psychiatry*, *37*, 489-501.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. H. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *The Journal of Neuroscience*, *19*, 8560-8572.

Merigan, W. H. (1996). Basic visual capacities and shape discrimination after lesions of extrastriate area V4 in macaques. *Visual Neuroscience*, *13*, 51-60.

Merigan, W., Freeman A., & Meyers S.P. (1997). Parallel processing streams in human visual cortex. *Neuroreport,* 8: 3985–3991.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369-402.

Merigan, W. H., & Pham, H. A. (1998) V4 lesions in macaques affect both single- and multiple-viewpoint shape discriminations. *Visual Neuroscience*, *15*, 359-367.

Michael, C. R. (1978a). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology*, *41*, 572-588.

Michael, C. R. (1978b). Color vision mechanisms in monkey striate cortex: Simple cells with dual opponent-color receptive fields. *Journal of Neurophysiology*, *41*, 1233-1249.

Michael, C. R. (1978c). Color-sensitive complex cells in monkey striate cortex. *Journal of Neurophysiology*, *41*, 1250-1266.

Michael, C. R. (1985). Laminar segregation of color cells in the monkey's striate cortex. *Vision Research*, *25*, 415-423.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, *6*, 414-417.

Mollon, J.D. (1989). “Tho’ she kneel’d in that place where they grew …” the uses and origins of primate colour vision, *The Journal of Experimental Biology*, *146*, 21-38.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*, 782-784.

Motter, B. C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *The Journal of Neuroscience*, *14*, 2178-2189.

Nathans, J., Thomas, D., & Hogness, D. S. (1986). Molecular genetics of human color vision: The genes encoding blue, green, and red pigments. *Science, 232*, 193-202.

Nealey, T. A., & Maunsell, J. H. R. (1994). Magnocellular and parvocellular contributions to the responses of neurons in macaque striate cortex. *The Journal of Neuroscience*, *14*, 2069-2079.

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesalum, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, *120*, 515-533.

Nystrom, L. E., Braver, T. S., Sabb, F. W., Delgado, M. R., Noll, D. C., & Cohen, J. D. (2000). Working memory for letter, shapes and locations: fMRI evidence against stimulus-based regional organization in human prefrontal cortex. *Neuroimage*, *11*, 424-446.

Optican, L. M., & Richmond, B. J. (1987). Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. III. Information theoretic analysis. *Journal of Neurophysiology*, *57*, 162-178.

Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology*, *82*, 2490-2502.

Pessoa, L., Thompson, E., & Noe, A. (1998). Finding out about filling-in: a guide to perceptual completion for visual science and the philosophy of perception. *The Behavioral and Brain Sciences*, *21*, 723-748.

Peterhans, E., & von der Heydt, R. (1993). Functional organization of area V2 in the alert macaque. *The European Journal of Neuroscience*, *5*, 509-524.

Poggio, G. F., Baker, F. H., Mansfield, R. J. W., Sillito, A., & Grigg, P. (1975). Spatial and chromatic properties of neurons subserving foveal and parafoveal vision in rhesus monkeys. *Brain Research*, *100*, 25-59.

Ptito, A., & Zatorre, R. J. (1988).Impaired stereoscopic detection thresholds after left or right temporal lobectomy. *Neuropsychologia*, *26*, 547-554.

Ptito, A., Zatorre, R. J., Larson, W. L., & Tosini, C. (1991). Stereopsis after unilateral anterior temporal lobectomy. Dissociation between local and global measures. *Brain*, *114*, 1323-1333.

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letter strings, and textures: A functional magnetic resonance imaging study. *The Journal of Neuroscience*, *16*, 5205-5215.

Reid, R. C., & Shapley, R. M. (1992). Spatial structure of cone inputs to receptive fields in primate lateral geniculate nucleus. *Nature*, *356*, 716-718.

Reynolds, J. H., & Desimone, R. (1999). The role of neural mechanisms of attention in solving the binding problem. *Neuron*, *24*, 19-29.

Rizzo, M., Nawrot, M., Blake, R., & Damasio, A. (1993). A human visual disorder resembling area V4 dysfunction in the monkey. *Neurology*, *42*, 1175-1180.

Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, *126*, 2381-2395.

Rossion, B., Dricot, L., Devolder, A., Bodart, J. M., Crommelinck, M., & De Gelder, B. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *12*, 793-802.

Saito, H., Tanaka, K., Isono, H., Yasuda, M., & Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research*, *75*, l-l 4.

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., & Lounasmaa, O. V. (1997). Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience*, *77*, 49-55.

Sáry, G., Vogels, R., Kovacs, G., & Orban, G. A. (1995). Responses of monkey inferior temporal neurons to luminance, motion, and texture-defined gratings. *Journal of Neurophysiology*, *73*, 1341-1354.

Schein, S. J., & Desimone, R. (1990). Spectral properties of V4 neurons in the macaque. *The Journal of Neuroscience, 10*, 3369-3389.

Schiller, P. H. (1995). Effect of lesions in visual cortical area V4 on the recognition of transformed objects. *Nature*, *376*, 342-344.

Schiller, P. H., & Lee, K. (1991). The role of primate extrastriate area V4 in vision. *Science*, *251*, 1251-1253.

Schiller, P. H., & Logothetis, N. K. (1990). The color-opponent and broad-band channels of the primate visual system. *Trends in Neurosciences*, *13*, 392-398.

Schoppig, A., Clarke, S., Walsh, V., Assal, G., Meuli, R., & Cowey, A. (1999). Short-term memory for colour following posterior hemispheric lesions in man. *Neuroreport*, *10*, 1379-1384.

Schwartz, E. L., Desimone, R., Albright, T. D., & Gross, C. G. (1983). Shape recognition and inferior temporal neurons. Proceedings of the National Academy of Sciences of the United States of America, *80*, 5776-5778.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., & Tootell, R. B. H. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*, 889-893.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. *Brain*, 115, 15-36.

Shipp, S., & Zeki, S. (1985). Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature*, *315*, 322-325.

Shipp, S., & Zeki, S. (2002). The functional organization of area V2, I: specialization across stripes and layers. *Visual Neuroscience*, *19*, 187-210.

Singer, W. (1999). Neuronal synchrony: A versatile code for the definition of relations? *Neuron*, *24*, 49-65.

Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology*, *66*, 170-189.

Tanaka, H., Uka, T., Yoshiyama, K., Kato, M., & Fujita, I. (2001). Processing of shape defined by disparity in monkey inferior temporal cortex. *Journal of Neurophysiology*, *85*, 735-744.

Takechi, H., Onoe, H., Shizuno, H., Yoshikawa, E., Sadato, N., Tsukada, H., & Watanabe, Y. (1997). Mapping of cortical areas involved in color vision in non-human primates. *Neuroscience Letters*, *230*, 17-20.

Thompson, K. G., Leventhal, A. G., Zhou, Y., & Liu, D. (1994). Stimulus dependence of orientation and direction sensitivity of cat LGNd relay cells without cortical inputs: a comparison with area 17 cells. *Visual Neuroscience*, *11*, 939-951.

Thorell, L. G., DeValois, R. L. & Albrecht, D. G. (1984). Spatial mapping of monkey Vl cells with pure color and luminance stimuli. *Vision Research*, 24, 75l-769.

Tootell, R. B. H., & Hadjikhani, N. (2001). Where is 'dorsal V4' in human visual cortex? Retinotopic, topographic and functional evidence. *Cerebral Cortex*, *11*, 298-311.

Tootell, R. B. H., Tsao, D., & Vanduffel, W. (2003). Neuroimaging weighs in: humans meet macaques in "primate" visual cortex. *The Journal of Neuroscience, 23*, 3981-3989.

Treisman, A. (1986). Features and objects in visual processing. *Scientific American*, *255*, 114-125.

Ts'o DY, & Gilbert CD (1988) The organization of chromatic and spatial interactions in the primate striate complex. *The Journal of Neuroscience*, *8*, 1712-1727.

Uka, T., Tanaka, H., Yoshiyama, K., Kato, M., & Fujita, I. (2000). Disparity selectivity of neurons in monkey inferior temporal cortex. *Journal of Neurophysiology*, *84*, 120-132.

Ungerleider, L. G., Courtney, S. M., & Haxby, J. V. (1998). A neural system for human visual working memory. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 883-890.

Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, *4*, 157-165.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In: Ingle, D. J., Goodale, M. A., & Mansfield, R. J. W. (Eds.), *Analysis of visual behavior* (pp. 549-586). Cambridge, M. A.: M. I. T. Press.

Van Essen, D. C., Maunsell, J. H., & Bixby, J. L. (1981). The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic organization. *The Journal of comparative neurology*, *199*, 293-326.

Vautin, R. G., & Dow, B. M. (1985). Color cell groups in foveal striate cortex of the behaving macaque. *Journal of Neurophysiology*, *54*, 273-292.

von der Heydt, R., Friedman, H. S., & Zhou, H. (2003). Searching for the neural mechanisms of color filling-in. In: Pessoa, L., & De Weerd, P. (Eds.), *Filling-in: From Perceptual Completion to Skill Learning* (pp. 106-127). New York: Oxford University Press.

Walls, G. L. (1954). The filling-in process. *American Journal of Optometry and Archives of American Academy of Optometry*, *31*, 329-341.

Walsh, V., Butler, S. R., Carden, D., & Kulikowski, J. J., (1992a). The effects of V4 lesions on the visual abilities of macaques: shape discrimination. *Behavioural Brain Research*, *50*, 115-126.

Walsh, V., Kulikowski, J. J., Butler, S. R., & Carden, D. (1992b). The effects of lesions of area V4 on the visual abilities of macaques: colour categorization. *Behavioural Brain Research*, *52*, 81-89.

Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology*, *29*, 1115-1156.

Wilson, H. R., Wilkinson, F., & Asaad, W. (1997). Concentric orientation summation in human form vision. *Vision Research*, *37*, 2325-2330.

Yarbus, A. L. (1967). *Eye Movements and Vision*. New York: Plenum Press.

Yoshioka, T., & Dow, B. M. (1996). Color, orientation and cytochrome oxidase reactivity in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, *76*, 71-88.

Yoshioka, T., Dow, B. M., & Vautin, R. G. (1996). Neuronal mechanisms of color categorization in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, *76*, 51-70.

Zeki, S. M. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *The Journal of Physiology*, *236*, 549-573.

Zeki, S. M. (1975). Colour coding in rhesus monkey prestriate cortex. *Brain Research, 53*, 422-427.

Zeki, S. (1980). The representation of colours in the cerebral cortex. *Nature*, 284, 412-418.

Zeki, S. (1983a). The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. *Proceedings of the Royal Society of London* (*Series B*), *217*, 449-470.

Zeki, S. (1983b). Colour coding in the cerebral cortex: the reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience*, *9*, 741-765.

Zeki, S. (1990). A century of cerebral achromatopsia. *Brain*, *113*, 1721-1777.

Zeki, S. (1993). *A vision of the brain*. Oxford: Blackwell.

Zeki, S., Aglioti, S., McKeefry, D., & Berlucchi, G. (1999). The neurological basis of conscious color perception in a blind patient. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 14124-14129.

Zeki, S., & Bartels, A. (1999). The clinical and functional measurement of cortical activity in the visual brain, with special reference to the two subdivisions (V4 and V4 alpha) of the human colour centre. *Philosophical transactions of the Royal Society of London* (*Series B*), *354*, 1371-1382.

Zeki, S., & Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain*, 121, 1669-1685.

Zeki, S., McKeefry, D. J., Bartels, A., & Frackowiak, R.S. (1998). Has a new color area been discovered? *Nature Neuroscience*, *1*, 335-336.

Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience*, *11*, 641-649.

Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *The Journal of Neuroscience*, *20*, 6594-6611.

Zipser, K., Lee, T. S., Lamme, V. A. E., & Schiller, P. H. (1994). Invariance of figure-ground segregation mechanisms in Vl for depth, orientation, luminance, and chrominance cues. *Abstracts - Association for Research in Vision and Ophthalmology* (*ARVO*), *35*, 1973.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 185-202

Chapter 6

IS COLOUR COMPOSITION PHENOMENAL?[*]

Vivian Mizrahi
Department of Philosophy, University of Fribourg, Switzerland

ABSTRACT

Colour composition divides colours into two types: unitary and binary colours. Colours which are not composed are said to be "unique" or "unitary" colours, whereas composed colours are always binary. Colour composition and the distinction between unitary and binary colours have played a major role in colour science and in the philosophy of colours. They have for example been invoked to introduce opponent-processes in the mechanisms underlying colour vision and have been used to criticize philosophers who defend a physicalist view on the nature of colours. Most philosophical or scientific theories suppose that colour composition judgments refer to the way colours appear to us. The dominant view is therefore *phenomenalist* in the sense that colour composition is *phenomenally* given to perceivers. This paper argues that there is no evidence for a phenomenalist view of colour composition and that a conventionalist approach should be favoured.

We can express a lot of judgments about the colours we perceive. Most observers judge for example that red is more similar to orange than it is to blue; that no shade of yellow is a shade of blue; or that red and green, orange and blue, and yellow and purple are pairs of maximally dissimilar colours. All those judgments express colour structural relations, i.e. relations that colours bear to each other. Among colour structural relations, colour composition has received tremendous attention by philosophers and scientists from fields as diverse as physics, physiology, psychology, artificial intelligence, linguistics, anthropology, etc.

Colour composition divides colours into two types: unitary and binary colours. Colours which are not composed (or unmixed) are said to be "unique" or "unitary" colours, whereas

---

[*] Thanks to M. Nida-Rümelin, J. Suarez, Y. Jraissati and D. Gross for helpful comments and criticisms. This paper was written with the support of a grant from the SNF (Swiss National Science Foundation).

composed (or mixed) colours are always binary. According to the prevailing view of colour science there are only six unitary colours: red, green, blue yellow black and white. The remaining colours are all binary colours: for example orange is always said to be somewhat reddish and somewhat yellowish, whereas purple is at the same time bluish and reddish.

The goal of this paper is to investigate the nature of colour composition and the foundation of the unitary/binary colours distinction. Colour composition and the distinction between unitary and binary colours have played a major role in colour science and in the philosophy of colours. They have for example been invoked to introduce opponent-processes in the mechanisms underlying colour vision[+] and have been used to criticize philosophers who defend a physicalist view on the nature of colours.[§] As I will try to show in this paper, most philosophical or scientific theories suppose that colour composition judgments refer to the way colours appear to us. The dominant view is that colour composition is *phenomenally* given to all human "normal" human observers. To judge for example if orange is binary or unitary or to evaluate its reddishness, we must turn to our colour experiences. As I will try to show, there is little evidence for the "phenomenalist" view of colour composition. Unlike the dominant phenomenalist view, which relies solely on individuals' colour experience, I will defend the idea that judgments about colour composition and the distinction between unitary and binary colours are essentially cultural and originate from communicational needs and constraints.

The paper will begin by a short overview of the historical background of the phenomenalist view about colour composition (§I). Then in §II and §III, I will argue that there is not enough evidence to conclude in favour of a phenomenalist view of the binary/unitary colours distinction and of colour composition. By exploiting an analogy with the perception of temperature, I will show that the phenomenalist approach to colour composition gives an unsatisfactory account of colour experiences and that a conventionalist view of the unitary/binary distinction is therefore preferable (§IV).

1. A SHORT HISTORICAL OVERVIEW OF THE PHENOMENALIST VIEW ABOUT COLOUR COMPOSITION

The publication in 1969 of Berlin & Kay's "Basic Colour Terms" has had a great impact on the scientific community in large part due to the fact that it helped linguists and anthropologists to give a scientific response to linguistic relativism. Linguistic relativism, which originated with the work of Herder [1772/2002] and von Humboldt [1820/1997] came to prominence through the work of Edward Sapir [1985] and his student Benjamin Lee Whorf [1956]. Linguistic relativism, today often referred as "the Sapir-Whorf hypothesis", is the thesis that the semantic structures of natural languages are incommensurable.[±] According to an extreme view of linguistic relativism, there is no way for speakers of different languages to

---

[+] See Jameson & Hurvich 1955.

[§] See for example Cohen 2003, Hardin 1988, Thompson 1995.

[±] Whorf tells us for example that: "We dissect nature along lines laid down by our native languages. The categories and types that we isolate from the world of phenomena we do not find there because they stare every observer in the face. [...] We cut nature up, organize it into concepts, and ascribe significances as we do, largely because we are parties to an agreement to organize it in this way - an agreement that holds throughout our speech community and is codified in the patterns of our language" [Whorf 1956: 214] have converging views on reality because each language structures reality in its own way.[§] In the challenge raised by linguistic relativism, colour naming has played a central role by providing linguists with abounding cross-cultural data. Because nothing in the physical reality can justify segmenting the colour spectrum into categories, the relativist assumption is that different languages deploy very different systems of colour naming and that different cultures partition the colour spectrum in dramatically different ways.[*]

In 1969, Berlin and Kay argued, against the Sapir-Whorf hypothesis, that colour categories across different cultures are not incommensurable. Relying on an extensive data collection across ninety-eight languages, they claimed that colour categories converge universally to shared basic colour categories. Contrarily to the relativist assumptions, the comparative colour naming survey of Berlin and Kay showed that the partitioning of the colour space by linguistic categories could be accounted for by universal principles.

Soon enough Berlin and Kay's powerful linguistic theory of colour categorization has been linked to theories about colour perception, and in particular to Hering's colour opponency model. In 1878[±] Hering hypothesized that colour vision was based on four chromatic and two achromatic elementary, or unitary, colour perceptions (*Urfarben*) organized in two opponent processes (red vs. green and yellow vs. blue) and one non-opponent process (black vs. white). Hering's evidence for his opponent process model is essentially phenomenal in the sense that a colour is considered to be elementary if it is not experienced as a mixture[€] and colours are said to be opponent just in case they are mutually exclusive.[+] In 1978, Kay and McDaniel argued that the most basic universally colour categories distinguished by Berlin and Kay were identical with Hering's six primaries, while all other colour categories were supposed to be fuzzy set recombination of those six unitary hues. Except notable criticisms[¥] and developments[£], current works in colour categorization continue to share Kay and McDaniel insights and consider Hering's primaries to be the most likely universal foundation for colour naming across cultures. Whereas it seemed that segmenting the colour spectrum into categories could not be derived from the physics of light or coloured objects, human colour perception, and in particular Hering's model of colour vision, seemed to offer a straightforward explanation of the universality of colour categories. Contrary to the previous relativist tradition, colour naming was not supposed to result from arbitrary internalized categories, but rather to be caused by innate perceptual processes.

While much research has been conducted in order to provide empirical data to confirm Hering's opponency model[≠], Hering's fundamental assumptions about colour experiences have never been closely scrutinized. What was presupposed by Hering, and what seems widely assumed to this day, is that colour composition and the distinction between unitary and binary colours are accessible through visual colour experiences and can therefore be

---

[§] According to Lucy, Whorf's view has been abusively assimilated to "a "prisonhouse" view of language in which one's thinking and behavior is completely and utterly shaped by one's language" [Lucy: 1992].

[*] See e.g. Boas 1911; Hoijer 1954.

[±] Hering 1920/1964.

[€] According to Hering [1920/1964] and contrarily to Helmoltz [1924] trichromatic model, yellow for example cannot be a mixture because the sensation of yellow is elementary.

[+] For instance, blue and yellow are said to be opponent pairs because "Yellow can have a red or green tinge, but not a blue one; blue can have only either a red or a green tinge, and red only either a yellow or a blue one"

[¥] See Saunders 2000; Saunders & van Brakel 1997; Jameson & D'Andrade 1997; Mausfeld 1997; Roberson, Davies and Davidoff 2000.

[£] See Regier, Kay & Cook 2005.

[≠] See Hurvich & Jameson 1957.

exploited by observers to differentiate and categorize colours. In particular, if Berlin and Kay's distinction between basic colour terms and non-basic colour terms is supposed to be explained by colour vision, it is because linguistic colour categories are supposed to reflect some basic facts about colour *experiences*. For example, Hardin asserts:

> It should now be apparent that, far from language carving out categories from a structureless colour space, the basic linguistic categories themselves have been induced by perceptual saliencies common to the human race [Hardin 1988: 168]

Universalism about colour categories which emerged from cross-cultural studies in colour naming research has therefore been connected to Hering's opponent theory of colour vision through the following two assumptions:

- universalism of colour categorization is explained by universalism of colour vision[*]
- Hering's opponent processes in colour vision are detectable through colour experiences.

To put it roughly, the traditional universalist view about colour categorization is that people categorize colours in almost the same way, because they perceive colours in approximately the same way.[+]

Contrarily to this general picture, and following recent studies in colour naming research and psychology, I will claim that there is no evidence for a distinction between unitary and binary colours *at the phenomenal level*. I will argue in particular that experiments in colour vision alone do not support Hering's distinction between unitary and binary colours and that it is only by using pre-established colour categories that colours are divided into unitary and binary colours. If this general approach is correct, then universal colour categorization, as well as colour lexical distinctions, is not directly supported by the structure of colour experiences but should receive a different explanation than the one provided by the phenomenalist view on colour categorization.

2. THE PHENOMENAL EVIDENCES FOR THE UNITARY/BINARY COLOUR DISTINCTION

Colour categories group together different colours and colour experiences. But according to the Berlin and Kay's tradition, colour naming does not rely on colour similarities only. Among the colour relations allegedly necessary to explain colour naming across cultures, colour composition plays a major role. The term color composition refers to the assumption

---

[*] The original view of universalism about colour categories, defended by Kay and McDaniel 1978, was that universals in colour naming could be explained by neurological properties of the visual system. Since several studies in neurophysiology [Abramov 1997; Abramov and Gordon 1994; Derrington et al. 1984] concluding that there is no evidence for a biological basis for Hering's oppency model, most universalists (see for example Kay and Maffi 1999: 746) take "universal constraints on colour naming to be based on presumed universals of colour appearance – for example, on opponent red/green and yellow/blue phenomenal channels – but on no specific neural substrate, retinal, geniculate, or cortical." [Kay 2005: 40].

that some colours or colour experiences can be analyzed into combinations of other, more basic, colours. Oranges, for example, - according to the prevailing view - seem to be both reddish and yellowish and purples seem to be both bluish and reddish. In contrast, there are particular shades of red, green, blue, and yellow which appear not to be composed of any other colours, or so it is commonly assumed.. Talk of colour composition relies therefore on a distinction between the "pure" colours, called unitary colours, and all the other colours which are assumed to be composed and called "binary colours".

Although the idea of colour composition is very old and can be traced back to antiquity, it is only with Hering that a consensus regarding the number and the choice of the unitary colours has emerged in the scientific community.* Hering justified the existence of six elementary colours by claiming that our visual system involves three opponent processes: one for red-green, one for yellow-blue, and a third, qualitatively different from the first two, for black-white. According to Hering and most colour specialists, the distinction between unitary and binary colours is primarily phenomenal.+ But how do unitary colours appear in experience and is there any evidence for a phenomenal distinction between unitary and binary colours?

The distinction between unitary and binary colours has been approached in the scientific literature in basically two types of studies: colour naming and cancellation experiments. The colour naming approach to unitary colour determination relies on direct introspection and asks observers to describe colour samples by assigning a percentage of a limited set of colour terms. Cancellation experiments on the other hand rely on psychophysical measurements of Hering's opponent processes. As we shall see, these two types of studies mirror in fact the two major claims hypothesized in Hering's opponent colour theory: first, there are only six colours that are perceived as "pure" or unitary; and, second, the six unitary colours organized in opponent pairs are sufficient to derive any other colour that we can experience. Contrary to what is usually assumed in the literature, I will claim that these experiments about unitary colours *do not show* that the unitary/binary distinction is a phenomenal distinction.

The colour naming test developed by Sternheim and Boynton [1966] is the most well-known psychophysical method for assigning uniqueness to a colour. Its goal is to identify the unitary colours by determining which colour terms are necessary and sufficient to describe the complete spectrum. In this test, the subject is asked to describe the appearance of coloured samples by assigning percentages from a specified set of colour terms. If a colour term appears to be both necessary and sufficient to describe a range of colour samples, the colour is classified as unitary. Thus, according to Sternheim and Boynton, the term 'orange' for example is unnecessary, since subjects are able to describe an orange-looking stimulus entirely in terms of yellow and red, whereas, on the contrary, stimuli appearing yellow cannot be described by any other term than "yellow". With this method, 'red', 'yellow', 'green' and 'blue' were proved to be both necessary and sufficient for the description of any perceived spectral colour.

But as stressed by Saunders and van Brake [1997: §4.2] asking the observer to use specific words to describe perceived colours tells us more about his mastery of colour

---

+ Or as Pinker put it: "The way we see colours determines how we learn words for them, not vice versa." [Pinker 1994: 63].

* See Dinah Gross (2009) and Martine Nida-Rümelin (2009) for an extended presentation of the various meanings of "primary colours" through history.

+ Ibid.

vocabulary than about the phenomenal content of his perception. The problem is that the task of describing colour appearances by using colour terms is constrained by the culture's consensus about colour terms. Far from being a test about the phenomenology of colour perception, colour naming experiments can be considered as a test about our colour naming structure. More generally, it seems doubtful to use verbal reports to study the particular properties of colour experiences, because there seems to be no congruent correlation between the way subjects use colour terms and the way they perceive colours. Various studies[*] show that subjects who classify colours in similar ways can nonetheless have very different colour experiences. The most remarkable example is certainly the case of protanopes who can learn to use the term "red" even if they are quite insensitive to the red end of the spectrum. Although similarity tests show that protanopic colour experience differs dramatically from normal trichromatic colour experience, some protanopes exhibit a colour naming behaviour that would not distinguish them from normal trichromats. [+]

If colour naming technique cannot demonstrate the phenomenal reality of the unitary colours, is the cancellation method used by Hurvich and Jameson more promising? Hurvich and Jameson's experiments are founded in Hering's opponent process theory which states that the human colour vision system operates with three independent opponent processes: red-green, blue-yellow and white-black. The basic idea behind Hurvich and Jameson's experiments is that opponency prevents both members of any opponent pairs to appear as "mixed" together: there are for example no reddish greens or yellowish blues.[§] When blue and yellow lights are mixed together they produce white and not bluish yellow, because blue and yellow cancel each other. If one starts with a mixed colour, like orange, it is therefore possible to mix orange with a unitary blue to cancel out the yellow component and obtain a pure red. This is the basic idea of Jameson and Hurvich's cancellation experiments: the strength of the cancelled colour component is determined by the amount of the cancellation colour used to reach the equilibrium of the opponent system.

The cancellation method is used to obtain the curves representing the colour opponency system. The first step when using this method is to identify for each observer their unitary red, green, yellow and blue. Then monochromatic lights are presented one after the other and the observer is asked to cancel out one of the perceived colours if the wavelength is not already a unitary colour. So, for example, when the observer is presented with an orange patch of light, he is instructed to cancel out the yellow component by using the unitary blue that has been formerly identified. The cancellation is total when the blue-yellow opponent system reaches the equilibrium, which is when unitary red is perceived by the observer. The amount of blue used to reach the equilibrium can then be taken as an indicator of the strength of the yellow component contained in the initial orange.

The cancellation experiments cannot however provide any empirical evidence for the phenomenal reality of the unitary/binary distinction because they rely on a *a priori* choice of the unitary colors. In order to be able to conclude for example that the yellow component of a perceived orange has been cancelled out, one must first acknowledge the existence of a unitary red which guarantees that the equilibrium has been reached. For this reason, it is

---

[*] Cf. Shepard and Cooper 1992; Jameson and Hurvich 1978.

[+] Cf. Jameson and Hurvich 1978.

[§] It appears however that in the occidental population many people consider green as composed of yellow and blue.

unwarranted to say that the existence of Hering’s opponent systems has been confirmed by Jameson and Hurvich’s cancellation experiments.

The mere fact that there is a systematic pattern in the way colours change cannot support the hypothesis that there is a phenomenal distinction between unitary and binary colours or the fact that apparent colours are generated by Hering’ antagonistic processes. In fact, there are as many different systematic patterns in additive colour mixtures as there are choices about what lights are first singled out and then used to perform the experiment. Take for example a green patch of light projected onto a white surface. If one add a blue light to a green light it turns into cyan. One could therefore argue from this experiment that green is a binary colour and that adding a blue light cancels its yellow component out yielding the coloured beam of light to appear cyan. One could also argue, as pointed out by Abramov and Gordon, that cancellation experiments show opponent processes to be chartreuse-violet and teal-cherry:

> hue cancellation studies demonstrate that hue is organized in opponent fashion: any stimulus that elicits some sensation of G can be added to one eliciting R in order to cancel R…However, there is no obvious a priori justification for these precise axes; the axes might be chartreuse-violet and teal-cherry. [Abramov & Gordon 1994: 468]

What is problematic about the cancellation tests is the preliminary choice of certain hues used for cancellation. What these experiments really show is that Hering’s distinction between unitary and binary colours is compatible with the way we perceive additive colour mixing.* But this is of course true of many alternative theories, including theories which deny that there is any phenomenal difference between unitary and binary colours. According to a theory that denies the theoretical distinction between unitary and binary colours, the cancellation experiments only show that systematic changes in the spectral composition of lights can be correlated with systematic changes in the colours perceived by a given observer. In other words, the cancellation experiments presented above shows that by adding a light perceived as blue in isolation to a light perceived as orange causes the perceived orange light to shift from orange to red and conversely that adding a light perceived in isolation as orange causes a blue light to shift from blue to red. But if cancellation experiments do not provide any decisive evidence for the claim that there is some yellow component in orange, why is this way of talking abundantly used in colour science and in every day life? Is the difference between unitary colours and binary colours not obvious?

