Negative feedback control of the visual system and systematic color vision model

Yan Liu

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Negative Feedback Control of the Visual System
and
Systematic Color Vision Model

by

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A thesis submitted for partial fulfillment of the requirements for the degree of Master of Science in the Center for Imaging Science of the Rochester Institute of Technology

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Title of Thesis: Negative Feedback Control of the Visual System and Systematic Color Vision Model

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Abstract

This thesis presents a physiological hypothesis of a systematic negative feedback control mechanism of the human visual system and a corresponding systematic color vision model. This model is based on the physiological hypothesis of systematic negative-feedback control of the visual system and both the stage color vision theory and Land's theory. According to this systematic color vision model, the color vision is processed as described by the stage theory, the negative feedback of the visual system adjusts the sensitivities of the cone photoreceptors and controls the
visual system to adapt to the visual surroundings. The dynamic ranges of relative visual signals are always from 0 through 100, just as stated by the Retinex theory. New terms, color vision excitation, visual reference point, and color vector are introduced for describing the color vision process. This systematic color vision model can combine physiological quantitative data and psychophysical quantitative data by the systematic color equations. This thesis also presents a quantitative control model of the visual system.
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Mr. K. Parton, for his great help in improving the grammar of this thesis.
DEDICATION

This thesis is dedicated to
my parent.
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Introduction

From the time of Sir Isaac Newton's finding that light can be dispersed by a glass prism into a spectrum of colors to the present, much about color vision has been learned. It may have been Thomas Young\(^1\) who first proposed trichromatic color vision theory. Helmholtz\(^2\) further developed Young's idea, so the trichromatic theory is also referenced as the Young-Helmholtz theory. The trichromatic theory is based on the fundamental assumption that three independent kinds of cone photoreceptors exist, each having different spectral sensitivities. Visual signals generated in three kinds of cone photoreceptors are transmitted directly to the brain where the color sensations are experienced. This theory explains the experimental data of foveal color-matching well by the means of additive mixture of color stimuli, but is inadequate to account for the way color stimuli appear to an observer. Hering\(^3\) proposed an opponent-color theory as an alternative to the trichromatic theory. The opponent-color theory assumes the existence of six basic sensations

(1)
occurring in opponent pairs: red-green, yellow-blue, and black-white. One member of each pair drives a catabolic (dissimilation), and other an anabolic (assimilation), process. The opponent-color theory can explain the subjective appearance of color stimuli. For many years the trichromatic theory was favored over the opponent theory.

Muller\(^4\) first introduced the stage-theory of color vision, which merged the trichromatic theory and the opponent-color theory into a single theory. The stage theory states that in the first stage there are three independent types of cone photoreceptors, just as in the basic assumption of the trichromatic theory. In the second stage the chromatic response signals are converted to three new signals, one achromatic signal and two antagonistic chromatic signals. The second stage complies with the basic assertions of the opponent-colors theory. Subsequent stages further process the signals of the second stage and finally send them to the last stage located in the cortex. Currently, the stage theory is widely accepted.

Land\(^5\)–\(^7\) proposed the Retinex theory of color vision. "This theory assumes that there are three independent cone
systems, each starting with a set of receptors peaking, respectively, in the long-, middle-, and short-wavelength regions of the visible spectrum. Each system forms a separate image of the world in terms of lightness that shows a strong correlation with reflectance within its particular band of wavelengths. These images are not mixed, but rather are compared to generate color sensations." Moreover, Retinex algorithms for estimating color appearance have been developed.\textsuperscript{7-11}

In the cone photoreceptors the calcium levels control the spectral sensitivities and the feedback of $\text{Ca}^{2+}$ primarily causes light adaptation.\textsuperscript{12-14} Many studies\textsuperscript{15-22} have shown the existence of negative feedback in the retina. The negative feedback control of the visual system is very important in the visual process. It could be that systematic negative feedback controls all of the color vision processing, keeping the visual system stable and making the visual system possess the suitable sensitivity and highest acuity. Unfortunately none of the previous color vision theories have considered the important function of systematic negative feedback control in color vision processing.
Boynton\textsuperscript{23} has suggested the separate processing of hue and brightness at the striate cortex. Gouras et al\textsuperscript{24,25} observed that some cells in the striate cortex respond mainly to brightness and others respond to color contrast, even though all of them share the same cone photoreceptors. Zeki\textsuperscript{26} pointed out that visual cortex is made up of a multiplicity of distinct areas, each distinct area having a special function. Zeki and Shipp\textsuperscript{27} additionally gave a model of cortical connections. Fletcher and Voke\textsuperscript{28} summarized that "the separation of luminance information for brightness perception and of wavelength information for colour perception begins early in the retina after the photoreceptor stage, following a (normally) trichromatic processing by three classes of cone pigments and activation of the rod pigment, rhodopsin. This separation is maintained throughout the visual pathway to the striate cortex." However, Lennie et al\textsuperscript{29} suggested that a very large number of R-G units carry both a chromatic and an achromatic signal, and that at some stage beyond the lateral geniculate nucleus (LGN) there is emergence of separate chromatic and achromatic pathways. Martinez-Uriegas\textsuperscript{30} suggested that chromatic and achromatic
information are intermixed at an early stage. However, at some stages there exists the separation of luminance and wavelength information which contributes to the process of color vision. The separation of colorfulness\textsuperscript{31} and brightness\textsuperscript{31} processing also suggests the separation of negative feedback control in the perception of colorfulness and brightness.

Paritsis and Stewart\textsuperscript{32} used cybernetics, the science of systems of control and communications, to study color vision and presented a neural network model for an adaptive classification system in color vision that is based in biology. They suggested that the property of the 'ultra-anastomotic' system can give a solution to the differences between Helmholtz's and Land's points of view. They also presented the idea of reference and equilibrium points. They wrote in their book:"It would be dangerous at this stage of knowledge to combine, in one model, quantitative data at the physiological level with quantitative data at the psychophysical level." They additionally pointed out that "However, quantitative biological data can be used in order to outline the connectivity of a neural network, which can be
further used as a constraint of framework about what is logically and biologically possible, on the basis of which, as a future step, psychophysical quantitative neural-network models could be developed to fit psychophysical data."

