The Physiology of Human Color Vision

Jiayang Song 1005781708

Abstract— **In this report, the basic physiology of human color appearance is discussed. Main goals can be separated to two sections. One is the structures, and functionalities inside the human eyes, and the second is the concepts of visual signal processing. Since the neural network is extremely complex at the stages behind the retina in brain fields. Thus, the majority concepts of this report are focusing on the visual signal reception and initial signal processing in the retina.**

I. INTRODUCTION

In human eyes, the entire world can be arranged by a seemingly unlimited types of hues, from the virility of the wild forest to the violet of the grand sky, from the silver of a star to the wonderful color mixture of the aurora. It is remarkable that for any color detected by our eyes can be reassembled by mixing three different wavelengths of light with specific intensities. It is fascinating that when different fixate on the same landscape, they may have different senses on the images they caught. This phenomenon is caused by variety elements in human visual system, thus, although most people have identical structures on their color to reception system, some weeny differences on human tissues may affect their perception to this world.

This project is working on understanding of the physiology that how the light is absorbed and projected on human retina and how the light incidents are transported to chemical and electrical signals. Some amazing phenomenon is discussed as well, like the lined spot, filling in phenomenon and Purkinje shift. This report is set to two bases, the first part is concentrating on the process, starting from the light absorbed by the cornea, then, end at the optic nerve activity in the retina. The structure of human eyes is illustrated in detail including the cornea, the lens, the humors, the iris, the retina, the fovea, the macula and the optic nerve. The second part is focusing on the virtual signal processing that happened in the stages above and the areas in the brain. Two well-known theories about mechanisms of color vision are discussed which are Trichromatic theory, and Herring's opponent color theory. These two theories are combined to establish a complete model to explain the complete color reception and processing system.

II. OPTICS OF THE EYE

Light is composed of a mixture of colors, so, it is just electromagnetic waves, with wavelengths ranging from 400-700 nm for a visible range. When the light arrives at a surface, wavelengths will not change upon reflection. For all valuable wavelength, some portions are reflected, and the rest is absorbed by the objects. At this point, we only concern about the light absorbed by the human eye.

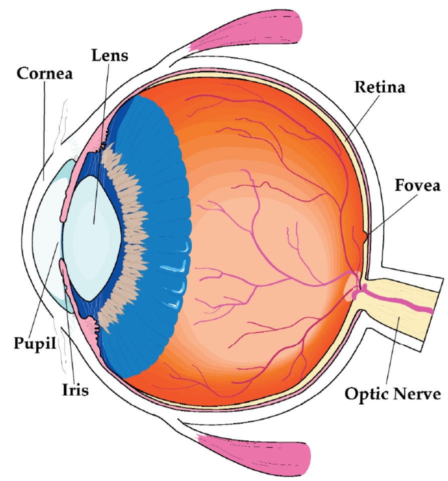

Fig. 1. Diagram of a human eye

The color perception of humans is mainly dominated by the complex structure and the incorporation of the components in the eye. Figure 1 illustrates a fundamental structure of the eye and the essential components are marked. A camera is a typical bionics example which simulates the activities inside a human eye. Thus, we can think about it reversely to consider the eye more intuitionistic. The cornea and lens are taking the role of a lens in a camera which passes the light and projects the image on the backside. The retina is like an image sensor of a camera which does the image detection job and signal processing in initial stage. Each component in the eye has distinct effect on the perception of color, but the combination of these elements performs a complete and precise system to explore the colorful world.

A. The Cornea

The cornea is a transparent layer in the first stage of the visual system which will absorb the incoming lights from the outer world. From figure 1 above we can find there are serval components covered by the cornea such as the Pupil, the Iris and the lens. It is obvious that the cornea has a curved shape which has the largest change in the index of the refraction. Thus, the cornea contributes the majority of optics power to human eyes. The cornea itself is avascular that no blood vessels found on the cornea, so, it gets the necessary nutrients and oxygen from the surrounding blood vessels and aqueous humour. If the inappropriate shaping happens on the cornea, the refractive errors will occur which can lead to nearsightedness, farsightedness or astigmatism.

