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A Mathematical Model of Retinal Receptive Fields Capable of Form & Color Analysis

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In an effort to understand the workings of the retinal receptive fields, Enroth-Cugell and Robson developed a mathematical model that utilized the difference-of-Gaussian (DOG) function, an equation in which the inhibitory portion of a receptive field is subtracted from the excitatory portion. Additions to the original Enroth-Cugell and Robson equation have been successful in modeling a two-dimensional array of different-sized receptive cells. However, this model could be greatly enhanced if it were able to respond to the chromatic characteristics of a stimulus. In this study, the existing model was extended to include chromatic analysis. Using Mathematica, the spectrally opponent nature of the receptive field and the trichromatic features of the cone pigment systems were added to the model via a filter placed before the existing equation. To validate this color sensitive model, the model was exposed to pure color fields that ranged in hue from 400nm to 700nm. The results obtained from this full-field stimulation were highly correlated to the findings of past physiological experiments. To further validate the model, two participants performed a series of psychophysical matching tasks involving simultaneous color contrast stimuli. The model was presented with an identical set of stimuli. The results obtained by the behavioral testing were highly correlated with those produced by the model indicating that the color-opponent processing responsible for simultaneous color contrast begin at the level of the ganglionic receptive fields.

Key Words: Vision; Retina; Receptive Fields; Computer Modeling; Simultaneous Contrast

Background

Color is an integral feature of how human beings perceive the surrounding world. We describe objects as if color were an integral feature of that object. However, color perception depends greatly upon the structure and function of the visual system. The way in which the visual system operates can cause the same object to appear to have more than one color in different circumstances and surroundings. For an example of the mutable nature of color look at Figure 1. In this illustration, there are two complimentary color fields with an identical gray square in the center of each. By examining the figure, one can see that the gray box in the blue field takes on a yellowish tint while the gray box in the yellow field appears blue-gray. The original gray hue has not changed, but our perception of the color has been effected. The hue shift caused by the interaction between two colors is known as simultaneous color contrast. Several researchers have postulated about the possible physiological mechanisms that cause simultaneous color contrast. Jameson and Hurvich (1964) suggested simultaneous color contrast occurs because of the inhibitory effects between adjacent neurons. To continue with the previous simultaneous color contrast example, Jameson and Hurvich proposed that retinal neurons which are part of a blue

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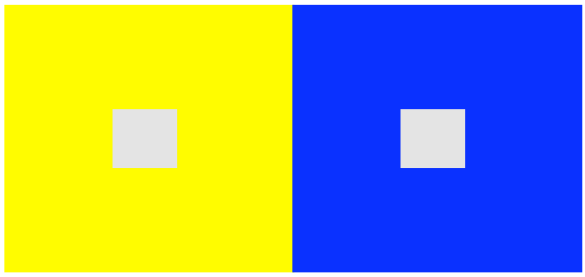

Figure 1: Simultaneous color contrast example.

response system are highly activated by the large blue field surrounding the gray box. Consequently, these activated neurons will inhibit the blue response in the adjacent retinal neurons which react to the gray square. The inhibition of a color offsets the typical balance that exists between that hue and its compliment. The compliment of blue is yellow, and the aforementioned blue inhibition causes the yellow compliment to be integrated into the gray response. Jameson and Hurvich used the term "neuron" when describing the location of the inhibitory actions responsible for simultaneous color contrast. Neuron is broad, especially when referring to highly specialized structures like the eye and the retina. Consequently, an understanding of more accurate and descriptive terminology is required before the discussion of simultaneous color contrast and color opponency can proceed. In 1953, Kuffler and Barlow independently described the structure of what came to be known as a receptive field. By inserting microelectrodes into individual ganglion cells, they found that the firing rate of some neurons increased when exposed to a concentrated light stimulus while the firing rates of other neurons decreased. Furthermore, these excitatory and inhibitory inputs are arranged in a very particular way, a center-surround organization (Figure 2). The example shows an off-center, on-surround arrangement; this basically means that if light falls on the surround the firing rate of the neuron would increase and if light hits only the center region the firing rate would decrease. The opponency created by the center-surround arrangement became a key feature in many later experiments and discoveries. Though the initial receptive field research was conducted in cats and frogs, center-surround receptive fields have since been found in the primate visual system (Hubel & Wiesel, 1960; DeValois et al, 1958). Receptive fields act as funneling system within the retina. There are over 125 million receptor cells and only 1 million ganglion cells in the retina. Thus, receptive fields must funnel the information from many receptor cells into a single ganglion cell. Yet, it is important to note that a single receptor is able to send outputs to multiple ganglion cells due to an intervening layers of intermediate cells . This overlapping arrangement in ganglionic receptive fields causes inhibitory effects known as lateral inhibition. Lateral inhibition was first described by Hartline and Ratliff (1957) using the compound eye of the Limulus as a model. Lateral inhibition is defined as the process of adjacent sensory units inhibiting one another. The process of lateral inhibition compiles information from adjoining cells and thereby heightens any existing differences within the stimulus pattern. Just like the ommatidia of the Limulus, center-surround receptive fields are sites of lateral inhibition in the primate visual system. The oppositional organization of the center and surround portions of the receptive field generates the lateral inhibition. The complete stimulation of the center cancels out total stimulation of surround. However, different stimulation patterns across the receptive field will yield different ganglionic firing rates. Lateral inhibition within receptive

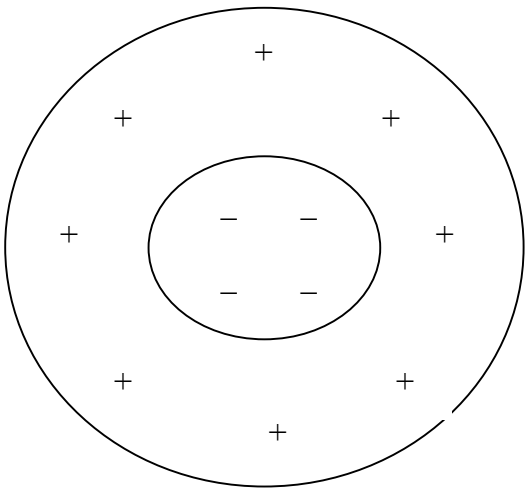

Figure 2: An off-center, on-surround receptive field.