This thesis presents a systematic color vision model based on the systematic negative feedback control of the visual system and both the stage color vision theory and Land's theory. This model assumes that the systematic negative feedback control of the visual system adjusts the sensitivity of three kinds of cones for light adaptation. It adjusts the absolute and relative sensitivity among the three kinds of cone photoreceptors for optimal adaptation to the light surroundings. The systematic color vision model is a more complete color vision model which can more correctly describe the color vision phenomena and can combine quantitative data at the physiological level with quantitative data at the psychophysical level.
Negative Feedback Control of the Visual System

The visual system should include two physiological parts: the main visual part and the system control part. The main visual part processes the color image from the photoreceptor stage through the final stage at the cortex. The other very important part of the visual system is the system control part. The system control performs the systematic negative feedback control (systematic NFC) to make the visual system optimally adapt to the visual surroundings and to possess both the suitable sensitivity and highest acuity of color perception. Here the term 'visual surrounding' is used instead of light source since the visual system needs to adapt to the visual surroundings, not only the light source, but also the color in the visual surrounding area affects the visual system's adaptation.

Because the chromatic information and achromatic information are mainly processed separately, the system control part should correspondingly include two loops: the absolute sensitivity NFC loop and the relative sensitivities
NFC loop. The absolute sensitivity is the sensitivity of the visual system to the overall radiance of the visual surroundings, and the relative sensitivity is the sensitivity of each of the three kinds of cones compared to each other. The absolute sensitivity NFC can control the visual system over very large ranges of luminances, from very dim through very bright. It can enable the visual system to adapt to a very large luminance change in the visual surroundings and still process color vision well. The absolute sensitivities of the three kinds of cone photoreceptors are supposed to be the same to adapt to the visual surroundings. So, the output visual signals of the three kinds of cone photoreceptors are different for the visual surroundings generally. The relative sensitivity NFC adjusts the relative sensitivities among the three kinds of cone photoreceptors to keep the visual system adapted to the chromaticity of the visual surroundings. Consequently the sensitivities of the three kinds of cone photoreceptors are not the same generally, but the output visual signals are supposed to be the same for the visual surroundings under full adaptation. The adjustment range of the relative sensitivity NFC for full adaptation is much
smaller than that of the absolute sensitivity NFC. Full adaptation for the relative sensitivities is limited to the region around the black body line on the chromaticity diagram. If the visual system fully adapts to the chromaticity of the visual surroundings under the relative NFC, the sensitivities of the three kinds of cone photoreceptors will generally be different, but the output visual signals of the three kinds of cone photoreceptors are assumed to be the same maximum values for the visual surroundings. The visual system processes color vision under both kinds of NFC throughout. The Ca$^{2+}$ in the cone photoreceptor adjusts the output visual signals of the three kinds cone photoreceptors to be equal, therefore it can adjust both absolute and relative sensitivities.

The process of absolute sensitivity NFC is that when the luminance of the visual surroundings is increased, the absolute NFC decreases the sensitivities of the three kinds of cone photoreceptor simultaneously. Similarly if the luminance of the visual surroundings is decreased, the absolute NFC increases the sensitivities of the three kinds of cone photoreceptors to adapt the luminance change of the

(9)
visual surroundings. In some limited luminance range, the absolute NFC also adjusts the size of the pupil with the change of the sensitivities of the three kinds of cone photoreceptor simultaneously. If the luminance is increased, the NFC decreases the size of pupil with simultaneous decrease of the brightness sensitivities of the cones. The absolute NFC signal for adjusting the size of the pupil is transmitted from the brain to the pupil though a pathway outside the eyes. For the relative sensitivity NFC, when the chromaticity, whatever hue or saturation, of the visual surroundings is changed, the relative sensitivity NFC will adjust the relative sensitivities among the three kinds of cone photoreceptor. For example, if the visual surroundings increase in redness, such as when the correlated color temperature of a light source is decreased, the relative NFC will decrease the relative sensitivity of the red cone photoreceptor. Since red and green are the antagonistic colors, with decreasing of the sensitivity of the red cone photoreceptor, the relative NFC will also increase the relative sensitivity of the green cone photoreceptor. Due to less blueness of the visual surroundings, the relative NFC
will increase the relative sensitivity of blue cone photoreceptor. At the same time, the relative NFC will also decrease the relative sensitivity to yellow, that is the relative sensitivities of both red and green. Because there are two opponent color pairs, as the relative sensitivity changes for one pair of cone photoreceptors, the relative sensitivity of the other pair of cone photoreceptors will be changed too by the relative NFC. The final result of the relative NFC should be the relative sensitivity of red cones decreased, the relative sensitivity of blue cones increased, and the relative sensitivity of green changed little. Any chromaticity change of the visual surroundings will bring the relative NFC to adjust the relative sensitivities of the three kinds of cone photoreceptors. The result of the systematic NFC is that the sensitivities of the three kinds of cone photoreceptor reach dynamic equilibrium. When the visual system reaches dynamic equilibrium each kind of cone maintains the most suitable sensitivity. For dynamic equilibrium to the color of the visual surroundings, the output visual electrical signals of two pairs of opponent colors should be zero, only achromatic signals reach the
brain, so the color sensation is white.

Whatever change in the luminance of visual surrounding, under the systematic NFC, the sensitivities of the three kinds of cone photoreceptors keep in their optimal state, the range of visual signals remain unchanged, the range can simply be supposed to be a relative number from 0 through 100. For example, under full adaptation for one visual surrounding, the equivalent output visual signals of the three kinds of cone photoreceptors are 0 for no light and 100 for the visual surroundings. If the visual surroundings change, whatever the changes of chromaticity and luminance, under the systematic NFC, the visual system will adapt to the changed visual surroundings again and will reach new dynamic equilibrium, the output range of equivalent output visual signal intensity of the three kinds of cone photoreceptors is still from 0 through 100 after fully adapting to the changed visual surroundings. If the chromaticity of the visual surroundings exceeds the maximum range of the relative NFC adjustment, that is the visual system cannot fully adapt to the chromaticity of the visual surroundings, the relative NFC cannot adjust the relative sensitivities of the three kinds
of cone photoreceptors to make the equivalent output visual signals be 100 for the visual surroundings, but around 100.