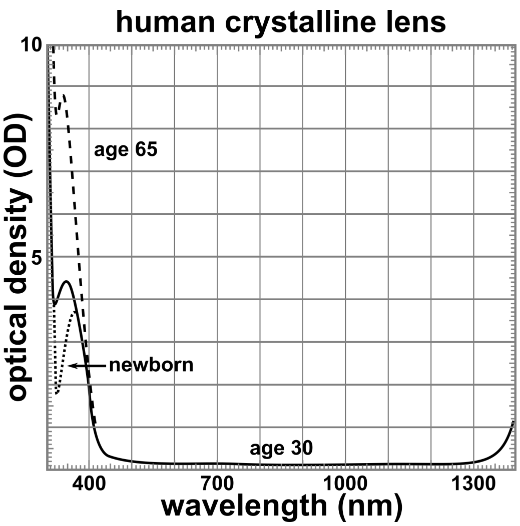

Fig. 2. Optical density of the human crystalline lens for different ages

B. The Lens

The lens is a transparent, biconvex entity behind the cornea, aims to refract the passing light and project on the retina. The functionality of the lens is accommodation, by changing the shape, it can adjust the focal distance to fixate the objects at various distances. The accommodation is similar to a photographic camera while moving its lens to get a clear vision for objects in different distances. In the center of the lens, due to the high refraction index, it can refract more light the the surrounding areas. This observation helps to attenuate some noisy lights that may be caught by a normal optic device.

The ciliary muscles are in charged to control the shape of the lens, which gives the lens the ability of accommodation. If we look at a object in a short distance, the lens behaves ‘fatter’ in which allows more optic power be transmitted to us to focus on the object. When we fixate on a far object, a ‘flatter’ lens will occur in our eyes to reduce the optic power. The lens loses its flexibility in shaping as our ages growing. Normally, the lens completely losses its flexibility at the age of 50, thus, elder people are no longer able to focus on the near object and glasses now are required.

Meanwhile, the lens becomes hardening as the decrement of its flexibility, the optical density will increase. As figure 2 shown above, the lens will absorb more energy from short-wavelength waves (blue and violet) thus, the colors from medium and long wavelengths will become more significant. This results in a phenomenon that while looking at a purple object, the elder people will find it is redder than the results observed by young people. Since the blue energy reflects from the purple object are absorbed much more by elder people due to their hardening lens and the red energy is not affected at all. So, the red color performs more significant to older people. The lens is the only structure in the human eye that influenced by human ageing.

C. The Humors

There are two types of humors filled in two gaps in the eye. One is the aqueous humor between the cornea and the lens, which is crystalline and basically water. One type of humor known as vitreous humor, which fills the gap between the lens and the retina and it has higher viscosity like gelatin. The aqueous humor has functions to allow the expansion of cornea, thus, it can against the dust and pressure from outside. As we discussed in the cornea section, the aqueous humor surrounding the cornea can transport nutrients. The main difference between vitreous humor and aqueous humor is that there is an amount of vitreous humor in the eye that does not move. These two humors provide slight pressure to the flexible eyeball to let it maintains its shape and dimensions. And the overall ability in the eyeball against the injury is also increased by this special structure. Since the index of refraction in both two humors are close to water, the surface of the lens only have ignorable ability on light absorption as known as low optical density.