One can argue that although there are no uncontroversial empirical evidences for the unitary binary distinction, the phenomenal evidences are undisputable: the way unitary colours look to me is different from the way binary colours look to me because when I have an experience of unitary colour I can only distinguish one component whereas when I have an experience of a binary colour I can distinguish two components. However, introspection has been criticized for not being a reliable source of evidence for phenomenal facts.* One could therefore argue that the fact that most people are willing to describe their own colour

---

* In fact, as noted since 1907, Hering’s opponent processes are not satisfactorily confirmed by spectral mixtures. It has been observed in particular that canceling unitary red with a green light always produce yellowish appearance instead of a whitish appearance as predicted by the theory.

* See Hurlburt and Schwitzgebel 2007.

experiences in terms of the unitary/binary distinction does not necessarily imply that the unitary/binary distinction is anchored in the phenomenology of colour.

It seems, moreover, that the evidences based on introspection are not as uncontroversial as they appear at first sight and that a careful examination of the character of one's own experience shows that the appearance of binary colours does not really differ from the appearance of unitary colours. The claim that a colour is binary seems to imply that a binary colour is complex in the following sense: when in a unitary colour we can distinguish only one component, in looking at a binary colour we can differentiate two components. The experience of a binary colour would therefore seem to be more complex than the experience of a unitary colour. But, contrary to this supposition, it seems difficult to hold that experiences of binary colours are somewhat more complex than experiences of unitary colours.

Consider an analogy with shapes.

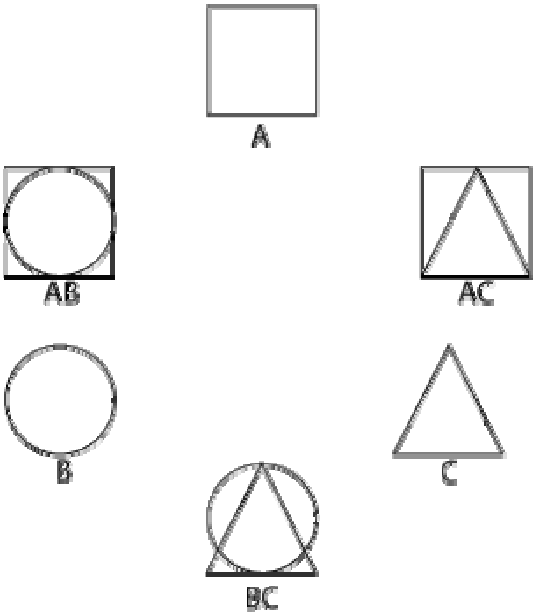


Figure 1.

Although there is nothing in common between A, B and C, they share a phenomenal "simplicity" that is not present in AB, AC and CB. Inversely, AB, AC and CB share a phenomenal "complexity" which A, B and C lack. Notice that each "composed" shape bears also some resemblance relations with the "simple" shapes. AC, for example, resembles both to A and C.

In the case of the above geometrical example it seems correct to say that there is a phenomenal difference in complexity between A, B and C, on the one hand, and AB, BC and AC on the other hand. It seems clear however that there is no equivalent difference in complexity between binary hues and unitary hues in the case of colours. With respect to simplicity, colours seem in effect to be all alike. As often stressed by philosophers, all colours appear to be “simple” and “unanalysable”.[*] Colours can be said to be unitary or binary, but introspection does not seem to confirm a corresponding distinction at the level of colour experiences. Of course, it could be argued that the distinction between unitary and binary colours does not imply any difference with respect to the complexity of colour experience, but such a claim would require a clarification of the notion of colour composition at issue in order to make it understandable in what sense one can say that a composed colour is not more complex than a pure colour.

3. THE PHENOMENAL EVIDENCES FOR COLOUR COMPOSITION

We have seen so far that there is no evidence for a phenomenal difference between unitary and binary colours. In other words, it appears that there is no evidence that observers can distinguish on the basis of their colour experience alone which colours are unitary and which colours are binary. What I would like to examine now are the possible phenomenal evidences in favour of colour composition itself. In other words, I would like to investigate the reasons given to say that a given colour is said for example to be composed of blue and red instead of violet or orange. I would like in other words to consider in what way colour composition is supposedly given in colour experience. However, to address this issue, we must first ask: what is “phenomenal colour composition”?

“Composition” is generally used in mereology to express the relation between the components and the whole they compose; where “components” are the parts available as individual units, regardless of their interaction with the other parts of the whole”.[+] A heap of rocks is for example composed of rocks and a sentence is composed of words.

If we follow this practice, colour composition should be understood as the relation between a binary colour and its chromatic parts. But as stressed for example by Hardin, there is no clear sense in which we can say that a binary colour has parts. To circumvent this difficulty Hardin proposes to understand colour composition not in terms of mereological relation, but in terms of a vector:

> There seems to have been tendency to think that if colours are analyzed they are analyzed into parts, whereas we might better think of them as being, like vectorial quantities in physics, analyzable into components. A component of a vector is not part of a vector. [Hardin 1988: 43-44]

The image of vectorial decomposition is different from parthood relations, but it is not clear how talk about vectors can help us to have a better understanding of colour composition and how it is accessible in colour experience.

Colour composition is expressed in terms of relative proportion: a given composed colour Cc is equivalent to a certain amount of colour C1 and colour C2. A common way to express colour composition is to give the relative proportion of a shade’s components (a given shade of orange can be for example 60% red and 40% yellow) or to express colour (di)similarities by comparing the amount of a shade’s components: a given chip of orange can have for

---

[*] See Locke 1689: Bk II, Ch. II, par. 1. See also Hume 1739/1983: Bk. I, Pt. VII, footnote.

[+] Varzi 2003.

example, more “red” or less “yellow” than another. What these examples show is that colour composition seems to involve quantity. But, as expressed here by Byrne & Hilbert, talking about the quantity of a property seems quite problematic:

Red, yellow, green, and blue are properties, and it does not make any sense to say that one object has more of a property than another object, or a relative amount of a property. An object either has a property or it doesn’t. [Byrne & Hilbert 2003: 14]

Assigning quantities to colours becomes more plausible if colour composition is considered as some kind of mixture. Unlike composition, mixture involves transformation and quantity. When one adds some milk to a cup of black coffee, one gets a cup of coffee-and-milk. Coffee-and-milk is not black coffee plus milk, it is a new beverage obtained by mixing black coffee and milk. Coffee-and-milk is no longer black coffee and no longer milk. By mixing the ingredients, one transforms the initial ingredients and obtains some new substance. Quantity plays an important role in mixture because the result directly varies according to the relative proportion of the ingredients. A mixture can be, for example, a medicine or a poison according to the relative proportion of the active ingredient it includes.

Many authors have tried to explain colour composition in terms of mixture. Michael Tye for example proposed to give an account of colour mixing in terms of physical colour mixing:

> As for the binary-unitary distinction, it can be preserved as a basic truth about colour mixing. Orange, for example, is the colour you get when you mix red and yellow pigments. These facts are arguably facts we have learned from training, not facts given to us in our colour experiences and extractable from them without any basic lessons or art classes on the various colours and their relationships. [Tye 1995: 148]

Colour composition accounts in physicalist terms have been strongly criticized because predictions based on such accounts are wrong.* According to the physicalist account, green is a mixture of blue and yellow in exactly the same sense in which orange is a mixture of red and yellow. But this result clearly contradicts the fact that most observers consider green to be a unitary colour. Conversely, some colours which can be obtained by mixing different pigments are not considered to be composed in a similar way. Painters for example can mix orange and green pigments to get yellow or blend green and red pigments to get grey, but neither yellow nor grey are considered to be composed of green. Lack of parallelism between physical colour mixing and colour descriptions in terms of colour composition has favoured a phenomenalist interpretation of colour composition which claims that the way colours are described is not anchored in the way colours are physically generated, but in the way they appear in colour experiences.

The phenomenalist is right in stressing the fact that colour composition cannot be accounted for by physical colour mixture. However, from the fact that colour composition cannot be equated with physical mixture, one cannot conclude that colour composition is phenomenal. It is possible for example to home colour composition in language rather than perception. And in fact a lot of empirical evidence seems to point in this direction. First, contrary to what has often been claimed, there appear to be many inter-linguistic as well as intra-linguistic discrepancies about colour categorization. If access to colour composition was

---

∗ Cf. Hardin 1988: 43; Byrne 2003: n.38.

essentially perceptual, one would expect those distinctions to be universally shared. Take for example, the blue and green categories. If blue and green are unitary colours, one expects blue and green to be categorized in different categories because blue and green enter as components of different colours. If the quadripartite division of colours is valid, lime contains green but no blue and violet contains blue but no green. Recent works[*] show however that on the contrary many languages do not have separate terms to designate "blue" and "green". In Berinmo for example green and blue are grouped under a GRUE category called nol. If colour composition characterizes the way we perceive colours, we must conclude that the Berinmo lack the linguistic tools to describe their phenomenology, while English speakers are better equipped. But there are also notable differences among English speakers which seem to undermine a phenomenalist view on colour composition. According to colour-naming studies, many English speakers consider green to be a combination of yellow and blue[+], whereas brown is rarely considered to be a combination of yellow and black. Those cases of course do not constitute a devastating objection to the phenomenalist view on colour composition, because the phenomenalist could claim for example that there are phenomenal differences among subjects or that observers can be wrong about their own experiences. However, I would like to show that there is a different approach to colour composition which is worth exploring because it has the advantage of explaining many of the difficulties and the controversies related to the question of colour composition and the selection of unitary hues.

I have argued that there is no phenomenal evidence for colour composition or the distinction between unitary and binary colours. However, it appears undisputable that describing orange as a mixture of yellow and red is acceptable, while talking about a shade of red as being a mixture of purple and orange is not. As stressed by Broackes, the use of any alternative colour system appears impracticable:

> Is the choice of red, green, yellow, and blue as unitary and basic terms of classification an arbitrary one? Could we have done just as well, for example, with lime, purple, orange, and teal?
>
> Suppose we imagine a colour classification system based on those four. What would be involved? Some shade of orange would need to strike us as unitary and pure – containing no hint of red or yellow, or any other colour. Similarly, teal would have to seem free of any hint of blue or green. What we now see as unitary blue we would have to see as containing purple and teal. We would need to be able to understand instructions like this: "Take this yellow patch of light, cancel the orangeness in it with as much teal as it takes, until you are finally left with the pure lime that is its other component." It is, I think, no mere accident of the 20th-century American English that we find it hard to imagine using these four hues in the way described. We might write the specification of a language for talking of colour in this way, but is it a language we could learn to speak? [Broakes 1997: 183]

If there is no reason other than conventions to categorize colours, why does an alternative colour system appear to be wrong and even impossible? Is the apparent naturalness which

---

[*] Jameson 2005a; Roberson, Davies & Davidoff 2000; Kay & Regier 2003.

[+] One famous example is Brentano who defended the view that green is phenomenally composed of yellow and blue against his contemporaries. For a careful and critical presentation of Brentano's arguments, see Schnetzer 2005.

goes with our use of Hering's colour system not evidence in favor of the view that Hering's unitary colours are rooted in our colour experiences?

Even though there is a strong tendency to assimilate the feeling of the "naturalness" of our colour system with the fact that it is rooted in experience or in our biological makeup, I would like to argue that internalized conventions can provide the same feeling. My claim is that the apparent appropriateness or naturalness of colour descriptions in terms of Hering's unitary hues is not incompatible with a conventionalist approach to colour categorization.

To illustrate this view, I will present an analogy with temperature perception. The analogy is designed to fulfil two purposes: it should make the thesis intuitively clear and it should also provide some support. Like temperature experiences colour experiences cannot be differentiated by their complexity. Like in the temperature case, the recognition of amounts of redness cannot and should not be explained by the assumption of the presence of redness as a phenomenal component in the perceived colour. The temperature case will help to understand the view I propose about how particular colours are singled out and used as landmarks in colour identification. It will also clarify the role played by mixture in colour categorization and it will illustrate how arbitrary colour categories can be internalized. Furthermore the analogy will illustrate that we cannot conclude from our capacity to recognize a certain amount of redness and a certain amount of blueness in a particular colour that red and blue are somehow phenomenally 'contained' to a specific degree in the resulting colour.

4. MIXING WATER AND MIXING COLOURS

Imagine you are diving in a tropical sea. The water is clear and you can admire wonderful fishes and colourful coral reefs. Continuing your descent, you dive deeper. Slowly, light diminishes and the colours vanish until there is only darkness surrounding you. You've left the visible world.

What are your perceptual experiences in the darkness of the abyss? We can suppose there is not much to be seen, heard, tasted or smelled. Your perceptual experiences are reduced to the awareness of your body and the perception of the water enwrapping you. Now, your skin is your only sense organ and the water the only external reality to be sensed. As poor as it can seem, your perceptual universe is not empty. Your perceptual experiences can vary according to the changes of the water's temperature, current or viscosity.

Suppose now that you want to order your different experiences according to the temperature of the water that you perceive. It would be quite natural, I suppose, to graphically represent their ordering using a straight line extending from the coldest to the hottest experiences. The ordering is apparently easy and straightforward. However, to order experiences of temperature one must be able to compare the experiences at issue and this comparison can be quite difficult according to the circumstances. Suppose for example you took a warm bath yesterday and wondered if it was the same temperature as the bath you took a week ago. How can you make this comparison? It seems quite difficult because your memory is not perfectly reliable and the absence of an external standard makes the comparison uncertain. Suppose now that the plumbing of your house is archaic and that the only way to have tepid water is to mix a certain quantity of cold water at a fixed temperature

C with a certain quantity of hot water at an invariable hot temperature H. Although not very convenient, this plumbing system provides an unexpected way to measure the temperature of the water in your house. With time and practice, you would know the relative proportions of hot and cold water needed to obtain water at a given temperature. In this manner comparing the temperature of the bath you took yesterday and the temperature of the bath you took last week could be performed through the comparison of the relative proportions of cold and hot water needed to obtain the temperature of both baths.

Although the tepidity of your bath is the result of mixing hot and cold water of determinate temperatures C and H, the exact same temperature of your bath could be obtained by mixing water of different temperatures. The practical choice of choosing C and H as the external reference should therefore not hide the arbitrariness of the choice. Water temperature could in effect be measured in the same manner by using reference temperatures other than H and C. Despite the arbitrariness of the measurement method, one can, I believe, easily imagine that this method, if regularly used, could be internalized and become a second-nature for estimating the temperature of water. Now, let’s leave the abyssal darkness and let’s surface to the world of colours.

Experiences of colours, like experiences of temperatures, can be ordered. But the task seems much more complex. Unlike experiences of temperature, there is a multiplicity of similarity relations between each pair of colours. Two colours can resemble each other according to their lightness, saturation, hue, glossiness, fluorescence, etc. I will defend the view that the complexity of colour similarity relations explains why some colours are singled out as unitary colours. I will maintain in particular that the distinction between unitary and binary colours result from the way we refer and classify colours and colour experiences and that the way we refer to colours and order them is not constrained by the nature of colours or colour experiences only. Contrary to what has been widely assumed, the fact that orange is steadily said to be both reddish and yellowish in not rooted in the phenomenology of colour experience, but in the fact that a given shade of red and a given shade of yellow can be used as references to locate orange in the complex web of colour similarity relations. To understand better how some colours can be used as referential landmarks, I propose to return to the analogy of the bath given above.

Suppose for example that the temperature of the bath has been obtained by filling the bathtub with 25% of hot water at a temperature H and 75% of cold water at a temperature C. It certainly makes sense to say that we could judge that the temperature of the bath corresponds to 25% of water at temperature H and 75% of water at temperature C, but it is very doubtful to say that, by touching the water of the bath, we experience the two quantities of water initially added to obtain the water of the bath. The tepid temperature of the bath T does not appear to be composed in any way. When I immerse my body in the water at T, I do not have a phenomenal access to the water at C and the water at H used to fill my bathtub. What I feel is simply the temperature T of the result of mixing some water at C with some water at H. Phenomenally, the temperature of the water of the bath does not appear more complex than the temperature of the water used to fill the bath initially. The felt temperature of the water of the bath and the felt temperature of the water used to fill the bath are different only in degree.

My proposal is to describe colour composition in a similar way. Judging that a given orange patch is 25% red and 75% yellow is not determined by the phenomenal presence of any red and yellow component. An orange patch does not look in any way more complex than a pure red patch or any other coloured patch. Like in the water example, red and yellow are not phenomenally given in the perceptual experience itself but can be used as references to describe actual experiences of orange. Yellow and red are not therefore contained in orange or in the experience of seeing an orange patch as suggested by the phenomenalist view of colour composition. They are stored in memory and used to locate colours, like orange, in the colour spectrum. Referring to some arbitrary colours can greatly simplify the task of ordering colour experiences and identify colours. We can in effect discriminate around ten million different shades of colour, but we are almost unable to reidentify a particular colour shade.* Our inability to directly identify or reidentify colours among the tremendous richness of possible colour experiences can be partly overcome by comparing our colour experiences with some particular colours used as landmarks. This is the reason paint companies provide colour charts of various shades. The fact that those colours are externally accessible like in Pantone® colour charts for example or internally accessible like in memorized experiences of "pure" red, yellow, blue, green, black or white does not make any relevant metaphysical difference. Being able to identify and reidentify colours by comparing them with some particular colour used as references is certainly remarkable. However there is no good reason to consider those referential colours to be metaphysically or phenomenally different from the other colours. Their distinctiveness among the plethora of colours is essentially linked to the role they play in our cognitive access to colours and colour experiences. Like in the bath example, the fact that we can use water at temperature C and H to compare temperatures does not make the temperatures C and H ontologically, phenomenally or biologically different. Other colours could have been chosen to play the referential role played by yellow, blue, green, white and black in our colour system, but it does not imply that the choice is fully arbitrary. It could be the case that the colours chosen to play this role have some specificity.+ However, the fact that some characteristics could have guided the choice of those particular colours does not imply that no other colours could have played the cognitive role at issue.

It is also important to notice that once a particular referential system has been established, it becomes so "natural" that any other referential system seems impracticable. Once again, imagine you've learned to estimate the water temperature in terms of the relative proportion of water at temperature C and water at temperature H. It would seem impossible for you to estimate the water temperature in using completely different referential temperatures. In the same way, to use any other referential colours to describe or identify colours can seem impossible.

It appears that the example of the bath exhibits many resemblances with the way we use referential colours to identify and classify colours. However, we can question how far the analogy goes. In particular, we can wonder if colour "composition" could be derived from some physical mixture. Remember that in the example of the bath, mixing water at given temperatures allows the subject to build a temperature scale expressed in terms of the relative quantity of water at temperature C and H needed to obtain water at temperature T . In the

---

* Raffman 1995.

+ Recent studies offer a new perspective on cross-cultural colour categorization and naming. Rather than founding universality of colour categorization on pan-human colour vision mechanisms, they argue that universality in colour categorization and naming emerges from cognitive universals and socio-cultural evolutionary processes. Jameson [2005c] argues for example that universality in colour categorization can be accounted from a purely pragmatic approach based on individual cognitive strategies (explaining, for example, how dichromat observers can communicate with the majority of trichromatic individuals) and social constraints aimed to optimize interpersonal communication.

colour case, one can wonder if some similar colour mixing can explain our ability to judge the relative proportion of “pure” yellow and “pure” red needed to obtain a given shade of orange. One can wonder in particular if the relative proportion of red and yellow identifying a particular shade of orange by a given observer can systematically be correlated to the relative proportion of a given yellow paint and red paint necessary to obtain this particular shade of orange. It should be noticed here that most objections against the assimilation of colour composition with physical colour mixture do not affect the present account. The fact, for example, that some particular shades of grey can be obtained by mixing red and green has been alleged[*] to refute accounts of colour composition in terms of colour physical mixing, because, unlike its physical composition, a given shade of colour, like grey, never looks to be composed of green and red. As discussed earlier, the present proposal denies that colour composition is phenomenal. It cannot therefore be affected by the claim that grey is phenomenally composed of black and white and not of red and green. According to the present account, we simply do not see whether some particular shade of grey is or is not composed of red and green, what we see is just a particular shade of grey.

But why is grey described as being whitish and blackish and not reddish and greenish? If colour mixture plays a role in classifying colours, why is green and red not used to identify shades of grey? I have claimed that the choice of primary colours is not rooted only in colour phenomenology but that linguistic conventions and pragmatical constraints play a major role in the way we refer to colors. According to this analysis, the way a particular shade has been obtained by colour mixing is irrelevant to the way we refer and describe the colours we perceive. And if the present account is correct, the choice of red, yellow, blue and green is partly arbitrary and could be replaced by other colours, like for example, cyan, magenta, yellow and black.[+]

However paint mixing can provide a method for comparing colours. Like with the example of the bath, variations of colours can be captured in an economical way by referring to the relative proportion of the ingredients entering a mixture. We learn to compare shades of orange by the way we combine red and yellow paints. We say that a shade of orange is more reddish than another, because we know that to obtain that particular shade by using red and yellow paint, we should add more red paint. It is however not necessary once we’ve learned this way of identifying colours, that the shade we perceive is actually obtained by the mixture of the colours used for its identification. As with the bath example, once we have learned how to estimate the temperature of a liquid by reference to a relative proportion of water at C and H, it is possible to use the same method to estimate the temperature of a liquid whatever its actual mixture is. If the present account is correct, the role of paint mixing is therefore restricted to setting up a comparison scale and learning how to use it.

The unitary/binary distinction has raised various philosophical controversies. Philosophers and scientists have fought over the number of primary colours or the question whether green is unitary or binary.[*] If the present account is correct, all these controversies

---

[*] *Cf* Nida-Rümelin & Schnetzer 2004.

[+] The present proposal predicts that people working in the printing industry who daily use four inks - cyan, magenta, yellow and black to reproduce the whole colour spectrum, will be disposed to describe colours in terms of the relative proportion of those four inks. An interesting experiment would therefore be to determine if red, which can be obtained by mixing magenta and yellow inks, is “perceived” as a primary colour by printer and graphic designers.

[*] *Cf* Schnetzer 2005.

miss the point, because the unitary/binary distinction does not concern colour phenomenology, nor colour ontology. The unitary/binary distinction is an epistemological tool built to identify and describe the variety of colours. As a tool, the only thing that matters is its effectiveness. As long as its efficiency is guaranteed, variations among subjects can be tolerated. If some people take green to be a unitary colour, whereas others consider green to be a binary colour, it's probably because it does not affect their capacity to identify colours. Using a thermometer whether in Celsius or Fahrenheit can both help us to select the right temperature of our bath, provided we have some familiarity with the scale we use.

REFERENCES

[1] Abramov, I. 1997. Physiological mechanisms of color vision, in *Color Categories in Thought and Language,* ed. Hardin and Maffi, UK: Cambridge University Press.

[2] Abramov, I., and Gordon, J. 1994. Color appearance: on seeing red - or yellow, or green, or blue. *Annual Review of Psychology*, 45: 451-485.

[3] Berlin, Brent and Paul Kay 1969. *Basic color terms: their universality and evolution,* Berkeley: University of California Press.

[4] Boas, F. 1911. *Handbook of American Indian languages*, Washington: The

[5] Smithsonian Institution.

[6] Broakes 1997. Could we take lime, purple, orange and teal as unique hues?, *Brain and Behavioral Sciences,* 20: 183-184.

[7] Byrne 2003. Color & similarity, *Philosophy and Phenomenological Research*, 66: 641-65.

[8] Cohen, J 2003. On The Structural Properties of the Colors, *Australasian Journal of Philosophy*, 81(1): 78-95.

[9] Derrington, A.M, J. Krauskopf and P. Lennie 1984. Chromatic mechanisms in lateral geniculate nucleus of macaque, *Journal of Physiology*, 357: 241-265.

[10] Gross, Dinah. "The evolution of the notion of primary colour in colour vision science", in M. Nida-Rümelin et al. (eds.), *Experiencing Colors : Philosophy, Phenomenology and Science,* in preparation.

[11] Hardin, C. L. 1988. *Color for Philosophers: Unweaving the Rainbow*, Indianapolis: Hackett.

[12] Helmholz, H. L. von. 1924. Treatise on Physiological Optics, translated from the third German edition by J. P. C. Southall, New York: Optical Society of America.

[13] Herder, J.G. 1772/2002. Treatise on the Origin of Language, in *Philosophical Writings*, ed. and trans. Michael N. Forster, Cambridge: CUP, 65-164.

[14] Hering E, 1920/1964. *Outlines of a Theory of the Light Sense,* Cambridge, Mass: Harvard University Press,

[15] Hoijer, H. 1954. *Language and culture.* Chicago: University of Chicago Press.

[16] Humboldt Wilhelm von 1820/1997. On the Comparative Study of Language and its Relation to the Different Periods of Language Development, in *Essays on Language*, ed. T. Harden and D. Farrelly. Frankfurt: Peter Lang.

[17] Hume, David 1739/1983, *Treatise of Human Nature*.

[18] Hurlburt Russell T. and Eric Schwitzgebel 2007. Describing Inner Experience? Proponent Meets Skeptic, MIT Press.

[19] Hurvich LM, Jameson D. 1957. An opponent-process theory of color vision, *Psychological Review*, 64: 384-404.

[20] Jameson, Kimberly A. 2005a. Why GRUE? An Interpoint-Distance Model Analysis of Composite Color Categories, *Cross-Cultural Research,* 39: 159-204.

[21] 2005b. Semantic and Perceptual Representations of Color, in *Fechner Day 2005: Proceedings of the 21st Annual Meeting of the International Society for Psychophysics,* ed. J.S. Monahan, S.M. Sheffert, & J.T. Townsend, Mt. Pleasant: Central Michigan University Printing Services.

[22] 2005c. Culture and Cognition: What is Universal about the Representation of Color Experience?, *The Journal of Cognition & Culture*, 5: 293-347.

[23] Jameson, Kimberly, and R. G. D'Andrade 1997. It's not really red, green, yellow and blue: an inquiry into perceptual color space, in *Color Categories in Thought and Language*, ed. C. L.Hardin and L. Maffi, Cambridge University Press, 295-319.

[24] Jameson, Dorothea and Leo M. Hurvich 1955. Some quantitative aspects of an opponent-colors theory: I.Chromatic responses and spectral saturation, *Journal of the Optical Society of America*, 45: 546–52.

[25] 1978. Dichromatic Color Language: `Reds' and `Greens' Don't Look Alike But Their Colors Do, *Sensory Processes*, 2:146--155.

[26] Kay, Paul 2005. Color Categories are Not Arbitrary*, Cross Cultural Research*, 39: 39-55

[27] Kay & McDaniel, 1978. The linguistic significance of the meanings of color terms, *Language*, 54, 610-646.

[28] Kay & Regier 2003. Resolving the question of color naming universals, *Proceedings of the National Academy of Sciences*, 100(15).

[29] Locke 1689. *An Essay Concerning Human Understanding.*

[30] Lucy, John A. 1992. *Grammatical Categories and Cognition: A Case Study of the Linguistic Relativity Hypothesis,* Cambridge: Cambridge University Press.

[31] Mausfeld, R. 1997. Why bother about opponency? Our theoretical ideas on elementary colour coding have changed our language of experience. *Behavioral and Brain Sciences*, 20(2): 203.

[32] Nida-Rümelin, Martine and and Achill Schnetzer 2004. Unique Hues, Binary Hues and Phenomenal Composition, draft.

[33] Pinker, Steven 1994. *The language instinct: How the mind creates language*, W.Morrow, New York.

[34] Raffman, Diana 1995. On the Persistence of Phenomenology, in *Conscious Experience*, ed. T. Metzinger, Paderborn: Ferdinand Schoningh.

[35] Regier, Kay & Cook 2005. Focal colors are universal after all, *Proceedings of the National Academy of Sciences*, 102(23).

[36] Roberson, D., Davies I. & Davidoff, J. 2000. Colour categories are not universal: Replications and new evidence from a Stone-age culture, *Journal of Experimental Psychology: General*, 129: 369-398.

[37] Sapir, Edward 1985. Selected Writings of Edward Sapir, in *Language, Culture, and Personality*, ed. David G. Mandelbaum, University of California Press.

[38] Saunders, B. 2000. Revisiting `Basic Color Terms', *The Journal of the Royal Anthropological Institute*, 6:81-99.

[39] Saunders, B. and J. van Brakel 1997. Are there non-trivial constraints on colour categorisation?, *Behavioural and Brain Sciences*, 20: 167-232.

[40] Schnetzer, Achill 2005. The Greenness of Green: Brentano on the status of Phenomenal Green, unpublished paper, <http://fns.unifr.ch/philocolor/Doc/Brentanodraftseptember05.doc>

[41] Shepard, R. N., & Cooper, L. A. 1992. Representation of colors in the blind, color-blind, and normally sighted, *Psychological Science*, 3: 97-104.

[42] Sternheim and Boynton 1966. Uniqueness of Perceived Hues Investigated with a Continuous Judgmental Technique; *Journal of Experimental Psychology*, 72:770-86.