fields accounts for a number of perceptual phenomena like simultaneous brightness contrast (Figure 3). Simultaneous brightness contrast occurs because of inhibitory interactions between adjacent receptive fields. The gray square surrounded by black will appear lighter than the identical gray square on the white background. The strong excitation caused by the white surround will yield greater levels of lateral inhibition in the gray box, and as a result the gray area appears darker than it truly is. Kuffler and Barlow's work with receptive fields only utilized achromatic stimuli, but their discoveries did stimulate other researchers to experiment with diverse types of stimuli and single-cell recording techniques. Three years after Kuffler and Barlow's landmark discovery, Svaetichin (1956) published findings from an experiment in which different wavelengths of light were found to cause varied response patterns in the retinal bipolar cells of goldfish. Svaetichin found response patterns which were very similar to the center-surround distribution noted by Kuffler and Barlow (Figure 4). Color-opponent receptive fields, as they came to be known, operate through the paired-opposition of a color and its compliment. Spectrally-opponent receptive fields can have a myriad of color combinations: red on-green off, red off-green on, blue on-yellow off, and blue off-yellow on. Receptive fields with color capabilities have also been found in the visual systems of primates (DeValois, Smith, Kitai & Karoly, 1958; DeValois, 1960). The discovery of the color-opponent receptive field gave physiological support to the color-opponent theory of vision. Proponents of color-opponent theory like Ewald Hering believed that people actually experience color as if it were composed of four primaries, not three. The primaries were

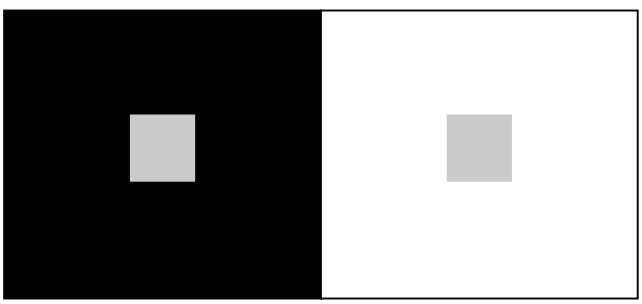

Figure 3: Simultaneous brightness contrast example.

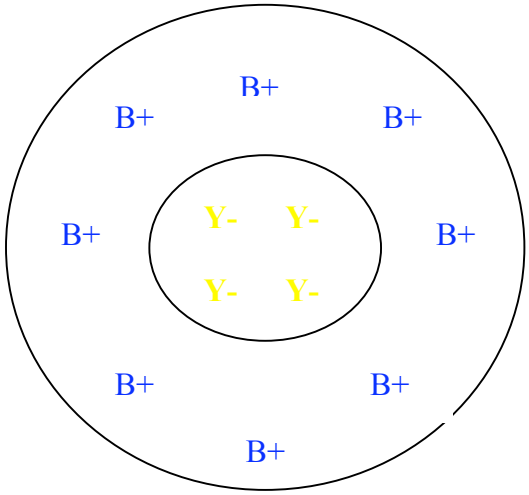

Figure 4: Color-opponent receptive field organization.

paired, red-green and blue-yellow. Within a given pair, it was hypothesized that the primaries would act in opposition to one another. For example if the red primary was fully stimulated, green primary would be totally inhibited. The color-opponent theory is also supported by perceptual phenomenon like the color aftereffects. If a man stares at a red wall for a few minutes and then looks at a bare wall, he will perceive a green tint on the bare wall. This green coloring appears because staring at the red wall fatigued the red channels in the man's eye. When the man looked away from the red wall, his red channels ceased to fire, and the opponent green channels were inversely stimulated. This color opponency processing is a salient factor in the simultaneous color contrast phenomenon, and it seems logical to conclude that the color-opponent receptive fields of the retinal ganglia may be the sites where this color-opponency principle exercises its effects. Currently, many researchers are concerned with investigating the interaction between the color-opponent systems and trichromatic systems in the eye. Many theories exist on how the information from the three cones is organized and then transferred into color-opponent receptive fields. If the simple receptive fields explained by Kuffler and Barlow can account for simultaneous brightness contrast, it is reasonable to contend that the color-opponent receptive fields have a role in simultaneous color contrast. Certain spectrally-opponent receptive fields within the retina are highly stimulated by one color while the adjacent receptive fields are

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inhibited by the compliment. The lateral inhibition occurring within the spectrally-opponent receptive fields may be the inhibitory process Jameson and Hurvich implicated in their simultaneous color contrast hypothesis. The color-opponent process that produces simultaneous color contrast seems fairly clear; however, opinions differ as to where the inhibitory interactions transpire within the visual system. Cells with spectrally-opponent capabilities have been found throughout the visual system. The lateral geniculate nucleus (LGN) contains color-opponent cells similar to those found in the ganglion cells (DeValois et. al, 1958; DeValois, Abramov & Jacobs, 1966). There are also cells within the visual cortex that have a more complex type of color-opponent arrangement known as double opponent (Michael, 1985). But despite the existence of color-opponent cells elsewhere in the brain, it is reasonable to contend that the inhibitory process that causes simultaneous color contrast starts at the retinal ganglion level just as it does in simultaneous brightness contrast. Retinal ganglia are the first cells in the visual system to generate action potentials, and they filter all of the information flowing to the other color sensitive receptive fields in the LGN and the striate cortex. Moreover, the disparity between the number of receptor cells and retinal ganglia would necessitate a process like lateral inhibition that combines and condenses the inputs from several receptors. Therefore, the color-opponent receptive fields of the retinal ganglia are the logical sites for the inhibitory interactions for the simultaneous color contrast process to begin. As previously stated, the goal of this study is to examine the possibility that simultaneous color contrast is a function of the color-opponent receptive fields in the retinal ganglion cells; this will be accomplished in a quantitative fashion.