D. The Iris

The iris is a thin, circular structure in the eye, which controls the size and the diameter of the pupil and thus changes the amount of light projected on the retina. People have different colors is due to the different resolution of the melanin in their iris. There is a hole located at the centre of the iris named pupil that lets the light passes. The size of the pupil is basically determined luminance levels passed into the eyes, but some experiments proved that the pupil size affected by arousal as well. When people get some emotional stimulus, the pupil will change its size as a type of response to the stimulus. Based on the control under iris, the size of pupil can vary from 3 mm to 7mm, which results in a 5-fold change in the pupil area, the same as the luminance levels on the retina. It is marvellous that the acceptable illuminance levels in human visual functionality vary over 10 orders of magnitude. Only the changes in pupil size cannot fully explain this excellent human ability in vision. Another important reason is in the signal reception section which we will talk about later, the cooperation of rod and cone photoreceptors also significantly expands the range of illuminance level.

E. The Retina

The retain is a thin surface formed by cells where the optic images projected on. The retina incorporates the functionalities of image reception, initial signal processing and signal transmission. Two types of receptors, cones and rods, are distributed in the retina. The detailed features and abilities of these two photoreceptors will be illustrated in later sections. In this part, we only focus on the structure of the retina. There is a layer called pigmented epithelium behind the retina, which aims to absorb the light that passes the retain but no being absorbed by the photoreceptors. This layer can prevent any light that reflected from the retina.

F. The Fovea

In the retina, there is a tiny spot that provides the clearest vision of all which called the fovea. In this area, we have the best color vision due to the highest density of the corn photoreceptors. When people stare or fixate on an object, they tend to move their heads or eyes to make the object fall on the fovea. When we are reading some texts we instinctively fixate our vision on the sentences we are concerning, so, it is hard for people to read the words using their peripheral area.

G. The Macula

The macula is oval-shaped filtering are near the center of the retina, which is used to protect the fovea. The macula is pigmented in order to protect the fovea from the exposures to the short-wavelength light. We can think about the equation of optical energy, that:

$$E = hf = h\frac{c}{\lambda} \tag{1}$$

where h is the Planck's constant, c is the speed of light and λ is the wavelength. From equation (1), we get the shorter wavelength is the light, the more energy can be carried and absorbed by the eye. To reduce the chromatic aberration which can make the red images be out of focus frequently, the yellow filter, the macula is at service. From the section of the lens, we know that the lens will become more yellow with the age increasing. However, the yellow filter, macula, prior to the fovea, does not have this feature. One thing that needs to be noticed is that the density of the pigment within the macula has a large variation, indifferent observers. The lens and macula are two filters that allow observers to have variability in color vision.

H. The Optic Nerve

The optic nerve is the last remaining component in human eyes. The optic nerve is composed of the axons from the ganglion cells and it is the last stage in the front level of optics of the eye. From the past research, we find that there are approximately 130 million photoreceptors spreading on the retina to collect image information, but only about 1 million fibres in the optic nerve to transmit them. The incredible ratio shows that there is a high compression of the revived signal comparing to transmitted signals in the later stages in the visual system.

To summary the structures we describe in previous sections, a clear view of the system of visual image processing is presented, that the light coming from the outer world firstly passes the cornea and the cornea controls its shape to get the best index of refraction. Then the pupil changes its diameter has adjusted the level of illumination that going to the lens. The lens and the macula modulate the spectral responsivity by their yellow filtering effect and project the filtered light onto the retina. The photoreceptors laying on the retina starts to collect the information and convert the image signal to the chemical and electrical signal. Finally, the optic nerve serves to transmit these signals to the high-level stages of the visual system in the brain.

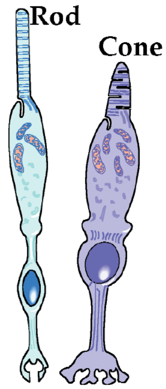

Fig. 3. Rod and Cone photoreceptors

III. Signal Processing In Visual System

The signal processing behind the retain is complex, and the later stages in the brain side are even more complex. This section takes a view on the signal reception and processing on the retina stage since it is extremely difficult to explain the functionality on a single cell in the later stages. Sometimes, it might not be meaningful to explore the ability of a single cell, because the perception of color vision is incorporated into the contributions that distributed across a wild collection of cells in the brain. Rather than exploring mist in the cortex, this section is focusing to explain the features of photoreceptors, rods and cones, the structure of the retina, the receptive fields and two important theories in color vision, Trichhromatic theory and Opponent theory.