Figure 1 shows two light sources with different relative power distributions, one is illuminant A and the other is an imaginary light source, S, that has relatively much more long wavelength power distribution and, would appear redder. Suppose the reflectance of the visual surroundings is nonselective, that is the relative spectral power distribution of the visual surroundings is the same as that of the light source. First if we use illuminant A to illuminate the visual surroundings, figure 2 gives the explanation for the process of systematic NFC for full adaptation of the visual system to the visual surroundings. In figure 2, the dark bars represent the equivalent output visual signal intensities of the three kinds of cone photoreceptors under the absolute NFC control only. Because of the assumption that the absolute NFC adjusts the three kinds of cone photoreceptor with the same absolute sensitivities, the ratio of the absolute output visual signal intensities of the three kinds of cone photoreceptors only depends on the relative spectral power distribution of the
Figure 1. Relative spectral power distribution of illuminant A and imaginary red light source S.
Figure 2. Intensity of the equivalent visual electrical signals for full adaptation under the process of NFC. Dark bars represent the intensity of the three equivalent visual electrical signals under the absolute NFC only. The light bars represent the same under the systematic NFC for full adaptation. In this figure, under the systematic NFC, the equivalent visual electrical signal intensities of the three kinds of cone photoreceptor are equal.
visual surroundings, so the ratio of the absolute signal intensities of the three kinds of cone photoreceptors is the same as that of the three integrations of the products of the three spectral sensitivities of cone photoreceptors and the relative spectral power distribution of the visual surroundings. The relative NFC adjusts the relative sensitivities of the three kinds of cone photoreceptors and makes the output visual signal intensities equal for full adaptation. Suppose that the relative NFC uses medium absolute signal intensity as a reference to adjust the other two relative sensitivities of the three kinds of cone photoreceptors, the relative NFC will decrease sensitivity of the cone photoreceptors with the large signal (R) and increase sensitivity of the cone photoreceptors with the smaller signal (B). The light bars of figure 2 show the result of the systematic NFC after both absolute and relative NFC. If the human visual system can fully adapt to illuminant A, the equivalent visual signal intensities are equal to 100. The opponent color signals transmitted to the brain are 0, the brain only receives the achromatic signal, therefore, and the color sensation is white. If we use the light source S
Figure 3. Intensity of the equivalent visual electrical signals for unfull adaptation under the process of NFC. Dark bars represent the intensity of the three equivalent visual electrical signals under the absolute NFC only. The light bars represent the same under the systematic NFC for full adaptation. In this figure, under the systematic NFC, the equivalent visual electrical signal intensities of the three kinds of cone photoreceptor are not equal.
**Figure 4.** Schematic diagram of the systematic color vision model. Bold lines represent the color vision processing network, thin lines form the relative NFC loop, the dashed lines form the absolute NFC loop, and the bold dashed lines of the cone photoreceptors belong to both relative and absolute NFC loops. The color vision processing network includes three stages: the cone photoreceptor stage, visual electrical signal processing stage, and the color sensation stage. Here the pupil belongs to the absolute NFC loop.
instead of illuminant A to light the visual surroundings, the result of NFC is shown in figure 3. Since the relative NFC has a maximum full adaptation adjustment range, but the light source S has too much long wavelength spectral distribution, the relative spectral power distribution of the visual surroundings is over the maximum range, the relative NFC cannot adjust the relative sensitivities in such a large range, so the equivalent output visual signals are not equal to 100, but as shown in figure 3. The ratio of the R and B equivalent output visual signals is not equal to 1, therefore, the opponent chromatic signals are not equal to 0 and the visual system does not fully adapt to the visual surroundings. As a result, the visual surroundings appear reddish.

The anatomy and physiology of systematic NFC is complex. Little about it is known. The Ca\(^{2+}\) levels provide negative feedback inside the cone photoreceptors and primarily control sensitivities of the three kinds of cone photoreceptors of the visual system for light adaptation.\(^{12-14}\) The function of the feedback loop between the horizontal cells and the cone photoreceptors may be mainly for relative NFC.\(^{15-22}\)

Figure 4 shows the scheme of the systematic color vision (19)
model. In the diagram, the dashed lines form the absolute NFC loop, the thin lines form the relative NFC loop, the bold dashed lines inside the cone photoreceptors belong to both relative and absolute NFC loops. The dark lines represent the main color vision process network. Calcium levels inside the cone photoreceptors primarily control the sensitivities of the three kinds of cone photoreceptors. For the absolute NFC loop, the cone photoreceptors, the brain and other part(s) of the visual system send the absolute NFC signals to the cone photoreceptors to adjust their absolute sensitivities. The brain also sends NFC signal to the pupils to adjust their size through the special nerve channels for achromaticity adaptation. For the relative NFC loop, Ca^{2+} feedback inside the cone photoreceptors essentially controls the chromaticity adaptation. The relative NFC signals are also initiated in the retina by horizontal cells and transmitted to the cone photoreceptors to adjust their relative sensitivities. Additionally, the brain send relative NFC signals to the retina. The signals sent by the brain will stimulate new relative NFC signals and interact with the relative NFC signals initiated in the retina to form supplementary

(20)
relative NFC signals for adjusting the relative sensitivities of the cone photoreceptors.
The systematic color vision model

In figure 4, the bold lines represent the main color vision network which is much like the color vision model scheme given by Walraven. In the network, the first stage is the trichromatic photoreceptor stage with the three kinds of cone photoreceptor, the second stage is the electronic visual signal processing stage, and the third stage is the color sensation stage. In the first stage, the three kinds of cone photoreceptors receive light and initiate three independent electronic visual signals. The initiated signals are separated into chromatic signals and achromatic signals and sent to the next electric visual signal processing stage. The red (R) and green (G) signals are involved in both the antagonistic and the nonantagonistic processes. The R and G signals are converted to an opponent R-G signal by antagonistic process and a yellow (Y) signal by nonantagonistic process. In figure 4, Y(R, G) is used to represent the nonantagonistic process by which the R and G signals are converted to a yellow signal. Here Y(R, G) means (22)
the yellow (Y) signal is an unknown function of R and G. The three signals of R, G, and B are converted to two pairs of opponent color signals and processed by the antagonistic processes, just as described by the opponent-color vision theory, processed, and transmitted to the brain for the colorfulness sensation. The achromatic signals are coded in a nonopponent way and sent to the brain for the brightness sensation through the achromatic pathway. At some stages chromatic and achromatic signals may be intermixed.\textsuperscript{29,30} It is known that there are fewer B cone photoreceptors than R and G cone photoreceptors in the primate retina.\textsuperscript{34,35} This may be because the B cone photoreceptors practically only participate in the antagonistic process of color vision. The R and G cones not only participate the antagonistic process of both R-G and Y-B, but they are also the main contributors to achromatic perception and visual resolution.