The Current Study

In this study, the inhibitory processes that occur within color-opponent receptive fields will be examined through mathematical modeling. By using a computer model, the experimenters will be able to simulate an array of receptive fields and confine the scope of inquiry to the retina and the ganglion cells. These parameters could not be attained with other methods of study like physiological recordings or psychophysical testing.

Background Models: Enroth-Cugell and Robson (1966, 1984) were the first researchers to create a mathematical model of the ganglion cell's receptive field. They developed a difference-of-Gaussian (DOG) function as a model of the typical receptive field response curves that had been found through physiological testing with drifting sine wave gratings. In equation format (1), the first gaussian represents the excitatory portion of a receptive field, and the second gaussian corresponds to the inhibitory regions of a receptive field.

$$\frac{1}{S_e\sqrt{2\pi}} - \frac{(i-w)^2}{2s_e^2} - \frac{1}{S_i\sqrt{2\pi}} - \frac{(i-w)^2}{2s_i^2} \qquad (1)$$

S_e represents the standard deviation of the excitatory field, and S_i represents the standard deviation of the inhibitory field. However, it is the magnitude of S_i and S_e variables that determines which portion of the equation represents the center and which represents the surround. The larger of the two values stands for the surround, and the smaller variable corresponds to the center. The DOG equation is simply the difference in magnitude between the two gaussians. Enroth-Cugell and Robson saw the responsivity curve based on sensitivity across a receptive filed as a unified whole, not separate curves representing the excitatory and inhibitory regions (Figure 5).

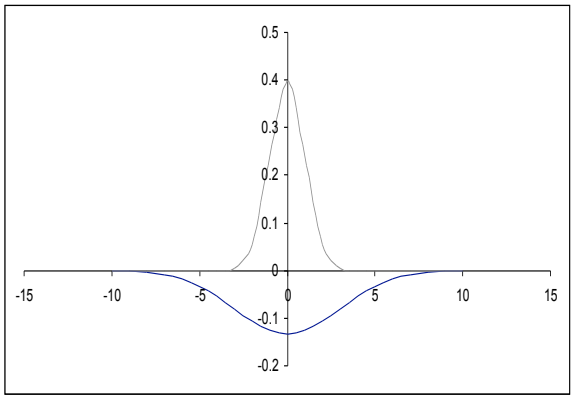
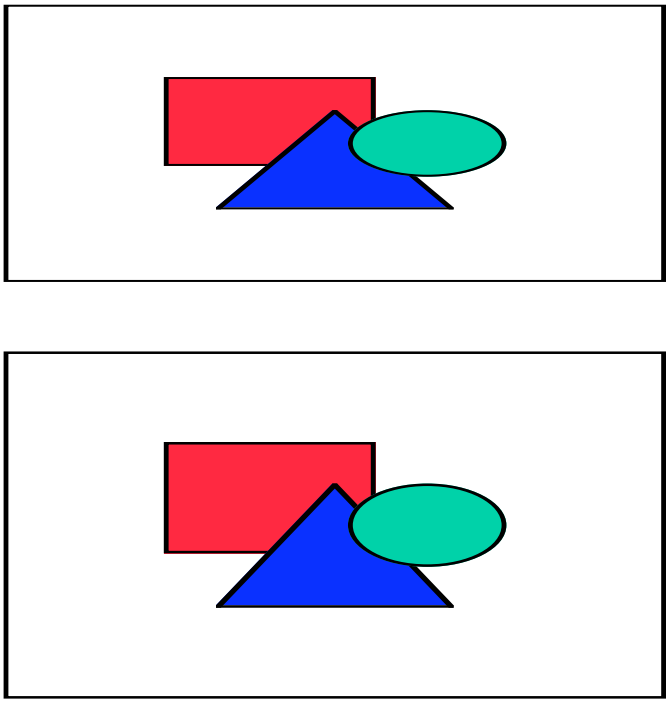


Figure 5: The difference-of-Gaussian equation.

The inhibitory portion of the function is inverted, but that has only been done for clarity's sake. In fact, the sole difference between the excitatory and inhibitory portions of the curve is the magnitude of the standard deviation, and it is this difference which that the DOG function exploits. Moreover, the Enroth-Cugell and Robson's model was able to predict the responsivity of a receptive field to a unique stimulus by utilizing only four parameters: two spatial dimensions and two responsivities at zero spatial frequency. Krantz (2000) amended Enroth-Cugell and Robson's DOG function to include additional information about the nature of the retinal receptive fields. When designing his model, Krantz considered the physical nature of the receptive field. Receptive fields and ganglion cells are two-dimensional structures; however, the DOG model only has one-dimensional capabilities. By including the $(j-w)^2$ component derived from the Pythagorean theorem, the Krantz model gained two-dimensional abilities. The addition of this two-dimensional feature required the substitution of S_i/S_e for 1 in the numerator position of the first gaussian to compensate for the unequal area increase between the inhibitory and excitatory regions.

$$\frac{\left(\frac{s_i}{s_e}\right)}{s_e\sqrt{2\pi}} e^{\frac{(i-W)^2+(j-W)^2}{2s_e^2}} - \frac{1}{s_i\sqrt{2\pi}} e^{\frac{(i-W)^2+(j-W)^2}{2s_i^2}} \quad (2)$$

Furthermore, the Krantz model is able to simulate an array of receptive fields. The Enroth-Cugell and Robson model only accounted for a single receptive field. It is important to remember that while a single receptive field is capable of lateral inhibition many stimuli are larger than a single receptive field. Thus, most stimuli are detected by an array of receptive fields. The standard DOG model with the Krantz modifications is able to analyze a variety of stimuli and produce predictive receptive field outputs. This updated model has been applied to a diverse number of stimuli including simultaneous brightness contrast (Figure 6 and Figure7). The Krantz model is able to analyze the receptive field response to achromatic bit-map file. Yet, the updated DOG function still does not offer a complete view of the



Figures 6 & 7: The input stimulus (top) and the model generated output (bottom).

activities of the receptive fields in the retina. Just as Svaetichin expanded Kuffler and Barlow's work with receptive fields by introducing color stimuli, this study will expand Krantz's augmented DOG model to account for chromatic stimuli. Color is certainly an integral part of the visual experience for humans and other primates. If the Krantz model could be expanded to account for color-opponent receptive fields, it could be used to predict the retinal ganglionic response to a wider variety of color stimuli. Another shortcoming of the Krantz model was a lack of a behavioral correlate. Thus, after the new color model is complete, its outputs will be compared to those obtained from psychophysical testing data. It is not expected that the model findings and the psychophysical findings will be an exact match. This incongruity stems from the fact that the model is merely an array of receptive fields in the retina while the participants are experiencing the stimulus through the retina and many additional layers of processing (LGN, visual cortex, etc.). However, the two data sets should show similar trends.