A. Rods and Cones

Figure 3 shows the shapes of two types of photoreceptors, the one with a long and thin structure is called rod, which is specialized for discriminating at a very low level of light. (scotopic vision) The second one is focusing on detecting images in high light level of illumination, (photopic vision), it is called cone since its conical shape. In the middle levels of illumination, both rods and cones cooperate to provide the viewing functionality under mesopic vision. Since these tow photoreceptors have their specialized operating light levels, so the transition between rods and cones is the core mechanism that gives a large range of acceptable levels of illumination to the human visual system. Combing the features of pupil size that we talked about in the prior section, now we can fully explain the appearance of the excellent range for acceptable luminance levels in the human eye. One is based on the changeable pupil size, the other is contributed by the transition mechanism between rods and cones.

All rods have equal sensitivity on spectra, they can not distinguish the spectral distributions from the light on different areas of the retina. Since light is electromagnetic waves distributed in a range of spectra, so for the night vision, we cannot see specific colors only shades of grey between black and white. The photosensitive pigment in the rods is called rhodopsin, which has the peak spectral responsivity at approximately 510nm.

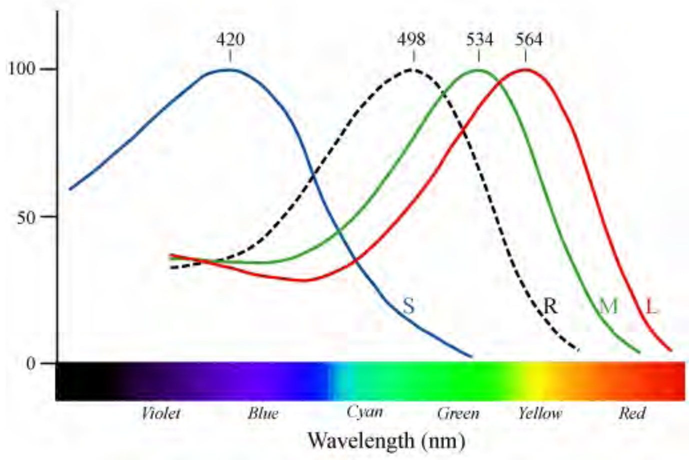

Fig. 4. Spectral sensitivity of rods and cones

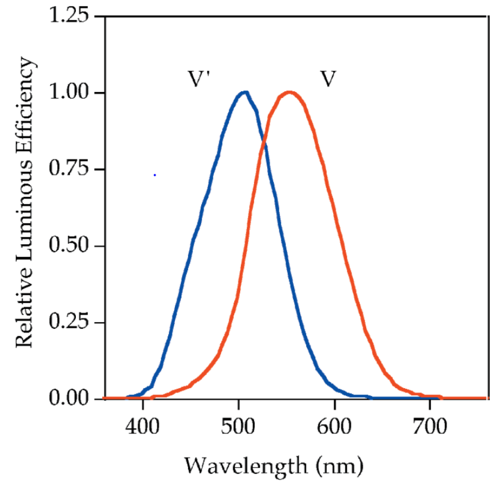

Fig. 5. CIE spectral luminous efficiency for scotopic vision V' and photopic vision V)

