On the possibility of scotopic color vision

An interdisciplinary approach

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Abstract

This interdisciplinary thesis is a collaboration between psychology and physics. Since there is no consensus in the literature about scotopic color vision, the aim of this study was to determine the threshold for color vision and investigate whether this threshold lies in the range of scotopic or mesopic vision, i.e. whether only the rod system is active or that both rods and cones mediate color vision at the threshold level. In this thesis, an introduction into color research is given and an experiment is reported with 15 Hz stimuli of different colors and scotopic light intensities. Subjects were asked to indicate the color of the stimulus. We found that the threshold for color vision seems to vary for different colors and is $-2.12 \pm 0.04$ log phot. Td. for blue, $-0.69 \pm 0.07$ log phot. Td. for green, $-1.35 \pm 0.05$ log phot. Td. for orange and $-1.59 \pm 0.06$ log phot. Td. for red. Although these values are below the cone threshold according to previous studies, our results indicate that color perception at these intensities is primarily mediated by cones, rather than rods. This implies that the threshold for color vision is within the range of mesopic vision.

Keywords: dim illumination, color vision, scotopic vision, primary and secondary rod pathways, mesopic vision, cone threshold
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"Color is neither physics nor psychology; it is both. Physics cannot predict the appearance of a given energy distribution nor can psychology predict the color of a subtractive mixture. Both together should be able to do both; this and similar aims should be the goal of the science of color."

Contents

1 Interdisciplinary introduction 5

2 The research process 8

3 Disciplinary introduction 11
   3.1 Research on color and color perception ............................................. 11
   3.2 Anatomy of the human visual system .................................................. 13
      3.2.1 Anatomy of the human eye ............................................................ 13
      3.2.2 Processing and pathways in the retina ......................................... 14
      3.2.3 Sensitivity and acuity ................................................................. 18
   3.3 The color of an object .......................................................................... 20
      3.3.1 Spectral content of the light source .............................................. 20
      3.3.2 Interaction with the object ............................................................. 20
      3.3.3 Light scattering in the medium ...................................................... 21
      3.3.4 Interaction with other objects ........................................................ 22
      3.3.5 Interaction in the eye .................................................................... 22
   3.4 Technical aspects of color and color perception .................................. 22
      3.4.1 Brightness ....................................................................................... 23
      3.4.2 Luminance ...................................................................................... 24
      3.4.3 Spectral sensitivity ......................................................................... 26
      3.4.4 Detectability .................................................................................... 27
      3.4.5 Univariance ..................................................................................... 28
   3.5 The perception of color .............................................................. 29
      3.5.1 LGN and opponent color channels ............................................... 29
Chapter 1

Interdisciplinary introduction

Most people are able to recognize colors in everyday life. While the number of colors discriminated by a person depends on culture, almost all cultures and languages possess a notion of color. For most people color is such an ordinary phenomenon that no attention is paid to it, except when picking out clothes or a car. This is not surprising from an evolutionary perspective: color vision is the reason why humans and other animals are capable of differentiating between edible and poisonous fruits and crops. It goes without saying, however, that color vision nowadays is no longer crucial for the survival of most humans.

From a scientific perspective, color is a highly interesting subject. Since the sixteenth century people have been reflecting on the origin of color. The main question then was where the color of an object originated: was it an intrinsic quality of the object or was it contained in the light that reflected on the object? Could humans perhaps perceive color in the absence of any physical attribute? In other words, did color only exist in the brain? These issues drew the attention of scientists from various disciplines who came up with heaps of new questions. They set out to investigate light and discovered that a beam of white light consists of a variety of colors. After instruments for detailed and precise scientific research on small structures had been developed, scientists studied the human eye and discovered the existence of cones in the retina. They concluded on the basis of experiments that these cones are responsible for the fact that humans have color vision.

Nowadays lots of research is done on the human visual system. Apart from a scientific curiosity, there is a great importance in doing research in this field: to recover and compensate for all kinds of blindness, such as color blindness. Knowing which processes are relevant for the perception of
color is indeed important in designing a treatment for visually impaired people.

In this thesis, the light intensity for which humans are able to see color will be studied. By establishing the threshold for color vision and inferring which type of photoreceptors are active at this threshold, more insights on the human visual system can be gained. This matter is worth investigating, for current research has demonstrated that, contrary to the current believes, it is possible for humans to perceive colors under dim illumination (Pokorny et al., 2006). However, the current leading consensus in human vision denies the necessity to investigate color perception under dim illumination: because of the dichotomy between rods and cones, people with normal vision are assumed not to be capable of perceiving colors in the dark. Recent research has however to a certain extent suggested the contrary: people are possibly able to discriminate colors under dim illumination. Therefore, the aim of this thesis is to examine at what light intensity humans are able to see colors. Little research in this field of study has been performed, meaning that there currently is a gap in the knowledge about the human visual system and extensive research on this topic could eventually lead to a paradigm shift.

With this research, also a public cause is pursued: research on the perception of color under dim illuminations can be meaningful for the understanding of diseases such as Retinis Pigmentosa, a progressive degeneration of the retina that affects night vision and peripheral vision (Wolfe et al., 2009). Treatment of this disease can be improved if more details of the visual system are known.

The question of at what light intensity humans are able to see colors requires an interdisciplinary approach, because of its complex nature: human vision is an object of study for several disciplines, including biology, physics and psychology. Moreover, not one of these disciplines covers all the relevant variables. Physics for example focuses mainly on the light reaching the eye and the measurable (electrical) eye responses, whereas psychology is concerned with the neural pathways and processing of neural signals from the eye and biology researches the physical structure of and the chemical processes within the human eye. When a colored light stimulus is observed by a person, very different effects can come into play: the physical content of a light stimulus does not determine the color one sees completely. Complicated effects in the retina and higher-order processes in the brain can be of great importance. Specifically, at low light intensities other information, such as prior experience can influence the ability of a person to perceive a certain color. For a complete
view of the concepts and insights associated with questions about human vision, it is important to combine the efforts of (some of) these disciplines.

Several disciplines are relevant for this research project. Biology is relevant, because it researches the human eye. Cognitive psychology researches the signal processing of human sensory mechanisms and is therefore able to shed light on the intricate pathways signals follow from the eye to the brain. In addition, cognitive psychology provides useful research methodologies. Physics as a discipline has developed several important research methods for human vision, including colorimetry and electro retinoscopy. Furthermore, physics studies light as a natural phenomenon.

In practice, these disciplines are not as divided as the preceding paragraph may suggest: researchers in the field of human vision use many results of research that has been done by other disciplines, because most topics lie in the scope of several disciplines. Therefore, in a way, almost all research in human vision is interdisciplinary. In the present thesis, the insights of physics and cognitive psychology are combined. However, since physics, biology and cognitive psychology are so intricately interlaced, relevant biological concepts and insights are also incorporated whenever necessary, thus making it possible to study all the relevant variables involved.

Since the topic of this thesis constitutes a gap in our scientific knowledge, not much literature is available. This led us to set up an experimental study, executed under the supervision of the Helmholtz Institute at Utrecht University. Given the experimental nature of the work reported in it, the thesis is structured as follows. It starts with an introduction into the field of color vision, containing both insights from physics and psychology. This introduction is followed by a report of the experiment. After that, a common ground is created for integration of insights of the two disciplines. Finally, an interdisciplinary conclusion is drawn which will contribute to a more complete understanding of color vision under dim illumination.
Chapter 2

The research process

An important aspect of every bachelor program is learning how to set up a research project. Writing a bachelor’s thesis is one of the best ways to learn this. The way research is done varies however from discipline to discipline: Most sciences use experimental studies, while most of the humanities perform literature-based studies. These differences are reflected in the way the bachelor’s theses at Utrecht University are incorporated in the curricula.

The bachelor’s thesis for Liberal Arts and Sciences usually has the form of a literature study. In a very early stage of the planning of this thesis (around December 2010), we came to the conclusion that an experimental approach seemed more suitable with regard to our potential research questions. The department Physics of Man at the Helmholtz Institute helped us to set up our research by allowing us to investigate an effect that was observed in a recent experiment by one of their PhD-students, Mieke Bijveld, who would become our advisor. Our advisor from Liberal Arts was supportive in our decision to start researching at the Helmholtz institute. The choice for an experimental research has changed a lot about our research process. We feel that it is important to make these differences known to the reader, because in the report of an experimental study a large part of the whole process is not discussed. A research article usually does not discuss all the thinking, the testing and the various tried experimental set ups needed to design a good experiment. Since we are supposed to learn how to do research, we think that it is important to discuss the process that led to our final experiment.

As a start, we went to the Bartiméus Institute for the Visually Impaired with our advisor Mieke Bijveld, who works there as a PhD-student, to see the equipment we would use in our experiment
as well as learn more about the practical implications of color research. We observed several sessions where children were diagnosed. We also conducted a first pilot experiment, in which Emma participated as a subject. This pilot showed us that the results that Mieke had observed in her previous research were easily reproducible, but also that our crude set-up of that pilot would not suffice if we wanted to make a proper analysis of our experiment.

Shortly after this intern day at Bartiméus, we discussed the design of our experiment in greater detail and came up with a couple of preliminary questions that needed answering before we could finish our design. To answer these questions, we spent another day at Bartiméus to conduct more pilot studies. Firstly, we determined the intensity ranges of our experiment, making sure that the highest intensity had an obvious color for all our subjects and that the lowest intensity was colorless for our subjects, but still visible. Secondly, we found out that with our possibilities, it was impossible to properly find an intensity range in which subjects would not detect a flicker (for more information on the origin and importance of flicker detection, see the Introduction of the research article). Thirdly, we tested whether presenting our stimuli in a random order would have an effect on perception. We found that the effect of dark adaptation, which makes the visual system more sensitive, was not significantly decreased when high-intensity stimuli were presented. In addition, presenting a high-intensity stimulus of a certain color followed by a colorless stimulus did not seem to alter the color judgments of our subjects significantly. As a final test, we also tried out different ways of asking a subject which color was shown and allowing different kinds of answers. It was immediately clear to us that leaving the way a subject could answer completely open would lead to very obscure color tags in our data, such as turquoise or magenta. This would make it very hard to analyze our data without making severe compromises. On the other hand, allowing a subject to choose only between the colors that were actually shown could leave out information that might be important for future research. Since our experiment was also meant as an exploratory study of the phenomenon, we found it important to collect that information and thus decided that subjects could choose from a specific set of colors to describe their perception.