There exist several kinds of cells connected with other kinds of cells horizontally, such as horizontal cells and amacrine cells. They may connect with both chromatic and achromatic channels and affect the independence of chromatic and achromatic visual signals. Therefore, they intermix and
process both chromatic and achromatic signals and output their function signals, for example the horizontal cells output NFC signals to photoreceptors.

The systematic color vision model is as follows:

1. The visual system includes two physiological parts: a color vision processing part and a systematic negative feedback control part. The systematic NFC part consists of two loops: an absolute sensitivity NFC loop and a relative sensitivity NFC loop. The color vision processing part processes electrical visual signals initiated by the cone photoreceptors. The systematic NFC part controls the color vision processing, makes the visual system optimally adapted to the visual surroundings, and keeps the visual system stable.

2. Under the systematic NFC, each of the three kinds of cones possess their own sensitivities. If the visual system fully adapts to the visual surroundings, the equivalent output visual signals of each kind of cone photoreceptor is assumed to be 100 for the visual
surroundings, and from 0 for no light to 100 for the highest lightness for any color sample. If the visual system cannot fully adapt to the chromaticity of the visual surroundings, the equivalent output visual signals of the three kinds of cone photoreceptors are not the same at 100, but different around 100, the range of the equivalent output visual signals will be from 0 to around 100 for any color sample. The relative NFC will maximally adjust the sensitivities of the three kinds of the cone photoreceptors to make the equivalent output visual signals be as equal as possible and near 100 for the visual surroundings.

3. The color vision processing is as described by the stage theory. There are three main stages: the cone photoreceptor stage, the visual processing stage, and the color sensation stage.

The first stage consists of the three kinds of cone photoreceptors in the retina. Each of the three kinds of cone photoreceptors possesses its own sensitivity which depends on the spectral power distribution, the luminance of the visual
surroundings, and the degree of adaptation to the visual surroundings. The electrical visual signals are initiated through the process of absorption of light in the photopigments of the cone photoreceptors and converted into electrical visual signals. Because each kind of cone photoreceptor possesses its own sensitivity, in the first stage, three independent color image electrical signals are initiated and transmitted to the next stage.

The visual processing stage includes many sub-stages, each sub-stage is a physiological visual processing function layer that can encode and decode the electrical visual signals inputted from previous stages. This stage processes the three independent color image electrical visual signals inputted from the cone photoreceptor stage. It encodes, decodes, transmits and finally outputs two pairs of antagonistic chromatic electrical visual signals for color sensation and a achromatic electrical visual signal for achromatic sensation through the visual pathway. This proceeds sub-stage by sub-stage, and
signals are finally sent to the brain. It may be that in some sub-stages the chromatic electrical visual signals and achromatic electrical visual signals intermix and involve in a multiplexing process.

In the third stage, the color sensation stage, the brain accepts both the two pairs of antagonistic chromatic electrical color visual signals and the achromatic electrical signal and finally evokes the color sensation.

4. Chromatic and achromatic information are processed essentially separately after the first stage. The negative feedback control part correspondingly adjusts the sensitivity for adapting to the lightness of the visual surroundings by the absolute NFC loop and adapting to the chromaticity of the visual surroundings by the relative NFC loop. The achromatic signals are not involved in the antagonistic process, but are processed more directly by the visual system. In this aspect, it is not as described by the opponent color vision theory.
Based on the assumption of the systematic color vision model, the color vision sensation depends on the spectral reflectance of the color sample, the visual surroundings, and the adaptation degree of the visual system. In order to describe the process of the systematic color vision model and the true color appearance of color samples under different visual surroundings and different degrees of adaptation, a term for color vision excitation is introduced as followings:

\[
E_R = \frac{\int S(\lambda)R(\lambda)\phi_R(\lambda)d\lambda}{\int S(\lambda)\phi_R(\lambda)d\lambda} \\
E_G = \frac{\int S(\lambda)R(\lambda)\phi_G(\lambda)d\lambda}{\int S(\lambda)\phi_G(\lambda)d\lambda} \\
E_B = \frac{\int S(\lambda)R(\lambda)\phi_B(\lambda)d\lambda}{\int S(\lambda)\phi_B(\lambda)d\lambda}
\]

where \(E_R\), \(E_G\) and \(E_B\) are the red, green and blue vision excitations (\(R\), \(G\), and \(B\) excitations for short), \(S(\lambda)\) is the relative spectral power distribution of the visual surroundings, \(R(\lambda)\) is the spectral reflectance of the color sample, \(\phi_R(\lambda)\), \(\phi_G(\lambda)\) and \(\phi_B(\lambda)\) are the relative spectral sensitivities of red, green and blue cone photoreceptors, which are basically like the curves described by Bowmaker et al. (28)
The color vision excitations can represent the responses of the three kinds of cone photoreceptors to color and the adaptation degree to the visual surroundings. The denominators of equation (1) represent the state of full adaptation of the three kinds of cone photoreceptors to the visual surroundings. The numerators represent responses of the three kinds of cone photoreceptors to the color of the sample.