Model Development: The Krantz model was augmented to encompass the color aspects of a stimulus. Chromatic analysis capabilities were added by placing a series of pre-equation "filters" to the existing Krantz program. These filters were designed in three by three matrix format in order to retain the three-dimensional nature of a color stimulus. The first matrix changed the computer's chromaticity values to CIE tri-stimulus coordinates.

$$\begin{pmatrix} 0.607 & 0.174 & 0.2000 \\ 0.299 & 0.587 & 0.114 \\ 0.00 & 0.066 & 1.116 \end{pmatrix} \quad (3)$$

The CIE values represent a standardized system for color description developed in 1931 by an international commission. The second matrix converted the CIE values to cone systems (Teufel & Wehrhahn, 1999).

$$\begin{pmatrix} 0.61209 & 2.14231 & -0.02966 \\ -0.969775 & 2.955775 & 0.305425 \\ 0 & 0 & 1.41183 \end{pmatrix} \quad (4)$$

The third and final matrix changed the cone system information into a color-opponent organization (Benzschawel, Brill, & Cohn, 1986).

$$\begin{pmatrix} 0.85 & 1.50 & 0.01 \\ 1.66 & -2.23 & .37 \\ 0.34 & 0.06 & -0.71 \end{pmatrix} \quad (5)$$

This opponency data was then analyzed by the gaussian-based equation designed by Krantz. It is important to note that several of the numbers in the second and third matrixes were changed from their original format to account for the effects of multiplying matrixes. The alterations merely countered the amplification effect caused by the multiplication process.

Simulation Environment: The color-inclusive model was programmed into Mathematica 4.2 (Wolfram Research Inc; Champaign, IL). Mathematica 4.2 is a multi-faceted software program. It is capable of performing a wide range of activities from relatively simple calculation functions to providing an integrated technical programming environment. Mathematica provided two key features necessary for this experiment. It was capable of producing graphic representations of the results, and it worked with problems symbolically. Furthermore, all of the stimuli designed in order to test the model utilized Mathematica's interface compatibility with Java.

Verification: The model was verified by programming a matrix containing CIE color space coordinates into the Mathematica notebook. The CIE values consisted of a list of wavelengths every 10 nanometers (nm) between 400nm and 700nm, the spectrum of visible light (Figure 8). Each color was quantified by a set of three numbers that placed the color in three-dimensional space according to a tri-stimulus value system, XYZ. This CIE matrix was identified as the input stimulus for the model to

$$\begin{pmatrix} 400 & 0.0143 & 0.0004 & 0.0679 \\ 410 & 0.0435 & 0.0012 & 0.2074 \\ 420 & 0.1344 & 0.0040 & 0.6456 \\ 430 & 0.2839 & 0.0116 & 1.3856 \\ 440 & 0.3483 & 0.0230 & 1.7471 \\ 450 & 0.3362 & 0.0380 & 1.7721 \\ 460 & 0.2908 & 0.0600 & 1.6692 \\ 470 & 0.1954 & 0.0910 & 1.2876 \\ 480 & 0.0956 & 0.1390 & 0.8130 \\ 490 & 0.0320 & 0.2080 & 0.4652 \\ 500 & 0.0049 & 0.3230 & 0.2720 \\ 510 & 0.0093 & 0.5030 & 0.1582 \\ 520 & 0.0633 & 0.7100 & 0.0782 \\ 530 & 0.1655 & 0.8620 & 0.0422 \\ 540 & 0.2904 & 0.9540 & 0.0203 \\ 550 & 0.4334 & 0.9950 & 0.0087 \\ 560 & 0.5945 & 0.9950 & 0.0039 \\ 570 & 0.7621 & 0.9520 & 0.0021 \\ 580 & 0.9163 & 0.8700 & 0.0017 \\ 590 & 1.0263 & 0.7570 & 0.0011 \\ 600 & 1.0622 & 0.6310 & 0.0008 \\ 610 & 1.0026 & 0.5030 & 0.0003 \\ 620 & 0.8544 & 0.3810 & 0.0002 \\ 630 & 0.6424 & 0.2650 & 0.0000 \\ 640 & 0.4479 & 0.1750 & 0.0000 \\ 650 & 0.2835 & 0.1070 & 0.0000 \\ 660 & 0.1649 & 0.0610 & 0.0000 \\ 670 & 0.0874 & 0.0320 & 0.0000 \\ 680 & 0.0468 & 0.0170 & 0.0000 \\ 690 & 0.0227 & 0.0082 & 0.0000 \\ 700 & 0.0114 & 0.0041 & 0.0000 \end{pmatrix}$$

Figure 8: CIE color space coordinate matrix.