After we had made a final design for our experiment using the data from our pilots, we made sure that we would not be surprised by unforeseen effects by testing our whole experiment using a naïve subject. This turned out to be a good decision, since some important changes were made: we altered the intensity levels slightly and also increased the number of times a stimulus was presented from
two to three. This was done to investigate whether subjects were consistent in their judgments. Finally, the actual experiment took place in mid-April and was spread over two days. In addition to our pilots, we also attended some of the weekly meetings of the department Physics of Man, to talk about our own progress as well as the work that other researchers were doing. We tried to attend the meetings as often as possible, or when our schedule would allow it. The feedback we got from those meetings was very valuable.
Chapter 3

Disciplinary introduction

In this chapter the fields of color research within psychology and physics will be explored. The concepts introduced in this chapter are important for our research. Since many aspects of color vision are closely related to the anatomical structure of the human eye, this anatomy will be discussed first. In particular, the pathways along which the neural signals travel through the retina and the photoreceptors are discussed. Subsequently, several variables that are important for the color of an object are reviewed, showing that color vision is not the simple concept it might seem. Furthermore, technical aspects regarding color will be dealt with and lastly, the process of perceiving color will be discussed as well as the complex effect of color constancy.

3.1 Research on color and color perception

Research in physics

The phenomenon of color vision has fascinated many of the great minds in physics, including Isaac Newton, James Clark Maxwell and Erwin Schrödinger. In a sense, these physicists were the founders of color research. The early scientists tried to find the origin of a color of an object, whether it was in the light or in the object itself. This led to discoveries like the fact that white light consists of many different wavelengths and that the mixing of colors can be modeled with mathematical tools. Later on, scientists started to include the human eye in the research as well as subjects. Maxwell in particular developed the important research methodology of colorimetry, in which a beam is compared with reference beams to determine its color, using a subject [Maxwell, 1872]. This has formed the basis of modern color science. At present, the questions in color science
are becoming more and more complex, because other variables come into play. Since the research that can be done on human neural systems and brain processing is rapidly increasing, problems can be solved using knowledge generated by scientists from many different fields, including biology, physics and psychology.

Research in psychology

Whereas physics is concerned with the physical properties of world, cognitive psychology deals with how the physical world is perceived by the interpretation of signals from the human senses. The field of cognitive psychology has blurry boundaries and has a significant overlap with other disciplines such as human biology. In the last decades, the interdisciplinary field of cognitive neuroscience has experienced a major growth and increasing popularity. To obtain a complete understanding of the human brain and mental processes is the aim of this field. Among the disciplines that have contributed to the foundations of cognitive science are artificial intelligence, human-computer interaction, linguistics, medicine, neuroscience, psychology and sociology [Schunn et al., 1998]. Insights from these disciplines are integrated to obtain a more complete understanding of the human brain. Research in cognitive sciences is done through experimental studies and through simulation of the functional anatomy of the brain by computer programs. Due to the development of modern non-invasive techniques for studying and simulating the brain, new insights quickly succeed one another in this meta-discipline. These insights even have a much wider scope as they influence theories in a broad range of disciplines, among them anthropology, philosophy and engineering. As perception in general is an important topic in cognitive neuroscience, the perception of color under dim illuminations lies within the scope of this discipline. Psychology investigates the perception of color as a higher cognitive process and examines questions about color constancy, color naming and experience of color.

Definition of color

Although in everyday life the term "color" is intuitively clear, it is impossible to give a correct, complete definition that is accurate for all color research. In trying so, one would encounter different aspects of human vision that make it the complex system that it is [Evans, 1948]. To make it possible to communicate meaningfully about color in this thesis, it is, however, important to have some kind of definition to start with: we define color as the quality of an object or substance that is
primarily dependent on the spectral energy distribution of the light that reflects from the object or substance. Moreover, we will make a distinction between color and color perception. Whereas color can be seen as the attribute of an object, the perception of color is a cognitive process that involves the interpretation of neural signals. These two concepts can not be studied separately since they interact: the colortag one is prepared to give to a particular object is dependent on many other variables than spectral content alone. To be able to discuss these variables properly, we will first discuss the anatomy of the human eye.

3.2 Anatomy of the human visual system

3.2.1 Anatomy of the human eye

The first step in visual perception starts at the eye, a complex system where light rays are captured and converted into neural signals (Duncan and Hart 2005). (see fig. 3.1) This important sense organ consists of multiple layers (see figure 3.1) : an outer layer of connective tissue forming the cornea and the sclera; a middle vascular layer composed of the iris, the ciliary body and the choroid; and lastly, the inner neural layer of the retina. (Duncan and Hart 2005).

Light enters the eye through the cornea, the transparent window into the eyeball that allows beams of light to enter the eye and helps to bring the rays into focus on the retina (Duncan and Hart 2005). From there the light passes through the aqueous humor, a watery fluid in the anterior chamber of the eye and the pupil, which is the dark circular opening at the center of the iris of the eye (Wolfe et al. 2009). The iris is a muscular diaphragm regulating the amount of light entering the eye by expanding and contracting the pupil. Right behind the pupil is the flexible lens that refracts the light and

Figure 3.1: The human eye and its components. Source: www.eyesandeyesight.com
enables focus by accommodation due to variation in curvature of the lens established by the zonules of Zinn and the ciliary muscles that are attached to them. When refracted by the lens, the light enters the vitreous chamber containing a transparent fluid that fills the posterior part of the eye. A large part of the light will be lost in this chamber and only a small portion will fall on the retina. This light-sensitive membrane in the back of the eye, which contains the macula and the optic disc (Duncan and Hart, 2005), translates the light into neural signals that are sent to the brain through the optic nerve (Duncan and Hart, 2005; Wolfe et al., 2009).

3.2.2 Processing and pathways in the retina

The retina is the part of eye where information processing takes place: this tissue converts light energy into a neural signal. The retina can be divided into different layers containing various types of cells that each have another function in the processing of visual information. These cells include photoreceptor, horizontal, bipolar, amacrine and ganglion cells (Bruce et al., 2003). The retina roughly consists of two pathways: a vertical and a horizontal one.

The vertical pathway

The vertical pathway that lies perpendicular to the retina, consists of photoreceptors, bipolar cells and ganglion cells. The human retina contains ciliary receptor types, so called photoreceptors, which form the first link in the pathway from the retina to the brain. These light-sensitive receptors lie in the posterior layer of the retina (Solomon and Lennie, 2007). To arrive at this layer, the photons have to pass all other layers of the retina.

Photoreceptors

The photoreceptors are composed of (1) an outer segment, containing photopigments that absorb photons; (2) the inner segment, containing the machinery for metabolism and the place where the pigments are made; (3) the outer fiber; a stalk, (4) the cilium, connecting the outer with the inner segment the cell body; and (5) the inner fiber, which terminates at the synaptic terminal (Duncan and Hart, 2005; Panga et al., 2010). (see fig. 3.2).

When not activated, the photoreceptors have a resting potential of $-40 \text{ mV}$ and release some amount of neurotransmitters. The pigment in the photoreceptor consists of a protein, the structure that determines which wavelengths are absorbed, and a chromophore, which captures light photons.
Figure 3.2: A schematic view of the photoreceptors. Source: Duncan and Hart, 2005, page 59.

(Wolfe et al., 2009). Whenever a photon hits the receptor and the pigment in the photoreceptor is broken down, the permeability of the membrane resulting in hyperpolarization till $-70$ mV. This hyperpolarization is unique for photoreceptors, as cells normally get depolarized when excited. When hyperpolarized, the release of neurotransmitters from the synaptic terminal is reduced. The
size of this receptor potential is proportional to the logarithm of the intensity of light striking the cell \cite{Bruce2003}.

The human visual system is highly specialized but at the same time functional in a broad range of light intensities. To be able to see under so variable lighting conditions, the system can adapt its capacity to respond in various levels of illumination due to the activation of different photoreceptors and the adaptation of photoreceptors \cite{Gegenfurtner2001}. The retina contains two types of photoreceptors, the rods and the cones each sensitive in another range of light intensities. The human eye has about 80 to 110 million rods and 4 to 5 million cones. During high luminance (photopic vision) the cones are most sensitive and the rods are saturated. Cones dominate photopic vision and, according to the current paradigm, mediate color vision \cite{Duncan2005}. However, during low luminance (scotopic vision), the rods are most active and the cones are not active \cite{Wolfe2009,Duncan2005}. Rods are extremely sensitive under dim illumination. When a critical mass of photons with the right amount of energy hits a receptor, the cell will send a signal to the next layer of cells, the bipolar cells \cite{Gegenfurtner2001}.

**Bipolar cells**

The bipolar cells are the second link in the visual vertical pathway. The dendrites of these cells are connected to photoreceptors and horizontal cells, and the axons of bipolar cell synapse with ganglion cells and amacrine cells \cite{Solomon2007}. Bipolar cells are part of both the vertical and horizontal pathway: they transmit information from photoreceptors to ganglion cells, horizontal and amacrine cells, and secondly, they receive feedback from the amacrine cells. There are many different types of bipolar cells known \cite{Duncan2005}, among them are the diffuse and midget bipolar cells. Diffuse bipolar cells are present in the periphery and receive input from multiple photoreceptors, either a population of rods or of cones. Another kind of bipolar cells, the so-called midget cells receive input from one cone and synapse with a single ganglion cell. This pathway is called the one-to-one cone pathway and can only be found in the center of the retina, the fovea \cite{Solomon2007}. The diffuse bipolar cells have a high sensitivity but a low acuity. The midget bipolar cell, however, has a low sensitivity but a high acuity. These bipolar cells can be subdivided into two kinds: ON and OFF bipolar cells. The ON bipolar cells respond to an increase in light captured by the cones by inverting the inhibitory signal from the cones into an excitatory signal. The OFF bipolar cell, on the other hand, responds to a decrease in light.
This cell does not invert the inhibiting signal from the photoreceptors but also hyperpolarizes when activated (Wolfe et al., 2009).

**Ganglion cells**

The bipolar cells synapse in turn with ganglion cells. The ganglion cells receive visual information from photoreceptors via two intermediate neuron types, the bipolar cells and amacrine cells (Duncan and Hart, 2005). There are three different kinds of ganglion cells. Firstly the P ganglion cells, which are small cells that receive excitatory input from single midget bipolar cells in the central retina. The P cells have a sustained response and are wavelength-selective (Zeki, 1993). These cells have small receptive fields and hence a high visual acuity. Secondly, there are M ganglion cells which receive excitatory input from diffuse bipolar cells. This type of ganglion cells responds transiently and is not selective for the wavelength of the stimulus (Zeki, 1993). These ganglion cells have large receptive fields and are therefore more sensitive under low lighting conditions. The last type of cell is the koniocellular ganglion cell (Wolfe et al., 2009). The axons of ganglion cells run over the surface of the retina to the blind spot, where they are bundled together to form the optic nerve.

**The horizontal pathway**

The horizontal pathway provides feedback to the retinal cells and modifies and integrates neural signals before they are sent to the brain. The pathway consists of three different types of cells: horizontal cells, amacrine cells and interplexiform neurons. Horizontal cells communicate with
photoreceptors, bipolar cells and other horizontal cells. These cells transmit information in the direction parallel to the retina. The axons of these cells terminate in the outer plexiform layer. The amacrine cell has large endings that terminate in the inner plexiform layer. The cell forms complex connections with bipolar cells, other amacrine cells, ganglion cells and interplexiform neurons (Duncan and Hart, 2005).