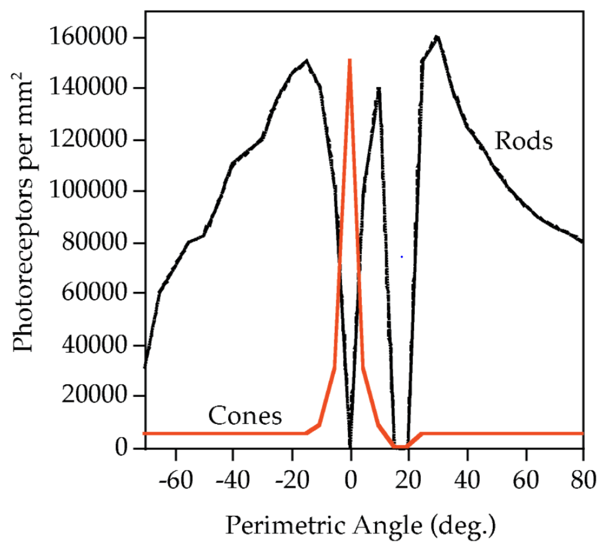

Fig. 6. Density of rods and cones on the human retina

In the daylight vision, a world with seemingly infinite colors has been presented to us. Under this typical photopic vision condition, the cones are fully operating, and the rods stops their jobs. As we mentioned previously, any color detected by our eyes can be represented by mixing three different wavelengths of light with specific intensities, this remarkable phenomenon owes to the work done by cone receptors. Thus, there must be three types of cones that exist named as L, M and S cones. These names are given to denote the cones sensitive to long, middle and short wavelengths. There is also an alternative naming manner for cone receptors, known as RGB, red, green and blue cones. This RGB naming manner is not really appropriate since there are broadly overlapping for three cones in the wavelength responsivity spectrum.

Refer to figure 4, we can easily find that the peak responsivity of three cones is not exactly located at the colors of red, green and blue. So, rather than differ these cones by color separation, the LMS names are more appropriate. The photosensitive pigment in the cones is called opsin. Pigments are the dominated elements in each cone to absorb a certain type of wavelength from the light better than others. All types of cones are filled with all kinds of opsin. For each subclass, the resolution of various opsin are different, thus there is one type of dominant opsin in each type of cones that gives the special peak sensitivity to the light spectrum to different cones.

Figure 5 shows the CIE spectral luminous responsivity, the blue curve V' on the left for scotopic vision and the curve V on the right representing the high-light vision. The only function receptor under scotopic vision is rods, thus, the appearance of curve V' mostly controlled by the spectral sensitivity of rhodopsin. Comparing the shapes in figure 3 and 4, we shall see that the curve of spectral sensitivity of rods match the CIE curve in scotopic vision, which is a solid proof to the point that only rods are functional in very low luminance levels. Different from the curve of rods, the V function in photopic vision is a mixture of three types of cones. All the spectral sensitives in LMS cones combined to form a distinct shape. As a consequence, in scotopic vision, we are more sensitivity to short-wavelength and long-wavelength for photopic vision. Thus, the effect is known as the Purkinje shift, which can be viewed by one red object and one blue object in different luminance levels. In the scotopic vision, the blue object seems light and the red object becomes darker due to the different spectral sensitivities.

From figure 5, it is interesting that the peak spectral sensitivity in photopic vision is around 560 nm which loses to the peak spectral sensitivity for long-wavelength cones. It points out that there are relatively fewer S cones spreading in the retina, and there are much more L and M cones populated throughout the retina. The population of L, M and S cones are approximately 12:6:1. Thus the long-wavelength cones dominate the performance of the CIE spectral sensitivity function in photopic vision.

Figure 6 illustrates the density of cones and rods populated

Fig. 7. Blind spot simulation, (a) the blind spot reffer to a spot (b) the blind spot reffer to a gap in a stright line

on the retina. There are some fantastic findings showing on the graph. One is that there are far more rods than cones in the retina, rods have an approximate population of 120 million per retina, and for cones are only 7 million per retina. This finding is somehow unintuitive to people since cones provide a better color vision to humans in photopic vision with high visual acuity. However, the rods which only work in low luminance levels with reduced visual acuity have a much greater population.