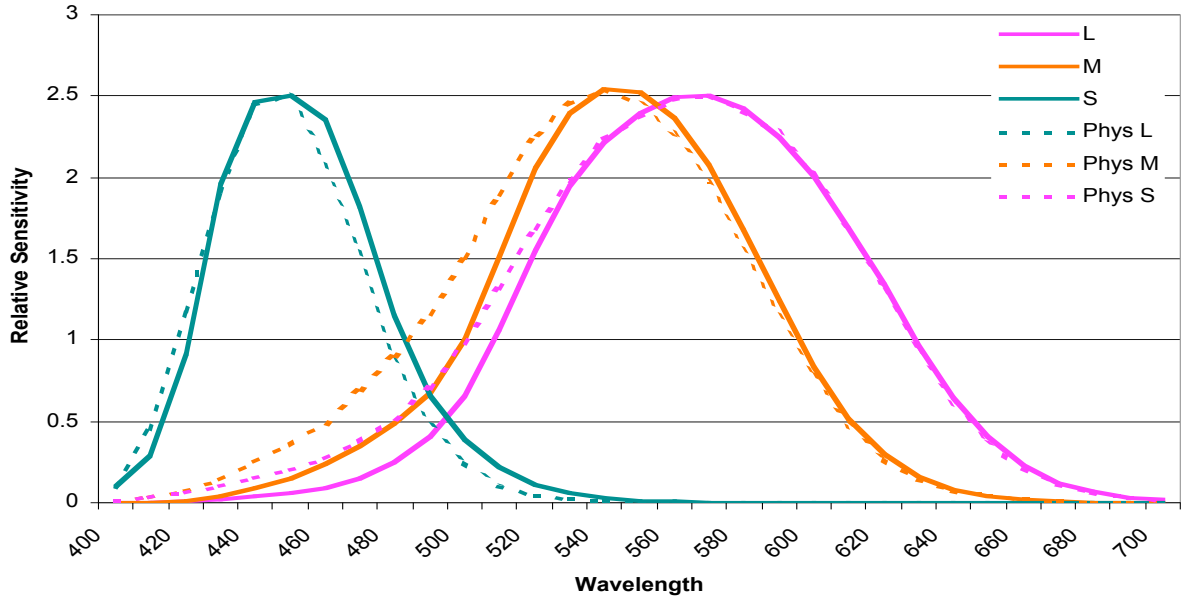
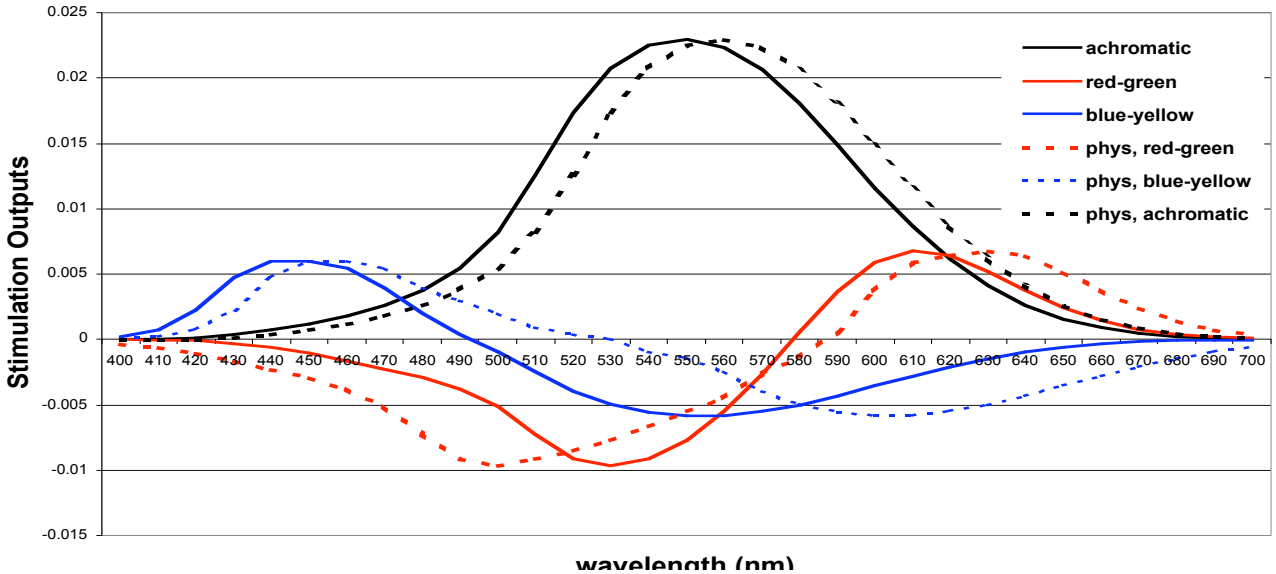


Figure 9: Model-generated cone systems compared to standard physiological findings.

analyze. A single field of pure color would cover the entire span of modeled receptive fields. All of the receptive fields were equally stimulated because the stimulus was composed of only a single color. Yet, it is important to note that the stimulation values obtained from the model are viewed as the equivalent of firing rates within neurons. To test the accuracy of the CIE to cone system matrix, the full field stimuli were run only through the first two filters. The values obtained were supposed to simulate the responsiveness patterns of the cone systems. The model's cone-like outputs were compared to accepted spectral sensitivity curves (Stockman, Sharpe, & Fache, 1999; Stockman & Sharpe, 2000). The cone system results obtained from the model were highly correlated with physiological findings. The long cone system generated by the model was nearly completely aligned with the physiological data (r = 1.00). The medium cone system and short cone system displayed correlations similar to those observed in the long cones (r = 1.00, r = 0.99), respectively. The graphic display of these three cone systems emphasizes the high degree of similarity with physiological finding (Figure 9). To test the accuracy of the entire filter system, the

Figure 10: Model-generated color opponency curves compared to standard physiological findings.



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full field stimuli were run through all three filters. The results derived from this analysis represented the color-opponent receptive fields. The color-opponent analysis revealed opponency curves that followed trends similar to accepted values (Figure 10).

Behavioral Testing

After the color-inclusive model was created and verified by past research, the model was tested with a series of specially designed simultaneous color contrast stimuli. All of the stimuli were composed of two identical grey squares each surrounded by a larger color field (Figure 1). The large fields were composed of complimentary colors like yellow and blue. A set of eight simultaneous color contrast stimuli were designed and saved as bit map files. The bit map format was utilized because bit maps are capable of retaining both form and color information. The same set of stimuli was then used in a psychophysical testing paradigm.

Participants: The psychophysical testing data was obtained from a small number of participants (n = 2). There was one male and one female subject. Both subjects had normal color vision, but the female participant required corrective lenses for near-sightedness. There was also a twenty-year age difference between the two participants.