The cells forming the horizontal pathway are crucial for vision and provide lateral inhibition: the ability to inhibit the response of neurons with a weak firing rate. When a stimulus is presented, photoreceptors begin to fire, some more intensely than others. The neural signal associated with the stimulus will therefore be noisy. The horizontal pathway can inhibit the neurons that fire most slowly. These photoreceptors will thus be filtered out as irrelevant. The cells with high firing rates are weakened in their response, thereby saving energy. Lateral inhibition leads to down regulation of the neural activity, the ability to filter the relevant information and thereby sharpening the neural signal (Wolfe et al., 2009). For an overview of the cells in the retina, see fig. 3.4).

3.2.3 Sensitivity and acuity

There are quite some differences between the rod and the cone system. The distribution of rods and cones is not homogenous over the retina and there is a greater convergence of rods than of cones onto ganglion cells which influences the acuity and sensitivity of the system (Bruce et al., 2003). The retina can be divided into two areas: the fovea in the center of the retina and the periphery. The fovea contains mostly cones and midget bipolar cells with small receptive fields. It has a low degree of convergence, a high visual acuity and low sensitivity. A relatively small number of cones connect to one cone bipolar cell, and a small number of cone bipolar cells synapse with a single ganglion cell. In some situations there is a 1:1 ratio between ganglion cells and cones, reflecting the amount of detail that the cones can discriminate (Duncan and Hart, 2005). The periphery however, contains mostly rods and diffuse bipolar cells with large receptive fields. There is a high ratio of rods to ganglion cells, resulting in high sensitivity for the detection of light. The acuity of this region is low and the sensitivity is high (Wolfe et al., 2009). Thus the cone-rich region provides high acuity vision in bright light, whilst the rod-rich area provides high sensitivity vision is dim light (Bruce et al., 2003). The peripheral retina therefore is suitable for detecting motion whereas the central fovea is specialized in fine details and color discrimination (Duncan and Hart, 2005). Lastly, the rods and cones differ in the speed of response and in their time-course. This is
due to temporal summation: the activity of a photoreceptor is integrated over a certain amount of time. Rods have a longer temporal window than cones, which results in a higher sensitivity: less photons are necessary to activate a rod. This longer temporal window also leads to lower acuity:
the inability to detect fast changes in the dark (Wolfe et al., 2009).

3.3 The color of an object

The color of an object at first glance does not seem a very difficult phenomenon: Light with a certain spectral energy distribution travels from a source to an object, interacts with the object, which changes its spectral energy distribution and then continues to travel to the observer’s eye. The spectral energy distribution of the light that enters the eye then determines what color the observer will ascribe to the object under observation.

In practice, this model is, however, too simple. Although the dependencies in this crude model definitely exist, their relation to the assignment of a particular color is non-trivial and other variables come into play as well. A typical situation in which color perception is studied consists of a light source, a medium, an object that is irradiated by the light source and an observer, who perceives the object. There are now at least five different variables that determine the color and the perception of color.

3.3.1 Spectral content of the light source

The light source can be a variety of things, such as the sun, a light bulb or a flame. It is possible to describe the light source by the wavelengths that are present in the light as well as the intensities of the different wavelengths. This is called the spectral energy distribution and is usually presented in a figure in which the intensity is shown as a function of wavelength. As an example, the spectral energy distribution of sunlight is shown in figure 3.5. The fact that the spectral energy distribution of the light source is important for the color one ascribes to the illuminated object is easily understood: Imagine a source which has a strong yellow filter in front of it. An object illuminated by such a source will in general appear to be yellow. If the filter is changed to a red filter, the object will in general appear to be red and so on (Evans, 1948).

3.3.2 Interaction with the object

When the light from the source falls onto the object under observation, typically three things can happen: the light can be reflected, absorbed or transmitted. In a normal situation all three occur, with a wavelength dependency for the proportion of each. Since energy is never lost, the
total incident energy should equal the energy of the reflected, absorbed and transmitted energy combined.

Some materials, such as glass, transmit most of the incoming energy, while others, such as some metals, transmit no light at all [Evans 1948]. Depending on the position of the observer relative to the object’s position as well as the position of the source, the transmitted or reflected light finds its way to the eye of the observer and therefore determines the color of the object. Because the amount of light that is reflected is wavelength-dependent, the spectral energy distribution of the light that travels to the eye can be changed due to interaction with the surface of an object. In more extreme cases, such as a light source which consists solely of wavelengths below 600 nm and an object which reflects only wavelengths above 600 nm (most likely a red object), the object will appear to be black, since no light is reflected from the object into the observer’s eye.

3.3.3 Light scattering in the medium

Light from the source can also partially scatter off particles in the medium. This forms a second "source" that irradiates the object. What happens is this: the incoming radiation falls on an atom in the medium, causing the electrons of the atom to move. These accelerating electrons then irradiate light. The light that falls on the object due to scattering may not contain all the frequencies that the light source contains, because the scattering intensity of a light ray is proportional to the fourth
power of the frequency of the light, thereby favoring "blue" lights. In some situations therefore, the additional source may be viewed as a primarily blue source (Feynman et al., 1964).

3.3.4 Interaction with other objects

In the same way that light scattering can cause additional light to fall on to the object, also interaction of the source light with other objects can lead to a different spectral energy distribution of the light that falls on the object under observation. When light from the source reflects or is transmitted through other objects, it is possible that this light travels to the object. As is shown before, this light may possess an entirely different spectral energy distribution than the source light and may therefore change the total spectral content of the incoming light. In addition, the presence of other objects in the observed scene may change the color of the observed object due to color constancy. The latter effect will be explored later in greater detail (Koenderink and Kappers, 2002).

3.3.5 Interaction in the eye

When the light of the object reaches the eye, its spectral energy distribution can still be changed, due to reflectance and absorption in the eye as well as scattering in the eye media. The biggest factor in the eye itself is the macular pigment, that can be found mainly in the center of the retina. It absorbs most strongly from 400 nm to 550 nm and thus removes a lot of "blue" from the incoming light. The amount of pigment present in a person’s eye differs greatly over the population and is thus responsible for the fact that different people may see the same color slightly different (Shevell, 2003; Wyszcki and Stiles, 2000).

Although the above list is not as excessive as it could be, it is clear from this list that color vision is not as straightforward as one might intuitively think.

3.4 Technical aspects of color and color perception

As many other scientific fields, color research has developed a rich disciplinary jargon, which reflects the fact that it is very difficult to define certain phenomena studied by the discipline. One can use many different terms to describe aspects of a color, for example, hue, saturation and brightness. These aspects are dependent on cognitive processes as well as the physical origin of the stimulus
and may differ from individual to individual [Evans, 1948].

Hue may be described as the quality in color that changes most noticeably when one changes the wavelength of the light. For example, in a red beam the hue of the beam will indicate the fact that the beam is red. For monochromatic beams, hue is thus closely related to the wavelength of the beam. The amount of hue present in the beam is called the saturation and reflects the vividness of the color. The brightness of a certain beam is closely related to the amount of light or total radiant energy in the beam and can be defined as the effect the amount of light has on an observer [Evans, 1948]. In colorless beams, brightness is the only aspect of a beam that can change without changing from colorless to colored [Grassmann, 1853].

These definitions are not as deeply rooted in the physical world as one might want: as shown before, assuming a direct relationship between these characteristics and the physical world would be erratic. Still, these terms are still widely used in the field, though need to be interpreted with care.

3.4.1 Brightness

For those who have studied the variables on which color is dependent, it may come as no surprise that the concept of brightness is a very complex one. Neurological processes play an important role in the judgment of a color on its brightness, explaining why the study of brightness has to consist of experiments with subjects. Since the differences between subjects can be great, this may lead to problems, as is illustrated by the next example.

In a typical colorimetric experiment, in which the color of a beam is judged by a subject, the subject sees a field through an eyepiece or a hole, half of which is filled with the beam one wants to measure. The other half of this field is filled with the reference beam from a source that is controlled by the experimenter. When the two halves of the field merge into one uniformly colored circle, the two beams appear to the observer to have the same color. When a comparable experiment is set up in which not the color, but only the brightness of a beam is compared to that of a reference beam, the merging of the two halves may not occur, since the hue or saturation of the beams may differ. The situations are therefore very different, as expressed by Erwin Schrödinger: "Whereas the condition of distinguishableness of two fields is logically absolutely clear and does not require any further
definition, this is by no means true of the condition of being equally bright, which is allegedly accomplished in this case” (Schrödinger 1926). This is why the question whether the two halves are equally bright is more complicated than the question whether there are two distinguishable halves and leaves room for interpretation. It is therefore not possible to test the brightness of a beam in the way just described, without accepting a certain amount of subjectivity, which in cognitive experiments has to be eliminated. Of course, even when the standard colorimetric set-up is used, some subjectivity remains: subjects still have to judge if the two halves are distinct or not. It is however impossible to design an experiment which is based on judgments of subjects that is not subjective: the subjectivity is an intrinsic property of judgments. An experimenter can only try to eliminate subjectivity as much as possible.

Of course there are other methods by which brightness can be defined. One could define brightness operationally, as a certain variable in a precise experimental setup, or in a theoretical way, as an aspect of a specific color in the mathematical framework. Both options have their problems: definitions that are based on an experimental setup are subject to arbitrariness. The theoretical options for definitions of brightness have as a common problem that they do not necessarily correspond to actual human observation and may ascribe very different values to colors that for humans look equally bright (Koenderink and Kappers 2002).

3.4.2 Luminance

As a way to eliminate cognitive processes as a factor in judging the intensity of a light beam, the term luminance, with unit candela per m², was created. As said before, the photoreceptors in the human eye detect light of different wavelengths with different efficiency. To account for this efficiency, a curve was introduced called the luminosity function \( V(\lambda) \) (see fig. 3.6) by the CIE, the Commission Internationale de l’Éclairage (Internation Committee on Illumination), which allows one to calculate under certain conditions the amount of light necessary for a certain color to be as bright as another given color. This curve was calculated by the CIE with the data from several psychophysical measurements. Since the first introduction of the curve in 1924, several other curves were introduced that can be used under other conditions than the first curve. For example, the CIE 1931 10°-curve can be used for visual fields of around 10°, whereas the original curve is valid only for fields smaller than 4° (Shevell 2003). With the CIE 1931 10°-curve, luminance is defined
Figure 3.6: **The photopic luminosity function, showing the relative efficiency of the receptors at different wavelengths**

as follows:

\[ L = \int_0^\infty E(\lambda)S(\lambda)d\lambda, \]

where \( E(\lambda) \) is the radiant energy per wavelength and \( S(\lambda) \) is the sensitivity of the eye of the standard observer. Luminance is usually expressed in candela, the intensity per star radians. The standard observer is a theoretical observer, who has the average properties of a large group of subjects. This definition was decreed by the CIE and has some nice properties, such as the fact that luminance is linear. This corresponds to reality only under certain conditions (Wagner and Boynton, 1972). However, strictly speaking, its applicability is limited to situations similar to those in which the data for the curve were collected, because the curve changes with adaptation (Gegenfurtner and Sharpe, 2001; De Vries, 1948; Koenderink and Kappers, 2002).