To explain this phenomenon in fact we need to step to the later stage about signal transmission in ganglion cells. In the layer of transmission between photoreceptors and ganglion cells that single cones transmit signals to ganglion cells while the rods gather the information from large number of receptors and transmitted into one signle ganglion cell. Due to the reduced visual acuity in scotopic vision while rods are the only operating receptors, more rods are required to be functional, to increase the sensitivity. This mechanism looks like a compensation strategy that compensates the reduced acuity by increasing sensitivity. This also explains the problem we have mentioned above that there is a high compression between the signal from receptors and the transmitting ganglion cells. The receptors and ganglion cells are not connected in a pointwise way, that one ganglion cell can receive information from hundreds of receptors.

If we look at the density distribution of these two receptors, they are not only different in total numbers but also a significant difference in density in the retina. The cones are highly concentrated at the centre point at 0 degrees in a perimetric angle where is the position of fovea. Unlike cones, rods are more populated throughout the peripheral retina with a relatively large number and there are few cones in these outer areas. We can notice that there two particular areas lacking rods, one is the fovea and the second is are with perimetric angles from 15 to 20 degrees. Now we consider the fovea area since the space on the retain is limited thus more cones while means the reduced number of rods. As we discussed in fovea section, this area has the best color and spatial vision, thus the lack of rods in the fovea gives more space for cones to produce the highest possible spatial acuity and color vision.

The second important area in figure 6 is in angles between 15 and 20 degrees. In this spot there are neither cones nor rods exist, this area is known as the blind spot. The optic nerve gathered at the blind spot, and no space left for receptors. This sounds unintuitive that in a particular angle our eyes cannot detect any images, and figure 7 is a good example to prove the blind spot exists. One reason that the blind spot is hard to be noticed is that it hides on the other side of the retina in human eyes. In fact, even we close one eye and keep the other opened, it is still to notice the blind spot.

So, we now use figure 7 to show that the blind spot truly exists. Looking at the cross with the eye on the right, then adjust the distance to paper until the spot is covered by the blind spot. Note that the black dot in (a) will disappear while it falls on to the blind spot, but the area disappeared is not left with a black region, but a plain blank area. This remarkable phenomenon is known as filling in. When the brain cannot receive any information representing as changes from the visual signals in the blind spot, it will automatically fill this area with the most probable stimulus. In the circumstance of (a), the black dot is surrounded by the plain white paper, so the brain fills the uniform stimulus from the surrounding area to the blind spot, thus, a blank is presented in the blind spot. The same mechanism can be applied to case (b) when the blind spot covers the gap in the line, a continuous line will appear with no gay at all. The brain fills the gap with the most probable uniform stimulus, a straight line, to the gap.

This filling in functionality also explains the fundamental operating rules of the vision system. Only the stimulus about changes can be presented in the ganglion cell. Moreover, only the information represents spatial or temporal changes that are transmitted to the brain. By the filling in ability, our brain can generate a uniform perception of the areas where no change is detected until a new transition is noticed. In this way, the required bandwidth to transmit the information is largely reduced.

B. The cells in the human retina

In this section, several layers in the retain are discussed with their functionalities and stages in the signal transmission. Figure 8 is a cross-section graph that shows how the layers distributed in the retina. Starting from the photoreceptors with are rods and cones, vertical transmission is established between the receptors and the bipolar cells which transduce the information to ganglion cells in the end. It