Materials: The stimulus screen was made up of a color wheel, three sliding control bars, three command buttons, and two center-surround boxes atop one another (Figure 11). The standard center and standard surround boxes were located on the top, left-hand corner of the screen, and the comparison center and comparison surround boxes were placed on the bottom, left-hand corner. The color wheel sat atop the sliding control bars on the right-hand portion of the screen. The sliding control bars controlled the hue, saturation, and brightness of the comparison center. The command buttons were located underneath these sliding control bars. The command buttons included: set colors, match, and reset. Pressing the "set colors" button accessed a

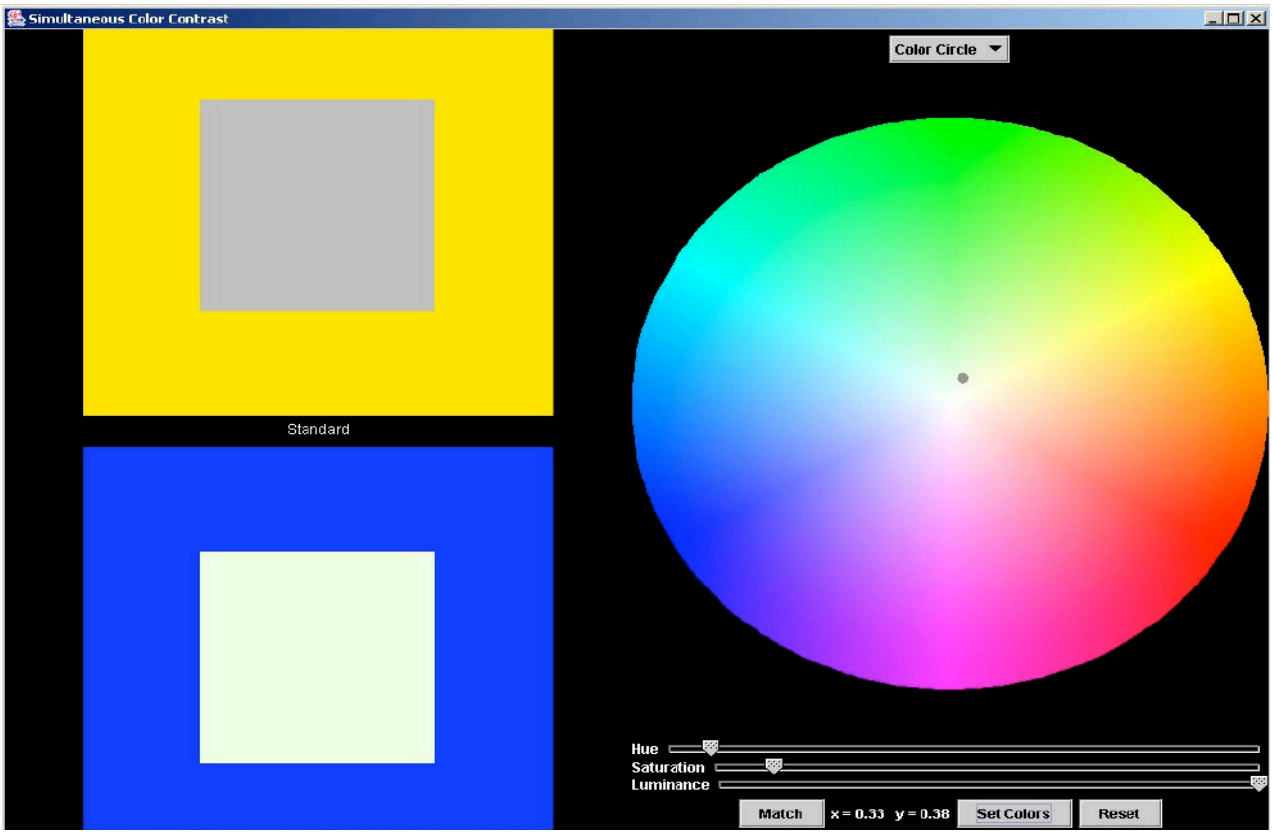

Figure 11: The stimulus screen consisted of two center-surround boxes, a color wheel, and three command boxes.