Because the efficiencies of the photoreceptors are different at low light (or scotopic) intensities, the scotopic luminosity function was developed, which describes the effectiveness of the receptors at scotopic light levels. This curve was constructed from data sets of brightness matching experiments at low light intensities and measurements of vision threshold as a function of wavelength (Shevell, 2003). This function has its peak not at 555 nm, but at 507 nm.
The luminosity curve is widely used in color research as a tool to express results in terms of a standard observer. Additionally, with the definition of luminance, the definition of the unit troland was created, to account for the dilation of a human’s pupil, as \( Td = L_v \cdot p \), where \( L_v \) is the luminance in \( \text{cd} \ \text{m}^{-2} \) and \( p \) is the area of the pupil in \( \text{mm}^2 \). In this thesis the unit scotopic troland will be used, the unit that is derived from the scotopic luminosity curve. Other units, such as the lumen and the lux are also important: lumen measures the luminous flux and lux measures the intensity of the light on a certain surface. 1 lumen is defined as the luminous flux of a light beam with an intensity of 1 candela and 1 star radian in angular area. If such a beam falls on a surface of 1 m\(^2\), the intensity at that surface is 1 lux (Wyszecki and Stiles, 2000).

3.4.3 Spectral sensitivity

When the light from the object has arrived at the posterior part of the retina, it falls onto the photoreceptors which are responsible for translating the light stimulus into neural signals. These photoreceptors detect light of different wavelengths with different efficiency. There are three different types of cones: S-system cones, M-system cones and L-system cones. Each type contains slightly different pigment molecules and each pigment molecule is activated by the absorption of light of a specific wavelength. The peaks of the absorptions lie at respectively 430 nm, 530 nm, and 560 nm (Solomon and Lennie, 2007) (see fig. 3.7). This wavelength-dependency is called the spectral sensitivity of the photoreceptors. The three kinds of cones in the eye thus all have different spectral sensitivity. In practice this means that at normal light intensities (comparable to daylight) for a standard observer (who has an spectral sensitivity which is an average of many subjects), light with wavelengths close to 560 nm is detected approximately twice as easy as light with wavelengths primarily around 500 nm.

![Figure 3.7: The spectral sensitivity of the L-, M- and S-cone and the rods (R). Source: www.reefcolors.de/HTML_Science/science_colors2.html](image)
However, the spectral sensitivity is different for different observers and is an important factor in the process of color perception (Evans 1948). The standard observer is most sensitive to wavelengths that correspond to the color green. If the photoreceptors had a uniform spectral sensitivity, i.e. if the photoreceptors were equally sensitive to all wavelengths, the world would look less green.

It is also important that the spectral sensitivity of the human eye is different at different illumination levels. At light levels where the rods are active and the cones are not (at dusk or night), the spectral sensitivity of the eye is dominated by the rods. This leads to the explanation of the empirical fact that since rods are more sensitive to short wavelengths than cones, at low light intensities everything looks bluer than at normal illumination levels: the so-called Purkinje shift (Shevell 2003).

3.4.4 Detectability

When no light from an object reaches the eye of an observer, it is obvious that the observer will be unable to detect the object. However, when only a very small amount of light reaches the eye, observers are typically still unable to detect the object. The threshold of how much light is necessary to detect an object, depends on several factors, such as the position of the object in the visual field and the size of the patch on the retina that is illuminated by the incident light from the object. This is mainly due to the location of rods and cones on the retina and the mechanisms that create signals in these photoreceptors.

Signals are created only when at least one photon is absorbed by a receptor. When light intensity is very low, the quantum nature of photons becomes important. The arrival of photons at a specific place at the retina can be modeled using a Poisson distribution. So even when the average number of photons is larger than zero, it is still possible that at a specific moment no photons arrive (Shevell 2003). This gives important insights concerning the threshold of vision: when a stimulus illuminates only a very small patch on the retina, has a very short duration and is of very low intensity, it is possible that an individual is unable to see the stimulus. This is especially true in the fovea, where the only receptors present are cones. Only a few cones connect to a single cone bipolar cell there, causing the chance that no signal is sent to the brain when photons fall on a small patch on the fovea to be significantly greater than zero. Of course, the larger the area that is stimulated by a light becomes, the smaller the chance that no signal is sent. For a very small stimulus (only 1’ (or
1 arc minute) at the cornea) that illuminates only the fovea, about 203 photons are needed for a subject to see the stimulus (Koenig and Hofer, 2011).

The rods operate in a slightly different manner. A single rod needs less photons to create a signal than a single cone due to temporal summation, which in rods is done over a longer time period than in cones. The number of rods that connect to a single bipolar cell is large, lowering the chance that quantum fluctuations in the stimulus are of great influence. Of course, when the number of incident photons is dropped, the fluctuations can still become important. A recent study has shown that for a stimulus with a diameter of 27’ (or 27 arc minutes) that illuminates the retina at 11 degrees temporal, only 50 photons are needed for a subject to detect the stimulus (Koenig and Hofer, 2011). This is only one-fourth of the number of photons per second needed to activate the cones.

### 3.4.5 Univariance

When it comes to seeing color, the output of a single photoreceptor is ambiguous. A difference in the spectral composition of light falling on two neighboring receptors containing the same pigment will cause a difference in their electrical response, but a difference in just the intensity of light can have exactly the same effect (Bruce et al., 2003). The spectral sensitivity of a photoreceptor is best understood as a measure of the probability that the receptor will absorb a photon of a particular wavelength. Once absorbed, the identity of the photon is lost, so no single photoreceptor can distinguish a change in the wavelength of light from a change in its intensity. This is the principle of univariance (Solomon and Lennie, 2007): an infinite set of different wavelengths-intensity combinations can elicit exactly the same response, so the output of a single photoreceptor cannot by itself give information about the wavelengths stimulating it (Duncan and Hart, 2005; Panga et al., 2010). Furthermore, the output of the photoreceptors is ambiguous since they do not give any absolute information about the spectral composition of the light due to the existence of metamers: different mixtures of wavelengths that elicit the same combination of responses in the photoreceptors. Metameric color stimuli are color stimuli with the same tristimulus values but different spectral radiant power distributions (Wyszecki and Stiles, 2000). This also means that they are perceived as the same color. More generally, metamers can be defined as any pair of stimuli that are perceived as identical in spite of physical differences (Wolfe et al., 2009). In a retina containing only one type of receptor cell, the pattern of receptor potentials therefore cannot provide separate
information about the patterns of intensity and of spectral composition and thus color vision is not possible (Bruce et al., 2003). This is also why, according to the current paradigm, color vision is not possible at scotopic light levels: all rods have the same spectral sensitivity and thus the problem of univariance makes it impossible to discriminate colors. Color vision, the ability to distinguish lights of different spectral composition, regardless of intensity, thus depends on the \textit{comparison} of activity from photoreceptors with different spectral sensitivities (Solomon and Lennie, 2007). The trichromatic theory of color vision states that the color of any light is defined by the relationships of three numbers, the outputs of three receptor types now known to be the three cones. If the combined output from the receptors is the same, the same color is perceived (Bruce et al., 2003).

Thus, due to the spectral sensitivity and the fact that univariance is not an issue, the cones are able to discriminate light beams of different spectral components. Based on the principle of univariance, one would infer that during scotopic vision, when only the rod system is active, color vision is not possible (Duncan and Hart, 2005).

### 3.5 The perception of color

Since the human brain is the final interpreter of the neural signals transmitted by the eye, it is not surprising that brain processes can influence color vision. In this section, the areas in the brain that interpret the incoming signals are discussed, as well as their functions. The signals from the retina are transmitted through the optic nerve via the Lateral Geniculate Nucleus (LGN) in the thalamus to the primary visual cortex (V1) in the brain (Stockman et al., 1995; Sharpe and Stockman, 1999).

#### 3.5.1 LGN and opponent color channels

LGN is the relay station situated in the thalamus for visual information. Most of the fibers arriving at LGN terminate in V1; only about 10% of the fibers terminate in another nucleus in the thalamus, the Superior Colliculus. LGN has a retinotopic and complex, six layered structure. It contains two lower magnocellular layers that receive input from the M ganglion cells and four upper parvocellular layers, receiving input from the P ganglion cells (Wolfe et al., 2009; Zeki, 1993). This nucleus, which is present in both hemispheres, gets information from both the contra- and the ipsalateral eye, which is segregated into different layers. Due to the organization of LGN, the retina is represented six times over in each LGN, three times for each eye (Wolfe et al., 2009). As mentioned earlier, P-ganglion cells have small receptive fields and some degree of wavelength specificity, whereas the
M-ganglion cells have large receptive fields and are not sensitive to different wavelengths. Since the P-ganglion cells project to the parvocellular layers in LGN, only these layers are concerned with color vision (Zeki, 1993).

In work done by Ewald Hering conducted in 1892, red, green, blue, and yellow were considered to be elementary colors that could not be described by a combination of any other colors. Moreover, he stated that red and green were opponent colors since the perception of red and of green never co-exist in the same color.

Blue and yellow were mutually exclusive, as were light and dark (Wolfe et al., 2009). The anatomical basis of this idea is found in LGN, which contains opponent color cells in which the output of the cones are added and subtracted. There are three kinds of opponent color cells: first (L+M) cells, a light-dark channel that adds the output of the L-cones and the M-cones; secondly (L - M) cells, a red-green channel that subtracts the output of the M-cones from the L-cones; and lastly the ([L+M] - S) cells, a blue-yellow channel that subtracts the S-cones from the combined output from L- and M-cones (Zeki, 1993) (see figure 3.8). The support for the opponent cells comes from afterimages: if one looks at a particular color for a while, an achromatic region will take on the color opposite to the original color (Gegenfurtner and Sharpe, 2001).

3.5.2 Cortical areas concerned with color

From LGN a majority of the fibers travels to V1 in the occipital lobe of the brain. V1 is divided into different layers, each concerned with another primary aspect of vision. The cells in this primary cortical area are organized in columns and hypercolumns. Within such hypercolumns so-called blobs and interblobs are distinguished that are respectively concerned with color and form. The output from the parvocellular layers of LGN is relayed to layers 2 and 3 of V1, where it feeds the

![The opponent color channels in LGN. Source: www.handprint.com](https://www.handprint.com/3.8.jpg)
blob cells and the interblob cells. Thus, the P-pathway is responsible for both form and color. The information from the magnocellular layers of LGN on the other hand is passed on the layer 4B of V1 and serves as input for the orientation and direction-selective cells layer of 4B that is concerned with motion. From V1 all signals are passed on to higher brain areas such as V2, V3, V4 and MT (V5) (Wolfe et al., 2009; Zeki, 1993).