[43] Thompson, Evan 1995. Colour vision, evolution, and perceptual content, *Synthese*, 104 (1995): 1-32.

[44] Tye, Michael 1995. *Ten Problems of Consciousness: A Representational Theory of the Phenomenal Mind,* Cambridge, Mass: MIT Press.

[45] Varzi, A. 2003. Mereology, in *Encyclopedia of Philosophy*, ed. E. N. Zalta, Stanford: Stanford: CSLI, internet publication, <http://plato.stanford.edu/entries/mereology/>

[46] Whorf, B. L.,1956. *Language, Thought and Reality,* ed. J. B. Carroll, Cambridge, MA: MIT Press

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 203-224

Chapter 7

COLOR IMAGE RESTORATION AND THE APPLICATION TO COLOR PHOTO DENOISING

Lei He*
Department of Information Technology, Armstrong Atlantic State University,
Savannah, Georgia, USA

1. INTRODUCTION

Image restoration has been a classical and significant topic of image processing, which refers to the techniques to reconstruct or recover an image from distortion (e.g. motion blur and noise) in different applications, such as satellite imaging, medical imaging, astronomical imaging, and family portraits. For motion blur, *image deblurring* techniques are used to estimate the actual blurring function and "undo" the blur to restore the original image. In cases where the image is corrupted by noise, *image denoising* methods are employed to compensate for the degradation the noise caused. In the past two decades, image denoising has been a fundamental and active research topic and widely used as a key step in a variety of image processing and computer vision applications, such as image segmentation, compression, object recognition, and tracking. This chapter focuses on image denoising, specifically for color image denoising and the application to color photo denoising.

Color image denoising has been an active area with the fast progress of optical camera techniques in past decades. There are several major color spaces to represent color images and the most common one is the Red, Green and Blue (RGB) model. Other color systems include YIQ (luminance, hue and saturation) system (NTSC), YCbCr (luminance, blue minus luminance and red minus luminance) system, CMY and CMYK (cyan, magenta, yellow and black) systems, HSV (hue, saturation and value) and HSI (hue, saturation and intensity) systems [29]. The selection of a system is generally application-specific, e.g. RGB for education and presentation, NTSC for television, YCbCr for digital video, HSV for color

---

* Lei.He@armstrong.edu

palette. Among these color spaces, HSI space has been well accepted for its favorable color description capability that is practical for human interpretation.

As a specific application of color image denoising, color photo noise removal is an important subject due to extensive use of digital cameras in recent years. Color photo noise is introduced in the process of image acquisition, filtering, compression and reconstruction. In digital photography, a high ISO setting of a digital camera is usually used to increase light sensitivity in dark environments, but the resultant image contains more sensor noise than a low ISO image taken with the same exposure*. The objective of our work is to denoise high ISO photos to achieve a low ISO photo quality without the use of expensive cameras or accessories. The motivation comes from the practical needs of digital camera users and manufacturers [30]. So far, most existing approaches are used to solve a general denoising problem (e.g. gray, color or multi-spectral images) based on an assumption of additive or multiplicative noise independent of signal and to the best of our knowledge, none of presented literatures focus on the unknown digital camera sensor noise in color photos.

Since the pioneering work in regularization methods [1,2,3], scale-based analysis has played an increasingly important role in signal (image) processing. The idea is to represent an image in multi-scale, so that only important features are preserved and unwanted features (e.g. noise) are removed in low scales. This is based on the conclusion that convolving a signal with a Gaussian kernel is equivalent to evolving it with a heat differential operator where time is the scale [2]. Such methods have direct applications for feature extraction and image denoising. For example, given an image I: $\Omega \subset \Re^2 \rightarrow \Re^m$, the corresponding heat diffusion equation is:

$$\frac{\partial I}{\partial t} = I_t = \mathbf{div}(\nabla I) = I_{\eta\eta} + I_{\xi\xi}, \tag{1}$$

where η and ξ refer to the normal and tangential directions respectively. For the denoising applications, this linear filtering approach corresponds to isotropic diffusion, which presents a major limitation: important details in an image also get smoothed away along with the noise. Therefore, a nonlinear filter or an anisotropic diffusion is needed to preserve those details from the smoothing process. Since the seminal model proposed by Perona and Malik [4] in the early 1990s, numerous literatures have been presented to recover the “true” image from noisy data through a nonlinear analysis, such as partial differential equation (PDE)-based anisotropic diffusions [5-10,33-40], variational approaches [11-23,32,43-48], robust statistics [24,25], as well as some transformation based approaches (e.g. wavelet [18,20], ridgelet and curvelet-based image denoising [26]), just to name a few. A complete review of current image denoising approaches can also be seen in several recent literatures [25,27,28].

This chapter presents a novel framework specifically for denoising color photos particularly those photos taken at a high ISO setting that resulted in noticeable sensor noise. Compared with existing literatures, there are two major contributions in the presented approach. The first is that the color photo denoising is conducted in the HSI space instead of the traditional RGB space, which is motivated by the fact that the HSI model has a better color description for human interpretation. Our algorithm is based on separating a color photo

---

* This is achieved by reducing the shutter speed or increasing the aperture.

into hue, saturation, and intensity components, and then processing each component with PDEs or diffusion flows. The intensity denoising is our main focus, which is implemented with a PDE that is a combination of a gradient vector flow (GVF)-based filter [31] and a fourth-order PDE filter [32]. This combined technique provides a robust and accurate denoising process, i.e., it preserves edges well and at the same time overcomes the staircase effect in smooth regions. The hue and saturation denoising are implemented by a weighted orientation diffusion and a modified curvature diffusion respectively. The second contribution is the algorithm performance assessment. In most existing literatures, synthetic noise (e.g. Gaussian, salt & pepper noise) has been used for algorithm performance evaluation. Furthermore, the denoising effect has been assessed mostly by human visual perception, few by the mean squared error (MSE) and the peak signal to noise ratio (PSNR). In contrast, the color photo noise produced by digital cameras is real sensor noise. In this chapter, the proposed algorithm is evaluated by comparing the denoised images with the ground truth. The ground truth and noisy images are produced by the same camera on the same scene with low and high ISO settings by maintaining the same exposure. Because ground truth images are available for those photos taken under a controlled environment, we could assess the performance of our proposed algorithm, several recognized methods, and commercial software using objective error measurements of MSE and PSNR, in addition to the commonly used subjective visual assessment. Both qualitative and quantitative validation shows that the proposed algorithm is more appropriate for color photo denoising than existing approaches.

2. BACKGROUND

2.1. Direct Partial Differential Equation-Based Anisotropic Diffusion

One major category of image denoising approach is implemented via anisotropic diffusion flows, either implemented directly in the form of partial differential equations (PDE) [4-10,33-40], or derived from certain optimization problems using variational approaches [11-23,43-48]. For direct PDE-based approaches, a continuous sequence of smoother images I_t are generated by $I_t = R(I)$, with $R(I)$ representing a space-based image regularization term. For anisotropic diffusion, this term restricts the smoothing in two principles: 1) the magnitude of smoothing, e.g. less smoothing at image features; 2) the direction of smoothing, e.g. less smoothing in the directions across image features. A diffusion equation using a general form of $R(I)$ can be formulated as

$$I_t = R(I) = r(|\nabla I|)I_{\eta\eta} + s(|\nabla I|)I_{\xi\xi}\,, \tag{2}$$

where $r(\cdot)$ and $s(\cdot)$ are gradient-based weighting functions (called "diffusivity" or "edge stopping" functions) to control the smoothing amount along the η-ξ directions.

The well-known Perona-Malik (PM) equation is formulated as

$$I_t = \mathbf{div}(\mathrm{g}(|\nabla I\,|\nabla I)) =(g(|\nabla I|)+|\nabla I\,|\,g'(|\nabla I|))I_{\eta\eta} + g(|\nabla I|)I_{\xi\xi}\,, \tag{3}$$

where $g(\cdot)$ is a decreasing function (e.g. $g(|\nabla I|) = \frac{1}{1+(\frac{|\nabla I|}{K_{PM}})^2}$ and $K_{PM}>0$). Though with some deficiencies [35-38], e.g. high noise sensitivity, unstable numerical process, staircasing effects, and no stopping criteria, the PM equation has opened a new door for later works. Based on the PM equation, selective image smoothing [35,36] is used to smooth image along the image feature (e.g. gradient) direction with a stable numeric implementation. In [36-38], different weighting functions have been proposed to diffuse image along the η-ξ directions for an adaptive smoothing, i.e., stronger diffusion along the tangential direction than in the normal direction. Moreover, when the normal direction coefficient is negative, inverse or backward diffusion [37,39] can be generated to enhance image edges. Similarly, shock filters [8,40] have been proposed to enhance the edges by assigning a negative weight to the normal direction diffusion. Recently, more advanced diffusion systems have been presented, such as complex diffusion [5] to overcome staircasing effects, color/vector image diffusion framework [6] which is based on a novel notion, color gradient [42]. Besides the diffusion in the η-ξ directions, other directions have been used for a more accurate or specific image feature preservation in the smoothing process, such as the eigenvectors of Hessian matrix [9] or a diffusion structure tensor [10] that is constructed by the outer product of image gradients.

2.2. Variational Approaches

Variational approaches [11-23,43-48] are usually formulated as an optimization problem, with an energy functional to be minimized,

$$E(I) = \int_{\Omega} \left(\psi(|\nabla I|) + \frac{\lambda}{2}(I - I_0)^2 \right) d\Omega, \tag{4}$$

With calculus of variations, the corresponding diffusion PDE can be derived as:

$$I_t = \mathbf{div}\left(\frac{\psi(|\nabla I|)\nabla I}{|\nabla I|}\right) - \lambda(I - I_0). \tag{5}$$

Numerous diffusion terms of $\psi(|\nabla I|)$ have been presented in past years, such as the image total variation (TV) [12,13,32,43-46], hypersurface areas [14,15], Mumford-Shah functional and its variations [16,17,47,48], and orientation diffusion [11,41] for angle signals (e.g. hue, chromaticity).

With the assumption that an image I_c is corrupted by additive noise N, TV-based methods are usually presented as a minimization of the image total variation with certain constraints, and the optimum produces the noise-free signal I_c. In [12], Rudin et al. formulates the denoising problem as a minimization of the image TV:

$$E(I) = \int_{\Omega} |\nabla I| \, dxdy, \tag{6}$$

with a constraint that the mean of the input image I_0 ($I_0=I_c+N$) is the same as the noise free signal I_c, and the standard deviation of I_0 is the same as the noise signal N. With the calculus of variations, the denoising process was implemented by a PDE as:

$$I_t = \frac{I_{xx}I_y^2 - 2I_xI_yI_{xy} + I_{yy}I_x^2}{|\nabla I|^3} - \lambda(I - I_0)\,. \tag{7}$$

The first component corresponds to the level set evolution [49] with the local curvature ($\kappa = \frac{I_{xx}I_y^2 - 2I_xI_yI_{xy} + I_{yy}I_x^2}{|\nabla I|^3}$) as the velocity. The second component is a data fidelity term to prevent the final result deviating far from the input image. This original TV model has shortcomings to preserve fine details like edges and textures. More general assumptions of the noise models (e.g. additive and multiplicative noise) and blurring process have been investigated in [45]. Later approaches with the similar idea to apply the curvature term in image denoising have been inspired, including the min/max curvature flow [7] and modified curvature flows [14,15]. In [14,15], an image is modeled/mapped as an embedding manifold (i.e., harmonic mapping) that flows (Beltrami flow) toward the minimal surface in a higher dimensional space, e.g. in the case of color images a 2D manifold in a 5D space. Based on the early works in [12,44,45], a discrete low pass TV filter has been implemented in [43], and color and texture applications can be seen in [13,46]. Particularly, to overcome the staircase effect, a dynamically changed weighting function has been created to combine the TV component with a higher (2nd) order functional [32], which reserves the good properties of both models and alleviates their difficulties, i.e., TV model is good at preserving image features (jumps and discontinuities) and the second-order functional is good at recovering the smooth regions. Another major category of variational approach is related to Mumford-Shah functional [51,52]. Since the proposition of the Mumford-Shah functional for image segmentation, many variations of the original functional have been proposed for image denoising [16,17,47,48]. For example, a single framework [16] combining Ambrosio-Tortorelli functional [53] (an elliptic approximation of the Mumford-Shah functional) and the geodesic active contour model [54] is applied for both segmentation and denoising, and it is implemented by iterating two coupled PDEs. Similar work can be seen in [17,47,48], which all use coupled PDEs for several objectives, including curve evolution for image segmentation, diffusion for noise elimination and image magnification [17].

2.3. Statistics-Based Anisotropic Diffusion

The nonlinear techniques introduced above do not explicitly account for the noise statistics in the diffusion PDEs. Robust statistical techniques have been widely used in image processing and computer vision [55], and their early applications in image restoration can be seen in [56-58]. In [24,59,60], image noise statistics has been embedded into the diffusion PDEs for image denoising. The approach in [24] interprets the PM equation as a robust statistical estimation that is to minimize the image intensity difference of local neighborhood, i.e., to estimate a piecewise constant image. New edge stopping functions based on Lorentzian error norm, Tukey's biweight and Huber's minmax estimator have been adopted to replace the traditional $g(\cdot)$ functions for a better edge preservation. A line process has also been included as a spatial coherence constraint to preserve edge continuity. In [59], Rabie improves the accuracy of the approach in [24] by using adaptive parameters in the edge stopping functions. In [60], the diffusion process is simulated as a Markov chain, with the intensity of each pixel being characterized by an evolving density from the initial state. Moreover, a bidirectional gradient-based weighting function is used to ensure that the final result resembles to the initial image, which performs as the data fidelity term used in many diffusion PDEs. Different from previous PDE-based iterative diffusions, a non-local mean algorithm [25] does not assume the strength or frequency of image noise (i.e., there are no $g(\cdot)$ functions to identify edges), and the denoising is based on image redundancies. In this algorithm, each image pixel intensity value is replaced by a weighted intensity summation of its neighbors that are determined by their context statistics of intensities and gradients. A novel noise measurement, method noise, is defined, and the algorithm performance has been validated with better results than several major approaches including Gaussian filter, PM equation, TV minimization, and neighborhood filtering.

2.4. Color Image Denoising and HSI Space

While most existing color image denoising methods are implemented in the RGB space, few exploit other color spaces, e.g. chromaticity and brightness (CB) space [11,21], HSV space [21-23]. These spaces are used because they are deemed to be closer to human visual perception. In these methods, chromaticity or hue denoising are usually the main focus. The models in [11,21-23] are extensions of the TV [12] and Beltrami flow [14] to CB and HSV spaces. Different from the general applications of these presented approaches, our approach is specifically developed for high ISO color photo denoising in the HSI color space for a better consistency with human visual perception. The components of the hue, saturation and intensity are processed by spatially varying weighted PDEs.

Hue is an attribute to describe a pure color and saturation gives a measure of the degree to which a pure color is diluted by white light. Intensity represents the image brightness. Figure 1 illustrates the geometric relationship of the RGB space and the HSI space. For a color point in a circle (e.g. I=0.5 in Figure 1), its hue value is computed as the angle counterclockwise from the red axis. The saturation value of a point is the distance to the center intensity axis. Particularly, the conversion equations from RGB to HSI and vice versa are listed as following.

Given a RGB image,

$$\begin{cases} H = \begin{cases} \theta & \mathrm{B} \le \mathrm{G} \\ 2\pi - \theta & \mathrm{B} > \mathrm{G} \end{cases}, \; \theta = \cos^{-1}\left(\dfrac{[(R-G)+(R-B)]/2}{[(R-G)^2 + (R-B)(G-B)]^{1/2}} \right); \\ S = 1 - \dfrac{3}{(R+G+B)} \min(R,G,B); \\ I = \dfrac{R+G+B}{3}. \end{cases} \tag{8}$$

Given an HSI image,

$$\begin{cases} \text{When } 0 \le H < \dfrac{2\pi}{3},\ B = I(1-S),\ R = I\left(1+\dfrac{S\cos H}{\cos(\frac{\pi}{3}-H)}\right),\ G = 3I-(R+B); \\ \text{When } \dfrac{2\pi}{3} \le H < \dfrac{4\pi}{3}, H = H-\dfrac{2\pi}{3}, \\ \qquad R = I(1-S),\ G = I\left(1+\dfrac{S\cos H}{\cos(\frac{\pi}{3}-H)}\right),\ B = 3I-(R+G); \\ \text{When } \dfrac{4\pi}{3} \le H \le 2\pi, H = H-\dfrac{4\pi}{3}, \\ \qquad G = I(1-S),\ B = I\left(1+\dfrac{S\cos H}{\cos(\frac{\pi}{3}-H)}\right),\ R = 3I-(G+B). \end{cases} \tag{9}$$

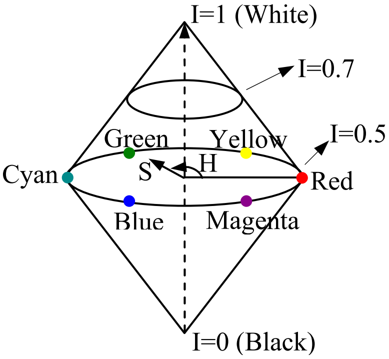


Figure 1. Relationship of the RGB and HSI spaces.

2.5. Gradient Vector Flow Field

The GVF field was first presented in the snake model for image segmentation [31], in which it was used as an external force field. The GVF field is computed as the diffusion of an image edge map (e.g. gradient magnitude map). For example, given an image edge map as $f(\mathbf{x}) = |\nabla(G_\sigma * I)|^2$, $\mathbf{x}\in\Re^2$ and G_σ is a Gaussian smoothing filter, the GVF field $\mathbf{v}(\mathbf{x})=(u(\mathbf{x}), v(\mathbf{x}))$ can be obtained as the solution minimizing the energy functional

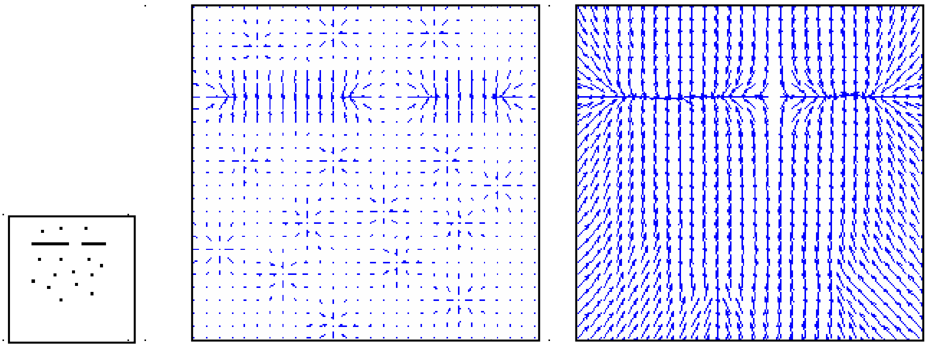
$$E(\mathbf{v}) = \int_{\Omega} \left(\mu |\nabla \mathbf{v}|^2 + |\nabla f|^2 |\mathbf{v} - \nabla f|^2 \right) d\Omega, \tag{10}$$

where μ is a regularization parameter. With a variational approach, the GVF field can be derived by solving the following diffusion equation:

$$\mathbf{v}_t = \mu \mathbf{div}(\nabla \mathbf{v}) - |\nabla f|^2 (\mathbf{v} - \nabla f), \tag{11}$$

with the initial condition $\mathbf{v}(\mathbf{x}, t=0)=\nabla f$ [31] and $\mathbf{v}$ is considered as a function of time. The first component in the diffusion equation is a smoothing term and it produces a slowly varying field when there is no data (edge). The second component is a data term that ensures the GVF field close to ∇f at edges. In other words, the diffusion equation produces a vector field that is close to the gradient of the edge map at boundaries, and is slowly varying in smooth regions. A more general functional (Generalized GVF) [61] has been proposed with the parameters μ and $|\nabla f|^2$ being replaced by weighting functions.

Compared with the gradient field, the GVF field has a wider boundary capture range and is more robust to image noise and small boundary gaps. Figure 2(b) and (c) compares the gradient field and the GVF field of an artificial image in Figure 2(a), which illustrates that the GVF field outperforms the gradient field on the noise sensitivity and gap problems. With these favorable features, the GVF direction is selected in our diffusion algorithm, instead of the traditional η-ξ direction. Experiments show that it produces a more stable and accurate result than η-ξ based diffusions. A recent GVF-based image denoising approach [33] has been proposed to apply the GVF field to replace the high-order derivative terms in several popular frameworks, including the original PM equation, shock filters and the mean curvature flow.



(a) An artificial image (b) The gradient field of (a) (c) The GVF field of (a)

Figure 2. Comparison of image gradient and GVF.

3. COLOR PHOTO DENOISING VIA HSI DIFFUSION

The HSI color system is adopted in our algorithm because it represents colors similarly as how the human eye senses colors. Given a color photo, the first step is to convert the image from the RGB space to the HSI space. After the iterative diffusion process on the hue, saturation and intensity channels, the final result is obtained by converting the diffusion result back to the RGB space.

3.1. Intensity Diffusion

The intensity component (I) of a color image is the average of the red, green and blue values, which corresponds to the gray version of the color image. Thus it transfers the most important information for human visual "feeling" on the image. Following the original PM equation (Eq. (3)) and many subsequent approaches, the proposed intensity diffusion also adopts the divergence format. The common diffusion directions such as η-ξ direction have difficulty in robust noise removal and boundary gap closing, which is critical for edge identification and preservation in image denoising. To address this problem, we restrict the diffusion flow along the GVF direction: $\mathbf{v}(\mathbf{x}) = (u(\mathbf{x}), v(\mathbf{x}))^T$, $\mathbf{x}\in\Re^2$, which was initially proposed for image segmentation and more robust on noise and small boundary gaps. Note that our proposed method shares the same objective for more stable and accurate denoising performance as the GVF-based denoising method in [33], but uses a different framework more targeted for the color photo denoising.

In order to restrict the diffusion along the GVF direction, we construct a diffusion tensor ($\mathbf{D}$) similar to the coherence-enhancing diffusion in [10], which sets the diffusion directions along the eigenvectors of $\mathbf{D}$ by constructing it as the outer product of image gradients. In our algorithm, the tensor $\mathbf{D}$ is also built as a 2 × 2 matrix, with its two eigenvectors ($\mathbf{p}$, $\mathbf{q}$) parallel and perpendicular to the GVF direction ($\mathbf{v}$), i.e., $\mathbf{p} \parallel \mathbf{v}$ and $\mathbf{q} \perp \mathbf{v}$. The two eigenvalues ($f_1$ and f_2) correspond to the $g(\cdot)$ functions to adaptively control the diffusions in the $\mathbf{p}$ and $\mathbf{q}$ directions. With the embedded GVF field, the diffusion has the advantage of more accurate noise removal and edge preservation than those along the η-ξ directions. However, it still suffers from the staircase effect due to the piecewise constant image modeling. To overcome this staircase effect, a fourth-order term in [32], is specifically added to the diffusion framework to overcome the staircase effect. This fourth-order term is derived from the minimization of a second-order functional, which models an image as a piecewise linear signal. More details and illustrations about this high order filter can be seen in [32]. Given these considerations, we define our proposed intensity diffusion formulation as follows:

$$I_t = \alpha I_{GVF} + \eta I_H, \tag{12}$$

where I_{GVF} is the GVF-based diffusion component, and I_H represents the fourth-order term, α>0 and η>0.

$$I_{GVF} = \mathrm{div}(\mathbf{D}\nabla I) - h(I - I_0), \tag{13}$$

where f_1 and f_2 are the eigenvalues of the diffusion tensor **D**, $h = 1 - f_1$, and I_0 is the initial intensity component. The fourth-order term is defined as:

$$I_H = -\left(\frac{I_{xx}}{|U^2 I|}\right)_{xx} - \left(\frac{I_{xy}}{|U^2 I|}\right)_{yx} - \left(\frac{I_{yx}}{|U^2 I|}\right)_{xy} - \left(\frac{I_{yy}}{|U^2 I|}\right)_{yy}, \tag{14}$$

where $|U^2 I| = (I_{xx}^2 + I_{xy}^2 + I_{yx}^2 + I_{yy}^2)^{1/2}$. In Eq. (13), the first component is in divergence format with the tensor **D** to restrict the diffusion along the **p-q** directions. Here the GVF-based diffusion tensor **D** is constructed as:

$$\mathbf{D} = (\mathbf{p}\ \mathbf{q})\begin{pmatrix} f_1 & \\ & f_2 \end{pmatrix}(\mathbf{p}\ \mathbf{q})^{-1} = \begin{pmatrix} u & -v \\ v & u \end{pmatrix}\begin{pmatrix} f_1 & \\ & f_2 \end{pmatrix}\begin{pmatrix} u & -v \\ v & u \end{pmatrix}^{-1} \tag{15}$$

$$= \frac{1}{u^2 + v^2}\begin{pmatrix} u^2 f_1 + v^2 f_2 & uv(f_1 - f_2) \\ uv(f_1 - f_2) & v^2 f_1 + u^2 f_2 \end{pmatrix},$$

where $u^2 + v^2 = 1$ for a normalized GVF field. With some mathematical operations, we can derive:

$$\mathbf{div}(\mathbf{D}\nabla I) = \text{Trace}\ (\mathbf{DH}) + \nabla I^{\mathrm{T}} \mathrm{div}(\mathbf{D}) \tag{16}$$

$$\begin{aligned} &= I_{xx}(u^2 f_1 + v^2 f_2) + 2I_{xy}uv(f_1 - f_2) + I_{yy}(u^2 f_2 + v^2 f_1) \\ &+ I_x(u_y v(f_1 - f_2) + uv_y(f_1 - f_2) + uv(f_{1y} - f_{2y})) + I_x(2uu_x f_1 + u^2 f_{1x} + 2vv_x f_2 + v^2 f_{2x}) \\ &+ I_y(u_x v(f_1 - f_2) + uv_x(f_1 - f_2) + uv(f_{1x} - f_{2x})) + I_y(2vv_y f_1 + v^2 f_{1y} + 2uu_y f_2 + u^2 f_{2y}), \end{aligned}$$

where **H** represents Hessian matrix. The second component in Eq. (13) is a data fidelity term for a convergent diffusion process. Similar to the Generalized GVF [61], a general weighting function ($h = 1 - f_1$) is used to balance the diffusion term and the data term. In practice, there can be many choices for f_1 and f_2 [24,27] for anisotropic diffusion purpose. Different from previous approaches, we construct

$$f_1(I, |\nabla I|) = \frac{\gamma(I)}{\tau_1(|\nabla I|)}, \quad f_2(I, |\nabla I|) = \frac{\gamma(I)}{\tau_2(|\nabla I|)}, \tag{17}$$

which depend on both image intensity and gradient. The intensity-based term is computed as

$$\gamma(I) = 1 - \frac{1}{1 + \exp(-\frac{(I - L_I)Z_I}{255})}, \tag{18}$$

where $255 \geq L_I \geq 0$ and $Z_I > 0$ are constants to control the smoothing degree according to image brightness. Examples of this term with different Z_I and L_I are shown in Figure 3. It can be seen that this term inhibits diffusion at bright locations and enhances diffusion at dark locations, which is inspired by observations that color photos usually have smaller signal to noise ratio in dark regions. The gradient-based terms are given as

$$\tau_1(|\nabla I|) = \frac{1}{1+(|\nabla I|/K_I)^2},\ \tau_2(|\nabla I|) = \frac{1}{\sqrt{1+(|\nabla I|/K_I)^2}},\ K_I > 0. \tag{19}$$

Note this is only one possible empiric choice (from the $g(\cdot)$ function overview in [6,27]) for the adaptive smoothing purpose.

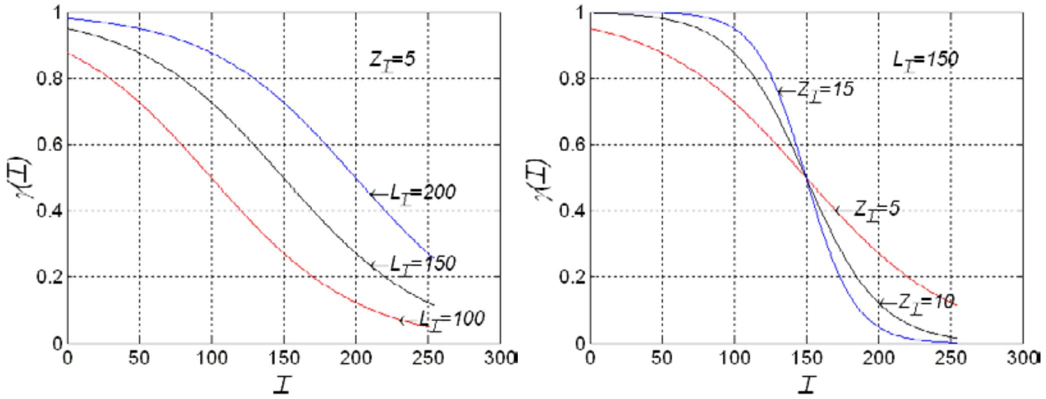


Figure 3. Intensity-based coefficient of Eq. (18).