If the visual system cannot fully adapt to the visual surroundings, then the visual system will adapt the visual surroundings to a maximum degree by the negative feedback control. In this case, the color vision excitations will become the adjusted color vision excitations:

$$E'_R(\lambda) = F[\phi_R(\lambda), S(\lambda), R(\lambda), L]$$
$$E'_G(\lambda) = F[\phi_G(\lambda), S(\lambda), R(\lambda), L]$$
$$E'_B(\lambda) = F[\phi_B(\lambda), S(\lambda), R(\lambda), L]$$

where $L$ is the luminance of the visual surroundings for the visual system. The adjusted color vision excitations are functions of the relative spectral power distribution and the
luminance of the visual surroundings, the spectral sensitivities of three kinds of the cone photoreceptors, and the spectral reflectance of the color sample. The previous models for chromatic adaptation given by von Kries,\textsuperscript{39} Nayatani,\textsuperscript{40} Hunt,\textsuperscript{41} and Fairchild\textsuperscript{42} and the integrated reflectance for quantitative studies in Retinex theory given by McCann et al\textsuperscript{43} all include terms like color vision excitation or generalized color vision excitations. It is also true of CIELAB color space, which includes X/X\textsubscript{n}, Y/Y\textsubscript{n}, Z/Z\textsubscript{n}. When the visual system cannot fully adapt to the visual surroundings, the S(\lambda) of the denominators is not the spectral distribution of the visual surroundings but the adapted spectral distribution S'(\lambda). When the adaptation of the visual system is incomplete to the visual surroundings, equation 1 becomes:

\[
E'_R = \frac{\int S(\lambda)R(\lambda)\phi_R(\lambda)d\lambda}{\int S'(\lambda)\phi_R(\lambda)d\lambda}
\]

\[
E'_G = \frac{\int S(\lambda)R(\lambda)\phi_G(\lambda)d\lambda}{\int S'(\lambda)\phi_G(\lambda)d\lambda}
\]

\[
E'_B = \frac{\int S(\lambda)R(\lambda)\phi_B(\lambda)d\lambda}{\int S'(\lambda)\phi_B(\lambda)d\lambda}
\]

Since the visual system can adapt well over a very large
luminance range, the luminance factor in equation (2) can be ignored. The adapted spectral distribution $S'(\lambda)$ depends on lightness of the visual surroundings.

In the first stage of color vision processing, the cone photoreceptor stage, the three kinds of cone photoreceptor absorb light and initiate visual electrical signals. Under full adaptation, equation (3) represents the assumed relative intensities of equivalent electrical visual signals output from the three kinds of cone photoreceptors:

\[
V_R = 100 \left[ \frac{\int S(\lambda)R(\lambda)\phi_R(\lambda)d\lambda}{\int S(\lambda)\phi_R(\lambda)d\lambda} \right]^{1/3}
\]
\[
V_G = 100 \left[ \frac{\int S(\lambda)R(\lambda)\phi_G(\lambda)d\lambda}{\int S(\lambda)\phi_G(\lambda)d\lambda} \right]^{1/3}
\]
\[
V_B = 100 \left[ \frac{\int S(\lambda)R(\lambda)\phi_B(\lambda)d\lambda}{\int S(\lambda)\phi_B(\lambda)d\lambda} \right]^{1/3}
\]

Since the response behavior of the three kinds of cone photoreceptors most likely obey a cube root power function,\textsuperscript{44} the terms of the power function are shown as $1/3$ in equation (3). The coefficient, 100, corresponds to the assumption of the systematic color vision model that the output visual

(31)
electrical signals range from 0 to 100 under the condition of full adaptation to the visual surroundings. If we let \( R(\lambda) = 1 \), then the color visual electrical signals are equal to 100, just as the assumption that the output visual signal from each kind of cone photoreceptor is 100 for visual surroundings.

Depending on the systematic color vision model, if the color vision excitations remain constant, then the color sensation will be unchanged. The same is true for color appearance when the visual system can totally adapt to the visual surroundings. From equation (3) we can see that when only the spectral distribution of the visual surroundings changed, the visual electrical signals change little. Generally the changes are smaller than that of the minimum discrimination of the visual system, so the color appearance remains unchanged.

In the visual processing stage, the visual electrical signals of the three kinds of cone photoreceptor are coded both in antagonistic and nonantagonistic ways. The process of combining the red and green visual electrical signals to produce the yellow visual electrical signal is

(32)
nonantagonistic processing. In figure 4, \( Y(R,G) \) is used to represent the nonantagonistic process of the red and green visual electrical signals being coded to become the yellow visual electrical signal. The results of antagonistic processing can be represented by the following equations:

\[
C(R-G) = F(V_R, V_G) \\
C(Y-B) = F(V_Y, V_B)
\]

(4)

where \( C(R-G) \) and \( C(Y-B) \) represent the red-green and yellow-blue opponent visual electrical signals being transmitted to the brain for color sensation. they are the functions of the visual electrical signals \( V_R \) & \( V_G \) and \( V_Y \) & \( V_B \) respectively. The functional form of equations (4) is not clear, but for a simplified case, if we suppose a unit amount of red visual electrical signal plus one and half unit amount of green visual electrical signal, the nonantagonistic process shown in equation (5) says that the result will be one unit amount of yellow visual electrical signal which is the smaller of the two input signals.
\[ V_Y = \text{Min}(V_R, V_G) \]  

(5)

The antagonistic processing is shown as a simple subtraction operation in equations (6):

\[ C(R-G) = m(V_R-V_G) \]  

(6)

\[ C(Y-B) = n(V_Y-V_B) \]

where \( m \) and \( n \) are undetermined coefficients. If \( C(R-G) > 0.0 \), then the color vision sensation is red; \( C(R-G) < 0.0 \), green; if \( C(Y-B) > 0.0 \), yellow; \( C(Y-B) < 0.0 \), blue. If both \( C(R-G) \) and \( C(Y-B) \) equal \( 0.0 \) then the color vision sensation is neutral.

The achromatic sensation is processed, in principle, separately from the antagonistic process above. The achromatic electrical visual signal is processed nonantagonistically after the cone photoreceptor stage. The achromatic sensation can be represented by the following:

\[ L = F(V_R, V_G, V_B) \]  

(7)

The achromatic sensation should primarily be the function of \( V_R, V_G \), but we know little about the form of above function.