To summarize the pathways of visual perception (see fig. 3.9): (1) The P-Pathway has its origin in the midget bipolar cells and the P-ganglion cells in the fovea. From the P layers of the LGN, these signals are relayed to layers V1 where they feed the blobs (color) and the interblobs (form); these subdivisions eventually relay to area V4 and inferotemporal areas through the thin stripes and interstripes of V2. (2) The M-Pathways has its origin in the diffuse bipolar cells and the M-ganglion cells in the periphery of the retina that project to the magnocellular layers of LGN. From layer 4 in V1 signals are transmitted to V3 and MT via the thick stripes in V2 (Wolfe et al., 2009; Zeki).
Studies on patients with lesions in LGN show that the magnocellular pathway responds to large, fast-moving objects, and the parvocellular pathway responds to details of stationary targets. More generally, it is said that the P-pathway is concerned with form and color while the M-pathway codes for motion (Shevell 2003).

### 3.5.3 Complex effect: Color constancy

Now that the path of visual perception has been explained, there remains one question: where is color generated? Since color perception and experience involves much more than the determination of the spectral composition of a light, color cannot be generated by low-level mechanisms of the pathway of color vision. Evidence that perception of color is not a straight-forward process, but a higher cognitive phenomenon involving knowledge about the world comes from the phenomenon of color constancy.

The same object illuminated by two different lights will generate two different patterns of activity in the cones. However, under certain circumstance, a shift in the perceived color may arise such that the object will be perceived as to have the same color under both illuminants. This phenomenon is known as color constancy (Zeki 1993; Lin and Sun 2008). To achieve color constancy, an object’s spectral reflectance is the constant color parameter that needs to be evaluated and the light source should be disregarded since it is a variable. A lot of variables are required to characterize both the surface reflectance function and the spectral power distribution of the illuminant. Any information that better describes these two parameters is a cue to color constancy (Gegenfurtner and Sharpe 2001).

The phenomenon of color constancy may arise due to low-level analysis in the retina such as the determination of local color contrast. Moreover, the depressions in the sensitivity of the photoreceptors, called color adaptation, seem to play an important role in color constancy: when the eye is exposed to, for example, green light, the M-cone will be temporarily depressed in sensitivity, causing subsequent lights to look less green. This effect is stronger when the first light is of higher intensity and can cause a subsequent yellow light to look orange (because the L-cone has a stronger response than the M-cone this case). In general, then, when the eye is exposed to light for a long time, the sensitivity of all cones is changed due to the energy distribution of the source. Since a higher intensity causes a greater deficiency, the spectral sensitivity of the eye is opposite to the
energy distribution of the source and causes an object with a flat reflectance curve to look white. This goes for all objects: every object will have approximately the same appearance as it would have had under standard illumination \cite{Evans1948}. This effect of color constancy is not complete however, in the sense that for sources with an energy distribution very different from average daylight or for objects with a sharp distribution, changes in colors may be observed:

Imagine a surface with a very sharp energy distribution in the yellow, illuminated by a source which is one-fifth as strong in the blue, one-third in the green as compared to the red. The eye is therefore five times as sensitive to blue, three times as sensitive to green as it is to red, compared to the situation in average daylight. The spectral content of the reflected light from the surface is changed only slightly, because the distribution of the surface is sharp. But with the adapted receptors, the output of the M-cone will be three times as high as the output of the L-cone causing the surface to look green-yellow instead of the yellow in normal daylight \cite{Evans1948}.

However, color constancy can not be fully explained by low-level processes, as higher-order processes in the brain are also of importance. An analysis that extracts the average chromaticity from the scene as a way to estimate the illuminant requires spatial integration that does not occur in the retina or LGN \cite{Gegenfurtner2001}. Therefore, higher-order processes, such as feedback and learning, are necessary for achieving color constancy. One V1 mechanism postulated to contribute to color constancy is a neuron with a double opponent receptive field \cite{Gegenfurtner2001}. Moreover, Zeki has suggested that the cortical area V4 has an important role in color constancy \cite{Zeki1993}. Some other cues to color constancy are global contrast and mutual reflections \cite{Wolfe2009}. Research suggests that when perceiving objects, people rely also heavily on form information and space information to achieve color constancy, as opposed to using only information about spectral reflectance or illumination chromaticity \cite{Lin2008}.

Color constancy has a more profound effect on every day vision than most people realize \cite{Evans1948}. But not only the colors (or hue) of objects seem constant under different illuminations, also brightness constancy occurs. In contrast, an effect called brightness enhancement is shown to exist for flickering lights. Flickering lights appear brighter than steady lights of equal luminance \cite{Evans1948,Wu1996}. Experiments concerning brightness enhancement have only detected enhancement at light intensities higher than 1 log phot. Td. \cite{Wu1996,VanDerHorst2003}.
Chapter 4

Research article

4.1 Introduction

4.1.1 Anatomy

Early anatomical studies showed that bipolar cells receive segregated rod and cone synaptic input. This traditional view has long been challenged (Panga et al., 2010). It has been known for decades that the pathways for rods and cones are not strictly separated. The rod pathway appears to be superimposed on the already existing cone pathways that allow multiple ways for signal transmission (Sharpe and Stockman, 1999).

The primary rod pathway connects rods to ON bipolar cells and AII amacrine cells. The latter connect to both midget and diffuse bipolar cells, hereby providing input to the P- and the M-pathway. These AII cells have the same response threshold, saturation levels and spectral sensitivity as rods and are therefore called 'rod amacrine cells' (Sharpe and Stockman, 1999). The signals from these cells are transmitted via two routes: either via the main cone pathway by synapsing on ON cone bipolar cells through gap junctions that are responsible for the electrical synaptic transmission between neurons (Bloomfield and Dacheux, 2001) or via OFF cone bipolar cells by conventional synapses (Stockman et al., 1995) or Sharpe and Stockman, 1999). This pathway is sensitive, slow and active mainly at low scotopic intensities (Stockman et al., 1995). The secondary rod pathway connects to the cone pathway at an earlier stage through a rod-cone gap junction. One rod spherule can have up to five gap junctions that link to L- or M-cones. Through these junctions, rod signals have direct access to ON and OFF cone bipolar cells and ganglion cells (Stockman et al., 1995) or Sharpe and Stockman, 1999). As light level increases to mesopic level, this fast and insensitive pathway becomes active (Sharpe and Stockman, 1999).

Evidence for the two rod pathways in the retina comes from (1) psychophysical, (2) electrophysiological and (3) anatomical and biochemical
Firstly, the flicker that could be perceived with rod vision, the scotopic critical flicker fusion frequency, grows in two stages as the intensity of the flicker is increased. It is suggested that this is the case because of two rod signals, each with a different speed of transmission. The signals are recombined before being transmitted to later stages of the visual pathway (Stockman et al., 1995). The flicker fusion curve supports a duality in the rod system since, as the intensity of the flickering target with a frequency of 15 Hz is increased, the flicker becomes visible at the so-called contrast threshold, but then disappears before reappearing again at higher intensities. This effect is even visible in achromats, observers who lack cones altogether (Stockman et al., 1995). It appears steady until the flicker threshold is exceeded. At 15 Hz the flicker disappears at an intensity above the flicker threshold and reappears at higher intensities. The region of invisible flicker lies below the cone flicker threshold, so it can be concluded that this phenomenon must be a property of rod vision (Stockman et al., 1995; Stockman and Sharpe, 2006). This disappearance might be explained by interference between the fast and the slow rod signal. Since the slow signal is delayed by 33.3 ms, the use of a flicker of 15 Hz produces a phase delay of 180 degrees resulting in cancelation of the flicker (Stockman et al., 1995; Sharpe and Stockman, 1999). Since the phase delay is only exactly 180 degrees at 15 Hz, self-cancelation is maximal at this frequency (Stockman et al., 1995). (see fig. 4.1) Self-cancelation of flicker can also be observed with electrophysiological research by means of electro-retinogram (ERG) where both the slow and the fast signals can be recorded (Stockman et al., 1995). When a 15 Hz flicker is used, there is an abrupt minimum in the signal around 0.2 log scot. Td, although this value differs for various studies (Stockman et al., 1995). Below this flicker threshold, it is assumed that the slow and sensitive rod signals dominate, while the fast signals dominate above the threshold (Stockman et al., 1995). The coincidence of the minimum in the ERG with

Figure 4.1: Self-cancelation of rod signals in humans using 15 Hz flicker. Source: (Sharpe and Stockman, 1999)
the perceptual invisible flicker is important because it suggests that the electrical cancelation measured electro-physiologically and the neural cancelation measured perceptually are manifestations of the same phenomenon \( \text{(Stockman and Sharpe, 2006)} \). Lastly, anatomical and biochemical studies have been executed on other mammals. Research on mice, for example, has shown, firstly that the rod bipolar cells receive input from cones and, secondly, that a subpopulation of the cone bipolar cells receives input from rods \( \text{(Panga et al., 2010)} \). Pharmacological experiments indicate that fast scotopic signals carried by the cone bipolar cells do not pass across the gap junction to AII amacrine cells but bypass them completely \( \text{(Bloomfield and Dacheux, 2001)} \). Experiments on mammals with similar retinal organization indicate a division between the rod pathways concerning innervations of different ganglion cell types and the signals they send to the brain \( \text{(Bloomfield and Dacheux, 2001)} \).

Thus, the existence of two different rod pathways is very plausible on the basis of psychophysical and electro-physiological studies on humans and anatomical and biochemical research on other mammals. Evidence for a third pathway for signal transmission in scotopic lighting in mammals is sparse \( \text{(Sharpe and Stockman, 1999)} \).

### 4.1.2 Perception

Although the presumed dichotomy between rods and cones in terms of anatomy and pathways in the retina has been rejected about a decade ago \( \text{(Stockman et al., 1995)} \), the dichotomy as regards the function of rods and cones still exists today. The understanding about color vision that the cones facilitate color vision during photopic lighting and the rods mediate vision in scotopic luminance is, however, being reconsidered. Because of the presumed dichotomy between rods and cones, people with normal vision are not at all supposed to be capable of perceiving colors in the dark. Yet, recent research has suggested the contrary, namely that people are able to discriminate colors under dim illumination \( \text{(Pokorny et al., 2006, 2008)} \).

As light intensity decreases, perception does not abruptly change, but the human visual system adapts gradually to the transition between daylight and twilight \( \text{(Pokorny et al., 2006)} \). In this middle range of mesopic vision, both rods and cones are active. Color appearance in mesopic vision differs from that in photopic vision and is not easily estimated only from knowledge of photopic and scotopic vision. To predict a color appearance in mesopic vision, it is necessary to determine the interactions between cone and rod signals at the levels of mesopic vision \( \text{(Shin et al., 2004)} \). It is known that
rods influence color perception. The most convincing evidence for this is the Purkinje shift (Wolfe et al., 2009): as rods become dominant in scotopic vision, the peak of visual sensitivity shifts towards shorter wavelengths due to the spectral sensitivity of the rods. As a result, objects reflecting mid and short wavelengths light appear relatively brighter than objects that reflect long wavelength light (Pokorny et al., 2006). When light intensity decreases and rods become the dominant photoreceptor type, temporal response slows down and temporal integration increases (Zele et al., 2008). Moreover, rod activation alters all three attributes of color perception (hue, saturation and brightness) and enhances brightness and decreases saturation of spectral lights (Cao et al., 2005). Since signals originating from rods or cones are transmitted in shared pathways, it is not surprising that rod-cone interactions can alter color perception (Cao et al., 2005).