3.2. Hue Diffusion

The hue component (H) is an attribute to describe a pure color and is measured as an angle. As indicated by Perona [41], the direct application from intensity diffusion to angle-valued quantities would cause ambiguity in the updating process due to the angle periodicity. Therefore, we implement the hue component denoising as an orientation diffusion. In [41], the orientation diffusion is defined as

$$\theta_t = \lambda \sum_{(i,j)\in Nb(x,y)} \left(\sin\left(\theta(i,j) - \theta(x,y)\right)\right) - \beta(\theta - \theta_0), \tag{20}$$

where $\lambda > 0$ is to control the diffusion strength. The first component is the diffusion term and $Nb(x, y)$ is the 3 × 3 neighborhood of a point (x, y). The constant $\beta > 0$ is to balance the diffusion term and the data term $(\theta - \theta_0)$.

With a constant λ to adjust the diffusion strength, the original orientation diffusion equation (Eq. (20)) is an isotropic filter that cannot adaptively control the smoothing, i.e. edges cannot be preserved in diffusion. To solve this problem, we propose an anisotropic orientation diffusion for the hue denoising, with a spatially varying weighting function incorporated in the equation.

$$H_t = \sum_{(i,j)\in Nb(x,y)} [w(i,j)\sin(H(i,j)-H(x,y))] - \beta(H-H_0), \tag{21}$$

where $w(i,j) = \dfrac{K_1}{1+\left(\sin(H(i,j)-H(x,y))/K_2\right)^2}$ is the weighting function and K_1 and K_2 are positive constants ($K_1 \geq 1 \geq K_2 > 0$) to control the diffusion strength. Note that other forms can also be used for the same purpose, for example. $w(i,j) = K_1 \exp\left(-(\sin(H(i,j)-H(x,y))/K_2)^2\right)$. H_0 is the initial hue component.

Figure 4 compares the original orientation diffusion and the proposed weighted orientation diffusion performance on color edges. Figure 4(a) is an artificial hue image with constant values along the y direction and gradually changed values in the x direction (a slope to include all values), except an edge in the middle. Thus any horizontal cross section along the x direction yields a step type function in the middle. Figure 4(b) is the corresponding color image with the hue component from Figure 4(a) and a maximum value of 255 assigned to the saturation and intensity components. With the original orientation diffusion (Eq. (20), $\lambda = 1$, $\beta = 0.03$), the resultant image is shown in Figure 4(c) after 10 iterations. It can be seen that the center edge becomes blurry. Figure 4(d) is the result generated by the weighted orientation diffusion (Eq. (21), $\lambda = 1$, $\beta = 0.03$, $K_1 = 1$, $K_2 = 0.01$) with 20 iterations, and the color edge is preserved well.

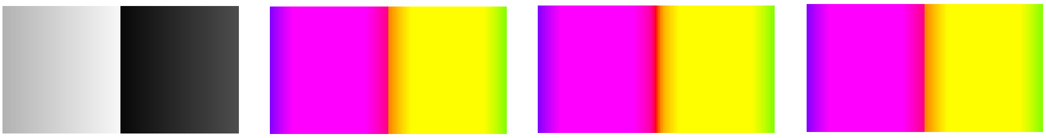

(a) Artificial hue image (b) Artificial color image (c) Orientation diffusion [41] (d) Weighted orientation diffusion

Figure 4. Weighted orientation diffusion.

3.3. Saturation Diffusion

The saturation component (S) gives a measure of the degree to which a pure color is diluted by white light and is represented as a distance map. The saturation diffusion here is based on a modified curvature flow [15]:

$$S_t = \frac{\Delta S + k^2 (S_x^2 S_{yy} - 2 S_x S_y S_{xy} + S_y^2 S_{xx})}{(1 + k^2 (S_x^2 + S_y^2))^2} - \varepsilon (S - S_0) , \tag{22}$$

$\varepsilon > 0$ and S_0 represents the initial saturation component. This is a simple extension from the mean curvature flow by projecting the mean curvature flow to the normal direction and rescaling the intensity component *I* to *kI*. Basically this flow smoothes an image in the direction parallel to the edges. The positive constant *k* is used to amplify image edges, and the anisotropic diffusion becomes the isotropic heat equation when $k = 0$. The interested reader is referred to [15] for more details and illustrations of this modified curvature flow.

4. EXPERIMENTS

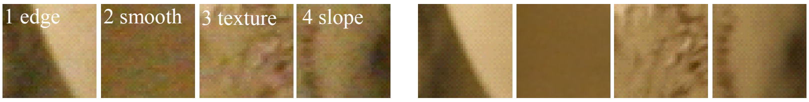
Two sets of color photos have been collected by a Canon 350D and 400D on the same indoor scenes with different ISO settings. The low and high ISO photos of one scene are used as the ground truth and the noise corrupted version. The photos are obtained with a carefully calibrated indoor setup to maintain the consistence of lighting between two photo captures. The photo scene contains only static objects to avoid any motion blur. Only shutter speed is adjusted to maintain the same exposure. Aperture is kept fixed to preserve the same depth of field in both low and high ISO photos. As introduced in Introduction, with the ground truth available, we can conduct a comprehensive performance comparison between our algorithm and 14 recognized approaches for different color spaces (CB [11,21], HSV [21,22] and RGB spaces [4,5,6,7,8,13,15,16,24,25]), and 2 commercial color photo denoising software (Noiseware$^{\text{TM}}$ [62] and Photoshop$^{\text{TM}}$), using both quantitative (PSNR and MSE) and qualitative (visual perception) measures. Here we present four approaches with the highest ranked performance from the quantitative comparison, i.e., the modified curvature flow [15], vector diffusion [6], non-local mean algorithm [25] and CB TV [13], as well as a photo denoising software (Noiseware$^{\text{TM}}$).

Figure 5(a) illustrates a low ISO photo (ISO=100, size=500×500)[*] as the ground truth. Figure 5(b) and 5(c) are the corresponding high ISO (ISO=1600) noisy photo and our GVF-based approach denoising result. In order to clearly view the performance of the selected approaches on different image features (e.g. edge, smooth region, slope and texture), we only display four enlarged regions (see Figure 5(a)) in the high and low ISO photos (Figure 5(d) and 5(e)) and the denoising results. The results of Figure 5(f)-(k) are sorted by the optimal PSNR and MSE values for visual comparison. Due to the close PSNR (MSE) values, these results look similar on the whole. Though, as the error increases, it can be seen some small features are smoothed away from the truth (e.g. at the left region 4). To test more varied images, we repeated this comparison on other four image pairs. Figure 8 illustrates the quantitative comparison of our approach with others by sorting the mean PSNR and MSE values. With these error measures, the GVF-based approach outperforms the other approaches in average.

---

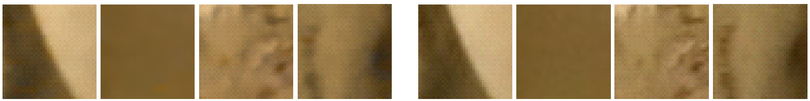
[*] The low and high ISO images were cut separately from big pictures (3456×2304 or 3888×2592) taken at the same scene with different ISO settings.

(a) Low ISO photo (b) High ISO photo of (a) (c) GVF-based approach result



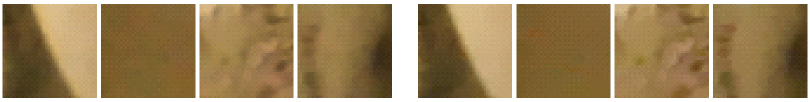
(d) High ISO photo regions (HIGH)
PSNR(db): 32.11; MSE: 40.01

(e) Low ISO photo regions



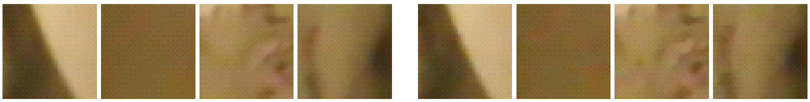
(f) GVF-based (GVF)
PSNR(db): 34.77; MSE: 21.67

(g) Noiseware (NOI)
PSNR(db): 34.69; MSE: 22.1



(h) CB TV (CBTV) [13]
PSNR(db): 34.41; MSE: 23.55

(i) Modified curvature (CUR) [15]
PSNR(db): 34.4; MSE: 23.59



(j) Non-Local (NON) [25]
PSNR(db): 34.11; MSE: 25.26

(k) Vector diffusion (VEC) [6]
PSNR(db): 33.91; MSE: 26.44

Figure 5. Denoising results sorted by the PSNR (MSE) values.

In order to highlight the behavior of the GVF-based approach on different image features, we draw four lines (see Figure 5(a)) in the intensity components of denoising results and compare the values on these lines with the ground truth pixel by pixel. Figure 6 demonstrates the intensity errors along the lines. For a clear view, we only compare four images in Figure 5(d), (f), (g) and (h) with the ground truth of Figure 5(e), instead of all the results in Figure 5. The results of Noiseware^{TM} (Figure 5(g)) and CB TV (Figure 5(h)) are included in this comparison because they are quantitatively ranked the second and third best. It can be seen that the GVF-based diffusion in overall performs better than other approaches on the image feature preservation and noise removal, i.e., closer to the ground truth (the low ISO photo).

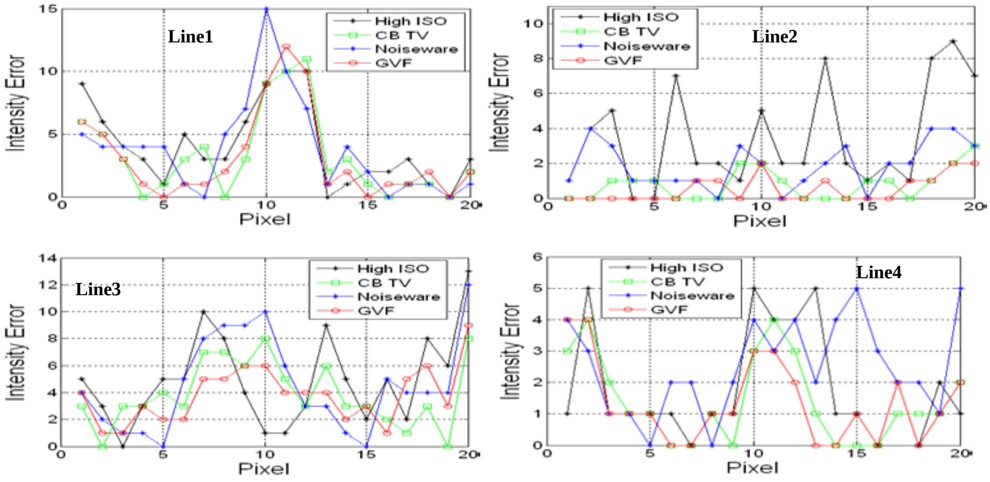
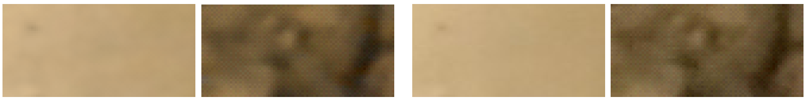


Figure 6. Denoising results line intensity comparison.

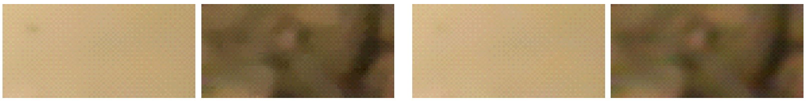
(a) Low ISO photo (b) High ISO photo of (a) (c) GVF-based approach result

(d) High ISO photo regions (HIGH)
PSNR(db): 31.94; MSE: 41.59

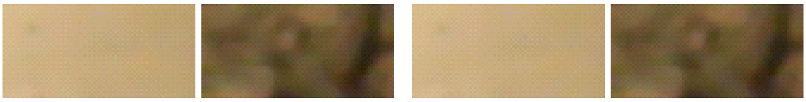
(e) Low ISO photo regions



(f) GVF. PSNR(db): 34.86; MSE: 21.23 (g) NOI. PSNR(db): 34.27; MSE: 24.31



(h) CUR. PSNR(db): 34.16; MSE: 24.92 (i) NON. PSNR(db): 33.95; MSE: 26.2

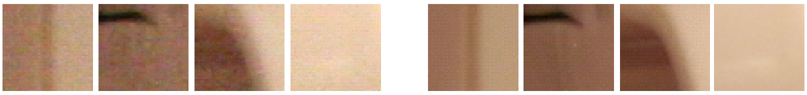


(j) VEC. PSNR(db): 33.81; MSE: 27.06 (k) CBTV. PSNR(db): 33.7; MSE: 27.71

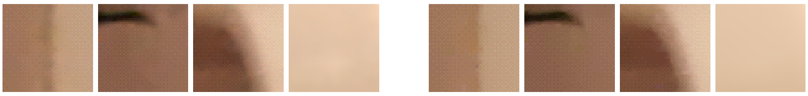
Figure 7. Denoising results sorted by the PSNR (MSE) values.

Another example is shown in Figure 7. The GVF-based diffusion outperforms all other approaches with the MSE and PSNR measures. Besides the quantitative error measures, an interesting visual effect can be observed in this example. There is a small concave part in the center of the bottom rectangle, which has been smoothed away in the results shown in Figure 7 except the GVF-based algorithm result in Figure 7(f). This visual observation again shows that the GVF-based diffusion can preserve image details better than other approaches.

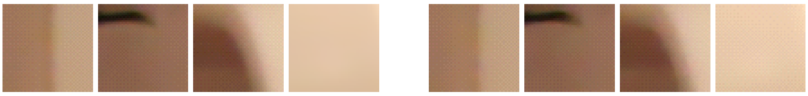
(a) Low ISO photo (b) High ISO photo of (a) (c) GVF-based approach result



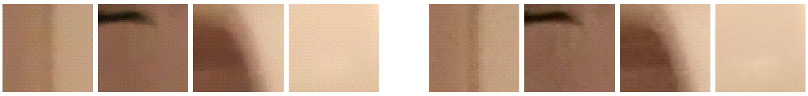
(d) HIGH ISO. PSNR(db): 97.26; MSE: 28.25 (e) Low ISO



(f) GVF. PSNR(db): 63.27; MSE: 30.12 (g) CUR. PSNR(db): 69.45; MSE: 29.71



(h) NON. PSNR(db): 71.04; MSE: 29.62 (i) VEC. PSNR(db) 71.52; MSE 29.59



(j) CBTV. PSNR(db): 72.24; MSE: 29.54 (k) NOI. PSNR(db): 77.25; MSE: 29.25

Figure 8. Denoising results sorted by the PSNR (MSE) values.

We repeat this comparison on other three sets of photos of different scenes and ISO settings. One more example is shown in Figure 8 with the results are sorted by the optimal PSNR and MSE values, in which our approach outperforms others in both quantitative and qualitative error measures. As shown in the enlarged regions, some fine details can be preserved only by the GVF-based approach and Noiseware^{TM}, while other approaches smooth them away (e.g. the weak lines/edges in the regions). The mean and standard deviation of the PSNR and MSE are computed on these five sets (including Figure 5 and Figure 7-8 results). Figure 9 shows the chart sorting the mean values of the PSNR, with the high ISO values listed as a reference. The corresponding MSE bars are also shown in Figure 9. The numbers above the bars are the corresponding mean values of the PSNR and MSE. The standard deviation values are marked as the vertical lines on the bars. It can be seen the proposed approach outperforms other methods with the quantitative measures in average.

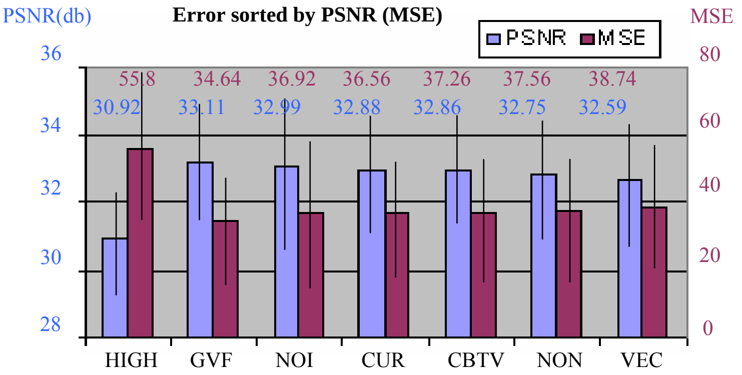


Figure 9. Error chart sorted by the average of PSNR (MSE).

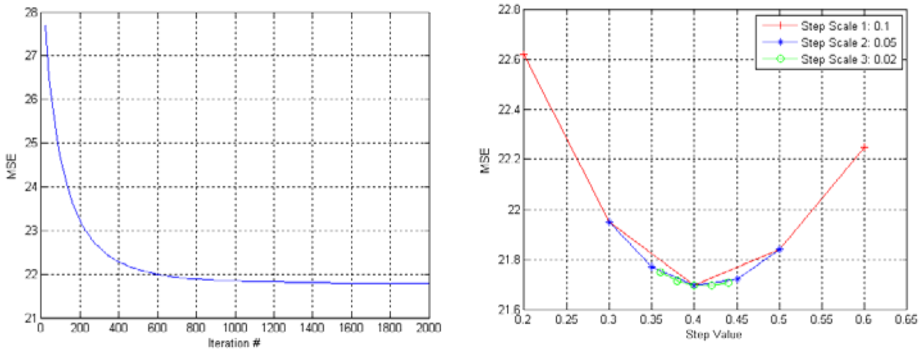
In our experiments, the algorithm parameters were fine-tuned for the "best"[*] results by a multi-scale coarse-to-fine scheme. Specifically, the data fidelity terms in the HSI diffusion equations (Eqs. (12), (21) and (22)) guarantee a convergent diffusion process. With all parameters being fixed except the iteration number, an example of the MSE convergence is shown in Figure 10(a), from which it can be seen that the diffusion process converges after about 1000 iterations. For the HSI diffusion algorithm, the iteration number was selected as 2000 for the optima. The GVF parameters are also fixed in our experiments with μ=0.2 and an iteration number 80 to compute the GVF fields for all images. Given a high ISO photo, the initial parameter settings are obtained by manually selecting the parameters, based on experience, and iterating the process until a quantitatively acceptable result was obtained (e.g. with the improved MSE and PSNR measures). Then we adjust the initial value for each parameter by both increasing and decreasing it until the result error measures become worse (e.g. an increase of the MSE), and the turning point is considered as the approximate optimum[§]. The steps to determine the approximate optimum proceed in a multi-scale fashion. For each parameter, we start with a coarse resolution consisting of large "jump" between step values to determine the approximate optimum, while other parameters are fixed with their initial or optimal values. Based on the approximate optimum, a variation range is selected for

---

[*] The parameter tuning was implemented in a semi-automatic way, i.e., a variation range for each parameter was manually selected at first, then a multi-scale searching scheme with different step values was applied to locate the optimum, or suboptimum results. The true optimum is determined by several factors, including the parameter resolution and dependency on each other. In our experiments, we record the intermediate results every 10 iterations in the diffusion process, and the step values (resolution) to update each parameter is changed dynamically as described in Footnote 5. Moreover, we assume that parameters are independent with each other, as described later in this paragraph.

[§] In fact only one turning point will be located in either increasing or decreasing direction due to the convergent process, i.e., the parameter curves are all unimodal, see Figure 10(b).

that parameter by using the approximate value as the range middle and its double[+] as the range radius. Finally a higher resolution with smaller step values is used in the variation range to locate the optimal parameter value[±]. This process is repeated for the other parameters with the assumption that the parameters are independent, thus the order in choosing parameters does not matter. Intuitively, if the parameters were dependent on each other then the diffusion process would not converge or provide accurate results. However, in practice this is not the case and the treatment of the parameters as independent variables provides accurate results. If needed, the above fine-tuning process can be repeated for finer resolution. An example of this unimodal parameter curve is shown in Figure 10(b), in which three step scales were used to locate the optimal k in Eq. (22). Similarly, this parameter tuning process is applied for other methods in our comparison except the non-local mean algorithm, whose parameters are not independent to each other, i.e., parameter curves are not unimodal. A brute force searching has been employed to identify the best size of the searching (learning) window and the comparison window[*].



(a) Convergence example by the MSE (b) Unimodal curve in multi-scale parameter tuning

Figure 10. Examples of convergence and multi-scale parameter tuning.

5. CONCLUSIONS

We present a novel model for color photo denoising in this chapter. The objective is to remove high ISO photo noise to obtain a low ISO photo quality. Unlike previous approaches, the proposed denoising process proceeds as a PDE-based diffusion framework that is

---

[+] The range radius can be adjusted for different parameters, e.g. double for α and triple for β. In fact, this radius is related to the coarse steps, i.e., the larger (coarser) the step value, the larger the radius. Meanwhile, if the optima is located at the boundary of the range, the whole range should be shifted toward that boundary direction, with the previous range boundary as the new range boundary on the other side, i.e., previous left boundary becomes current range's right boundary.

[±] In fact, the process to determine the parameter range is not sensitive to the step values due to the convergence of the diffusion process.

[*] For computational efficiency, we restrict the window radiuses within 1 to 10 (sizes from 3×3 to 21×21), i.e., for each searching window radius from 1 to 10, we repeat the denoising by changing the comparison window radius from 1 to 10.

conducted in the HSI color space. The hue denoising is implemented with a new weighted orientation diffusion that preserves color edge better than previous orientation diffusion. A modified curvature flow is applied in the saturation denoising. The intensity diffusion is our major contribution in this framework, which combines a GVF-based component and a fourth-order filter in one PDE. This combination employs the favorable features of both the GVF and the fourth-order term to implement a robust and accurate denoising process, and to overcome the staircase effect in smooth regions. The performance of the proposed algorithm has been assessed quantitatively and qualitatively in the experimental comparison with other recognized approaches and commercial software. The results indicate that the proposed approach accomplishes our goal and is competitive with the current state of the art.

REFERENCE

[1] L. Alvarez, F. Guichard, P.L. Lions, and J.M. Morel. Axioms and fundamental equations of image processing. *Archive for Rational Mechanics and Analysis*, 123(3):199-257, 1993.

[2] A.L. Yuille, T. Poggio. Scaling theorems for zero-crossings. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 8(1):15-25, 1986.

[3] A.P. Witkin. Scale space filtering. *In Proc. International Joint Conf. Artificial Intelligence,* pp.1019-1023, 1983.

[4] P. Perona, J. Malik. Scale-space and edge detection using anisotropic diffusion. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 12(7):629-639, 1990.

[5] G. Gilboa, N. Sochen, and Y. Zeevi. Image enhancement and denoising by complex diffusion processes. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 26(8):1020-1036, 2004.

[6] D. Tschumperle, R. Deriche. Vector-valued image regularization with PDEs: a common framework for different applications. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 27(4):506-517, 2005.

[7] R. Malladi, J.A. Sethian. Image processing: flows under min/max curvature and mean curvature. *Graphical Models and Image Processing*, 58(2):127-141, 1996.

[8] L. Alvarez, L. Mazorra. Signal and image restoration using shock filters and anisotropic diffusion. *SIAM Journal of Numerical Analysis*, 31(2):590-605, 1994.

[9] R. Carmona, S. Zhong. Adaptive smoothing respecting feature directions. *IEEE Transactions on Image Processing*, 7(3):353-358, 1998.

[10] J. Weickert. Coherence-enhancing diffusion filtering. *International Journal of Computer Vision*, 31(2/3):111-127, 1999.

[11] B. Tang, G. Sapiro, and V. Caselles. Color image enhancement via chromaticity diffusion. *IEEE Transactions on Image Processing*, 10(5):701-707, 2001.

[12] L. Rudin, S. Osher, and E. Fatemi. Nonlinear total variation based noise removal algorithms. *Physica D*, 60:259-268, 1992.

[13] P. Blomgren, T.F. Chan. Color TV: total variation methods for restoration of vector-valued images. *IEEE Transactions on Image Processing*, 7(3):304-309, 1998.

[14] N. Sochen, R. Kimmel, and R. Malladi. A general framework for low level vision. *IEEE Transactions on Image Processing*, 7(3):310-318, 1998.

[15] Yezzi. Modified curvature motion for image smoothing and enhancement. *IEEE Transactions on Image Processing*, 7(3):345-352, 1998.

[16] J. Shah. A common framework for curve evolution, segmentation and anisotropic diffusion. *In Proc. IEEE Conf. Computer Vision and Pattern Recognition*, pp.136-142, 1996.

[17] Tsai, A. Yezzi, and A. Willsky. Curve evolution implementation of the Mumford–Shah functional for image segmentation, denoising, interpolation, and magnification. *IEEE Transactions on Image Processing*, 10(8):1169-1186, 2001.

[18] J. Portilla, V. Strela, M.J. Wainwright, and E.P. Simoncelli. Image denoising using scale mixtures of Gaussian in the wavelet domain. *IEEE Transactions on Image Processing,* 12(11):1338-1351, 2003.

[19] S. Roth, M.J. Black. Fields of experts: a framework for learning image priors. In Proc. *IEEE Conf. Computer Vision and Pattern Recognition*, pp.860-867, 2005.

[20] M. Malfait, D. Roose. Wavelet-based image denoising using a Markov random field a priori model. *IEEE Transactions on Image Processing*, 6(4):549-565, 1997.

[21] T. Chan, S.H. Kang, and J. Shen. Total variation denoising and enhancement of color images based on the CB and HSV color models. *Journal of Visual Communication and Image Representation*, 12(4):422-435, 2001.

[22] R. Kimmel, N. Sochen. Orientation diffusion or how to comb a porcupine. *Journal of Visual Communication and Image Representation*, 13(1-2):238-248, 2002.

[23] N. Sochen, C. Sagiv, R. Kimmel. Stereographic combing a porcupine or studies on direction diffusion in image processing. SIAM Journal of Applied Mathematics, 64(5):1477-1508, 2004.

[24] M. Black, G. Sapiro, D. Marimont, and D. Heeger. Robust anisotropic diffusion. *IEEE Transactions on Image Processing,* 7(3):421-432, 1998.

[25] Buades, B. Coll, and J.M. Morel. A review of image denoising algorithms, with a new one. *Multiscale Modeling and Simulation*, 4(2):490-530, 2005.

[26] J.L. Starck, E.J. Candès, and D.L. Donoho. The curvelet transform for image denoising. *IEEE Transactions on Image Processing*, 11(6):670-684, 2002.

[27] J. Weickert. Anisotropic Diffusion in Image Processing. Teubner-Verlag, 1998.

[28] G. Aubert, P. Kornprobst. Mathematical Problems in Image Processing. Springer, 2001.

[29] R.C. Gonzalez, R.E. Woods. *Digital Image Processing*. 3rd Ed. Pearson Prentice Hall, 2008.

[30] Professional Photographer Magazine,http://www.ppmag.com/bonus/2006/08/review-imagenomic-noiseware.html.

[31] C. Xu, J.L. Prince. Snakes, shapes, and gradient vector flow. *IEEE Transactions on Image Processing*, 7(3):359-369, 1998.

[32] M. Lysaker, X. Tai. Iterative image restoration combining total variation minimization and a second-order functional. *International Journal of Computer Vision*, 66(1):5-18, 2006.

[33] H. Yu, C. Chua. GVF-based anisotropic diffusion models. *IEEE Transactions on Image Processing*, 15(6):1517-1524, 2006.

[34] Y. You, W. Xu, A. Tannenbaum, and M. Kaveh. Behavioral analysis of anisotropic diffusion in image processing. *IEEE Transactions on Image Processing*, 5(11):1539-1553, 1996.

[35] F. Catte, T. Coll, P.L. Lions, and J.M. Morel. Image selective smoothing and edge detection by nonlinear diffusion. *SIAM Journal of numerical analysis*, 29:182-193, 1992.

[36] L. Alvarez, P.L. Lions, and J.M. Morel. Image selective smoothing and edge detection by nonlinear diffusion (ii). *SIAM Journal of numerical analysis*, 29:845-866, 1992.

[37] P. Kornprobst, R. Deriche, and G. Aubert. Image coupling, restoration and enhancement via PDEs. *In Proc. IEEE International Conf. on Image Processing*, pp.458-461, 1997.

[38] P. Kornprobst, R. Deriche, and G. Aubert. Nonlinear operators in image restoration. *In Proc. IEEE Conf. Computer Vision and Pattern Recognition*, pp.325-330, 1997.

[39] G. Gilboa, N. Sochen, and Y Zeevi. Forward-and-backward diffusion processes for adaptive image enhancement and denoising. *IEEE Transactions on Image Processing*, 11(7):689-703, 2002.

[40] S. Osher, L. Rudin. Feature oriented image enhancement using shock filters. *SIAM Journal of Numerical Analysis*, 27(4):919-940, 1990.

[41] P. Perona. Orientation diffusions. *IEEE Transactions on Image Processing,* 7(3):457-467, 1998.

[42] G. Sapiro, D.L. Ringach. Anisotropic diffusion of multivalued images with applications to color filtering. *IEEE Transactions on Image Processing*, 5(11):1582-1586, 1996.

[43] T. Chan, S. Osher, and J. Shen. The digital TV filter and nonlinear denoising. *IEEE Transactions on Image Processing*, 10(2):231-241, 2001.

[44] T. Chan, C. Wong. Total variation blind deconvolution. *IEEE Transactions on Image Processing,* 7(3):370-375, 1998.

[45] L. Rudin, S. Osher. Total variation based image restoration with free local constraints. In Proc. *IEEE International Conf. on Image Processing*, Vol. I, pp.31-35, 1994.

[46] L.A. Vese, S. Osher. Image denoising and decomposition with total variation minimization and oscillatory functions. *Journal of Mathematical Imaging and Vision*, 20:7-18, 2004.