Equations (5), (6), and (7) combine both physiological
and psychophysical quantitative data, where \( V_R, V_G, \) and \( V_B \) represent the physiological quantitative data, \( C(R-G), C(Y-B) \), and \( L \) represent the color sensations which are psychophysical quantitative data. We call these the systematic color vision equations. \( C(R-G), C(Y-B) \), and \( L \) describe a color space for the systematic color vision model.
A quantitative control model of the visual system

The control theory offers us a tool for studying systems in general. The physiological feedback mechanisms have been studied from the control theory viewpoint.\textsuperscript{49,50} For the visual system, some feedback control models have been built for different sub-systems.\textsuperscript{50-55}

Based on the systematic color vision model, a physiological NFC model is proposed as shown in figure 5. In figure 5, R.C, G.C, and B.C represent red, green, and blue cone photoreceptors, Hr, Hg, and Hb represent red, green, and blue comparators of horizontal cells, V represents incident photons.

In the retinal rods and cones, the calcium ions provide negative feedback. The calcium level may mainly contribute to control the absolute sensitivities of the cone photoreceptors and the brightness adaptation of the visual system. There also exists negative feedback from the horizontal cells to the cone photoreceptors. The horizontal cells receive synapses from many photoreceptors in a large area of the
Figure 5. The schema for quantitative control model of the visual system.
retina. They also synapse on both horizontal cells and bipolar cells. So the horizontal cells can compare the visual signals over wide fields of the retina and then give overall negative feedback signals to the photoreceptors. Here, it is presumed that the horizontal cells first sum the three visual signals input from photoreceptors and other horizontal cells. They then compare the three summed visual signals of the cone photoreceptors and the summed visual signals of the horizontal cells connected with it. Lastly, they send negative feedback signals to the photoreceptors to control the sensitivities of the photoreceptors. In figure 5, there exit negative feedback pathways inside the cone photoreceptors and from the horizontal cells to the cone photoreceptors.

The negative feedback signals inside the cone photoreceptors control both relative and absolute sensitivities. The NFC signals of horizontal cells join the NFC signals from the brain to adjust the relative sensitivities of the cone photoreceptors. The brain also feeds back NFC signals to adjust the size of the pupil. The four kinds of NFC signals control the visual system for
adapting the visual surroundings.

The four summed visual signals of horizontal cells are supposed to be as follows:

\[
\begin{align*}
v_r &= \iint_s e_r(E'^r, x, y) dx dy \\
v_g &= \iint_s e_g(E'^g, x, y) dx dy \\
v_b &= \iint_s e_b(E'^b, x, y) dx dy \\
v_h &= \iint_s e_h(E'^h, x, y) dx dy
\end{align*}
\]  \hspace{1cm} (8)

where \( e_r, e_g \) and \( e_b \) are the distribution functions of R, G, and B visual signals in the retina for the horizontal cell, \( e_h \) is the distribution functions of visual signals of other horizontal cells connected with the horizontal cell, \( E'^r, E'^g \) and \( E'^b \) are the numerators of visual excitations, \( E_h \) is the output signal of other horizontal cells to the horizontal cell, \( x, y \) are the plane coordinates for the retina. The distribution functions of the visual signals are the functions of \( E'^r, E'^g, E'^b, E_h, x \) and \( y \). Since the horizontal cells have extensive arborisation of axon terminals, we can imagine that the distribution functions may be very complex.
and quite difference to each other. Currently, there is little known about the distribution functions.

Equation (8) can be simplified as a summation:

\[
\begin{align*}
\nu_r &= \sum_{i \in s} E_{ri}' \\
\nu_g &= \sum_{i \in s} E_{gi}' \\
\nu_b &= \sum_{i \in s} E_{bi}' \\
\nu_h &= \sum_{i \in s} E_{hi}'
\end{align*}
\]

where \( E_{ri}' \), \( E_{gi}' \), \( E_{bi}' \), and \( E_{hi}' \) are the input visual signals from \( i \)th R, G, and B cone photoreceptors and \( i \)th horizontal cells to the horizontal cell. The \((i \in s)\) means the summation includes all the arborisation areas of the horizontal cell.

The horizontal cells serve as comparators. They compare the three summed visual signals and output a negative feedback signal to the photoreceptor. The negative feedback signal joins the negative signal from the brain inside or outside the horizontal cells. The converged negative feedback signal input the photoreceptors and control the sensitivities together with the negative feedback inside the photoreceptor.
The negative feedback signals $N_r$, $N_g$ and $N_b$ of the horizontal cells are supposed to be functions of summed visual signals:

$$N_r = F(v_r, v_g, v_b, v_h, c_1)$$
$$N_g = F(v_r, v_g, v_b, v_h, c_2)$$
$$N_b = F(v_r, v_g, v_b, v_h, c_3)$$  \(9\)

where $v_r$, $v_g$, $v_b$ and $v_h$ are summed visual signals from the three kinds of photoreceptors and other horizontal cells which when connected with the horizontal cell, $c_1$, $c_2$, and $c_3$, are constants as the pre-existing negative feedback signals of the three kinds of horizontal cells.

The brain gives two negative feedback signals: achromatic and achromatic negative feedback signals. The brightness feedback signals are sent to two locations: the pupil and photoreceptor. The absolute feedback signals should be a integration of the function of visual signals over all of the retina:

$$N_1 = \iint_{S_0} F(V_r, V_g, V_b) dx dy$$  \(10\)

where $S_0$ means the integration area of brightness feedback.
signal is all over the retina. The brightness feedback signal F_1 will be divided into four parts, N_{1r}, N_{1g}, N_{1b} and N_p:

\[ N_i = N_{lr} + N_{lg} + N_{lb} + N_p \tag{11} \]

where N_{1r}, N_{1g}, and N_{1b} are the partial negative feedback signals of the R, G, and B cone photoreceptors, N_p is the negative feedback signal of the pupil. The three relative feedback signals N_{cr}, N_{cg}, and N_{cb} should be the integrations of comparing functions of the visual signals over all of the retina:

\[ N_{cr} = \int \int_{S_\theta} F_r(v_r, v_g, v_b) \, dx \, dy \]
\[ N_{cg} = \int \int_{S_\theta} F_g(v_r, v_g, v_b) \, dx \, dy \tag{12} \]
\[ N_{cb} = \int \int_{S_\theta} F_b(v_r, v_g, v_b) \, dx \, dy \]