Evidence that rods alone can mediate the perception of color, and that even in the absence of cone contributions various color percepts can be observed (Pokorny et al., 2006), is less abundant. (Pokorny et al., 2006, 2008) concluded that there were salient and diverse color percepts mediated by the rods at light intensities between −2.5 and −3.5 log Lux. At these light levels, color-normal observers consistently reported color names. These percepts were based on relative sample scotopic lightness and therefore the authors suggested that colors seen under conditions where rods exclusively mediate vision are relational (Pokorny et al., 2008).

Overcoming the problem of univariance, ‘scotopic color vision’ according to Cao et al., arises because rod stimulation mimics activation of the M-cones, thereby maintaining some distinction between long and short wavelength color appearance (Cao et al., 2005). According to Pokorny, scotopic color vision can be explained by experience in photopic color vision: given the experience with viewing familiar objects in the natural environment under dim illumination, it can be inferred that bright appearing objects are richer in short wavelength light compared to dim appearing objects. Pokorny speculates that in scotopic vision with input solely from rods, the visual system estimates probable colors based on natural visual experience (Pokorny et al., 2006). Some evidence for this hypothesis comes from a study with color defective observers (Pokorny et al., 2008). The color categories of these observers at scotopic luminance levels do not reveal an association of scotopic brightness and spectral composition. This can be explained by the fact that dichromats have a reduced color gamut at photopic light levels, which may contribute to their limited association of rod color perception with the spectral composition of objects differing in sco-
topic reflectance (Pokorny et al., 2008).

4.1.3 Thresholds

Determining the exact transition between scotopic and mesopic vision, i.e. determining the thresholds for rod and cone activity in the human visual system, is very difficult. Several thresholds have been defined that are not in agreement with each other. This is due to the fact that different kinds of stimuli can have a different effect on an observer, especially in the range of mesopic vision (Stockman and Sharpe, 2006). We can therefore only compare thresholds found using the same kind of stimuli.

In a study conducted by Sharpe and Stockman in 2006, measurements of a cone threshold using flicker stimuli with a flicker frequency of 15 Hz yielded a result of $0.8 \pm 0.1 \text{ log } \text{scot. Td.}$ using a 500 nm stimulus with a visual angle of 6 degrees. This is approximately $0.17 \pm 0.1 \text{ log phot. Td.}$ (Stockman and Sharpe, 2006).

Another study by Bijveld et al. on color perception under dim illuminance of large stimuli using both behavioral and electrophysiological methods also reports a threshold, namely $12.5 \text{ log quanta-deg}^{-2}$ (Bijveld et al., 2010). This unit does not correct for spectral sensitivity. We can express the intensity in phot. Td. for different colors using $T = N \cdot c_{ph} \frac{V(\lambda)}{X}$, where $T$ is the intensity in phot. Td., $c_{ph}$ is a constant with a value of $4.454 \cdot 10^{-13}$ and $N$ is the intensity in quanta-deg$^{-2}$.

The aim of the present study is to go further into the findings of (Stockman and Sharpe, 2006) and make a first guess at the threshold for color vision, in order to determine the lowest light intensity at which humans are able to perceive colors. Furthermore, after the threshold has been set, we infer, based on previous research on the cone threshold and our own experiment, which types of photoreceptors were most likely to be active at the threshold, in order to eventually be able to conclude whether or not color vision is possible with rods as the only active photoreceptors. Based on (Stockman and Sharpe, 2006) we expect that it is possible to perceive colors at light intensities between 11 and 12.5 log quanta-deg$^{-2}$ or perhaps even at lower intensity levels.

4.2 Methods

4.2.1 Subjects

Fourteen subjects, twelve females and two males took part in the study. All of them were between the age of 20 and 27. All had normal color vision as assessed by the Farnsworth’s dichotomus test 15D type and the Ishahara Test for Color Blindness (38 plates edition). The subjects were naïve about the subject of the study, participated voluntarily and did not re-
4.2.2 Stimuli

The stimuli consisted of 15 Hz lights with a particular color and a particular intensity. Five different colors were used: red, amber, blue, green and white. Light intensity was classified in nine levels ranging from $1.58 \cdot 10^{10}$ quanta·deg$^{-2}$ to $1.51 \cdot 10^{12}$ quanta·deg$^{-2}$. Each stimulus with one of five possible spectral compositions and one of nine intensity levels was presented three times. Duration of presentation was 5 seconds and the stimuli covered the entire visual field. Since the software of the sphere automatically corrected for the V-lambda curve, the input for each stimulus was converted so that the number of photons reaching the eye was equal for each color for a particular intensity level. To be able to give the subject stimuli of very low light intensities, glasses were used that only let through 1% of all light. In total there were five colors, nine intensity levels, and each combination of color and intensity level was presented three times. The actual experiment thus consisted of 135 stimuli which were presented in random order. For a detailed description of the stimuli, see Appendix A.

4.2.3 Apparatus

The study was executed in Bartiméus Institute for the Visually Impaired at Zeist. Stimuli were presented in a sphere: a Ganzfeld stimulator (whole field stimulator) of the type Standalone Colordome system (Diagnosys LLC). The room was completely dark and the sphere had no background illumination. The program Espion versie 5 (Diagnosys LLC) was used to control the sphere.

4.2.4 Procedure

The subjects were seated in front of the sphere. The curtains were closed and 20 minutes of dark-adaptation followed during which the experimenter explained the subject about the procedure of the experiment. 15 test stimuli were included for the subjects to get used to the range of colors and intensities. Each of the five colors was presented with a low, average and high intensity level. The test stimuli were presented in random order. Subjects were asked to respond to each stimulus by naming which color they perceived. For their response, they could choose from a number of colors: black, gray, white, red, blue, green and orange. A response could consist of a combination of a main color and a sub-color, for example blue-gray, or merely a main color. After completion of the test phase, the actual experiment consisting of 135 stimuli began. After presentation of
a stimulus, the subjects gave a verbal response and the experimenter wrote the response down on a personal form and entered the response in Open Office Calc. 3.2.0. After the experiment, subjects performed two tests to assess color vision: the Farnsworth’s dichotomus test and the Ishahara Test for Color Blindness. The results were written down on the personal form that the subjects were asked to sign. Lastly, they were offered a piece of pie as a reward for their partaking in the study. In total 150 stimuli were presented, each with a duration of 5 seconds. One trial consisting of presentation of the stimulus and a response took about 15 seconds. The whole study, including 20 minutes of dark-adaptation, explanation and the tests for color vision, took about 1 hour per subject.

4.2.5 Data-analysis

Wolfram Mathematica 7.0 and Open Office Calc. 3.2.0 were used to compute the light intensity levels, to generate random lists for the stimuli, to analyze the data and to create all the graphics. First, the responses of all subjects for one color were plotted in a chart; secondly, the data from each color was fit onto a standard psychometric function; and lastly, the above-change threshold for the perception of color was determined for each color. To be able to determine a threshold, it was necessary to decide which responses from subjects are ‘correct’ and which are incorrect. It is obvious that responses that do not contain the color of the given stimulus are incorrect, such as ”Red-Gray” for a green stimulus. In our view, responses like ”Blue-Gray” suggest that a subject recognized the stimulus as blue, but wanted to include the overall brightness of the stimulus in the addition of a colorless subcolor. If a subject would not have had the opportunity to assign a subcolor, he would have given the response ”Blue”. This can of course be disputed, but seems reasonable in this phase of the research. We will therefore define ‘correct’ to be those responses which match the color of the given stimulus, with the possibility that a colorless subtag was given. All other responses are incorrect. With this sense of correctness, a performance analysis could be made. Since each unique combination of intensity and color was represented three times to each subject, three answers per subject were collected for every intensity-color tuple. Those three answers are a dependent set, because they stem from the same subject. However, the set consisting of the averages of such a set is independent, because the averages come from different subjects. This set contains thus 14 data points per intensity.
Figure 4.2: Overview of the data. The color tags consist of combinations of Blue (B), Green (Gr), Orange (O), Red (R), White (W), Gray (G) and Black (Bl). The darkness of a square indicates how many times a particular color tag was given at a given intensity (see legend) on a continuous scale.
The averages of those sets reflect the average performance of the subjects for different intensities, with a certain internal uncertainty at each intensity level. Now we can fit psychometric curves to the average performance as a function of intensity, given by

\[ f(x) = \frac{1}{2} \left( \text{erf} \left( \frac{x - \alpha}{\sqrt{2} \beta} \right) + 1 \right), \quad (4.1) \]

where Erf is the Errorfunction, \( x \) is the intensity and \( \alpha \) and \( \beta \) are parameters. Using these psychometric curves, we determined the intensity thresholds for color vision, setting a success rate of 75 percent to see color.

4.3 Results

4.3.1 General

The data from this experiment is summarized in figure 4.2. As one would intuitively expect, at high intensities subjects were able to assign a color tag to a stimulus that one would call 'correct', such as "Green", for a green stimulus, or "Blue" for a blue stimulus. On the other hand, at low intensities, most subjects assigned a colorless tag to the given stimulus, such as "Gray", or "Black-Gray". This suggests that the intensity range from 10.2 to 11.96 quanta-deg\(^{-2}\) for the blue and green stimuli and 10.42 to 12.18 quanta-deg\(^{-2}\) for the orange and red stimuli contained all the stages of discrimination, from no discrimination until certain discrimination. This also suggests that the threshold for color vision lies in this range. It can also be seen in figure 4.2 that at medium intensity levels, subjects more often made mistakes than at the lowest and highest intensities. Specifically, these mistakes can be categorized: orange stimuli were most often mistaken to be red stimuli and vice versa. Green stimuli were most often mistaken to be blue. Blue stimuli were almost never mistaken to be a different color, but the subcolor given to most blue stimuli was green.

4.3.2 Psychometric curves

In figure 4.3 psychometric fits to this data are presented for each color, using the formula for the psychometric function in (4.1). The fits for the blue, orange and red stimuli show little noise. The green fit does not seem to be as close as those three, suggesting a lot of noise exists in the data, which is consistent with the overview of the data in figure 4.2. This is in accordance with our experimental experiences: one subject (subject 12) did not recognize the green stimulus as a green one, but consistently judged it to be blue. Another subject (subject 3) judged the green stimulus to be blue-green, also consistently. Although reasons for these apparent anomalies can be given, we will continue to analyze the data including the results from those subjects.
4.3.3 The psychometric curves in other units

In figure 4.4, the psychometric curves are plotted as a function of intensity in the units quanta·deg$^{-2}$, log photopic Troland and log scotopic Troland (abbreviated respectively as log phot. Td. and log scot. Td.). One sees that the curves are further apart when a correction for the spectral sensitivity of the rods is applied than with a correction for the cone spectral sensitivity.