[47] S. Teboul, L. Blanc-Feraud, G. Aubert, and M. Barlaud. Variational approach for edge-preserving regularization using coupled PDE's. *IEEE Transactions on Image Processing,* 7:387-397, 1998.

[48] S. Gao, T.D. Bui. Image segmentation and selective smoothing by using Mumford-Shah model. *IEEE Transactions on Image Processing,* 14(10):1537-1549, 2005.

[49] R. Malladi, J. Sethian, and B. Vemuri. Shape modeling with front propagation. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 17(2):158-171, 1995.

[50] R. Malladi, J. Sethian. Image processing: flows under min/max curvature and mean curvature. *Graphical Models and Image Processing*, 58(2):127-141, 1996.

[51] D. Mumford, J. Shah. Boundary detection by minimizing functionals. *In Proc. IEEE Conf. Computer Vision and Pattern Recognition*, pp.22-26, 1985.

[52] D. Mumford, J. Shah. Optimal approximation by piecewise smooth functions and associated variational problems. *Communications on Pure and Applied Mathematics*, 42:577-685, 1989.

[53] L. Ambrosio, V.M. Tortorelli. On the approximation of functionals depending on jumps by quadratic, elliptic functionals. *Boll. Un. Mat. Ital.,* 46-b:105-123, 1992.

[54] V. Caselles, R. Kimmel, and G. Sapiro. Geodesic active contours. *International Journal of Computer Vision*, 22(1):61-79, 1997.

[55] P. Meer, D. Mintz, A. Rosenfeld, and D. Y. Kim. Robust regression methods for computer vision: a review. *International Journal of Computer Vision*, 6:59-70, 1991.

[56] S. Geman, D. Geman. Stochastic relaxation, Gibbs distributions and the Bayesian restoration of images. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 6:721-741, 1984.

[57] S. Geman, G. Reynolds. Constrained restoration and the recovery of discontinuities. IEEE Transactions on Pattern Analysis and Machine Intelligence, 14:367-383, 1992.

[58] C. Bouman, K. Sauer. A generalized Gaussian image model for edge-preserving MAP estimation. *IEEE Transactions on Image Processing*, 2:296-310, 1993.

[59] T. Rabie. Robust estimation approach for blind denoising. *IEEE Transactions on Image Processing*, 14(11):1755-1765, 2005.

[60] Y. Bao, H. Krim. Smart nonlinear diffusion: a probabilistic approach. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 26(1):63-72, 2004.

[61] C. Xu, J.L. Prince. Generalized gradient vector flow external forces for active contours. Signal Processing, 71(2):131-139, 1998.

[62] Noiseware^{TM}, http://www.imagenomic.com/products.aspx.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 225-237

Chapter 8

COLOR IN PSYCHOLOGICAL RESEARCH: TOWARD A SYSTEMATIC METHOD OF MEASUREMENT

Roger Feltman and Andrew Elliot
University of Rochester, Rochester, New York, USA

Psychology is a discipline that prides itself on being an empirical science. As such, rigorous statistical and methodological controls must be used to ensure the validity of every result. Ostensibly, each submission for publication is peer reviewed, and needs to be replicated by other scientists in other locations to confirm or disconfirm the results. This is how a scientific discipline must operate if it wishes to produce meaningful, accurate results. When a discipline strays from these procedures, it leaves itself open to criticism and more importantly, to the possibility of inaccurate or misleading conclusions. All research needs to ascribe to these standards, regardless of how time consuming, inefficient, or difficult they may be.

One area of research that has failed to live up to these standards is the study of color and psychological functioning. The aesthetic property of color may at first consideration make it seem like a trivial topic for study, but recent research (Elliot, Maier, Moller, Friedman, & Meinhardt, 2007) indicates exactly the opposite. Color has been shown to influence affect, cognition, and behavior (Elliot, Maier, Binser, Friedman, & Pekrun, 2009; Elliot et al., 2007; Lichtenfeld, Maier, Elliot, & Pekrun, In Press**;** Maier, Elliot, & Lichtenfeld, 2008). The degree and type of influence has varied from study to study, some more psychologically consequential (e.g. color and performance: Elliot et al., 2007) than others (e.g. shoe color preference: Trinkaus, 1991). None of these results, however, can be considered valid if they fail to live up the methodological rigors of science.

An in depth examination of the color research of the past and present makes it clear that most of the work fails to meet scientific standards (Fehrman & Fehrman, 2004). Too many studies have failed to take into account the three basic properties of color. Others have failed to consider the unconscious associations people have with color that could act as possible confounds. Stated differently, color used in an experiment may affect the experiment's dependent variable in unwanted and unaccounted for ways. In either case, it is impossible to draw meaningful conclusions from these studies, as their results could be due to any number of variables. This is the primary argument that will be made throughout this chapter. The aim is not to criticize or demean the existing research or researchers. Rather, it is hoped that this analysis will lead to more systematic, scientifically valid empirical work on color psychology. By learning about and avoiding the mistakes documented below, researchers will be able to meaningfully add to the growing body of work in on color psychology.

Before a critical analysis can be conducted of past research, it is necessary to briefly review the physical characteristics of both color and the mechanisms by which people perceive color (for a more in-depth overview see: Levine, 2000). Color is part of a small band of electromagnetic radiation that the human eye is able to perceive. The wavelength of visible light ranges from about 400 to 700 nanometers; it is within this small range of the electromagnetic spectrum that humans perceive the world with their eyes. Color theorists define color using three components that explain where it falls along this spectrum: hue, chroma (or saturation), and lightness (or brightness).

Hue is the property of color most commonly considered in everyday life (Fehrman et al., 2004). The color terms we use every day -- red, orange, yellow, green, blue, indigo, and violet -- are all descriptions of hue. When a person exclaims that an apple is red, she is remarking primarily about the apple's hue. Black, white, and gray are not considered from this standpoint. Instead, each are merely neutrals as they lack the defining characteristic of color, hue.

Lightness, as its name suggests, is how much light is present in a given color (Fehrman et al., 2004). It describes the subjective brightness of a given color. Some color models refer to this as a color's value (see: Munsell, 1905). Finally, a color is defined by its saturation or chroma (Fehrman et al., 2004). When referring to saturation, a color's fullness or vividness is being described. A more parsimonious way to think about chroma is to consider how much white or black has been mixed in with the color. A light pink would have low chroma, for instance, while a deep crimson would have high chroma.

The importance of these three characteristics of color cannot be overstated; they lead to a precise definition of what color is being utilized. It is not sufficient to merely report that red and green, for example, were used in an experiment, as such terms could indicate a wide range of different colors. Is it a light red that is low in saturation or is it a deeper, darker red? Does the green have any yellow or blue mixed in or is it a "pure" green? Each of the three characteristics of color has a profound impact on what is observed in any given experiment.

Failing to consider the three properties of color not only leaves the research open to confounds, but, ultimately, there is no way for other researchers to reliably replicate the work. If one experiment used a dark, deeply saturated red and another, attempting to replicate the results of the first, using a light, unsaturated red, any effects due to lightness or chroma in the first study will not be present and could lead to a failure to replicate.

It is also important that colors *within* experiments be controlled when two or more colors are used simultaneously. While hue will obviously differ, the lightness and chroma of the colors need to be matched. This is a critical point that must not be overlooked. Without ensuring that the only difference between colors is their hue, the value of any results obtained will be diminished by the inability to distinguish the ultimate cause of the effect. Are the results due to hue differences, or is it differences in lightness or chroma that produce the results? This question cannot be answered if strict control is not maintained over the colors used.

Additionally, three potentially unanticipated factors come into play when color is used as an independent variable in research: 1) Combinations of colors may be perceived differently than each color would be observed in isolation (e.g. Kjelldahl & Schenkman, 2007). Yellow may look different when presented in the context of blue and red, for example. 2) The lighting of a space has a tremendous impact on how the colors are perceived (Hunt, 1991). A red in natural daylight will appear quite different than a red under fluorescent light; and 3) Any experiment with color must take into account possible color associations participants bring with them into the lab (Kaya & Epps, 2004). As will be seen, color associations are as diverse as they are many and vary from culture to culture (e.g. Hupka, Zaleski, Otto, Reidl, & Tarabrina, 1997). It is important to consider the effect of these associations when interpreting results.

Before examining the shortcomings of previous research, brief mention should be made of the various color models currently in use. Some research (mostly in the physiology and perception areas) has already implemented the color controls mentioned above. One such method is the Munsell color model (Munsell, 1905). This model assigns notations to every color based on lightness, chroma, and hue. In this way, researchers using the Munsell Model make use of a color's previously defined properties which are documented in the Munsell Book of Color (Munsell, 1905). A brief literature search reveals its position as the prevalent color model in use today in research on color physiology and color perception (e.g. Choo & Kim, 2003; Franklin & Davies, 2004; Indow, 1999; Kaya & Crosby, 2006; Lindsey & Brown, 2002; Perez-Carpinell, Camps, Trottini, & Perez-Baylach, 2006; Rodrigues & Murre, 2007). Alternatives to the Munsell model include the LCH color system described above (Wyszecki & Stiles, 2000) as well as the Lab color space (Wyszecki et al., 2000). The latter two color systems were both developed by the International Commission on Illumination (CIE).

The preceding discussion has highlighted the complexity of color and outlined the characteristics that must be considered when conducting research involving color. Several studies will now be evaluated to demonstrate the shortcomings of prior psychologically-based research on color. The purpose of this review is not to simply reject the results of each study. Instead, the aim is to use past research to provide clear examples of how the principles detailed above can be used to improve research on color psychology.

One of the most studied issues in the color psychology literature is people's color preferences (e.g. Coad & Coad, 2008; Dittmar, 2001; Ellis & Ficek, 2001; Eysenck, 1941; Guilford & Smith, 1959; Ou, Luo, Woodcock, & Wright, 2004; Rosenbloom, 2006; Wijk, Berg, Sivik, & Steen, 1999). The aim of investigating color preference varies across researchers. Some are interested in how color preferences indicate or influence personality (Lange & Rentfrow, 2007) while others seek to understand how people with psychopathologies differ in their color preferences from those without psychopathology (Strenski, Payson, Muzekari, & Bohr, 1970). Still others are interested in making a profit using color preference information, such as marketers (Singh, 2006) and advertisers (Lichtle, 2007). Color preferences have also been studied across age groups (Terwogt & Hoeksma, 2001; Zentner, 2001) and across cultures (Garth & Collado, 1929; Saito, 1996).

Unfortunately, most of the early research in this area, and most contemporary research as well, used methods that fail to yield conclusive results. For instance, in an early color preference study by Washburn (1911), the researcher states that different "tints" (presumably lightness values) and saturations were used. However, no mention was made of how tinted or saturated each color was. The researcher can be commended for his efforts to consider the multiple properties of color, but ultimately, without knowing the degree of tint or saturation, his results are inconclusive. Of course this criticism must be tempered by the fact that the technology available to researchers in the early 1910's was far more primitive than what is available today. Nevertheless, Washburn's (1911) attempts at color control are admirable, but they do not meet the standards for well-controlled empirical color research.

This same criticism can be directed toward all color research conducted prior to standardized color systems and spectrophotometry. Ideally, color research prior to these inventions would have used whatever methods available at the time to control color properties. There are examples of researchers taking this important step. Pressey (1921), for example, used an episcotister and light bulbs of equal intensity to equate brightness. Luckiesh (1916) used Wundt papers to standardize the colors used, and thus allowed for further tests to be conducted with the same materials.

The use of standardized papers from a manufacturer was a common method for controlling lightness and chroma prior to the development of spectrophotometry (e.g. Garth et al., 1929; Eysenck, 1941) and is still used today (e.g. Bellizzi & Hite, 1992). Conducting research with manufactured papers that ostensibly have the same lightness, chroma, and hue values is a step in the right direction, but it is not sufficient. A mistake, however minor, in the manufacturing process may result in inaccurate color values; what is claimed by the manufacturer may not reflect the actual characteristics of the paper. In the past, when the sophisticated technology that is available today had yet to be invented, the use of such papers may have been necessary, and in fact probably led to the most empirically sound research of the time. Their use today, however, is not advised due to potential irregularities. Researchers have available to them the methods that render reliance on papers unnecessary. Far more precise color control can be obtained using a spectrophotometer to determine the exact lightness and chroma values of any color at the spectral level. Manufactured papers, if used in experiments today, must be examined with spectrophotometry equipment, or the equivalent, to ensure that they indeed represent what they claim to represent. We will return to this issue toward the end of the chapter.

Terwogt and colleagues (2001) conducted a study of color preferences and failed to use any color controls; not even manufactured papers were used. This is particularly surprising considering that they cited several articles that explicated many of the same concerns being discussed here (e.g. Norman & Scott, 1952). Several other recent studies suffer from similar methodological shortcomings. An examination of the research on color preferences conducted in the last 15 years demonstrates how little control over the various properties of color has been attended to (e.g. Boyatzis & Varghese, 1994; Hemphill, 1996). Research on non-human animals is not immune from these deficiencies (Wells, McDonald, & Ringland, 2008).

Color preference is an interesting aspect of psychological study. In addition to work on color preferences per se, researchers have examined the link between color associations and affect (e.g., Wexner, 1954), personality (e.g., Schaie, 1963), and attention (e.g., Noiwan & Norcio, 2006). Researchers have attempted to discern which colors are "energizing" and which are "calming" (Stone & English, 1998). Colors have been found to be "hot" and "cold" (Taft, 1997), "heavy" and "light" (Lee & Lee, 2006), "happy" and "sad" (Hemphill, 1996). Unfortunately, most of these studies have the same methodological flaws as the color preference studies. Instead of using colors that have been carefully equated for lightness and chroma, researchers seem to have relied on their individual perceptions to pick colors for their study. A study by Weller and Livingston (1988) may be used in representative fashion. In this study, participants were presented with questionnaires on pink, blue, or white paper after reading a vignette about a crime. They were asked to indicate their thoughts about the crime, the judgment (guilty or not guilty), and their thoughts about the defendant. It was found that the pink questionnaires produced less emotionality than the blue or white questionnaires. Were the results due to differences in hue or did the brightness or saturation of the pink (or blue) produce the differences? Without knowing the specific properties of the colors used, it is impossible to know; clear results will depend on a replication with color carefully controlled. (An interesting aside is that the authors of this study mentioned that the brightness contrast between the ink and the paper was not the same for the blue paper as for the pink and white papers, pointing to an additional, idiosyncratic, confound).

Color and personality is another area that has been extensively studied with little concern for appropriate color controls. The care and fastidiousness with which personality researchers approach various aspects of personality structure and process has not generalized to their use of color. For instance, the Color Pyramid Test (e.g. Schaie, 1963) is a non-verbal test of personality that asks participants to arrange colored squares to make both “pretty” and “ugly” pyramids. The analysis of the composition of these pyramids, which is based exclusively on hue, is presumed to reveal the respondent’s personality. However, none of the colors used in the Color Pyramid Test have had their lightness or chroma measured. Thus, choices perceived to be made with regard to hue, may actually be made with regard to lightness, saturation, or an interaction of color properties. Another personality test using unstandardized colors is the Lüscher Color Test (Luscher, 1969). Respondents chose colors ranging from most favorite to least favorite and a respondent’s choices are said to reflect his or her personality. Again, all analyses are made based on uncontrolled hues, and no consideration is given to the other properties of color.

These color-based personality trait tests are not widely used by researchers and clinicians today and their validity is strongly doubted (Fernando, Cernovsky, & Harricharan, 1992; Picco & Dzindolet, 1994), but their popularity remains high among the general public. It is common to hear people “diagnose” their or their friend’s personality based on their favorite color. The internet is also filled with personality tests based on color (Fuentes).

Researchers have also been interested in how color is able to influence or alter emotional states in work and retail environments. It has long been claimed that red is an exciting color while blue is calming in such settings (see: Fehrman et al., 2004). What have researchers found? Yildirim, Akalin-Baskaya, & Hidayetoglu (2007) found that violet interiors were preferred to yellow in a restaurant setting. Kuller, Mikellides, & Janssens (2009) found that when employees subjectively rated the “colorfulness” of their work environments, those in the most colorful work spaces reported the highest degree of emotionality (e.g., happiness). Bellizzi and colleagues (1992) found that blue retail environments produce more positive customer feelings than red retail environments. Bellizzi, Crowley, and Hasty (1983) report that “warm” (long wavelength) colors draw people in closer, but are seen as less pleasant than “cool” (short wavelength) colors. None of these studies has used proper procedures to control for non-hue properties of color. Nevertheless, in the past decade the retailing industry has become very interested in the effects color can have on shopping behavior. Entire articles have been devoted to reviewing how to use color most effectively (e.g. Singh, 2006), and an issue of the Journal of Business Research has concentrated on the aesthetics used in retailing, including to a large extent, the use of color (August 2000).

Another area of research that has received attention is that on the effect of color on performance, on both strength-based and intellectual tasks. Hill and Barton (2005) recently demonstrated that Olympic competitors wearing red did better than those wearing blue. O'Connell, Harper, and McAndrew (1985) measured the impact color has on grip strength and found that looking at a red wall increased grip force (see also Green, et al., 1982). The effect of color has also been examined in the virtual world; Ilie, Ioan, Zagrean, and Moldovan (2008) replicated the results of Hill and colleagues (2005) using a virtual reality computer game. Another study (Wolfson & Case, 2000) found that a red background in a computer game decreased performance after multiple trials and a blue background in the same game resulted in increasing heart rates as the sessions continued. Sinclair, Soldat, and Mark (1998) found that participants did worse on classroom tests printed on red than blue paper (see also James & Domingos, 1953). Again, none of these studies controlled for lightness and saturation in examining hue effects. This is understandable in field research (e.g., Hill et al., 2005), but is less so in experimental work in the lab. Research that has examined color in a controlled manner has repeatedly demonstrated that red undermines intellectual performance (Elliot et al., 2007; 2009; Lichtenfeld et al., 2009), and has additionally shown that this is due to red evoking concern about the danger of failure that, in turn, undermines performance (Maier et al., 2008).

If, as this more controlled work suggests, red undermines intellectual performance, the use of color in experiments designed to examine other issues raises important questions. Indeed, almost any study that uses red in an achievement context as a marker or cue suffers from this confound. In one study (Trommershauser, Maloney, & Landy, 2003) participants were asked to touch a green part of a computer screen as quickly as possible while also avoiding a nearby red region in order to earn as much money as possible. The effects of hue were not being investigated here; hue was only used as an instructional marker for participants. Given the inimical effect of red shown in controlled experiments (e.g., Elliot et al., 2007), this seems problematic. The performance of participants was likely affected by the red color per se, as well as by the focal manipulation of the researchers. Furthermore, it is possible that green carries psychological meaning (it has been used to prime money; Mandel & Johnson, 2002), and could influence behavior in unintended ways as well. Unfortunately, the use of green to stand for gain/success and red to stand for loss/failure is not unique to this study. This same confound can be found in lottery studies (e.g., Rothermund, Wentura, & Bak, 2001), studies using the IAT (e.g., Dijksterhuis & Smith, 2002), go/no go tasks (e.g., Swainson, et al., 2003; Mostofsky, et al., 2003), group membership studies (e.g., Vanbeselaere, 1996), and research on the mechanisms of stereotyping (e.g., Bigler, 1995).

This unintentional color confounding is also important to consider in studies using a Stroop paradigm (Stroop, 1935). The quantity of studies using the Stroop task is very high, and it is vital that the mechanisms operative in the task are clearly understood and taken into consideration when interpreting results. The Stroop task is essentially an achievement oriented task in that it requires participants to state the correct word as quickly as possible. As such, it is likely that seeing red during this task will evoke failure associations (see Moller, Elliot, & Maier, In Press) that may disrupt concentration and influence responding throughout the task.

Two studies may be considered as illustrative representatives of the wider body of literature using the Stroop paradigm. The first study used the Stroop task to determine how the co-morbidity of depression and anxiety influences attentional bias (Grant & Beck, 2006).

Words like despair, defeated, and pathetic were presented in a variety of colors, one of which was red. Given the documented link between red and failure (Moeller et al., 2009), red likely influenced responses to these achievement-relevant words, unbeknown to the investigator. A second study utilized the Stroop task in investigating attentional bias for smoking-related and affective words in smokers (Drobes, Elibero, & Evans, 2006). The word “failure” was used as a target word in the study, as was the color red. Again, given the red-failure link, this color-word association undoubtedly influenced participants’ responses with unknown effects on the final results obtained.

It is encouraging to note that some researchers, particularly in the sensation and perception area, have realized and attended to the importance of strict color measurement. Almost all of the recent work submitted to *Color Research and Application*, for instance, has included quite strict color controls (e.g., Küller et al., 2008). This rigor, however, remains absent even in research published in such premier journals as *Science*. For example, Mehta and Zhu (2009) recently published a paper showing that red increases performance on low-level, detail oriented tasks and that blue increase creativity. These results have been widely disseminated in the public arena, and are likely accepted as fact by most who hear that the work was published in *Science*. Unfortunately, this work did not include proper procedures for equating hues on lightness and chroma. This is not to say that the results are necessarily incorrect (see Maier et al., 2008, for similar predictions), but it remains unclear, at present, whether the findings are indeed due to variations in hue rather than other properties of color.

Now that the deficiencies in much extant research on color and psychological functioning have been reviewed, we turn our attention to how to address the challenges presented by color research. A straightforward and effective way to control for color properties is to use a device known as a spectrophotometer. This device is able to provide precise information on lightness, chroma, and hue using data at the spectral level. Using a spectrophotometer, each and every color used in an experiment can be individually tested and verified (see: Lee & Honson, 2003). This is true regardless of whether the color is printed on paper or displayed on a computer monitor. Operating the spectrophotometer is not difficult, but it does require some investment of time to learn the proper procedures. In addition to being rather straightforward to use, specrophotometers are able to produce output in several different color spaces. Switching from an lcH color space to another CIE color space presents no problems for the researcher, and can be very helpful in comparing colors used in various published articles.

It should be noted that as in all research, putting method into practice is more difficult than might appear on the surface. While it is indeed easy to obtain spectral data on color stimuli, it is more difficult to ensure that the hues used in an experiment have the same lightness and saturation (or, more generally stated, that only one property of color varied at a time). A small change in the paper on which the colors are printed, the ink used to print the colors, and the lighting of the room in which the measurements are taken, can all impact the readings of the spectrophotometer. It is thus necessary to enforce strict controls over all of these factors: Ensure that the paper (or whatever material the color is being printed on) is of high quality and from the same packet for different colors, use ink manufactured in the same batch within a given printing of stimulus materials, and measure the colors in a room in which the lighting is consistent. Failure to account for any of these variables could result in the same unwanted variation present in the research reviewed earlier.

These issues notwithstanding, the use of a spectrophotometer (or similar method for equating color values using spectral data) is called for in experiments using color as an independent variable. This is particularly the case when printed color is used in experiments. For color presented on a computer monitor, two other techniques are available that provide rigorous color control.

One of these techniques is called heterochromatic flicker photometry (HFP: Jordan, Sherman, & Tonkin, 2007; Wagner & Boynton, 1972). Predominantly used in the field of brain imaging and neuropsychology, it has proven to be effective in equating the luminance of colors as observed by individual participants (Wagner et al., 1972). Typically, a target color is presented on a background of a different color or a baseline color (e.g. white). The target color is flashed very quickly (e.g. 12Hz or 20Hz; Jordan et al., 2007) while the background color remains constant. Participants are asked to adjust the luminance of the target color until the appearance of a flicker stops. This is the point at which the two colors are said to equiluminant (Jordan et al., 2007). Saturation is not controlled for in HFP, and thus a spectrophotometer would need to be used to ensure that each color selected has matching saturation values.

Similar to HFP is a method for equating the luminance of colors known as the minimally distinct border technique (MDB: Lindsey & Teller, 1989). In this technique, color consistency is obtained by presenting two colors adjacent to each other and asking the participant to adjust the brightness of one of them until the border between the two becomes as indistinct as possible. It has been suggested that the MDB method of equating color properties is superior to HFP, because it is able to equate for saturation as well as lightness (Wagner et al., 1972).

Thus, when color stimuli are presented on a computer display, it appears that MDB provides a way of controlling color properties that is as good as that provided by use of a spectrophotometer. Indeed, given that there are individuals differences in color perception (Webster, Miyahara, Malkoc, & Raker, 2000a; 2000b) the MDB approach might be seen as somewhat superior to using a spectrophotometer. However, the MDB approach can only be used in experiments in which color is an explicit aspect of the study; when the subtle or implicit use of color is under investigation, MDB is not a viable option. In addition, using a spectrophotometer is clearly the only rigorous way to control color properties with printed color.

Perhaps in the future, ensuring that two or more colors have the same lightness and saturation will be as easy as clicking on a color in a computer program or programming a printer to produce equiluminant and equally saturated colors. Unfortunately, technology has not yet advanced to this level of sophistication and, as such, it is imperative that researchers exert the necessary effort to establish proper color control using a spectrophotometer or MDB. Failure to do so will continue to hamstring a literature on color and psychology that remains at a nascent level of development.

REFERENCES

[1] (2000). *Journal of Business Research , 49* (2), 89-211.

[2] Bellizzi, J. A., & Hite, R. E. (1992). Environmental color, consumer feelings, and purchase likelihood. *Psychology & Marketing , 9*, 347-363.

[3] Bellizzi, J. A., Crowley, A. E., & Hasty, R. W. (1983). The effects of color in store design. *Journal of Retailing , 59*, 21-45.

[4] Bigler, R. S. (1995). The role of classification skill in moderating environmental influences on children's gender stereotyping: A study of the functional use of gender in the classroom. *Child Development , 66*, 1072-1087.

[5] Boyatzis, C. J., & Varghese, R. (1994). Children's emotional associations with colors. *Journal of Genetic Psychology , 155*, 77-85.

[6] Choo, S., & Kim, Y. (2003). Effect of color on fashion fabric color image. *Color Research and Application , 28*, 221-226.

[7] Coad, J., & Coad, N. (2008). Children and young people's preference of thematic design and colour for their hospital environment. *Journal of Child Health Care , 12*, 33-48.

[8] Dijksterhuis, A., & Smith, P. K. (2002). Affective habituation: Subliminal exposure to extreme stimuli decreases their extremity. *Emotion , 2*, 203-214.

[9] Dittmar, M. (2001). Changing color preferences with ageing: A comparative study on younger and older native Germans aged 19-90 years. *Gerontology , 47*, 219-226.

[10] Drobes, D. J., Elibero, A., & Evans, D. E. (2006). Attentional bias for smoking and affective stimuli: A Stroop task study. *Psychology of Addictive Behaviors , 20*, 490-495.

[11] Elliot, A. J., Maier, M. A., Binser, M. A., Friedman, R., & Pekrun, R. (2009). The effect of red on avoidance behavior in achievement contexts. *Personality and Social Psychology Bulletin , 35*, 365-375.

[12] Elliot, A., Maier, M., Moller, A., Friedman, R., & Meinhardt, J. (2007). Color and psychological functioning: The effect of red on performance attainment. *Journal of Experimental Psychology: General , 136*, 154-168.

[13] Ellis, L., & Ficek, C. (2001). Color preferences according to gender and sexual orientation. *Personality and Individual Differences , 31*, 1375-1379.

[14] Eysenck, H. J. (1941). A critical and experimental study of colour preferences. *The American Journal of Psychology , 54*, 385-394.

[15] Fehrman, K., & Fehrman, C. (2004). *Color: The secret influence* (2nd ed.). Upper Saddle River, NJ: Prentice Hall.

[16] Fernando, M. L., Cernovsky, Z. Z., & Harricharan, R. (1992). Color preference of DSM-III-R bipolars and normal controls. *Social Behavior and Personality , 20*, 247-250.

[17] Franklin, A., & Davies, R. L. (2004). New evidence for infant colour categories. *British Journal of Developmental Psychology , 22*, 349-377.

[18] Fuentes, G. (n.d.). *Color preferences reveal your personality*. Retrieved March 1, 2009, from The psychology of color: http://www.viewzone.com/luscher.html

[19] Garth, T. R., & Collado, I. R. (1929). The color preferences of Filipino children. *Journal of Comaprative Psychology , 9*, 397-404.

[20] Grant, D. M., & Beck, J. G. (2006). Attentional biases in social anxiety and dysphoria: Does comorbidity make a difference? *Anxiety Disorders , 20*, 520-529.

[21] Green, W. K., Hasson, S. M., Mohammed, S. K., Phillips, C. L., Richards, P. E., Smith Jr, M. E., et al. (1982). Effect of viewing selected colors on the performance of gross and fine motor tasks. *Perceptual and Motor Skills , 54*, 778.

[22] Guilford, J. P., & Smith, P. C. (1959). A system of color-preferences. *The American Journal of Psychology , 72*, 487-502.

[23] Hemphill, M. (1996). A note on adults' color-emotion associations. *Journal of Genetic Psychology , 157*, 275-280.

[24] Hill, R. A., & Barton, R. A. (2005). Red enhances human performance in contests. *Nature , 435*, 293.

[25] Hunt, R. W. (1991). *Measuring Color* (2nd ed.). Chichester: Ellis Horwood Ltd.

[26] Hupka, R. B., Zaleski, Z., Otto, J., Reidl, L., & Tarabrina, N. V. (1997). The colors of anger, envy, fear, and jealousy: A cross cultural study. *Journal of Cross-Cultural Psychology , 28*, 156-171.