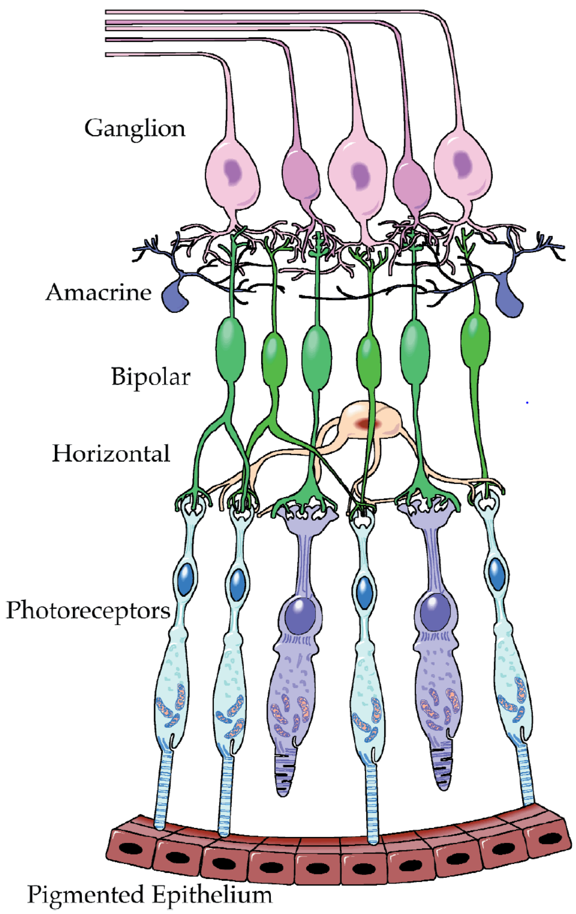

Fig. 8. Diagram of cells in the human retina

is important to know that the transmission in between of these cells is not pointwise. In other words, many receptors transmit signals to multiple bipolar cells and these bipolar cells give the information to also a great number of ganglion cells. During the transmission, two types of cells are playing important roles, one is horizontal cells and the other is amacrine cells.

The horizontal cells connect the photoreceptors and the bipolar cells and the amacrine cells conduct the bipolar cells and the ganglion cells. In fact, there are still many unknowns within these cells, but it is clear that the information transmitted from the retina to the brain is not simply pointwise. So, each synapse between cells is providing a multi-functional mathematical operation including adding, subtracting, multiply and dividing. These operations give the cells the ability to amplify, gain and control the activities within the cells in a nonlinear representation. Also, before the detected light passes to the photoreceptors, it will go across all the neural machinery inside the retina, but these cells have little impact on the vison generation since they are transparent and fixed in positions. These cells also transport the required nutrients to the receptors and waste produced from the retina.

C. Young-Helmholtz trichromatic theory

At its most basic, the Young-Helmholtz theory states that there must be three types of receptors with human eyes to form the color vision. These three receptors are sensitive to different regions in the spectrum and they combined to create the entire visual spectrum of light. The trichromatic theory states that the visual world is established by three layes of images transmitted to the brain and the ratio of strength in the signals is different in order to sort out the color appearance. The three-receptors hypothesis in this theory is proofed, but the idea of signals from receptors directly transmitting to the brain is not appropriate. Since serval observed phenomenon in human vision cannot be fully explained by trichromatic theory.

D. Hering's opponent-process theory

Based on serval observations including the appearance of hues, after images and deficiencies on certain color combinations, Hering came up with an opponent-process theory. Hering noticed that human can never perceive certain hue combinations, such as red-green or yellow-blue. Moreover, the the afterimages of the colors above are opponent. Hering explained these findings in terms of the colors complementing because of the ability of adaptation in the visual system supported by the trichromatic theory. Also, the people with color blindness lose the functionality to discriminate the colors between red and green or blue and yellow. This points out that the color perception in human vision system has some certain correlated hue pairs.

Thus, Hering stated that the three types of photoreceptors have bipolar responses to light-dark, red-green and yellow-blue. The opponent-process theory states three different pigmented photoreceptors which support the human ability to distinguish colors with opposing actions. From the previous section about the opponent-process, two signals from two cones combined to form an input to a bipolar cell, and the output of the bipolar cells is only relating to one inputted color, thus only one type of color signal can be presented by the opponent-processing at each time. The opponent-process is established based on a process of excitatory and inhibitory responses. For example, red and green are two hums inhibited each other, the input color of red can be treated as a positive response while the input of green is the negative response. Thus, the positive and negative responses cannot be presented at the same time by one bipolar cell.