The threshold for color vision, expressed in log phot. Td., is $-2.12 \pm 0.04$ log phot. Td. for blue, $-0.69 \pm 0.07$ log phot. Td. for green, $-1.35 \pm 0.05$ log phot. Td. for orange and $-1.59 \pm 0.06$ log phot. Td. for red.
Figure 4.4: The psychometric curves in different units
4.4 Discussion

The most important results from this experiment are as follows: the threshold for color vision seems to vary for different colors, between $-0.62$ and $-2.16$ log phot. Td.; The results also indicate that color perception at the intensities used in this experimental set-up is primarily mediated by cones, rather than rods. This is seen from figure 4.4: one would expect that when a correction for the spectral sensitivity of the dominant photoreceptor is applied, the curves would coincide. It is shown in figure 4.4 that the curves that are corrected for the cone spectral sensitivity (expressed in log phot. Td.) are much closer together than those that are corrected for the rod spectral sensitivity (expressed in log scot. Td.) and thus suggest that the perception of color at threshold level seems to be dominated by cones.

4.4.1 Threshold for color vision

Our finding that humans are able to distinguish colors at intensities below $-1.5$ log phot. Td. is in accordance with the results of Pokorny (Pokorny et al. 2006). In addition, our results also corroborate the findings of Pokorny that colors at very dim illumination levels can be ordered in a blue-green- and a red-orange group; mistakes between red and orange and between blue and green were significantly more frequent than confusions between for example orange and blue. Our findings corroborate the conclusion of Bijveld et al., namely that it is possible to perceive colors at intensities below $12.5$ log quanta-deg$^{-2}$ (Bijveld et al. 2010).

4.4.2 Mesopic or scotopic color vision

The mesopic region is defined as the intensity region where both rods and cones are active and spans thus from the intensity range beyond cone threshold for which rods are not yet fully saturated. There is no consensus yet on which type of photoreceptor is active at the light intensity of our threshold.

On the one hand, there is some support the claim that only rods were active at threshold level: Pokorny states that at the lowest illumination levels used in his studies (of $-3.5$ until $-2.5$ log lux or equivalently for fully darkness-adapted eyes with pupil diameter of 6.5 mm approximately $-1.7$ until $-0.7$ log phot td) only rods mediate vision (Pokorny et al. 2006). Furthermore, Sharpe and Stockman reported a cone threshold of $0.17 \pm 0.1$ log phot. Td., which is well above our threshold for a comparable stimulus (Stockman and Sharpe 2006). Indeed, the difference between our threshold for a green stimulus with an average wavelength of approximately 517 nm of $-0.69 \pm 0.07$ log phot. Td. and the one found by Sharpe and Stockman is $0.86 \pm 0.2$ log phot. Td. (Stockman and Sharpe 2006). Thus, according to Sharpe and
Stockman at our threshold level only the rod system was active.

On the other hand, there is some support for the claim that both rods and cones were active at threshold level. Our analysis of the data suggests that cones are possibly the dominant photoreceptor at light intensities higher than $-2 \log \text{phot td}$ (although this has been argued on the basis of the V-lambda curve, which might not correctly reflect the spectral sensitivity of the receptors in our experiment, due to the large stimuli). Moreover, there is current research on the absolute cone threshold that states that cones are active above approximately 203 photons at the cornea (Koenig and Hofer, 2011) which is far below our threshold. This threshold however holds merely for the fovea and not the periphery.

To sum up, based on our data and the literature, there is no decisive answer whether or not cones were active at the intensity of the threshold, i.e. if our threshold was within the range of mesopic or scotopic vision.

If we assume that only the rod system was active, there are two explanations for the possibility of scotopic color vision: the low-level explanation of the secondary rod pathway, and the higher cognitive learning effect.

Firstly, it is plausible that the secondary rod pathway, which is faster and less sensitive than the primary rod pathway, was mainly active during the course of the experiment. This pathway includes rod-cone gap junctions, so that rod signals are transmitted via cone-related cells from early on in the pathway. It can be suggested that the fact that rod signals are transmitted through the cone pathway can elicit the perception of color. Once converged onto bipolar cells, it can not be traced whether the signal originated from rods or cones. Thus, the output of the cone pathway does not give any information about the photoreceptors that have elicited a response. The signals can therefore be interpreted by the brain as originating from cones and give rise to the perception of a color. How in this case the problem of univariance has to be addressed is unknown, since the present paradigm states that all the rods connected to a secondary rod pathway have the same output: if every kind of cone has the same amount of rods connected to their pathway, the summed output of the cone pathway should be the electrical signal of a colorless stimulus.

Secondly, it is also possible that cone activity is not the cause for the color perception of our subjects. Rather past experience has taught participants how certain colors look under dim illuminations in terms of intensity. This possible 'learning'-effect was already stipulated by Pokorny et al. as a possible explanation for
color vision under cone threshold (Pokorny et al., 2006). However, if the 'learning'-effect was indeed the main reason for the color vision below threshold, its presence is stronger than in the experiment conducted by Pokorny et al.: in our experiment, subjects made only a few mistakes between colors from the two groups that existed in Pokorny’s experiment, indicating that subjects were not alone able to distinguish colors with a primarily short or long wavelength spectrum, but also between colors from the same group.

If we on the other hand assume that both rods and cones were active, this would imply that the absolute cone threshold is lower than Sharpe and Stockman state (Stockman and Sharpe, 2006). This difference can be accounted for by the fact that they measured the threshold for flicker detection after short periods of dark-adaptation as a measure of cone threshold. It could however have been the case that the period of dark-adaptation was not long enough for the cones to desaturate, thereby determining the boundary between photopic and mesopic vision rather than the boundary between mesopic and scotopic vision. Also, assuming that our threshold lies within the range of mesopic vision and thus has to be extended to such low intensity levels, many difficulties may arise: the additivity of luminous efficiency is likely to fail at mesopic levels, since more than one photoreceptor is operative. The mesopic luminous efficiency also changes abruptly if rod saturation starts, which makes it very difficult to measure. Since rods and cones have a different spatial distribution, the spatial location and size of a stimulus can be a very important factor. The difference in temporal integration window of the rod and cone signals can also have a large impact on measurements of visual performance, because the temporal characteristics of the stimuli can influence the output (see fig. 4.5). Lastly, other complexities of mesopic vision include rod-cone interactions, rod saturation, different rod and cone retinal distributions and mixed photoreceptor spectral sensitivities (Stockman and Sharpe, 2006).

4.4.3 Points of consideration

During experimentation, it became apparent that asking a subject which color was shown led to problems: two subjects were consistent in their judgment of the green stimuli of respectively blue-green and blue, but also had perfect color vision as tested by the Farnsworth’s dichotomus test 15D type and the Ishahara Test for Color Blindness (38 plates edition). A possible explanation is that the boundaries of the
Figure 4.5: The convergence of signals from the photoreceptors. Source: (Stockman and Sharpe, 2006)

Linguistic categories are somewhat different for different subjects, leading to different judgments. It seems that in particular our green stimulus had a color that was close to such a boundary. In addition, due to the fact that also color tags could be given that did not directly correspond to a particular stimulus, a precise threshold determination could not be completed.

Moreover, measuring a threshold means determining the boundary between the perception of a colored or a colorless stimulus. This boundary may differ among different subjects. In our experiment, subjects were asked to describe their percepts. Therefore, the tag that is given to stimuli that lie in the range of the transition from colorless to colored, will depend partially on the subject, introducing a source of subjectivity. Thus it is well possible that the judging itself may differ between subjects. In addition, there is a possibility that different subjects actually see different percepts, due to a difference in their visual system (Evans, 1948).

Our study differs from the mentioned studies in some essential aspects: whereas most studies presented a small stimulus with a visual angle of maximum 10 degrees with a duration of less than 1 second, this study used a large stimulus, covering both visual fields, with a presentation duration of 5 seconds. Since a threshold measurement can be influenced by many variables, differences in measured threshold can partly be attributed to differences in methodology. Determining a cone threshold can be done in various ways, all of which are useful, but all share the problem of non-generalizability. Since the rod and cone system differ with regard to spatial summation and temporal integration properties, it is plausible that aspects such as cone saturation, rod desaturation and rod-cone interactions change significantly when the size and exposure time of the test stimuli varies (Stabell and Stabell, 1993). Lastly, the V-lambda curve may actually only be applied to stimuli with a size up to 10 degrees in visual angle (Shevell, 2003). For the spectral sensi-
tivity correction of larger stimuli, there is no special V-lambda curve.

### 4.4.4 Further research

The findings of this research have strengthened the results of Bijveld and Pokorny that color vision is possible below $-1.5 \log$ phot. Td. (Bijveld et al., 2010; Pokorny et al., 2006). The threshold determination using the psychometric fits can be improved, for example using a staircase measurement, a widely accepted method for determining thresholds (Wolfe et al., 2009). To prevent problems with linguistic categories, separate measurement series should be used for different colors, using only one color and gray for every series.

The study of Bijveld that measures color perception under dim illuminance of large stimuli using both behavioral and electrophysiological methods reports a threshold of 12.5 log quanta-deg$^{-2}$ (Bijveld et al., 2010). Our results suggest that there is cone activity well below this value, namely below 11.8 log quanta-deg$^{-2}$, corroborating their hypothesis that using ERG very small but significant signals from bipolar cells cannot be detected. Thus, it could well be that the critical mass of cones necessary for color vision is less than the critical mass of cones necessary for detection using ERG. Further investigation is necessary to determine the exact possibilities and limitations of ERG research. Although Pokorny’s study on color defective observers has provided some support for the hypothesis (Pokorny et al., 2008), more research should be done to investigate the validity of the 'learning'-effect that under dim illuminations, subjects estimate the color using the observed intensity and prior experience.

In addition, to be able to draw proper conclusions concerning the activity of photoreceptors, the absolute cone threshold for stimuli with a large visual angle should be determined.
Chapter 5

Interdisciplinary reflection

5.1 Conflicts

Our research points out that the threshold for color vision varies for different colors, between $-0.69 \pm 0.07$ and $-2.12 \pm 0.04 \log \text{phot. Td}$. Moreover, the possibility of the perception of color at this light intensity can be accounted for by different explanations. The anatomy of the eye, containing two rod pathways, can be important, due to the fact that the second rod pathway is connected to the pathways of cones. In addition, the spectral sensitivity of the human photoreceptors can be important, because a difference in sensitivity allows for differentiating between different colors. Moreover, the so-called learning effect that Pokorny suggested can be important, since higher-order processes can compensate for the lack of information from the cones. All these explanations contribute to the understanding of scotopic color vision, but none of these is in itself sufficient for accounting for this phenomenon.