[27] Ilie, A., Ioan, S., Zagrean, L., & Moldovan, M. (2008). Better to be red than blue in virtual competition. *CyberPsychology & Behavior , 11*, 375-377.

[28] Indow, T. (1999). Predictions based on Munsell notation I: Perceptual color differences. *Color Research and Application , 24*, 10-18.

[29] James, W. T., & Domingos, W. R. (1953). The effect of color shock on motor performance and tremor. *The Journal of General Psychology , 48*, 187-193.

[30] Jordan, T. R., Sherman, S. M., & Tonkin, R. P. (2007). Constructing isoluminant stimuli for word recognition research: A precautionary study. *Behavior Research Methods , 39*, 494-501.

[31] Kaya, N., & Crosby, M. (2006). Color associations with different building types: An experimental study on American college students. *Color Research and Application , 31*, 67-71.

[32] Kaya, N., & Epps, H. H. (2004). Relationship between color and emotion: A study of college students. *College Student Journal , 38*, 396-405.

[33] Kjelldahl, L., & Schenkman, B. N. (2007). Color induction on computer displays: Adjacency and shape effects. *Behaviour & Information Technology , 26*, 261-272.

[34] Kuller, R., Mikellides, B., & Janssens, J. (2009). Color, arousal, and performance - A comparison of three experiments. *Color Research and Application , 34*, 141-152.

[35] Lange, R., & Rentfrow, J. (2007). Color and Personality: Strong's interest inventory and Cattell's 16PF. *North American Journal of Psychology , 9*, 423-438.

[36] Lee, D. Y., & Honson, M. (2003). Chromatic variation of Ishihara diagnostic plates. *Color Research and Application , 28*, 267-276.

[37] Lee, Y.-J., & Lee, J. (2006). The development of an emotion model based on color combinations. *International Journal of Consumer Studies , 30*, 122-136.

[38] Levine, M. (2000). *Levine & Shefner's fundamentals of sensation and perception* (3rd ed.). Oxford: Oxford University Press.

[39] Lichtenfeld, S., Maier, M. A., Elliot, A. J., & Pekrun, R. (In Press). The semantic red effect: Processing the word red undermines intellectual performance. *Psychological Sccience .*

[40] Lichtle, M.-C. (2007). The effect of an advertisement's colour on emotions evoked by an ad and attitude towards the ad: The moderating role of the optimal stimulation level. *International Journal of Advertising , 26*, 37-62.

[41] Lindsey, D. T., & Brown, A. M. (2002). Color naming and the phototoxic effects on the eye. *Psychological Science , 13*, 506-512.

[42] Lindsey, D. T., & Teller, D. Y. (1989). Influence of variations in edge blur on minimally distinct border judgments: A theoretical and empirical investigation. *Journal of the Optical Society of America: A , 6*, 446-458.

[43] Luckiesh, M. (1916). A note on color preference. *The American Journal of Psychology , 27*, 251-255.

[44] Luscher, M. (1969). *The Luscher Color Test.* (I. Scott, Ed.) New York: Random House.

[45] Maier, M., Elliot, A., & Lichtenfeld, S. (2008). Mediation of the negative effect of red on intellectual performance. *Personality and Social Psychology Bulletin , 34*, 1530-1540.

[46] Mandel, N., & Johnson, E. J. (2002). When web pages influence choice: Effects of visual primes on experts and novices. *Journal of Consumer Research , 29*, 235-245.

[47] Mehta, R., & Zhu, R. (2009). Blue or red? Exploring the effect of color on cognitive task performances. *Science* .

[48] Moller, A. C., Elliot, A. J., & Maier, M. A. (In Press). Basic hue-meaning associations. *Emotion* .

[49] Mostofsky, S. H., Schafer, J. G., Abrams, M. T., Goldberg, M. C., Flower, A. A., Boyce, A., et al. (2003). fMRI evidence that the neural basis of response inhibition is task dependent. *Cognitive Brain Research , 17*, 419-430.

[50] Munsell, A. H. (1905). *Book of Color.* Boston: Ellis & Co.

[51] Noiwan, J., & Norcio, A. F. (2006). Cultural differences on attention and perceived usability: Investigating color combinations of animated graphics. *International Journal of Human-Computer Studies , 64*, 103-122.

[52] Norman, R. D., & Scott, W. A. (1952). Color and affect: A review and semantic evaluation. *Journal of General Psychology , 46*, 185-225.

[53] O'Connell, B. J., Harper, R. S., & McAndrew, F. T. (1985). Grip strength as a function of exposure to red or green visual stimulation. *Perceptual and Motor Skills , 61*, 1157-1158.

[54] Ou, L.-C., Luo, M. R., Woodcock, A., & Wright, A. (2004). A study of colour emotion and colour preference. Part I: Colour emotions for single colors. *Color Research and Application , 29*, 232-240.

[55] Perez-Carpinell, J., Camps, V. J., Trottini, M., & Perez-Baylach, C. M. (2006). Color memory in elderly adults. *Color Research and Application , 31*, 458-467.

[56] Picco, R. D., & Dzindolet, M. T. (1994). Examining the Luscher color test. *Perceptual and Motor Skills , 79*, 1555-1558.

[57] Pressey, S. L. (1921). The influence of color upon mental and motor efficiency. *The American Journal of Psychology , 32*, 326-356.

[58] Rodrigues, P. M., & Murre, J. M. (2007). Selective attention along arbitrary axes. *European Journal of Cognitive Psychology , 19*, 769-788.

[59] Rosenbloom, T. (2006). Color preferences of high and low sensation seekers. *Creativity Research Journal , 18*, 229-235.

[60] Rothermund, K., Wentura, D., & Bak, P. M. (2001). Automatic attention to stimuli signalling chances and dangers: Moderating effects of positive and negative goal and action contexts. *Cognition & Emotion , 15*, 231-248.

[61] Saito, M. (1996). A comparative study of color preferences in Japan, China and Indonesia, with emphasis on the preference for white. *Perceptual and Motor Skills , 83*, 115-128.

[62] Schaie, K. W. (1963). The color pyramid test: A nonverbal technique for personality assessment. *Psychological Bulletin , 60*, 530-547.

[63] Sinclair, R. C., Soldat, A. S., & Mark, M. M. (1998). Affective cues and processing strategy: Color-coded examination forms influence performance. *Teaching of Psychology , 25*, 130-132.

[64] Singh, S. (2006). Impact of color on marketing. *Management Decision , 44*, 783-789.

[65] Stone, N. J., & English, A. J. (1998). Task type, posters, and workspace color on mood, satisfaction, and performance. *Journal of Environmental Psychology , 18*, 175-185.

[66] Strenski, A., Payson, J. M., Muzekari, L. H., & Bohr, R. H. (1970). Preferences and dislikes for color among chronic schizophrenics. *Journal of Clinical Psychology , 26*, 310-311.

[67] Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology , 18*, 643-662.

[68] Swainson, R., Cunnington, R., Jackson, G. M., Rorden, C., Peters, A. M., Morris, P. G., et al. (2003). Cognitive control mechanisms revealed by ERP and fMRI: Evidence from repeated task switching. *Journal of Cognitive Nueroscience , 15*, 785-799.

[69] Taft, C. (1997). Color meaning and context: Comparisons of semantic ratings of colors on samples and objects. *Color Research and Application , 22*, 40-50.

[70] Terwogt, M. M., & Hoeksma, J. B. (2001). Colors and emotions: Preferences and combinations. *The Journal of General Psychology , 122*, 5-17.

[71] Trinkaus, J. (1991). Color preference in sports shoes: An informal look. *Perceptual and Motor Skills , 73*, 613-614.

[72] Trommershauser, J., Maloney, L. T., & Landy, M. S. (2003). Statistical decision theory and the selection of rapid. goal-directed movements. *Journal of the Optical Society of America , 20*, 1419-1433.

[73] Vanbeselaere, N. (1996). The impact of differentially valued overlapping categorizations upon the differentiation between positively, negatively, and neutrally evaluated social groups. *European Journal of Social psychology , 26*, 75-96.

[74] Wagner, G., & Boynton, R. M. (1972). Comparison of four methods of heterchromatic photometry. *Journal of the Optical Society of America , 62*, 1508-1515.

[75] Washburn, M. F. (1911). A note on the affective values of colors. *The American Journal of Psychology , 22*, 114-115.

[76] Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000). Variations in normal color vision. I: Cone opponent axes. *Journal of the Optical Society of America: A , 17*, 1535-1544.

[77] Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000). Variations in normal color vision. II: Unique hues. *Journal of the Optical Socieity of America: A , 17*, 1545-1555.

[78] Weller, L., & Livingston, R. (1988). Effect of color of questionnaire on emotional responses. *The Journal of General Psychology , 115*, 433-440.

[79] Wells, D. L., McDonald, C. L., & Ringland, J. E. (2008). Color preferences in gorillas (Gorilla gorilla gorilla) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology , 122*, 213-219.

[80] Wexner, L. B. (1954). The degree to which colors (hues) are associated with mood-tones. *The Journal of Applied Psychology , 38*, 432-435.

[81] Wijk, H., Berg, S., Sivik, L., & Steen, B. (1999). Colour discrimination , colour naming and colour preferences among individuals with alzheimer's disease. *International Journal of Geriatric Psychiatry , 14*, 1000-1005.

[82] Wolfson, S., & Case, G. (2000). The effects of sound and colour on responses to a computer game. *Interacting with Computers , 13*, 183-192.

[83] Wyszecki, G., & Stiles, W. S. (2000). *Color science: Concepts and methods, quantitative data and formulae* (2nd ed.). New York: John Wiley & Sons Inc.

[84] Yildirim, K., Akalin-Baskaya, A., & Hidayetoglu, M. L. (2007). Effects of indoor color on mood and cognitive performance. *Building and Environment , 42*, 3233-3240.

[85] Zentner, M. R. (2001). Preferences for colours and colour-emotion combinations in early childhood. *Developmental Science , 4*, 389-398.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 239-252

Chapter 9

COLOR IN AQUACULTURE. AN IMPORTANCE OF CAROTENOIDS PIGMENTS IN AQUACULTURE OF SALMON AND ECHINODERMS

Pavel A. Zadorozhny*[2]*, Marianna V. Kalinina*[1]*, Eugene V. Yakush*[1]*,
***Eugene E. Borisovets*[1]**
1- Pacific Fisheries Research Centre (TINRO), Vladivostok, Russia
2-Institute of Chemistry, Far Eastern Branch of Russian Academy of Science,
Vladivostok, Russia

ABSTRACT

Carotenoids are widely used in aquaculture to achieve natural coloring of salmon flesh, improvement of trade quality (color) of sea urchin roe and in aquaculture of Crustaceans.For salmon, it has been found, that the relationship between pigment content and color parameters is complex and nonlinear. Nevertheless, there is an evident correlation between the total concentration of carotenoids (mainly astaxanthin) and the red, most valued by consumers, color of a muscular tissue of salmon (i.e. the higher the pigment content the better). Assimilation of carotenoids in salmon usually does not exceed 10-15 per cent, and cost of astaxanthin makes up about 6-8 % from the cost of filleted fish. Thus, researches in this field are directed on improvement of feed composition increasing of carotenoid assimilation and search of new sources of these pigments; optimization of processing and storage conditions of production, allowing keeping natural color. Ability to reach desirable color of roe is crucial condition for commercial echinoculture. A number of studies were devoted to developing of composition of artificial feed giving desirable color characteristics. Considering macroalgae, the best results have been reached with species of Laminaria, Alaria, Palmaria, and Ulva. It has been proved great significance of carotenoids as essential micronutrients for sea urchin aquaculture. A promising source of carotenoids in aquaculture may be microalga Duneliella salina. Carotenoid content correlates with redness of the gonads, but unlike salmon, for sea urchins there is a certain optimum of the pigment concentrations in gonads, excess or, on the contrary, lack of the pigments lead to falling into less desirable for customers color grades.

INTRODUCTION

There are two main causes doing color researches interesting for aquaculture. First, the appearance of a food plays the important role not only at a customer's choice of a product (Calvo, 1992), but it affects taste characteristics, influences the pleasantness and acceptability of foods (Clydesdale, 1993). Secondly, the physiological role of the compounds causing color, is important for organisms. One of the most widespread pigments of sea and fresh-water organisms are carotenoids – lipophilic tetraterpenoid pigments, de novo synthesised only by plants and microorganisms and on food chains be received at higher trophic levels (Britton, 1983).

Carotenoids are widely used in aquaculture, mainly to obtain of natural coloring of salmon flesh, at rearing of Crustaceans (Meyers, 1994), and molluscs (Tsushima & Matsuno, 1998). A source of pigments can be microalgae, a processing waste of Crustacean, synthetic carotenoids identical to natural ones. Invertebrates are able to converse assimilated β-carotene to carotenoids necessary for them (for example astaxanthin for Crustaceans), but Salmonoids are deprived of such metabolism.

Carotenoids can occur free and associated with proteins. Formation of a carotenoprotein complex may lead to considerable bathochromic shift in an absorption spectrum and therefore these complexes often have purple, blue or green color, unlike yellow or orange color of free carotenoids (Britton, 1983). Color of shell is caused with crustacyanin in many Crustacean species. In ovaries a share of carotenoids can be associated with high-molecular protein - vitellin (Wallace et al., 1967). During vitellogenesis presence of this complex imparts bright color of ovaries (Meusy, Payen, 1988).

The major carotenoids of Crustacean species is astaxanthin, some authors proposed that it is a "semi-essential" nutrient for these animals. Its content is critical to a survival of larvae, sensibility of adult animals to stressful conditions, reproductive success etc. (Chien et al., 2003; Higuera-Ciapara et al., 2006). Sometimes alterations in carotenoid metabolism lead to change of usual appearances of cultivated animals.

CAROTENOIDS AS COLORANTS OF SALMONOID FLESH

However, in Crustacean aquaculture carotenoid pigments have mostly physiological function and they are not as important for color formation as in a case with salmon fish. It is well known, that pink coloring of a muscular tissue at salmon is caused first by the concentration of astaxanthin (in some cases of canthaxanthin). Unlike invertebrates, fish cannot synthesize astaxanthin from β-carotene, in their natural habitat major source of pigments for them is their feed, small crustaceans. At artificial rearing addition of astaxanthin (of astaxanthin containing components) to feed is considered more preferable, in comparison with canthaxanthin as former does not give undesirable increase in yellowness of a tissue (Screde & Storebakken, 1986). In case of uncontrollable growth of microalgae containing high quantity of β-carotene in ponds for cultivation, muscular tissue salmon can become yellow because of accumulation of this pigment that is unattractive to customers who prefer usual red color. In one's turn, it leads to substantial losses for aquaculture farms.

Ability of different salmon species to accumulation of carotenoid pigments varies. Usually among a *pink salmon* (*Oncorhynchus gorbuscha*), a *Chum salmon* (*Oncorhynchus keta*), Coho salmon (*Oncorhynchus kisutch*), *Sockeye salmon* (*Oncorhynchus nerka*) the content of pigments increases (Vorontsov et al., 1986), also as well as cost of a fillet of these fish. Though the interrelation between the carotenoids content and color parameters of flesh is complex and has nonlinear character (Screde and Storebakken, 1986; Hatlen et al., 1998; Bjerkeng, 2000), nevertheless, there is an evident correlation between the total content of pigments (mainly astaxantin) and the red, most valued by consumers, color of a muscular tissue of salmon (i.e. the higher the pigment content, the better).

It happens often that at the identical content of pigments color characteristics of fillet samples in the same species are various, and the reasons of this are difficult to establish. Thus, Little et al. (1978) have found out, that color of a fillet can depend on the content of lipids, however No and Storebakken (1991) have not found such relation; suppositions of importance of a chemical microenvironment of pigment molecules of a pigment have been suggested (Hatlen et al., 1998). It should be noted also, that unlike Crustaceans, in salmon formation of carotenoproteins with considerable batochromic shift is not typical. Thus, interaction of muscular proteins and carotenoids leads to insignificant shift in absorption spectrum (about several nanometers) to long-wave area - i.e. color of a fillet is defined with free carotenoids.

It was found, that assimilation in salmon fish usually does not exceed 10-15 % from containing in feed (Torrissen et al., 1989; Storebakken and No, 1992). At the same time, cost of astaxanthin makes up to 15-20 % of a total cost of an artificial feed or to 6-8 % of fillet cost (Torrissen, 1995). Therefore, studies in this area are directed on improvement of feed composition to raise carotenoids assimilating, search of new perspective sources of these pigments, optimization of conditions of storage and processing of production to keep intense red color (Meyers, 1994; Akhtar et al., 1999; Bjerkeng, 2000).

SEA URCHIN AQUACULTURE

Another example when getting product with certain color characteristics is the important condition for successful aquaculture is cultivation of sea urchins. Their roe is high-valuable sea delicacy and it has a steady great demand at the markets of southeast Asia mostly Japan. Sea urchin roe or gonads are used for food fresh, salted, canned or as biologically active food additives. Color of gonads, along with its yield, texture and taste, is one of the major index of their commercial value. In sea urchins color of gonads varies extremely - from pale yellow to red, brown or terracotta, however the most preferable for consumers, that is "best" quality, are considered bright yellow and orange hues (Kawamura, 1993; Vadas et al., 2000). Most often at a commercial estimation of gonads its color is delineated into three market grades: A - yellow, yellow-orange, orange, the most desirable quality; B - light brown, orange-brown; C - rust, dark brown, the least desirable quality (Kalinina et al., 2000; Sedova et al., 2000; Vadas et al, 2000). Discrepancy of gonads to color criterion can make aquaculture of these species unprofitable (Kelly et al., 2001).

Trade qualities of sea urchin gonads are directly related to annual reproductive cycle of these animals. During growth and maturing of sexual glands their size, structure and color vary greatly. In sea urchin gonads, except gametes (sexual cells), there is a considerable quantity of auxiliary cells which provide former with trophic and energy resources (Varaksina, 1980; Khotimchenko et al., 1993). At early stages of gametogenesis sexual tubules are mostly filled with the auxiliary cells containing yellow-orange globules due to presence of carotenoids (Varaksina, 1985, Jondeung and Czihak, 1983). In the process of growth, maturing and accumulation of gametes there is a carrying of nutrients (including carotenoids) from auxiliary cell into sexual ones. However, presence of carotenoids is detected only in female gametes (Lawrence, 2001).

CAROTENOIDS OF SEA URCHINS AND THEIR EFFECTS ON ANIMAL HEALTH

Systematic study of the carotenoids in sea urchins, carried out by M. Tsushima and co-workers (Tsushima and Matsuno, 1990; Tsushima et al., 1993a), has shown that gonads, gut walls, tests and spines contain these pigments. Though the authors identified a significant number of minor pigments, the major carotenoids in gonads are β-echinenone, α-echinenone and β-carotene. Tsushima and Matsuno (1990) for the first time have separated fraction of echinenones in sea urchins and have identified of isomer of β-echinenone - α-echinenone. The only species at which the predominant carotenoids in gonads and gut walls were astaxanthin was *Peronella japonica*. It is not clear however, whether this species is capable to oxidize β-carotene to astaxantin, or it gets astaxantin from feed.

The metabolism of carotenoids in sea urchins has been studied for species *Pseudocentrotus depressus* (Tsushima et al., 1993b; Tsushima, 1995). Feeding experiments showed, that assimilated from feed β- and α-carotenes are oxidized to corresponding echinenones, the further transformation of β-echinenone into canthaxanthin and astaxanthin does not occur. The same authors have studied the importance of carotenoids, also vitamins A and E for oogenesis and a survival of larvae of *P. depressus* (Tsushima et al., 1997). It was found, that the greatest number of larvae and the best survival have been observed for β-carotene and β-echinenone groups of animals. According to de Jong-Westman et al. (1995b), larvae of *S. droebachiensis*, rearing at laboratory conditions, the greatest sizes, highest survival rate and a metamorphosis were observed if parental individuals received feed containing β-carotene.

It has been established, that unlike Crustaceans and vertebrates sea urchins does not contain vitamin A (Tsushima et al., 1997). Later, it has been confirmed for *Paracentrotus lividus* Rodriguez-Bernaldo de Quirós et al. (2001).

In the many of the studies on sea urchin carotenoids, the geometrical configuration of echinenone has not been specified. Usually presence of a cis-isomer was considered as an artifact. However, for sea urchins, apparently, it is not true. For the first time occurrence of significant amounts of cis-isomer in *P. lividus* have been reported by de Nicola and Goodwin (1954). In gonads of *Tripneustes gratila* cis-echinenon was found as predominant isomer (Shina et al., 1978). Tsushima & Matsuno (1997) identified cis-isomer as 9′Z-β-echinenone in *P. depressus*. It was confirmed as major carotenoids in *Paracentrotus lividus* also (Symonds et al., 2007). Thus, cis-form of echinenone is dominant and widespread in sea urchins, but its function is not clear yet.

Effect of β-carotene, β-echinenone, astaxanthin, vitamins A and E, and fucoxanthin on the biological defense of the sea urchin *P. depressus* has been investigated by Kawakami et al. (1998). The authors found the highest phagocytic index in group getting β-echinenone with feed. It is interesting that fucoxanthin (major carotenoid of brown seaweeds) does not accumulate in the gonads but have significant effect on phagocytic activity and quantity of ovulated eggs. Feeding experiments with *Lytechinus variegatus* have shown significance of dihydroxycarotenoids (lutein and zeaxanthin on development of eggs and the subsequent growth and a survival of larvae (George et al., 2001).

One of the important factors, which are crucial for accumulation and utilization carotenoids in organism of sea urchins, is sex and stage of gonad maturity. It is known, that the carotenoids content in males of sea urchins *Dendraster excentrias* and *Strongylocentrotus franciscanus* is higher than in females (Goodwin, 1984). For females and males of *S. intermedius* and *S. nudus* differences in carotenoids content during annual reproductive cycle exert influence on their gonad coloring (Borisovets et al., 2002, Zadorozhny et al., 2003). For these species, color grade of gonads according to market color scale is better for females than males (Kalinina et al., 2002). In addition, the certain interrelation between color and maturity of gonads was observed: improvement of color characteristics occurs in process of growth of gonads, both in females and males.

Consequently, all these data testify to activity and importance of carotenoid metabolism in a reproduction of sea urchins. In addition to β-carotene and echinenone, several carotenoids, not accumulating in gonads but present in significant amounts in natural food of sea urchins (lutein is primary xanthophyll of green algae (Goodwin, 1980), fucoxanthin – in brown seaweeds (Haugan & Liaaen-Jensen, 1994), zeaxanthin is typical for red algae (Carnicas et al., 1999)) may play an important role in processes of reproduction and biological defense of animals.

Effect of a Diet on Roe Color

Basis of a diet of sea urchins makes up of macrophytes, however under certain circumstances they also consume animal feed and detritus. Effect of various kinds of feed on color characteristics of gonads has been investigated in a number of studies. The majority of researchers agree in opinion, that gonadal index (relative mass of gonads) first of all depend on quantity of accessible food (Kawamura, 1973; Pearse, 1981; Brewin et al., 2000), its color and taste - from its quality (Hagen, 1996; Minor, Scheibing, 1997; Hoshikawa et al., 1998). However, among researchers there is no common opinion concerning specific composition of algae at which consumption sea urchins, in particular genus *Strongylocentrotus*, have the most preferable roe color. One authors consider brown seaweed as those, namely *Laminaria* (Levin, 1987; Hoshikawa et al., 1998; Krupnova & Pavlyuchkov 2000), others mention green algae (e.g. *Ulva*) (Smiths, 1946; Fuji, 1967), and the third consider red seaweed and even sea grasses (Yevseyeva, 1999). Some researchers suggest that the animals on mixed algae diet have the best color parameters of gonads (Lozano et al., 1995; Vadas et al., 2000).

For the sea urchins living at sublittoral – an area with high, as a rule, phytoproduction - the food availability is the second, after temperature, the factor of an environment having essential influence on their reproductive characteristics (Thompson, 1984; Pearse, 1981;

Nichols et al., 1985). Nevertheless, food factor is a primary importance for the market qualities of sea urchin gonads (roe) (Agatsuma et al., 1996; Minor, Scheibling, 1997; Hoshikawa et al., 1998).

Our studies on cumulative influence of biotic and abiotic environment factors on a reproduction and trade qualities of gonads have also shown the sea urchins living in a coastal zone of Primorski Krai of Russia (Sea of Japan), that gonadal index depends on quantity of accessible food, and color parameters - on feed composition (Kalinina et al., 2004 a, b; Viktorovskfya et al., 2005). In spring good color of gonads (season of active gametogenesis) were detected for animals consuming green algae (mainly *Ulva*), in summer months (active growth and maturation of gonads) - mixed algal food with prevalence of *Laminaria spp.*, and in the autumn (during active secondary gametogenesis) – dead algae with presence *Ulva*, *Laminaria* and *Polisiphonia*. Presence *Desmarestia* in a diet considerably worsened gonad color.

Processes of feeding of sea urchins in natural habitats are well investigated, but it is much less known about effects of artificial feed on color of gonads.

It is usually accepted desirable color characteristics at artificial cultivation can be attained by feeding animals with algal food (Fuji, 1967; Lawrence, 1975; Lemire, Himmelman, 1996; Shpigel et al., 2005). Vadas et al. (2000) have studied effects of several species of macrophytes on gonad color of sea urchins and have come to conclusion, that improvement of color, in comparison with the control ("wild" population), is reached using species of *Laminaria*, *Alaria*, *Palmaria*, *Ulva.*

However, use of fresh seaweeds is not always possible and profitable. Its food value is not stable (sensible to conditions of storage) and can become unacceptable at all because of environment pollutants. Therefore, successful industrial echinoculture, according to many authors (Klinger et al., 1986, 1998; Lawrence et al., 1997; Williams, Harris, 1998), is possible only based on balanced artificial feeds. The diets containing various macroseaweed (*Laminaria*, *Palmaria*, *Ulva*) promote color improvement гонад (Vadas et al., 2000), at the same time algal meal source slightly affects on gonad color (Pearce, 2000). In addition to macrophyte species, artificial feeds with addition of microalgae can be a promising source of carotenoids for aquaculture. McLaughlin and Kelly (2001) have found positive effect of the artificial diets containing rich carotenoid microalgae on growth and gonad color of *Psammechinus miliaris*. Robinson et al. (2002) have stated that dried microalga *Duneliella salina* (Algro™) may be a promising source β-carotene for sea urchin aquaculture.

Usually algal or plant meal (corn etc.) can be used as a major component for a diet; using fish minced meat can worsen of flavour of sea urchins gonads (Hoshikawa et al., 1998). According to Pearce (2000) use of β-carotene containing additive Rovimix™ also negatively affects on taste of roe. However using of purer β-carotene sources does not give such effect, hence, taste deterioration, most likely, is caused with non-carotenoid components of Rovimix™. Granulated feeds on the basis of minced meat of pollack with various additives and land plants (for example, *Polygonum orientale*) were tested by Sedova et al. (2000). It was shown that composition consisted of meal of *Laminaria japonica*, minced pollack meat, carrot puree and sodium alginate (as a binding component) could improve gonad development and its color. Pearce et al. (2002) have observed improvement of gonad color depending on the type of a binding component. They proposed using of starch as it produced better color than any other binder.

Introduction of carotenoids (or components with their high content) in a feed at artificial culture of some species - *Evechinus chloroticus* (Goebel and Barker, 1998), *Strongylocentrotus droebachiensis* (de Jong-Westman et al., 1995; Harvardsson et al., 1999; Pearce 2000; Robinson et al., 2002, Liyana-Pathirana et al., 2002), *Psammechinus miliaris* (McLaughlin and Kelly, 2001), *Lytechinus variegatus* (Plank et al., 2002), *Paracentrotus lividus* (Shpigel et al., 2005) have been carried out.

Goebel and Barker (1998) have shown that without carotenoids gonads become pale cream unsuitable for market. Astaxanthin addition to feed composition leads to improving the yellow-orange colors of gonads. Experimental group of the urchins supplemented astaxanthin as well as algal feed (*Ulva latuca* and *Macrocystis pyrifera*) showed the best results in terms of gonad color. Similar results have been obtained by Kelly et al. (2001): best color characteristics of gonads have been reached at feeding of sea urchins by feed mix used for rearing salmon, which containing astaxanthin and canthaxanthin. At the same time, astaxanthin is not typical pigment for sea urchins and degree of its accumulation remains not clear. It is known, though sea urchins are able to assimilate some astaxanthin but in much smaller quantities, than β-carotene (Tsushima et al, 1993b; Harvardsson et al., 1999).

Pearce has shown (2000), that rather high concentration of carotenoids is capable to improve gonad color in sea urchins. Such color improvement has been been attained by adding β-carotene in concentration of 200 mg/kg, and optimum concentration of the pigment is 250 mg/kg of a feed. At the same time, number of authors have found that carotenoid content in sea urchins decreases in the course of feeding experiments (Motnikar et al., 1997; Plank et al., 2002). Probably, it is caused by relatively low concentration of pigments in a feed.