The brain will send three negative feedback signals:

\[ N_r' = N_{cr} + N_{lr} \]
\[ N_g' = N_{cg} + N_{lg} \tag{13} \]
\[ N_b' = N_{cb} + N_{lb} \]

back to the three kinds of cone photoreceptors, and send the negative feedback signal N_p to the pupil. The pupil size is only controlled by the absolute negative feedback from the
brain. The three negative feedback signals sent back to the three kinds of cone photoreceptors will first join the negative feedback signals of the horizontal cells, and then the joined negative feedback signals input to the cone photoreceptors to control the sensitivities. The total negative feedback signals which input to the three kinds of the cone photoreceptors are:

\[
\begin{align*}
N_r &= N_r + N_r' \\
N_g &= N_g + N_g' \\
N_b &= N_b + N_b' \quad (14)
\end{align*}
\]

The adjustment of the sensitivities of the cone photoreceptors cannot be completed by the negative feedback signals immediately.
Discussion

Land and McCann\textsuperscript{8} have demonstrated a color constancy experiment using three light sources to illuminate an arrangement of color papers that was called a color Mondrian scene. When one of the light sources was gradually reduced the colors appeared unchanged. From the point of view of the systematic color vision model, this is because the systematic NFC can adjust the sensitivities of the three kinds of cone photoreceptors simultaneously with the change of light source to keep the visual system always fully adapted to the visual surroundings. The color vision excitations change slightly, but the change is not large enough to be discriminated by the visual system. The above is the explanation for the "color constancy" phenomenon via the systematic color vision model. From equation (1) we can see that when the relative spectral power distribution of the visual surroundings change, if the visual system can totally adapt to the visual surroundings (and the spectral reflectance of the observed color sample does not change), the color vision excitations will change
little. Also for the opponent visual electrical signals, a change in the above conditions causes a change in the opponent color, but not large enough to be perceived by the visual system, so the color appears "constant."

The adjustment process of negative feedback control needs time to finish. The larger the change of the spectral distribution and the brightness of the visual surroundings, the longer the time needed to adjust the visual system to full adaptation to the changed visual surroundings by the systematic NFC. The visual system also adapts partially to different areas of the surroundings. If we gaze at a colored spot, the color gradually appears less saturated and reaches a stable appearance after a while. During the above process, the cones in the retinal area receiving the light from the colored spot will change in absolute and relative sensitivity under the systematic NFC to adapt to the colored spot. When the color of the spot appears stable, by quickly moving the eyes to gaze at a neutral background, we can see the same size and shape but an opponent color after image on the gazed position. This is because the adaptation state in the corresponding area of the color spot has not changed much,
but the spectral power distribution of the area has changed. So, the color vision excitations have changed and the color sensation appears different. From equations (1) and (6) we can see that if the denominator remains unchanged, but the numerator has changed corresponding to the neutral surroundings, there will be a change in the color vision excitations and the opponent visual signals will cause a color sensation opponent to the original color of the adapted color spot.

For a better description of how the systematic NFC adjusts the sensitivities of the three kinds of cone photoreceptors to adapt to the visual surroundings in an \((x, y)\) chromaticity diagram, the term "visual reference point" is introduced. The visual reference point is an \((x, y)\) coordinate that represents the adaptation state of the visual system in the \((x, y)\) chromaticity diagram. If the visual system fully adapts to the visual surroundings then the visual reference point is located at the \((x, y)\) coordinate of the visual surroundings. The visual reference point corresponds to the denominators of the color vision excitations in the equations (1) and refers to the
physiological state of the cone photoreceptors under the adaptation to the visual surroundings. A color vector in the \((x, y)\) chromaticity diagram can better describe color appearance than just the chromaticity coordinates of the color sample. The color vector consists of the visual reference point and the chromaticity coordinate of the color sample. The vector points from the visual reference point to the position of the color sample in the chromaticity diagram. The length of color vector represents saturation and direction represents the hue of color appearance.

If we gaze at a color spot for a while, the visual reference point will move towards the \((x, y)\) coordinates of the color. Because the incomplete adaptation state of the visual surroundings may not be stable, when we quickly move our eyes to gaze at another neutral background, the visual point will somewhat jump to a point near the neutral point (for example, the point of equal spectral light source E). The visual system does not fully adapt to the visual surroundings by the systematic NFC in time. That is the visual reference point has not moved to the point of the visual surroundings, but the gazed color has changed to be
neutral, so we see an opponent color after image. The after image phenomenon that has been described is known as a successive color contrast effect. The successive color contrast can be simply explained by the color vector shown in figure 6, a CIE(x, y) chromaticity diagram. In the diagram, A is the chromaticity point of visual surroundings, B is the chromaticity point of the gazed color sample, and C is the chromaticity point of visual reference point after stable, but not full, adaptation. In the diagram, the point D is where the visual system jumps to (from point C) when the eyes are quickly move to gaze at the background. When we gaze at the color spot, the reference point of the partial retina will eventually move from A to point C. With the moving of the reference point, that is with the reduced length of the color vector $\mathbf{P}(C,B)$ as in Fig.6-1, the color of the spot will gradually appear less saturated. Finally, the reference point is stable at point C, the color vector becomes $\mathbf{P}(C,B)$. The length of color vector $\mathbf{P}(C,B)$ represents the saturation of the color's appearance. After this, we quickly move our eyes to gaze at then neutral background. Because the incomplete adaptation reference point may not be stable, it will jump to
Figure 6. Successive color contrast (afterimage). A is the chromaticity point of visual surroundings, B for gazed color sample, C for reference point of the stable unfull adaptation, and D for original reference point jumps from C when the eyes are quickly moved to gaze at the background. Color vector \( \mathbf{P}(C,B) \), on Figure 6-1, represents the color appearance of the color spot when the visual reference point is stable in C, \( \mathbf{P}(D,A) \), on Figure 6-2, represents the color appearance when the eyes are quickly moved to gaze at the background.
point D. The color should be represented at the point of visual surroundings, point A. The color vector becomes \( \mathbf{P(D,A)} \) as shown in Fig.6-2. These two color vision vectors are in the opposite direction, so we see an opponent color image. After a while, the opponent color image will disappear with the adaptation of the visual system to the new visual surroundings. The reference point moves from point D to point A under the process of systematic NFC. Finally the visual vector equals zero, there will be no chromatic sensation, and the visual system fully adapts to the new visual surroundings.