The insights can be distinguished on the basis of their disciplinary character. The issue of spectral sensitivity and detectibility lie in the scope of physics, whereas the learning effect is a higher-cognitive process studied by psychology. The issue of the pathways in the retina does not fit into either two disciplines but actually belongs to biology. When one is studying perception, it is possible to distinguish three main parameters: the thing that is perceived, the signal that contains information about the perceived thing, and the perceiver, who receives this signal. The first step of perception, the traveling of a signal through a medium to a perceiver and the first interactions between the signal and the human receptors, is what one intuitively would ascribe to the realm of physics. The second step, the further processing of the signal in the brain, belongs to the
realm of psychology. The realm of biology starts from the first interactions of the signal with the human receptors, since part of the research subject of biology includes the human body and its interactions with the outside world. One could argue that the realm of biology usually stops where the processes become too complicated to study them using chemical methods, EEG or other measuring techniques. There they become the subject of psychology alone.

In practice, most researchers do not respect the above boundaries. When a subject is studied that lies very near such a boundary, knowledge from both adjacent disciplines is used to create a complete understanding of the studied phenomenon. An example of such a subject is the pathway of the signals from the receptors to the brain. This subject can be studied using ERG, dissection of a retina or flicker detection experiments. These methods typically belong to different disciplines.

One could thus say that in the process of perception, physics, biology and psychology are all relevant, respectively, for the characteristics of the light entering the eye, for the anatomy of the sense organ and the neural pathways transmitting signals to the brain, and lastly for the interpretation of neural signals. The respective disciplines overlap at various points: physics and biology both study the spectral sensitivity of the photoreceptors as well as other measurable aspects of the human eye. In addition, all three disciplines investigate the path followed by the signals from the photoreceptors to the brain. In this thesis, the biological gap in the process of perception can be filled with knowledge from both physics and psychology, because all the relevant knowledge is also used and researched in these two disciplines. Moreover, since scientific disciplines tend to extend their research field, new disciplines arise in the form of combinations of primary disciplines, such as biophysics, biochemistry and neurobiological psychology. We feel that the aspects of biology that are relevant for this thesis can be understood from the frameworks of biophysics and neurobiological psychology, which are part of our disciplines.

The concepts concerning color vision that are used in physics and psychology are for a large part the same. Although concepts like 'V-lambda curve' and 'spectral energy distribution' are mainly used in physics, their contents is not different when used in the context of psychology. This also holds for psychological concepts used in physics. Thus, although concepts are created in one discipline, after their content has been determined they are adopted by other disciplines. This has led to a rich and conflict-free terminology regarding color vision. One exception is 'color constancy'.
Although the content of this concept is the same in physics and psychology, the explanations related to it have a different emphasis: whereas physical 'color constancy' states that altering spectral sensitivity compensates for small changes in illumination, psychological 'color constancy' focuses on a higher-order cognitive process in which experience and learning are essential. Whenever necessary, we always use the phrase 'physical color constancy' when discussing spectral sensitivity and 'psychological color constancy' when discussing higher-order processes. Thus, regarding insights and terminology, physics and psychology are mostly complementary. Also, none of these disciplines alone is sufficient for explaining scotopic color vision.

5.2 Common ground

The common ground needs not to be created but can be discovered easily. Since the disciplinary insights are merely complementary and do not contradict each other in the area in which they overlap, our common ground theory results from the accumulation of all disciplinary insights, resulting in a theory of scotopic color vision. The area of overlap consists of the path followed by a signal entering the eye until it reaches the brain.

5.3 Desintegration

It has become clear to us that research on color constitutes a separate discipline where researchers from a wide range of disciplines cooperate. Although the emphasis of the researchers will differ depending on their academic background, they all investigate aspects of color vision using the same assumptions and terminology without worrying about the boundaries of their respective disciplines. The interdisciplinary character of color science is reflected in the literature: the important journals in this field, Vision research, Visual Neuroscience and Ophthal. Physiol. Opt. include contributions from physics, medial sciences and psychology. The quote on page 2 above, repeated here, describes the intimate relation between physics and psychology when it comes to color research: "Color is neither physics nor psychology; it is both. Physics cannot predict the appearance of a given energy distribution nor can psychology predict the color of a subtractive mixture. Both together should be able to do both; this and similar aims should be the goal of the science of color." (Evans, 1948).

We have, however, noticed our difference in academic background while working on this thesis. The division of labor was quite clear: while physicist Rob studied the V-lambda curve and did all the
calculations, psychologist Emma investigated the pathways of the retina and the higher cognitive processes. It was sometimes hard for us to understand the work of our partner since each lacked some knowledge of the other’s discipline. Therefore, close teamwork was essential, particularly at the early stages. It was very rewarding to see that towards the end, differences in knowledge began to disappear, due to the fact that we both felt the necessity to understand every relevant aspect. This meant that our partnership was no longer one between a psychologist and a physicist, but one between two color researchers. The fact that this transition was possible also corroborates that the field is highly interdisciplinary.
Chapter 6

Conclusion

This thesis is an investigation into the possibility of scotopic color vision. Our study has shown that it is possible to see colors at intensities as low as \(-2\) log phot. Td., depending on the color. Using the spectral sensitivity of the receptors, we were able to give counterevidence against the claim that, at these intensities, rods mediate vision. However, this evidence is not convincing enough to reject the possibility of rod color vision altogether, due to the possibility that using a learning effect, people are able to correctly 'guess' the color of an object using past experience. In addition, our research has given evidence that not all the cone activity is measured when ERG is used; it is possible that small cone populations are active in situations where an ERG shows no activity. Since determining the cone threshold is difficult and the boundary between scotopic and mesopic vision remains blurry, more research to further investigate the possibility of scotopic color vision is necessary.
Appendix A: Stimuli and apparatus

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Figure 6.1: The nine intensity levels used in the experiment with the intensity in quanta-deg$^{-2}$

Figure 6.2: Spectra of the lights used in the experiment
Figure 6.3: Characteristics of the filter used

Figure 6.4: The sphere. Source: www.diagnosysllc.com/products/product2.php.
Appendix B: Additional results

Figure 6.5: An overview of the data from the colorless stimuli.
Appendix C: Glossary

**Absolute cone threshold:** the light intensity at which the cones become active.

**Brightness:** The effect the amount of light has on an observer. In colorless beams, brightness is the only aspect of a beam that can change without changing from colorless to colored.

**Color constancy:** the effect that, in specific situations, if the same object is illuminated by two different light sources, it will be perceived as having the same color under both illuminants.

**Cones:** the photoreceptor type that are active at high luminance and mediate color vision. There are three different types of cones: S-system cones, M-system cones and L-system cones.

**Dark-adaption:** a period of darkness in which the rods desaturate. After a period of approximately 20 minutes, a person’s rods are completely desaturated and at their maximum sensitivity.

**Detectability:** A property of a stimulus; a stimulus is detectable if an observer is able to see the stimulus.

**ERG:** Electroretinogram, a technique to determine the activity of photoreceptors by measuring electrical signals at the cornea.

**Fovea:** the center of the retina with a very high acuity, containing small receptive fields and only cones, no rods.

**Illuminance:** The total luminous flux on a particular area. It measures the intensity of incident light per time unit. Usually illuminance is expressed in lux (or log lux).

**Log lux:** the unit of illuminance. It is derived from the SI unit cd · sr · m⁻², where sr is star radians.

**Log quanta-deg⁻²:** A unit that measures intensity. It expresses the photon flux through an angle of 1 star radian.

**Luminance:** The intensity of a given light beam in a given direction per unit area. It is measured
in \text{cd}\cdot\text{m}^{-2}. If the spectral energy distribution \(E(\lambda)\) of the beam is known, one can calculate the intensity of the beam using \(L = \int E(\lambda)V(\lambda)d\lambda\), where \(V(\lambda)\) is the photopic \(V\)-lambda curve (if the intensity is in the range of photopic vision) or by using \(L' = \int E(\lambda)V'(\lambda)d\lambda\), where \(V'(\lambda)\) is the scotopic \(V\)-lambda curve.

**Mesopic vision:** the range of light intensities in which both rods and cones are active.

**Metamers:** different mixtures of wavelengths that elicit the same combination of responses in the photoreceptors.

**Periphery:** the edges of the retina that contain larger receptive fields and both rods and cones.

**Photon flux:** The amount of photons through a particular area per unit time (usually measured in star radians per second or \(\text{m}^{-2}\text{s}^{-1}\)).

**Photopic vision:** the range of light intensities in which only cones are active.

**Photopic troland:** a unit of intensity that corrects for the spectral sensitivity of the cones using the photopic \(V\)-lambda curve and takes into account the area of the pupil. The formula for the intensity of a light beam in scotopic troland is \(I = L'_\lambda \cdot p\), where \(L'_\lambda\) is the intensity in \text{cd}\cdot\text{m}^{-2} and \(p\) is the area of the pupil in \text{mm}^2. This unit is sometimes abbreviated as phot. Td..

**Retina:** the light-sensitive neural tissue at the posterior part of the eye where light energy is converted into neural signals.

**Rods:** the photoreceptor type active at low light intensities.

**Rod saturation:** the process that the rods become saturated when light intensity increases.

**Scotopic vision:** the range of light intensities in which only rods are active.

**Scotopic color vision:** the effect that color perception is possible at light intensities where only rods are active.

**Scotopic troland:** a unit of intensity that corrects for the spectral sensitivity of the rods using
the scotopic V-lambda curve and takes into account the area of the pupil. The formula for the intensity of a light beam in photopic troland is \( I = L'_{\lambda} \cdot p \), where \( L'_{\lambda} \) is the intensity in \( \text{cd} \cdot \text{m}^{-2} \) and \( p \) is the area of the pupil in \( \text{mm}^2 \). This unit is sometimes abbreviated as scot. Td..

**Self-cancelation of flicker:** the effect due to the 33.3 ms delay of the slow rod signal, that when using a 15 Hz flicker, a phase delay of 180 degrees will result in interference of the slow and fast rod signal, so that the flicker will be cancelled.

**Spatial summation:** the summation of neural signals over a spatial window.

**Spectral energy distribution:** A table, graph or function that expresses the intensity of the beam at every wavelength.

**Spectral sensitivity:** the phenomenon that the human photoreceptors detect light with different wavelengths with different efficiency. The spectral sensitivity of the rods and cones is different; both are expressed using a function, the so-called V-lambda (for the cone sensitivity) and V'-lambda curve (for the rod sensitivity). These curves are averages from a large amount of subjects. The actual spectral sensitivity of a particular observer may be very different from the standard observer’s spectral sensitivity, not only when an observer is color blind.

**Temporal integration:** the summation of neural signals over a temporal window.

**Univariance:** the effect that an infinite set of different wavelengths-intensity combinations can elicit exactly the same response, so that the output of a single photoreceptor cannot by itself give information about the wavelengths stimulating it.

**V-lambda curve (and V'-lambda curve):** Functions that express the spectral sensitivity of the human photoreceptors. The V-lambda curve expresses the sensitivity of the cones and the V'-lambda curve the sensitivity of the rods. These functions are decreed by the CIE and are derived from experimentations. The actual spectral sensitivity of a particular observer may be very different from the spectral sensitivity of the standard observer, not only when an observer is color blind.
Bibliography


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