Relationship between Roe Color and Carotenoid Content

It should be noted, that an objective estimation and comparison of organoleptic parameters, such as color, offers some difficulties. It is known, that color can be measured using reflecting spectrophotometers or colorimeters or visually with color atlases or special scales (Jadd & Wyszecki, 1975). In the studies devoted to research of color characteristics of sea urchin gonads instrumental (Agatsuma, 1998; Borisovets et al., 1999; Robinson et al., 2000; Robinson et al., 2002), and visual methods (Kalinina et al., 2000; Goebel and Barker, 1998; Pearce, 2000; Vadas et al, 2000; Pearce et al., 2002) were applied. At a visual estimation commercial scale with three grade (Kalinina el al., 2000; Sedova et al., 2000; Vadas et al, 2000), or more detailed one-dimensional scales with the bigger number of grades (Goebel and Barker, 1998; Vadas et al., 2000; Pearce et al., 2002) were used. As natural color of gonads varies in considerable limits major disadvantage of one-dimensional scales is their subjectivity - ambiguity and inaccuracy in description of color.

Another possibility is using three-dimensional color systems. Usually CIE $L^*a^*b^*$ (1976) system was used for evaluation color of sea urchin roe (Agatsuma 1998; Borisovets et al., 1999; Robinson et al., 2000, 2002). The data obtained in the CIE $L^*a^*b^*$ (1976) are convenient for the subsequent statistical analysis. Additionally, recalculation of L*a*b* color characteristics into Munsell's system is possible. Along with the convenience in usage and visualization, Munsell’s system is three-dimensional too and describes the physical nature of color objectively.

It has been shown, that change in carotenoids concentration usually leads to change of gonads color hue in terms of Munsell’s renotation (Zadorozhny et al., 2003). For species *Strongylocentrotus intermedius* and *S. nudus* carotenoid concentration increases with increasing of red hue of gonads (Table 1). Correlations between color, expressed in a market scale, and carotenoid were not found. These are several factors to explain this:

1) when ascribing to one or another grade of the market scale, sample’s value and chroma are taken into account first, hue does not play determining role;
2) hue of the gonads first of all depends on the total concentration of carotenoids. In the number of samples with hues 2.5YR→10YR concentration of carotenoids gradually decreases;
3) within the same hue, the samples with the grade A usually have lower concentration of carotenoids;

Table 1. Relationship between color characteristics of gonads, expressed in Munsell’s system (hue/value/chroma) and market grade with total carotenoids concentration.

Hue	Market grade	Value/chroma	Carotenoids concentration, mg/100 g of tissue		
			25% quartile	median	75% quartile
S. intermedius					
	whole		11.11	**20.40**	23.31
2.5 YR	A	7/12; 6/12, 6/14	9.68	11.11	20.31
	B	5/10	23.27	30.62	37.97
	C	4/6, 4/8	18.48	20.48	27.04
	whole		6.29	**9.70**	14.73
5 YR	A	7/10, 7/12; 6/12	5.71	6.29	10.70
	B	6/10; 5/8	9.22	12.02	19.16
	C	4/6; 3/2; 2/1	12.00	26.19	40.55
7.5 YR	whole		4.62	**6.30**	7.93
	A	8/10; 7/12	4.46	5.03	6.54
	B	6/6, 6/8, 6/10; 5/8	5.17	6.64	8.10
	C	4/6; 3/2	4.78	6.57	7.93
S. nudus					
7.5 YR	whole		1.21	**3.40**	4.45
	A	8/8; 7/8, 7/6 6/10, 6/8, 6/6	3.34	3.67	4.45
	B	8/6; 7/8, 7/6 6/8, 6/4;5/4	0.93	1.21	2.52
	C	6/8; 5/8; 4/6; 3/2	4.40	7.53	8.64
	whole		0.89	**1.98**	2.20
10 YR	A	8/6; 7/6	0.45	0.80	1.15
	B	8/8, 8/6, 8/4 7/6, 7/4 6/8, 6/6, 6/4	0.80	1.49	1.69
	C	6/6; 5/4; 4/4 3/1	1.50	2.20	2.83

Combined influence of these factors leads to the situation when correlation between gonads' color characteristics in the market scale and carotenoids concentration cannot be found. For example, the minimal concentration of pigments within 2.5YR tone (the color gradation A) practically equals to carotenoids concentration for grade B at samples with 5YR hue and substantially higher than corresponding values of the concentration for grade 3 in 7.5YR hue (Table 1).

It should be noted, that the difference between samples of grade B and C is not so clear, and, probably, can be attributed to influence non-carotenoid pigments. Thus, Carolsfeld et al. (1999) have found correlation of dark gonad color with the content of "hydroquinone-like compounds".

Thus, studying of relationship of color, carotenoid content and customer preferences for Echinoderms shows both similar pattern found earlier for salmon - the increase in red color stimulus with growth of concentration of pigments, and some differences. As well as in salmon fishes (though they contain other carotenoids) we observed increase of red color stimulus and decrease yellow one with increase of carotenoid content in sea urchins *S. intermedius* and *S. nudus.* Unlike salmon fishes, sea urchins have certain optimum of pigment concentration, excess of which leads to ascribing samples to grade B (dark red color, less desirable by customers). Then, it is necessary use three-dimensional color scales for studying relationship between color and pigment content.

REFERENCES

[1] Agatsuma, Y., Matsuyama, K., & Nakata, A. (1996). Seasonal Changes in Feeding Activity of the Sea Urchin Strongylocentrotus nudus in Oshoro Bay, Southwestern Hokkaido . *Nippon Suisan Gakkaishi, 62,* 592-597.

[2] Agatsuma, Y. (1998). Aquaculture of the sea urchin (*Strongylocentrotus nudus*) transplanted from coralline flats in Hokkaido, Japan. *J. Shellfish Res, 17,* 1541-1547.

[3] Bjerkeng, B. Carotenoid pigmentation of salmonid fishes – recent progress. In: Cruz-Suarez L.E., Ricque-Marie D., Tapia-Salazar M., Olvera-Novoa M.A., Civera-Cerecedo R. (Eds) *Avances en Nutricion Acuicola V. Memorias del V Simposium Internacional de Nutricion Acuicola. 19-22 Noviembre, 2000.* Merida, Yucatan. 2000;71-89.

[4] Borisovets, E.E., Lepskaya, N.V., Yakush E.V., Zadorozhny, P.A. Biological and biochemical features of gonad colour formation in two *Strongylocentrotus* species (Echinoidea). In: Candia Carnevali, M., Bonasoro F. (Eds), Echinoderm Research 1998, Proc. 5th European Conf. Echinoderm, Milan, 7-12 September, 1998. Rotterdam:Balkema. 1999; 3-6.

[5] Borisovets, E.E., Zadorozhny P.A., Kalinina M.V., Lepskaya N.V. & Yakush E.V. (2002). Changes of major carotenoids in gonads of sea urchins (*Strongylocentrotus intermedius* and *S. nudus*) at maturation. *Comp. Biochem. Physiol., 132B*, 781-792.

[6] Brevin, P.E., Lamare, M.D., Keogh, J.A., & Mladenov P. V. (2000). Reproductive variability over a four-year period in the sea urchin Evechinus chloroticus (Echinoidea: Echinodermata) from differing habitats in New Zealand . *Mar. Biol. 137.* 543-557.

[7] Britton, G. The Biochemistry of Natural Pigments, Cambridge: Cambridge Univ. Press, 1983.

[8] Calvo, C. (1992).Use of colour carts for visual evaluation of colour. *Rev. Esp. Cienc. Technol. Aliment., 32 (6),* 589-602.

[9] Carnicas, E., Jimenes, C., & Niel F.X. (1999).Effects of changes of irradiance on pigment composition of *Gracilaria tenuistipitata* var. *liui* Zang et Xia. *J. Photochem. Photobiol. B: Biol., 50,* 149-158.

[10] Carolsfeld J., Montgomery P., Ceska O., Liall M. Gonad pigmentation – of green sea urchins // Materials of Aquaculture Canada '99 Conference, Victoria, British Colombia, October 27, 1999**.** http://www.aquacultureassociation.ca/abst_99/contribabstracts.htm

[11] Chien, Y., Pan, C., & Hunter B. (2003). The resistance to physical stresses by *Penaeus monodon* juveniles fed diets supplemented with astaxanthin. *Aquaculture, 216*, 199-191.

[12] Clydesdale, F.M. (1993).Color as a factor in food choice. *Crit. Rev. Food Sci Nutr., 33 (1),* 83-101.

[13] Evseyeva, N.V. (1999). Feeding sea urchin Strongylocentrotus intermedius at the coast of Kuril Islands. In: Abstracts of the conference "Biomonitoring and efficient using of sea and fresh water hydrobionts", Vladivostok, 24-26 May, 1999. Vladivostok: TINRO; 34-36. (In Russian)

[14] Fuji, A. (1967). Ecological studies on the growth and food consumption of Japanese common littoral sea urchin, Strongylocentrotus intermedius (A. Agassiz). *Mem. Fac. Fish. Hokkaido Univ. 15. 2.* 83-160.

[15] George, S.B., Lawrence, J.M., Lawrence, A.L., Smiley, J., & Plank, L. (2001).Carotenoids in the adult diet enhance egg and juvenile production in the sea urchin *Lytechinus variegates. Aquaculture, 199,* 353-369.

[16] Goebel, N., Barker M.F. Artificial diets supplemented with carotenoid pigments as feeds for sea urchins / In R. Mooi & M. Telford (eds), *Echinoderms: San Francisco, 9th Int. Echinoderm Conf., San Francisco, 5-9 August,1996.* Rotterdam: Balkema, 1998. P. 667-672.

[17] Goodwin, T.W. The biochemistry of the carotenoids. Vol. 1: Plants. London: Chapman & Hall, 1980

[18] Goodwin, T.W. The biochemistry of the carotenoids. Vol. 2. Animals, London: Chapman & Hall, 1984.

[19] Hagen, N.T. (1996). Echinoculture: from fishery enhancement to closed cycle cultivation. *Word Aquaculture, (December),* 6-19.

[20] Harvardsson, B., Imsland, A.K., & Christiansen, R. (1999).The effect of astaxanthin in feed and environmental temperature on carotenoid concentration in the gonads of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *J. World Aquacult. Soc., 30,* 208-218.

[21] Hatlen, B., Jobling, M., & Bjerkeng, B. (1998). Relationship between carotenoid concentration and colour of fillets of Arctic charr, *Salvelinus alpinus* (L.), fed astaxanthin. *Aquacult. Res., 29,* 191-202.

[22] Haugan, J.A., & Liaaen-Jensen, S. (1994). Algal carotenoids. 54. Carotenoids of brown algae (Phaeophyceae). *Biochem. Syst. Ecol., 22,* 31-41.

[23] Higuera-Ciapara, I., Felix-Valenzuela, L., & Goycoolea, F.M. (2006).Astaxanthin: A review of its chemistry and applications. *Crit. Rev. Food Sci Nutr., 46,* 185-196.

[24] Hoshikawa, H., Takahashi, K., Sugimoto, T. (1998). The effects of fish meal feeding on the gonad quality of cultivated sea urchin Strongylocentrotus nudus (A. Agassiz). *Sci. Rep. Hokkaido Fish. Exp. Stn. 52.* 17-24.

[25] Jadd, D. & Wyszecki, G., Color in Business Science and Industry, New York: Wiley, 1975

[26] de Jong-Westman, M., March, B.E., & Carefoot, T.H. (1995a). The effect of different nutrient formulations in artificial diets on gonad growth in the sea urchin *Strongylocentrotus droebachiensis. Can. J. Zool., 73,* 1495-1502.

[27] de Jong-Westman, M., Qian P.-Y., March B.E., & Carefoot T.H. (1995b) Artificial diets in sea urchin culture: effects of dietary protein level and other additives on egg quality, larval morphometrics, and larval survival in the green sea urchin, *Strongylocentrotus droebachiensis. Can. J. Zool., Vol. 73,* 2080-2090.

[28] Kalinina, M.V., Gusarova I.S., G.S.Gavrilova, Viktorovskaya G.I. (2000). The features of sea urchenes reproduction at different biotopes of the Peater the Great Bay. *Izv. TINRO, 127,* 490-511. (In Russian)

[29] Kalinina, M.V., Victorovskaya G.I., Borisovets E.E., Bregman Ju.E., Kulepanov V.H. (2002). The biologycal of gray sea urchins at the north-western Coast of Japan Sea. II. The reprodactive characteristic. *Izv. TINRO,131,* 249-265. (In Russian)

[30] Kalinina, M.V., Soukhin I. J., Victorovskaya G.I. (2004a). Biotic condition effect on gonad'stat of grey sea urchin Strongylocentrotus intermedius Peter the Great Bay, Japan Sea). *Problems of Fisheries, 5,* 147-164. (In Russian)

[31] Kalinina, M.V., Soukhin I. J., Victorovskaya G.I. (2004b). Biotic condition effect on gonad'stat of black sea urchin Strongylocentrotus nudus Peter the Great Bay, Japan Sea). *Problems of Fisheries, 5,* 691-707. (In Russian)

[32] Kawakami, T., Tsushima, M., Katabami, Y., Mine, M., Ishida A., & Matsuno T. (1998).Effect of β,β-carotene, β-echinenone, astaxanthin, fucoxanthin, vitamin A and vitamin E on the biological defence of the sea urchin *Pseudocentrotus depressus. J. Exp. Mar. Biol. Ecol., 226,* 165-174.

[33] Kawamura, K. (1973). Fishery Biological Studies on a Sea Urchin, Strongylocentrotus intermedius (A. Agassiz). *Sci. Rep. Hokk. Fish. Exp. St., 16.* 1-54.

[34] Kawamura, K. (ed.) (1993). *Sea urchin. Breeding, processing and sale.* Sapporo: Hokkai suisan shimbunsha (In Japanese)

[35] Kelly, M.S., Owen, P.V., & Pantazis, P. (2001). The commercial potential of the common sea urchin *Echinus esculentus* from the west coast of Scotland. *Hydrobiologia, 465,* 85-94.

[36] Khotimchenko, Yu. S., Deridovich, I.I., Motavkin, P.A., (1993). The biology of reproduction and gametogenes and spawns regulation in Echinoderms. *Nauka, Moscow. (In Russian).*

[37] Klinger, T.S., Hsieh, H.L., & Pangallo, R.A. (1986). The effect of temperature on feeding, digestion, and absorption of Lytechinus variegates (Lamarck) (Echinodermata: Echinoidea. *Physiol. Zool. 59.* 332-336.

[38] Klinger, T.S., Lawrence, J.M., & Lawrence, A.L. (1998). Digestion, Absorption, and assimilation of prepared feeds by echinoids. In: Mooi, R., & Telford M,. (Eds). *Proceedings of the 9th International Echinoderm Conference, San Francisco,* Rotterdam: Balkema*.,* 713-721.

[39] Krupnova, T.N., & Pavlyuchkov, V.A. (2000). Nutrition of the grey urchin (Strongylocentrotus intermedius) in the north-western part of the Japan Sea. *Izv. TINRO, 127,* 372-381. (In Russian)

[40] Kuznetsov, V.V. (1946) Feeding and growth herbivore sea invertebrates of Eastern Murman. Doklady Biological Sciences (Doklady Akademii Nauk), (4), 109-124. (In Russian)

[41] Lawrence, J.M. (1975). On the relationship between marine plants and sea urchins. *Oceanogr. Mar. Biol. Annu. Rev, 13,* 213-286.

[42] Lawrence, J.M. (Ed.) (2001). Edible Sea Urchins: Biology And Ecology. Amsterdam: Elsevier.

[43] Lawrence, J.M., Olave S., Otaiza R. et al. (1997). Enhancement of gonad production in the sea urchin Loxechinus albus in Chile fed extruded feeds. *J. Word Aquac. Soc. 28.* 91-96.

[44] Lemire, M., & Himmelman, J.H. (1996). Relation of food preference to fitness for the green sea urchin, *Strongylocentrotus droebachiensis. Mar. Biol., 127,* 73-78.

[45] Levin, V.S., & Naydenko, V.P. (1987). Impact of the artificial food on sea urchin Strongylocentrotus intermedius at the laboratory. *Russian J. Mar. Biol.* 6, 50-56.

[46] Little, A.C., Martinsen, C., & Sceurman, L. (1979). Color assessment of experimentally pigmented rainbow trout. *Color Res. Appl., 4,* 92-95.

[47] Liyana-Pathirana, C., Shahidi, F., & Whittick, A. (2002). The effect of an artificial diet on the biochemical composition of the gonads of the sea urchin (*Strongylocentrotus droebachiensis*). *Food Chemistry, 79 (4),* 461-472.

[48] Lozano, J., Galera, J., & Lopes, S. (1995). Biological cycles and recruitment of *Paracentrotus lividus* in two contrasting habitats. *Mar. Ecol. Prog. Ser., 122.* 179-191.

[49] McLaughlin, G. & Kelly, M.S. (2001). Effect of artificial diets containing carotenoid-rich microalgae on gonad growth and colour in the sea urchin *Psammechinus miliaris* (Gmelin). *J. Shellfish Res., 20*, 377 – 382.

[50] Meusy, J.-J., & Payen, G. (1988). Female reproduction in malacostracan Crustacea. *Zool. Sci., 5*, 217-265.

[51] Meyers, S.P. (1994). Developments in word aquaculture, feed formulations, and role of carotenoids. *Pure & Appl. Chem., 66,* 1069-1076.

[52] Minor, M.A., & Scheibling, R.E. (1997). Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Biol., 129,* 159-167.

[53] Motnikar, S., Bryl, P., & Boyer, J. (1997). Conditioning green sea urchin in tanks: the effect of semi-moist diets on gonad quality. Bull. Aquacult. Assoc. Canada., 97 (1), 21-25.

[54] Nichols, D., Bishop, G.M., & Sime, A.A. (1985). Reproductive and nutritional periodicities in populations of the European sea-urchin, Echinus esculentus (Echinodermata; Echinoidea) from the English Channel. *J.Mar. Biol. Ass. UK. 65. 1.* 203-220.

[55] de Nicola, M., & Goodwin, T.W. (1954).Carotenoids in developing eggs of the sea urchin *Paracentrotus lividus. Expl. Cell Res., 7,* 23-31.

[56] No, H.K., & Storebakken, T. (1991). Pigmentation of rainbow trout with astaxanthin at different water temperature. *Aquaculture, 97,* 203-216.

[57] Pearse, J.S. (1981). Synchronization of gametogenesis in the sea urchins Strongylocentrotus purpuratus and S. Franciscanus. In: *Advances in Invertebrate reproduction. Amsterdam: Elsevier,* 53-68.

[58] Pearce, C.M. Gonad enhancement of the green sea urchin, *Strongylocentrotus droebachiensis*, fed prepared diets: the effect of starch type, algal meal source, and β-carotene concentration / *The workshop on the co-cordination of Green sea urchin research in Atlantic Canada*. Moncton, 1-2 June 2000. http://crdpm.cus.ca/oursin

[59] Pearce, C.M., Daggett, T.L., & Robinson, S.M.C. (2002). Effect of binder type and concentration on prepared feed stability and gonad yield and quality of the green sea urchin, *Strongylocentrotus droebachiensis*. *Aquaqulture, 205,* 301-323.

[60] Plank, L.R., Lawrence, J. M., Lawrence, A. L., & Olvera, R.M. (2002).The effect of dietary carotenoids on gonad production and carotenoid profiles in the sea urchin *Lytechinus variegates*. *J. World Aquacult. Soc., 33*, 127-137.

[61] Robinson, S., Castell J., Kennedy E., Peters L. A summary of sea urchin culture at the St. Andrews biological station / *The workshop on the co-cordination of Green sea urchin research in Atlantic Canada*. Moncton, 1-2 June 2000. http://crdpm. cus.ca/ oursin

[62] Robinson, S., Castell, J., & Kennedy, E. (2002). Developing suitable colour in the gonads of cultured green sea urchin (*Strongylocentrotus droebachiensis*). *Aquaculture, 206,* 289-303.

[63] Rodriguez-Bernaldo de Quirós, A., López-Hernández, J., & Simal-Lozano, J. (2001). Determination of carotenoids and liposoluble vitamins in sea urchin (*Paracentrotus lividus*) by high performance liquid chromatography. *Eur. Food Res. Technol., 212,* 687-690.

[64] Screde, G., & Storebakken, T. (1986).Characteristic of color in raw, baked and smoked wild and pen-reared Atlantic salmon. *J. Food Sci., 51,* 804-808.

[65] Sedova, L.G., Bregman Yu.E., Aminina N.M., Podkorytova A.V. (2000). Impact of artificial foods on feeding and gonads growth rate of sea urchin *Strongylocentrotus intermedius*. *Izv. TINRO, 127,* 512-523. (In Russian)

[66] Shina, A., Gross, J., Lifshitz, A., & Sklarz, B. (1978).Carotenoids of the invertebrates of the Red Sea (Eilat shore)- II. Carotenoid pigments in the gonads of the sea urchin *Tripneustes gratila* (Echinodermata). *Comp. Biochem. Physiol., 61B,* 123-128.

[67] Shpigel, M.,. McBride, S. C, Marciano, S., Ron, S., & Ben-Amotz, A. (2005). Improving gonad colour and somatic index in the European sea urchin *Paracentrotus lividus*. *Aquaculture, 245,* 101-109.

[68] Storebakken, T., & No, H.K. (1992.) Pigmentation of rainbow trout. *Aquaculture, 100,* 209-229.

[69] Symonds, R.C., Kelly, M.S., Caris-Veyrat, C., & Young, A.J. (2007). Carotenoids in the sea urchin *Paracentrotus lividus*: Occurrence of 9′-cis-echinenone as the dominant carotenoid in gonad colour determination. *Comp. Biochem. Physiol., 148 B (4),* 432-444.

[70] Thompson, R.J. (1984). Partitioning of energy between growth and reproduction in three populations of the sea urchin *Strongylocentrotus droebachiensis*. *Adv. Invertebr. Reprod, 3*. 425-432.

[71] Torrissen, O.J. (1995).Strategies for salmonoid pigmentation. *J. Appl. Ichthyol., 11,* 276-281.

[72] Torrissen, O.J., Hardy, R.W., & Shearer, K.D. 1989. Pigmentation of salmonoids – carotenoid deposition and metabolism. *CRC Crit. Rev. Aquat. Sci., 1,* P. 209-205.

[73] Tsushima, M., & Matsuno, T. (1990). Comparative biochemical studies of carotenoids in sea-urchins-I. *Comp. Biochem. Physiol., 96B*, 801-810.

[74] Tsushima, M., & Matsuno, T. (1997). Occurrence of 9′Z-β-echinenone in the sea urchin *Pseudocentrotus depressu*s. *Comp. Biochem. Physiol., 118B (4),* 921-925.

[75] Tsushima, M., Amemiya, S., & Matsuno, T. (1993a).Comparative biochemical studies of carotenoids in sea-urchins- II. The more primitive sea urchins belonging to the orders Cidaroida, Echinothuroida, Diadematoida and Arbacioida. *Comp. Biochem. Physiol., 106B*, 729-735.

[76] Tsushima, M., Kawakami, T., & Matsuno, T. (1993b). Metabolism of carotenoids in sea-urchin *Pseudocentrotus depressus. Comp. Biochem. Physiol., 106B*, 737-741.

[77] Tsushima, M. Biochemical study of echinoderm carotenoids: sea urchins and holothurians: Dr. thesis. Kyoto Pharmaceutical University, 1995. (in Japanese)

[78] Tsushima, M., & Matsuno, T. (1998). The role of β,β-carotene on growth and survival of juvenile Japanese abalone *Haliotis discus*. *Fisheries Sci., 64*, 660-661.

[79] Tsushima, M., Kawakami, T., Mine, M., & Matsuno, T. (1997). The role of carotenoids in the development of the sea urchin *Pseudocentrotus depressus. Inver. Reprod. Devl., 32,* 149-153.

[80] Vadas Sr., R.L., Beal, B., Dowling, T., & Fegley, J.C. (2000). Experimental field tests of natural algal index and quality in the green sea urchin, *Strongylocentrotus droebachiensis*: a case for rapid summer production in post-spawning animals. *Aquaculture, 182,* 115-135.

[81] Varaksina, G.S. (1980). Morphology of accessory cells during the reproductive cycle of sea urchins. *Russian J. Mar. Biol., 5*, 38-44.

[82] Varaksina, G.S. (1985). The cytoplasmic inclusions of the accessory cells of the sea urchins ovaries. *Russian J. Mar. Biol., 4*, 40-46.

[83] Victorovskaya, G. I., Sedova L.G., Borisovets E.E., Matveev V.I., Kalinina M.V., Bregman I.E.(2004). The biological characteristics of sea urchins Strongylocentrotus intermedius (Agassiz) concentrations at the Northern Primorye Coast (Sea of Japan). *Izv. TINRO, 139,* 225-259. (In Russian)

[84] Vorontsov, S.N., Yakush, E.V., & Yarochkin, A. P. Method for objective estimate of muscular tissue colour in salted salmon. In: Investigation on technology of hydrobionts of the Soviet Far East seas. Vladivostok: TINRO; 1986; 46-56. (In Russian)

[85] Wallace, R.A., Walker S.L., Hauschka P.V. (1967). Crustacean lipovitellin. Isolation and characterization of the major high density lipoprotein from the eggs of decapods. *Biochemistry, 6,* 1582–1590.

[86] Williams, C.T., Harris L.G. (1998). Growth of juvenile green sea urchins on natural and artificial diets. In: Mooi, R., & Telford M,. (Eds). *Proceedings of the 9th International Echinoderm Conference, San Francisco,* Rotterdam: Balkema., 887-892.

[87] Zadorozhny, P.A., Lepskaya, N.V., Borisovets, E.E., Kalinina, M.V., & Yakush, E.V. Gonad colouring and its dynamics in the maturation process of sea urchins S*trongylocentrotus intermedius* and *S. nudus*. In: Feral, J.-P., David, B. (Eds), *Echinoderm Research 2001, Proc. 6th European Conf. Echinoderm Research, Banyuls-sur-mer, France, 3-7 September, 2001*. Lisse: Swets & Zeitlinger. 2003, 295-300.

In: Color Perception: Physiology, Processes and Analysis
Editors: D. Skusevich, P. Matikas, pp. 253-259
ISBN: 978-1-60876-077-0

Chapter 10

BLACK ENOUGH?: NEEDED EXAMINATION OF SKIN COLOR AMONG CORPORATE AMERICA

Matthew S. Harrison and Wendy Reynolds-Dobbs
The University of Georgia, Athens, GA 30602 , USA

ABSTRACT

A common problem among social scientists who group all members of a race/ethnicity together is that they assume that all of the life experiences of those individuals are the same, and thereby, overlook the prevalence of heterogeneity within ethnicities. One such example is a global phenomenon present in all cultures where there is skin tone variation—colorism. This longstanding ideology which suggests preference within ethnic groups is closely linked with skin color is often ignored. Recent research, however, has found that among Blacks, lighter skin has major implications in the job selection process—where one is better off if he/she is lighter-skinned. Due to issues of attractiveness and general levels of comfort, individuals tend to feel a lighter-skinned black is more competent or less threatening, respectively. Though many companies are now concentrating efforts on enhancing diversity—with race being one of the primary focuses—one has to wonder if these "advancements" in diversity are resulting in more lighter-skinned Blacks being hired over their equally-qualified darker-skinned counterparts. This research commentary intends to look broadly at the executive boards of corporate America to investigate if this "lopsidedness" is indeed present. It is expected that greater numbers of light-skinned Blacks will be found in these positions, which will support prior research and illustrate the need for greater discussion and future research regarding this very issue.

INTRODUCTION

"You boys stay out of that terrible sun…God knows you're dark enough already" (p. 2)—though quoted by Lawrence Otis Graham in the opening of his best selling novel *Our Kind of People,* while reflecting on what he would routinely hear his great-grandmother say while he and his family would vacation at Martha's Vineyard, statements similar to that espoused by Graham's great-grandmother have been heard by many young Black adolescents for generations. Though continuously reinforced throughout life via the media, most Blacks are somewhat acculturated, from a very young age to believe in the notion that he or she is, or at the very least will be, better off if they are light-skinned. Although this phenomenon is incredibly prevalent and powerful, this incessant focus on skin color among and within the Black race is very rarely discussed. Most people know about its presence, most people see how it is reinforced in advertisements, television, movies, even politics; yet, very little focus is given to the topic. Instead, the notion and pervasiveness of colorism is basically overlooked as all attention is given to the prevalence of general racism (most usually viewed as a Black vs. White issue) in America.

Given the longstanding history of the relationship between Blacks and Whites in America, it should not be terribly surprising that race relations in the U.S. of this dichotomous manner are most discussed. Ultimately in these conversations, each race is generalized and homogenized into one grouping (Celious & Oyserman, 2001). Even racial identity theories follow this same inexplicit categorization, where race is viewed as a simple binary relationship between Blacks and Whites, and any potential diversity within each race is simply ignored or overlooked. While race is a social construction, and while these theories are accurate in their assumption that similarities do exist within racial groups (Celious & Oyserman, 2001); it is important to note that there is the potential for differences to exist within races. Blacks may have very different life experiences depending on their gender, socioeconomic status, and (the focus of this commentary) skin color—all of these demographic elements potentially play a significant role in the life they may lead, in addition to the treatment they may receive from others.