Another familiar color vision phenomenon is that of simultaneous color contrast. This phenomenon has the effect of an induced contrast due to adjacent colors that are opponent in nature. Simultaneous contrast is an induced effect due to the surround. The reason for simultaneous color contrast is that the visual system can partially adapt to the visual surroundings. The visual reference point of one area of the retina corresponding to one color will slightly shift to its opponent color, so the color vision vector is larger than that with no surrounding color, so the color appears to
be more saturated. In figure 7, point A represents a yellow color and point B represents a blue color. The two samples are arranged as shown in figure 8 such that the yellow color surrounds the blue color. Point E represents the visual surroundings. When observing this color sample, the adaptation of the partial area of the retina, which corresponds to the observed blue color area, will be affected by the surrounding yellow color. In this case, the visual reference point will move somewhat towards the yellow point from point E. The resulting color vector is \( \mathbf{P}(C, B) \) which is larger than \( \mathbf{P}(E, B) \), so the blue appears to be more saturated than if it were viewed on a neutral background.

Because the sensitivity of the three kinds of cones are adjusted separately by the negative feedback control, each kind of cone photoreceptor has its own sensitivity and processes its own image. The range of the equivalent visual electrical signals is from 0 through 100 for full adaptation. The final color image in the brain is the mixture of the three individual processed images that are encoded and decoded by the antagonistic and nonantagonistic processes. The systematic color vision model can explain the color
Figure 7. Simultaneous color contrast. A is the chromaticity coordinate of surrounding yellow color, B is that of blue sample, C is visual reference point of the retinal area which is used to observe the blue area, E is that of visual surroundings. The visual reference point of the retinal area for observing the blue area is affected by the surrounding yellow color, it slightly moves towards point C, the color vector $\mathbf{P}(C,B)$ is more saturated than $\mathbf{P}(E,B)$.
Figure 8. Color sample used for demonstrating simultaneous color contrast. Blue color surrounded by yellow color.
vision phenomena introduced by Land.\textsuperscript{45,46} For Karp's demonstration,\textsuperscript{47} the term visual reference point can be used to replace the term 'white cue' to explain the observed full color phenomenon. Under the conditions of the visual surroundings, the visual system will adapt to the mixture of colored light and white light in the visual surroundings. The visual reference point will shift towards the point of the colored light, so we have the color sensation of the colored light and its opponent color. Because of the continuous spectral power distribution of the white and red lights, we can see the colors around the reference visual point.

From the systematic color vision model we can get the simplified mathematical equations (6) and (7) which are much like the CIELAB equations. In equations (6) and (7), the equivalent visual electrical signals are physiologically quantitative data and the results \( C(R-G), C(Y-B) \), and \( L \) represent the psychophysically quantitative data. Thus equations (6) and (7), as well as the systematic color vision model, make it possible to combine the physiological and psychophysical quantitative data into one model. If we select suitable coefficients, and use the transformed \( X, Y, Z \) values
of Hunt and Pointer\textsuperscript{46} as pseudo spectral sensitivities of cone photoreceptors, then we can get a real color space represented by the systematic color model. If we use the equivalent spectral power distribution of the light source at the reference point for incomplete adaptation to calculate the denominator of the color vision excitations, we can predict color appearance accurately.

This thesis give a qualitative control model of the systematic color vision model. Because of the extensive arborisation of the axon terminal of horizontal cell and the complexity of the brain, it is impossible to know the distribution function of the visual signals for horizontal cells and the corresponding functions of the brain. The author will continue to work on this topic and try to give a simplified quantitative control model. It is hoped that the simplified quantitative control model can be used as a better and more practical color vision model for physiological research of the human visual system and for robot machine color vision.
Conclusions

The systematic color vision model is based on the systematic negative feedback control of visual system and previous color vision theories. This systematic color vision model can explain color vision phenomena and can provides a better understanding of the color vision process. This systematic color vision model also gives a outline of vision processing of the visual system.

The systematic NFC includes the Ca\textsuperscript{2+} negative feedback inside the cone photoreceptors, negative feedback of the horizontal cells, and negative feedback of the brain. Among the three kinds of NFC, the Ca\textsuperscript{2+} negative feedback primarily contributes to the light adaptation of the visual system, controlling both absolute and relative sensitivities of the cone photoreceptors. The negative feedback of horizontal cells may mainly adjust the relative sensitivities of the cone photoreceptors and contributes to the chromatic adaptation. The negative feedback of the brain includes two
parts. One is controls the sensitivities of the cone photoreceptors for both chromatic and achromatic adaptation. The other controls the size of the pupil for only achromatic adaptation.

The visual system includes three main stages, cone photoreceptors stage, visual signal processing stage, and the color sensation stage, described as the stage theory. The cone photoreceptors stage receives light and initializes visual electrical signals. The visual signal processing stage antagonistically and directly process the visual electrical signals initiated by the cone photoreceptors. The color sensation stage receives the processed visual electrical signals and evokes color sensation. Under the systematic NFC, every kind of cone photoreceptors possesses its own sensitivity and forms its own image, just as described as Land's theory.

The systematic color vision equation can combine physiological quantitative data and psychophysical quantitative data. Based on the systematic color vision model and experimental data, suitable coefficients can be selected for the systematic color vision equation to build a more
uniform color space. The color vision space uses the pseudo relative spectral sensitivities of cone photoreceptors, but not CIE color-matching functions. So the color vision space can more correctly represent the human color vision and color appearance.

The reference point of the visual system represents the adaptation degree and adapted chromaticity of visual system. It can give us a definite sign of chromatic adaptation degree on a chromaticity diagram.

The quantitative control model of the visual system can be used to quantitatively study the visual signals processing and to develop analogue model for robot color machine vision.
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