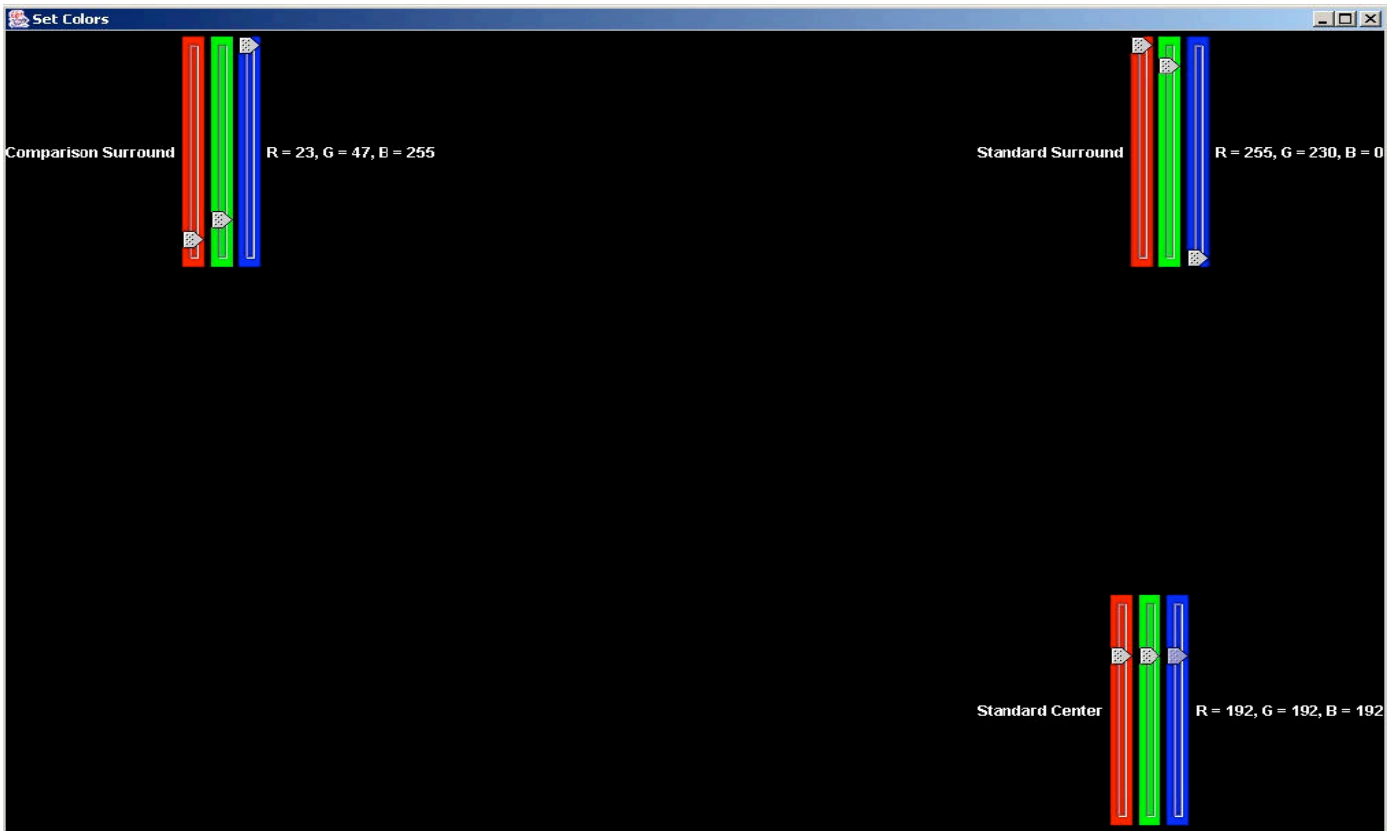

Figure 12: The settings screen which determined the appearance of the center-surround boxes.

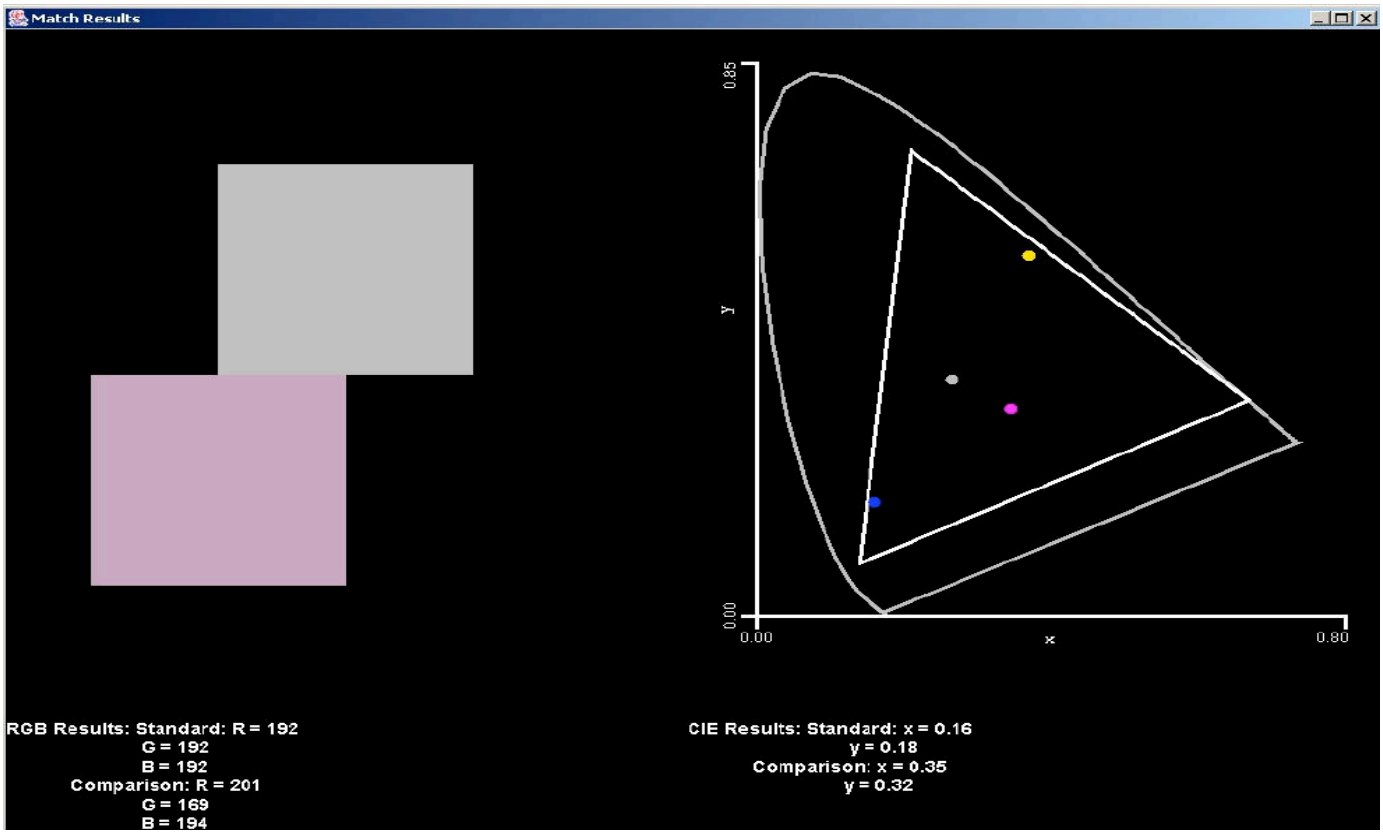

Figure 13: The results screen displayed in the behavioral testing portion of the study.

settings screen. This settings screen allowed the participants to set the color values for the standard center, standard surround, and comparison surround (Figure 12). The color values were entered by adjusting three sliding tool bars: red, green, and blue. Moreover, selecting the "match" button on the stimulus screen presented the results for a given trial (Figure 13). The results were presented in RGB and CIE values. There was also a CIE diagram on which the values of the various centers and surrounds were plotted.