Black Americans may very well live in the same society, but their life experiences may vary greatly depending on whether or not one is light or dark-skinned. Edwards (1973) claims that of the many characteristics people of America are divided into, none has greater significance than one's skin color. Skin color remains divisive in America, and in most other western cultures, because whiteness and blackness are (and have always been) in binary opposition to one another. Whiteness is most often associated with beauty, purity, and graciousness, while blackness symbolizes ugliness, evilness, and incivility (Hunter, 2002). These contradicting views of what "black" and "white" represent are extremely powerful and have even been extended into the symbolic differences between "dark" and "light," respectively. In other words, the dichotomy between Blacks and Whites really expands into a stratification system within the Black race itself, where light-skinned Blacks take on the aforementioned characteristics associated with Whites, while dark-skinned Blacks are ascribed the negative characteristics commonly associated with blackness. It is therefore no surprise that research studies have found that lighter-skinned Blacks receive preferential treatment (particularly in the workplace) over their darker-skinned counterparts (Thompson & Keith, 2001; Harrison & Thomas, 2009).

Thus, as our title suggests, this commentary will focus on the need to closely examine the executive boards of corporate America. As more and more companies and corporations have affirmative action policies in place, or make claim to being equal opportunity employers, more and more people of color, Blacks in particular, are being hired and given certain seats around the boardroom table that they were never granted before. Given the power and prevalence of colorism in our society, however, we question exactly "how Black" are these Blacks who are granted access to these positions. Is it that more Blacks are now in corporate

America than ever before, or is that more *light*-skinned Blacks are there? This commentary will answer this very question, while explaining the historical significance of colorism in America, its implications on the present, and how all of this manifests itself on the boards within corporate America.

History & Current Ramifications of Colorism/Skin Color Bias

Issues of partisan behavior due to skin tone dates back to the chattel system of slavery in America, where the division of work chores among slaves was based on skin color (Hunter, 2002). Slaves who were dark-skinned, or of pure African ancestry, typically worked in the fields and were viewed as having the more physically-demanding tasks; while slaves who were lighter (due to mixed parentage—as it was common for slave masters to have nonconsensual and consensual sexual relationships with their slaves) were given the more "desirable" and prestigious positions within the chattel system (Keith & Herring, 1991). These work chore divisions not only engulfed a great deal of bitterness between slaves, but it also reinforced the notion that the lighter one's complexion, "the better off he or she was in the eyes of the majority group members" (Ross, 1997, p. 555).

What is most shocking is that this statement still holds true nearly 200 years later. According to the findings of researchers, Hughes and Hertel, lighter-skinned Blacks are more likely to have completed more years of schooling, have higher salaries, and have more prominent jobs than their darker-skinned counterparts (1990). Even more compelling, perhaps, is that they found that skin color has such a profound effect that the gap in educational attainment and socioeconomic status between light- and dark-skinned Blacks is equivalent to the gap between Whites and Blacks in general. These findings, combined with studies juxtaposing socioeconomic attainment between mulattoes (i.e., Blacks from mixed heritage) and Blacks, clearly detail the importance and prevalence of, colorism, and further illustrate the prominence of color-based stratification in American society (Hill, 2000). Thus, lighter-skinned Blacks tend to be more advantaged educationally, economically, and more likely to experience status advancement than those with darker skin (Seltzer & Smith, 1991; Udry, Bauman & Chase, 1971). These social advantages that are allotted to this group of lighter-skinned Blacks emphasize and reinforce a system in our society that privileges light skin over dark skin—this classification structure and system of preference is the general definition and form the building blocks of colorism (Hunter, 2002).

Colorism in the Workplace

Considering the fact that skin color has historic implications for biased and preferential treatment in social arenas, skin color may also have significant implications in the workplace. Research illustrates that in the "real world" there is a positive correlation between attractiveness and perceptions of ability and success (Umberson & Hughes, 1987). Ideologies surrounding colorism suggest that Blacks are perceived as being more attractive when their phenotypic features (e.g., nose shape, lip size, hair texture, etc.) are more closely analogous to that of European descent than African ancestry (Fears, 1998; Maddox & Gray, 2002; Oliver, Jackson, Moses & Dangerfield, 2004). Thus, it is common for lighter-skinned

Black women to have higher salaries than Black women with darker skin who have very similar résumés (Hunter, 2002). Furthermore, in a 2001 study focusing on Black women's career satisfaction, researchers found that light-skinned Black women, who are deemed "less ethnic," were more likely to be satisfied with their pay and opportunities for advancement than darker-skinned ("more ethnic") Black females (Catalyst). In a more recent study focusing on the effects of skin color on job selection, researchers found that a Black man with lighter skin, a bachelor's degree, and typical work experience was preferred for positions over a darker skinned Black man with an MBA degree and more extensive managerial experience. Additionally, in the same study, when education and past experience were similar, lighter skinned Black women were preferred for positions over darker skinned Black women (Harrison & Thomas, 2009). Thus, research has shown that skin color not only affects our experiences in social situations, but also in the workplace where one's skin color can have detrimental effects on career progression and overall experience.

Since attractiveness correlates with people's perceptions of ability, and lighter skin tone is somewhat viewed as being more attractive in American culture, it is no wonder that for African Americans, skin color may play an important part in moving up the corporate ladder. To investigate this concept further, in the February 2009 issue of Black Enterprise magazine, which is a long standing minority business publication, the cover story highlighted the top 100 most powerful Black executives in corporate America. Out of the 100 executives listed, the majority of top executives had brown to lighter skin tones rather than darker skin tones. For the most part, both Black women and men had lighter variations of brown skin tones which suggest that in the "real world" where decisions matter, skin tone may subconsciously play a part in people's perceptions of one's ability to be a successful leader. For instance, when looking specifically at the CEO position, 7 out of the 9 Black CEOs had medium brown to light brown skin tones while only 2 had darker brown skin tones. In addition to skin tone, other characteristics such as hair styles were more Eurocentric than Afrocentric for most of the executives, with women wearing straighter hair styles and men wearing short cropped hair cuts rather than more ethnic options such as dreadlocks, afros, or braids styles. Therefore, research, along with current Black executives in corporate America, suggest that appearance specifically skin tone can potentially affect one's move from the cubicle to the C class suite.

Although some may feel that we have moved past skin color when it comes to preferential treatment, a person's skin tone may still subconsciously affect people's perceptions of others. It is true that people may not solely rely on skin tone when it comes to preferred treatment regarding job selection and promotion, but one's attractiveness level which is highly connected to skin complexion can subconsciously affect a hiring manager's feelings towards a job incumbent. The idea that one's color can either help or hinder one's career progression is a viable discussion especially during times of severe economic turbulence where employers have the upper hand in the race for talent. Although it is true that education level and past experience is also taken into consideration when it comes to career advancement, color may still be a hidden factor in making decisions about selection. Certainly Black people with darker skin can still succeed in the workplace and lead extremely successful careers; however, it may prove to be more of a challenge compared to their lighter skin counterparts.

CONCLUSION

This commentary has intended to shed light on the need for research and discussion that emphasizes the prevalence of preference based on skin color in America's workforce—particularly within the boards of corporate America. Most past research neglects to look at discrimination outside of the normal dichotomous comparisons of Blacks and Whites as groups consisting of homogenous individuals. Given the increasing number of biracial and multiracial Americans, more research in this area should be performed so that Americans can become more aware of the prevalence of color bias in our society. Studies of this nature will perhaps not only enhance their awareness, but also challenge their acceptance of the common belief that whiteness signifies graciousness and beauty (Hill, 2000).

Additionally, research and discussions of this nature will help to substantiate, and in some ways expand, current theories regarding privilege and similarity attraction. It is no secret we live in a society where being White affords many privileges that are not equally awarded to those who are not White (McIntosh, 1993). Possibly, however, the privilege one receives extends beyond their race, and is deeply rooted in their skin color—where darker skin equates to fewer privileges. Similarly, ideologies surrounding colorism seem to further confirm Byrne's Similarity Attraction Theory, which states people tend to be more attracted to and have a greater comfort level around individuals who are similar to themselves (1971). It is therefore not surprising that lighter-skinned Blacks would be advantaged in the workplace where Whites are most likely making the hiring decisions.

Further, discussion and research of this nature could also help combat some of the irony that has long existed in social science research of race and race relations. While most social scientist who perform research of this nature make claim that the purpose of their research is to address, and hopefully falsify, negative perceptions and stereotypes surrounding various races, their grouping of individuals into homogenous groups, and assuming life experiences must all be the same for all Blacks or all Whites, does nothing more than perpetuate those very stereotypes they are attempting to falsify. When people are forced to look at races and ethnicities through a heterogeneous lens, it causes them to look at a racial or ethnic group in a way where longstanding stereotypes no longer seem accurate or appropriate.

Moreover, as mentioned earlier, given the increasing number of companies and organizations that are employing affirmative action policies in their selection processes, determining the possible presence of skin tone preference is paramount. Companies must be more cognizant of the colorism issue in many of their human resource related procedures. While statistics may continue to show that the number of minorities in corporate America is continuing to rise, they are not reporting the possibility that there is a disproportionate number of lighter complexioned minorities getting these jobs (particularly those at the senior executive level).

The only way we are going to begin to combat some of the inequities that result due to common beliefs and ideologies associated with colorism, is by becoming more aware of the prejudices we have regarding skin tone. Society and the media paints us a picture of lighter skin equating to intelligence, likeability, competency, attractiveness, etc., and a much more dismal and bleak picture is given for those who have darker skin. These images are extremely powerful, in that they alter our immediate perceptions of individuals who must then "fit" into the pictures we have been exposed to. For instance, if one was to imagine a

Black physician, attorney, politician, or CEO, more than likely, most of these images would be of a light-skinned Black. Whereas, if images of a Black factory worker, garbage collector, janitor, or prisoner were conjured up, more than likely they would be of darker pigmentation than those previously listed.

We must begin to combat these negative associations of dark skin and lower expectations, incited fear, and basic incivility. There was a brief period of time during the Black Power Movement where the Black community began to contest these notions that have damaging effects to the self-esteem of Blacks. This period, however, was short-lived, and chants of “Black is beautiful” are not too often still heard. Mantras of this nature must be recited once more if society and the media’s representation of Blackness and dark skin are going to change. The more we challenge these images, and our own belief systems, the greater the likelihood Black children of future generations will only be encouraged to come out of the sun because of the potentially harmful effects of UV radiation, and not because of the probable negative ramifications of having dark skin.

REFERENCES

[1] Alleyne, S. & Lott, A.M. (2009). The 100 most powerful executives in corporate America. *Black Enterprise Magazine, 39 (7),* 100-118.

[2] Byrne, D. (1971). *The Attraction Paradigm.* New York: Academic Press.

[3] Catalyst. (2001). *Women of color in corporate management: Three years later.* Retrieved December 20, 2008, from http://www.catalyst.org.

[4] Celious, A. & Oyserman, D. (2001). Race from the inside: An emerging heterogeneous race model. *Journal of Social Issues, 57 (1),* 149-165.

[5] Edwards, O. L. (1973). Skin color as a variable in racial attitudes of Black urbanites. *Journal of Black Studies, 3 (4),* 473-483.

[6] Fears, L. M. (1998). Colorism of Black women in news editorial photos. *The Western Journal of Black Studies, 22 (1),* 30-36.Graham, L. O. (1999). *Our Kind of People*. New York: HarperCollins Publishers, Inc.

[7] Harrison, M. S. & Thomas, K. M. (2009). The hidden prejudice in selection: A research investigation on skin color bias. *Journal of Applied Social Psychology, 39 (1),* 134-168.

[8] Hill, M. E. (2000). Color differences in the socioeconomic status of African American men: Results of a longitudinal study. *Social Forces, 78 (4)*, 1437-1460.

[9] Hughes, M. & Hertel, B. R. (1990). The significance of color remains: A study of life chances, mate selection, and ethnic consciousness among Black Americans. *Social Forces, 68 (4),* 1105-1120.

[10] Hunter, M. L. (2002). “If you’re light you’re alright”—Light skin color as social capital for women of color. *Gender & Society, 16 (2)*, 1750193.

[11] Keith, V. M. & Herring, C. (1991). Skin tone and stratification in the Black community. *The American Journal of Sociology, 97 (3),* 760-778.

[12] Maddox, K. B. & Gray, S. A. (2002). Cognitive representations of Black Americans: Reexploring the role of skin tone. *Personality and Social Psychology Bulletin, 28 (2),* 250-259.

[13] McIntosh, P. (1993). White male privilege: A personal account of coming to see correspondence through work in women’s studies. In A. Minas (Ed.), *Gender Basics.* 30-38. CA: Wadsworth.

[14] Oliver, M. B., Jackson, R. L., Moses, N. N. & Dangerfield, C. L. (2004). The face of crime: Viewers’ memory of race-related facial features of individuals pictured in the news. *Journal of Communications, 54 (1),* 88-104.

[15] Ross, L. E. (1997). Mate selection preferences among African American college students. *Journal of Black Studies, 27 (4),* 554-569.

[16] Seltzer, R. & Smith, R. C. (1991). Color differences in the Afro-American community and the differences they make. *Journal of Black Studies, 21 (3),* 279-286.

[17] Thompson, M. S. & Keith, V. M. (2001). The blacker the berry—Gender, skin tone, self-esteem, and self-efficacy. *Gender & Society, 15 (3),* 336-357.

[18] Udry, J. R., Bauman, K. E. & Chase, C. (1971). Skin color, status, and mate selection. *The American Journal of Sociology, 76 (4),* 722-733.

[19] Umberson, D. & Hughes, M. (1987). The impact of physical attractiveness on achievement and psychological well-being. *Social Psychology Quarterly, 50 (3),* 227-236.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 261-264 © 2010 Nova Science Publishers, Inc.

Short Communication 1

COLOR IN WEIGHTLESSNESS CONDITIONS: "µGORIENTING" PROJECT

Irene Lia Schlacht[1][*], Matthias Rötting[2][+] and Melchiorre Masali[3][§]

[1]PhD Student, Chair of Human-Machine Systems, Dept. of Psychology and Ergonomics, Technische Universität Berlin, Germany
[2]Chair of Human-Machine Systems, Dept. of Psychology and Ergonomics, Technische Universität Berlin, Germany
[3]Cattedra di Antropologia, Dipartimento di Biologia animale e dell´uomo, Università di Torino, Italy

ABSTRACT

In outer space habitats, where the weightlessness and isolation deeply influence human life**,** color perception, processing and reaction to color are subjects for analysis in Human Factors investigation. The "µgOrienting" project aims to improve the life quality in outer space by research on colors and other visual stimuli.

Picture 1. Color Design research in International Space Station (ISS), Schlacht 2007.

---

[*] (isc@mms-tu-Berlin.de www.mms.tu-berlin.de or Irene.Schlacht@gmail.com www.extreme-design.eu) I. L. Schlacht, TU-Berlin, IPA Fach MMS, Sekr. FR 2-7/1, Franklinstr.28-29, D-10587 Berlin

[+] (mro@mms-tu-Berlin.de)

[§] (Melchiorre.Masali@gmail.com)

Keywords: Color Perception, Color Design, Outer Space Habitats, Human Factors.

In a new project intended to increase habitability in outer space, a dedicated European team is carrying out research on colors and visual stimuli affecting astronauts' reliability. The goal of the project, called µgOrienting, is to increase well-being and orientation skills in outer space missions through color and visual stimuli.

Color research for human space habitats is aimed at the design of ergonomically-oriented spacecraft. As reported in the NASA standard Living Aloft (Connors *et al*., 2003), considering the importance of vision to the accomplishment of space missions, spacecraft's visual design has to bear in mind the strong psycho-physiological modifications that occur in the extreme environment of the outer space. Consequently, a major field of study is the development of human factors in technological habitat design, especially in view of the adaptation of Man in his challenge to live in outer space (Schlacht, 2008).

The µgOrienting project breaks down into three experiments: CROMOS, WIUD and ZEROgYMN.

- CROMOS: investigates color and visual perception in microgravity.
- WIUD: researches color and visual reactions vital for orientation during weightlessness.
- ZEROgYMN: researches the potential for color and visual stimuli to affect movement and a sense of rhythm.

CROMOS, successfully performed in 2007 during the European Space Agency (ESA) Student Parabolic Flight Campaign, analyzed changes in sensitivity to chromatic and achromatic perception in microgravity conditions. During CROMOS six European students tested color (Red, Blue, Green) sensitivity during a microgravity condition parabolic flight and in normal 1G earth conditions, using software developed by Stefano Brambillasca. The experiment used the Anolamoscope method, measuring the "range of color equality", that is, the range in which two slightly different colors were perceived as the same.

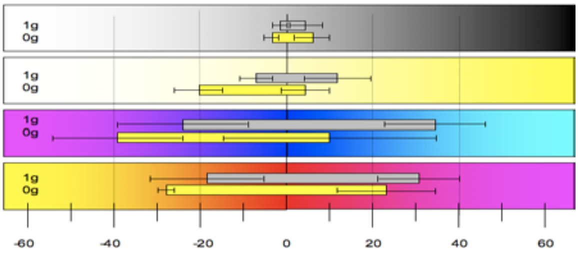


Diagram 1. CROMOS RESULT, Schlacht 2007. Mean Value of deviation from "Equal color" and RMS-value of the function in µgravity (0g) and normal gravity (1g) conditions. From the bottom to the top: Test 1 hue-Red; Test 2 Blue-hue; Test 3 yellow-saturation; Test 4 grey-lightness. A validation experiment with inverted color orders in each test is suggested for future experiments.

The CROMOS color results (RGB) show an increase of sensitivity in µg in the short wavelength (B) area of the visible spectrum and a decrease in the long wavelength area (R).

- Test 1. Hue: red. In µg, as a component of Red, G pixels were perceived 4.4 % less intensely and B pixels were perceived 3% more intensely in µg.
- Test 2. Hue: blue. In µg, as a component of Blue, G pixels were perceived 10.8% more intensely.

- Test 3. Saturation: yellow. Yellow is perceived more saturated in µg with a shift of mean value in the low saturation area by 2.9%.

- Test 4. Brightness: grey. In µg there is a weakening of sensitivity to achromatic luminosity.

The hypothesized cause of the observations is the physiological effect of weightlessness. The crystalline lens of the eye becomes more spherical which causes the chromatic aberration and consequent focus of images onto a different area of the retina with different concentrations of RGB receptors.

As a result, stimulation of Blue cones and rods are probably increased. The hypothesis relating physiology is consistent with the experiment's findings (Schlacht, 2009).

WIUD was conducted as a second phase of the µgOrientation requiring the subjects to recline to study instinctual reactions to color and symbols for up-and-down orientation in outer space habitats.

The results, currently estimated following 40 subjects' tests, were derived using images of ISS modules and orientation labels. The Russian module, based on color configuration with chaotic instrument set up, was easier for orientation in comparison with the American module, configured to have a clean instrument set up. Statistically, the findings suggest that a pictogram label system might improve orientation in ambiguous ISS module configurations.

ZEROgYM, the last µgOrientation phase, is in a developmental stage, in collaboration with Turin University (Italy) and Ki Productions (Kitsou Dubois). It is focused on the relationship between movement and visual input in weightlessness conditions. It is based on the consideration that vestibular systems responsible for orientation become silent in µG (Mallowe E., 2001), consequently colors and visual configurations are of primary importance for orientation. The experiment is envisaged to be performed in neutral buoyancy using gymnastics students from the Movement Science Dept. at Turin University.

ACKNOWLEDGMENT

We thank all the colleagues of the Man Machine Systems Chief of Technische Universität Berlin for their help, in particular M.Sc. Shengguang Lei and PhD Jeronimo Dzaack, and the people who took part in the experiments. A special ancknowledgment goes to the German Academic Exchange Service (DAAD), Paweł Domagała DAAD student at the TU-Berlin, Prof. Cesare Cardani and Amalia Finzi from the Aerospace Engineering Faculty of Politecnico di Milano, for their help and support, to PhD Marinella Ferrino, Arch. Giorgio Musso and Ing. Enrico Gaia from Thales Alenia Italy for consultings. A special thanks also goes to ESA for the parabolic flight and Prof. Franca Ligabue Stricker from the Chair of Anthropology of Università di Torino, the text reviewers Monica Argenta and Andrew Tweedie from Silberzeilen.de and all the people and organisations that collaborate with or support this research.

REFERENCES

[1] Bortz, J., Döring, N.(1995). *Forschungs-methoden und Evaluation.* Heidelberg, Germany: Springer. (Pag. 575 Signifikanztest Differenz (Xa-Xb) a= 0,05 Versuchtpersonen= klein 310, mittel 50, groß 20).

[2] Connors, M.M.; Harrison, A.A.; Akins, F.R.; (2004). *Human Requirements for Extended Spaceflight.* Washington, D.C: NASA. Retreived March '09 from: //history.nasa.gov/SP-483/cover.htm

[3] Mallowe, E.(2001). *Mission to Explore Motion Sickness*. Teach Talk. Cambridge, Mass: MIT News Office at the Massachusetts Institute of Technology. Retrieved from http://web.mit.edu/newsoffice/tt/1991/may22/ 24740.html

[4] Schlacht, I.L.; Brambillaca, S.; Birke, H. (2009). Color Perception in Microgravity Conditions: The Results of CROMOS Parabolic Flight Experiment. *Microgravity Science and Technology*: Volume 21, Issue 1; Page 21-30. Heidelberg, Germany: Springer.

[5] Schlacht, I.L., Masali, M., Ferrino, M., Rötting, M. & Riccò, D. (2008). Visual stimuli for outer space habitability IAC-08-E5.I.1. *International Astronautical Congress*. Papers on DVD. UK: IAC.

In: Color Perception: Physiology, Processes and Analysis ISBN: 978-1-60876-077-0
Editors: D. Skusevich, P. Matikas, pp. 265-268

Short Communication 2

WIUD EXPERIMENT: COLORS AND VISUAL STIMULI FOR OUTER SPACE HABITABILITY

Irene Lia Schlacht,[1*] Matthias Rötting[2+] and Melchiorre Masali[3§]
[1]Chair of Human-Machine Systems, Dept. of Psychology and Ergonomics,
Technische Universität Berlin, Germany
[2]Chair of Human-Machine Systems, Dept. of Psychology and Ergonomics,
Technische Universität Berlin, Germany
[3]Cattedra di Antropologia, Dipartimento di Biologia animale e dell´uomo,
Università di Torino, Italy

ABSTRACT

In microgravity under weightlessness conditions, where 'Up' and 'Down' have no meaning, orientation is of primary importance. Instinctual reactions to color and symbols are investigated in the WIUD experiment to help implement Up and Down orientation in Outer Space Habitats.

Image 1. Expedition 9, Astronaut Mike Fincke juggles oranges in zero gravity. (c) NASA

---

[*] (isc@mms-tu-Berlin.de www.mms.tu-berlin.de or Irene.Schlacht@gmail.com www.extreme-design.eu)
I. L. Schlacht, TU-Berlin, IPA Fach MMS, Sekr. FR 2-7/1, Franklinstr.28-29, D-10587 Berlin

[+] (mro@mms-tu-Berlin.de)

[§] (Melchiorre.Masali@gmail.com)

Keywords:

Colors influence and interact with our everyday life. In extreme environments, as in outer space, it has a crucial impact on astronauts' lives.

In outer space habitats, orientation can only be achieved visually, since the vestibular system becomes silent (Mallowe E., 2001). In this extreme environment, where astronauts experience isolation, body microgravity adaptation and the consequent psycho-physiological problems, colors can support both the orientation and well-being (Schlacht, I.L., 2008).

WIUD is an acronym for "Where is Up and Down", an experiment that studies instinctual reactions toward colors and symbols for "up" and "down" orientation in a microgravity environment. In this experiment the subject, lying in "bed rest" posture and watching the ceiling, is asked to give the correct up and down orientations of different images projected on the ceiling. The images are photos of the International Space Station (ISS) interiors, symbols and color configurations.

WIUD is a phase of a project called µgOrienting which investigates the visual stimuli needed to improve space habitability. This is team project with the Chair of Human-Machine Systems, Technische Universität Berlin, and SUISM Torino and Torino University Lab of Anthropometry and Ergonomics (Dr. Margherita Micheletti Cremasco).

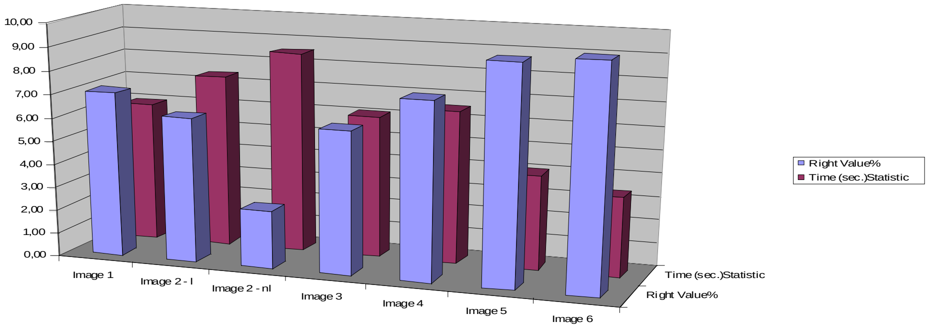
Table 1. WIUD experiment; images and results. Images (c) NASA and I.L. Schlacht

IMAGE		Right orientation	Time (sec.) Mean: 6,239	IMAGE		Right orientation	Time (sec.) Mean: 6,239
Image 1 *URSS ISS module (chaotic colors)*		Subjects: 29/40; %70,7	Mean: 6,032; Std. Deviation: 5,098	Image 4 *Earth in space image (blue down, black up)*		Subjects: 31/40; %75,6	Mean: 6,559; Std. Deviation: 10,039
Image 2 - 1 *Columbus ISS module (with orientation label)*		Subjects: 13/20; %61,9	Mean: 7,421; Std. Deviation: 5,334	Image 5 *Up down orientation label (blue up, brown down)*		Subjects: 38/40; %92,7	Mean: 4,073; Std. Deviation: 3,589
Image 2 - nl *Columbus ISS module (without orientation label)*		Subjects: 5/20; %25,0	Mean: 8,593; Std. Deviation: 5,822	Image 6 *Man pictogram orientation label (brown line as down)*		Subjects: 39/40; %95,1	Mean: 3,385; Std. Deviation: 2,674
Image 3 *USA ISS module (stripped off)*		Subjects: 25/40; %61,0	Mean: 6,103; Std. Deviation: 3,569				

In total 41 subjects (29 males, 12 females; Max. age 60, Min. age 23, average age 33) were involved, and one person's data was excluded for the final analysis.

The images were projected with a circular shape by the WIUD program (© MMS TU-Berlin 2008 Christian Kothe) in random order and with a random angle of alignment obtained using the Mersenne Twister random number generator.

The task was to orient as fast as possible 6 images using a computer mouse. The data recorded were: the subject's personal data; order of sequence and initial angle of the images; final angle and length of time in which the image is oriented by the subject (RT=reaction time).



Graphic 1. Results of WIUD experiment. (c) I.L. Schlacht

The results showed that, although the Russian module (Image 1) has more colors and chaotic configurations, it showed a greater number of right and faster oriented images compared to the American module (Image 3). However, this inverse correlation between reaction time and number of correct results didn't show a valid statistical relevance.

Use of orientation labels in the Columbus ISS module facilitated orientation, since reaction time of Image 2l is lower than Image 2nl, and the percentage of correct orientation of Image 2l is greater than Image 2nl, with a statistically valid relevance of $0.025 < 0.05$ (Bortz, 1995), [Image 2l, Image 2nl Pearson Chi-Square: value 5,013a; df 1; Asymptotic Significace (2-tails) .025].

Man pictogram (Image 6) was the easiest to orient (faster and higher percent of correct orientation) followed by the "up and down" label (Image 5). The "Earth in space" image (Image 4) showing blue earth and black sky was more difficult to orient. However, the comparison of Images 4, 5, 6 showed no statistical relevance.

Comments: The experiment will be further developed to explore the statistical relevance of the relationship between chaotic visual configuration and orientation in the interior ISS module, with and without the use of orientation labels.

ACKNOWLEDGMENTS

We thank all the colleagues of the Man Machine Systems Chief of Technische Universität Berlin for their help, in particular M.Sc. Shengguang Lei and PhD Jeronimo Dzaack, and the people who took part in the experiment. A special ancknowledgment goes to the German Academic Exchange Service (DAAD), Paweł Domagała DAAD student at the TU-Berlin, Prof. Cesare Cardani and Amalia Finzi from the Aerospace Engineering Faculty of Politecnico di Milano, for their help and support, to the reviewer Monica Argenta and Andrew Tweedie from Silberzeilen.de as well to PhD Marinella Ferrino, Arch. Giorgio Musso and Ing. Enrico Gaia from Thales Alenia Italy.

REFERENCES

[1] Bortz, J., Döring, N.(1995). *Forschungs-methoden und Evaluation*. Pag. 575. Heidelberg, Germany: Springer.

[2] Mallowe, E.(2001). *Mission to Explore Motion Sickness*. Teach Talk. Cambridge, Mass: MIT News Office at the Massachusetts Institute of Technology. Retrieved from http://web.mit.edu/newsoffice/tt/1991/may22/ 24740.html

[3] Schlacht, I.L., Masali, M., Ferrino, M., Rötting, M. & Riccò, D. (2008). Visual stimuli for outer space habitability IAC-08-E5.I.1. *International Astronautical Congress*, papers on DVD. UK:IAC.

INDEX