E. The connection between two theories

The trichromatic theory is concentrating on how the three types of cones working on various types of light wavelengths, while opponent-process theory tries to understand the connection between the cones and the ganglion cells. In the ganglion cells the color signals from the cones behaves an inhibited relationship in certain types. On the receptor level, the trichromatic theory describes the structure and the functionalities of the cone photoreceptors. Opponent process theory offers an explanation for how it operates at the neural level. The opponent-process theory gives an

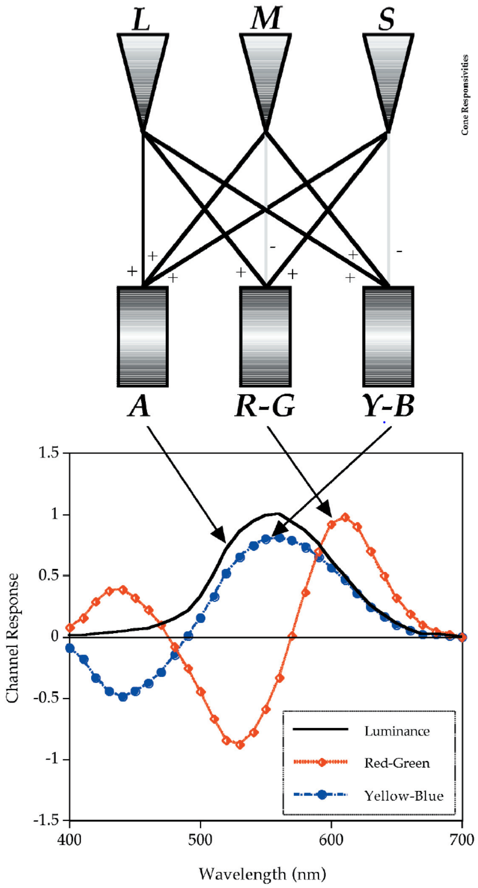

Fig. 9. Diagram of opponentcolors signals in the human visual system

explanation that how the color vision is resulted from a way in which the bipolar cells do an opponent-processing system. The opponent-process theory can be used to explain many phenomena in serval layers of the neural system. Once we step forward from the retina layer to the later stages in the brain, the mechanism of the cell responses is behaved in an opponent fashion.

Figure 9 shows the first stage of the color reception, as what hypothesized by the trichromatic theory, there are indeed three receptors sensitive to different regions in the visual light spectrum. However, the signals generated by these receptors are not directly transmitted to the brain. Instead, the bipolar cells in the retina transduce the colors into opponent signals. One is the red-green (L – M + S) signal and the other is yellow-blue (L + M - S). The LMS signals from receptors are converted to opponent signals which decorrelate the color information in three channels. Thus, the complexity of signal transmission is prominently reduced and noise reduction is achieved as well during this opponent process.

IV. CONCLUSIONS

This report has presented the basic physiology of human color appearance. The color vision in the human eye is a complex system with remarkable incorporation in serval stages. This report focused the physiology ending at the retain stage, due to the difficulty and complexity of analyzing the activities inside the brain. Moreover, some of the signal processing happened in the retina can be counted as an extension of the functionalities from the cortex, since the neural responses are highly correlated. In addition, come cells in the V1 area of cortex can be found that having linearly combine inputs from the LGN cell. It is not difficult to imagine how complex the visual system will be in a network of approximately 30 visual areas.

The amazing abilities that the human visual system has are not completed by sing cell or organ. The large acceptable range of the lamination level is achieved by the pupil and the opponent processing in the bipolar cells. In this report, a process is discussed how the light passed into human eyes are detected, converted and transmitted. The entire system is the front end is divided into serval sections, since it becomes much simpler to explore the functionalities of the various models if the fundamental anatomy, physiology and the performance of each section are understood.

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