Procedure: The participant opened the program and selected the "set colors" button. The subject would then set the values for the standard surround, standard center, and comparison surround for a given simultaneous color contrast stimulus. The participant then selected the "done" button to save these values. The stimulus screen reappeared, and the participant used the sliding control bars to adjust the comparison center to match the standard center. The participant could opt to forgo using the sliding control bars and utilize the pointer on the color wheel instead. In the color wheel option, the subject would simply move the pointer around the color wheel until a color match was obtained. When a color match was obtained, the participants would select the "match" button. The results screen would then appear, and the subjects recorded their RGB results for that particular trial. The participants conducted the experiment on the same computer and monitor in a darkened room. The subjects performed twenty trials of each of the eight simultaneous color contrast stimuli. The subjects would only conduct five to ten trials with the same stimulus at time and then switch the settings to another simultaneous color contrast stimuli. To prevent fatigue, the participants were allowed to complete the 160 trials over several testing sessions.

Results

The model produced three output channels: achromatic, red- green, and blue-yellow. Each channel output contained a graphic representation of the relative receptive field stimulation values (Figure 14) and both a maximum and a minimum stimulation number. When analyzing the results,

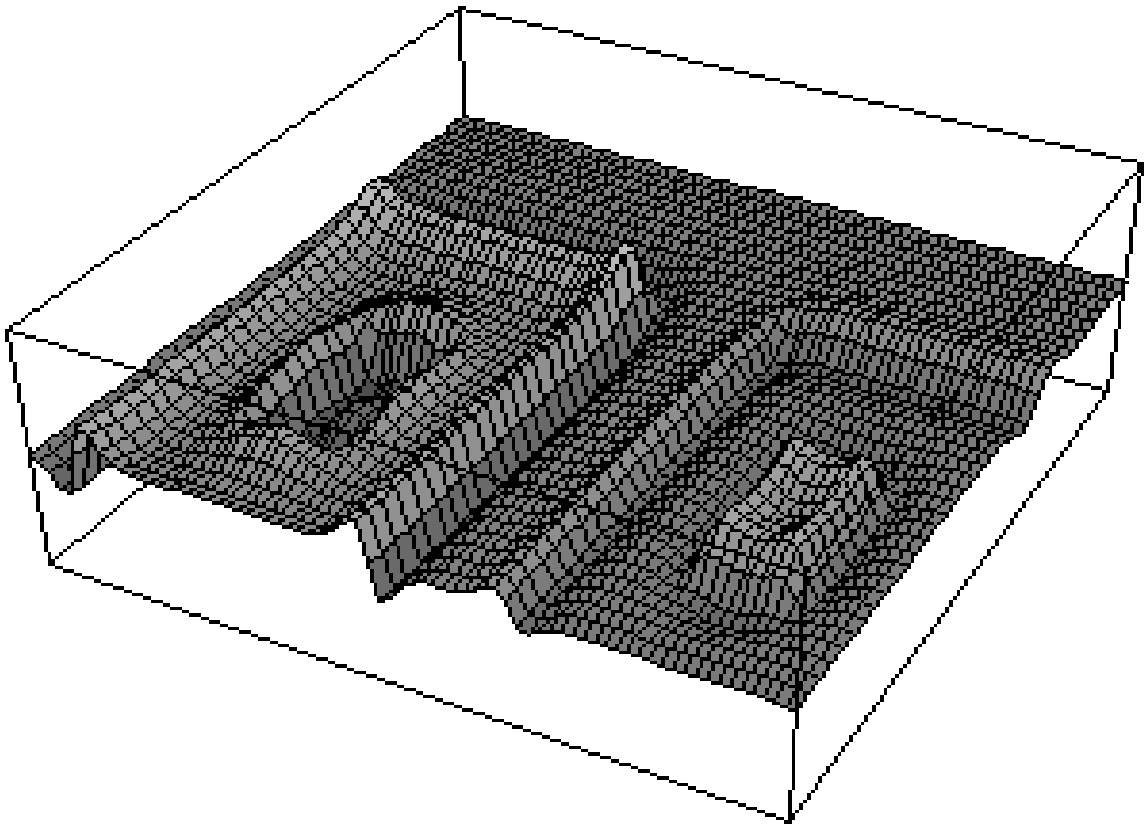

Figure 14: A graphic representation of the relative receptive field stimulation values.

the minimum value was subtracted from the maximum value to obtain the range of values that stimulated the receptive fields.

$$\text{distance} = \sqrt{\{(\text{red/green}_{[\![\max]\!]} - \text{red/green}_{[\![\min]\!]})^2 + (\text{blue/yellow}_{[\![\max]\!]} - \text{blue/yellow}_{[\![\min]\!]})^2 + (\text{achromatic}_{[\![\max]\!]} - \text{achromatic}_{[\![\min]\!]})^2\}} \quad (6)$$

The square of the red-green channel range was added to the square of the blue-yellow range and to the squared range of the achromatic channel to yield the squared distance between the variables. This distance variable was calculated for all eight stimuli. Then, the participants' results were compiled and analyzed. The means of the R, G, and B values for the comparison square were calculated for each stimulus. The mean of the R comparison was then subtracted from the standard R, and the resulting value was squared. The same procedure was used for the G and B values. The squared differences for all three values were added together to obtain the squared distance.

$$\text{distance} = \sqrt{(R_{[\![\text{standard}]\!]} - R_{[\![\text{comparison}]\!]})^2 + (G_{[\![\text{standard}]\!]} - G_{[\![\text{comparison}]\!]})^2 + (B_{[\![\text{standard}]\!]} - B_{[\![\text{comparison}]\!]})^2} \quad (7)$$

Subject one's results were highly correlated with subject two's results (r = .82). Next, the outputs produced by the model were compared to the psychophysical results obtained from the two participants. A correlation analysis was performed between the participant's calculated RGB distance data and the calculated distance values derived from the model. Individual subject results were highly correlated with the computer generated results (r = .71, r = .70). The average of the subjects' results were also highly correlated the computer generated results (r = .74).

Discussion

A mathematical model which simulated the properties of color-opponent receptive fields was developed to investigate the role of lateral inhibition in simultaneous color contrast. Based on colorless mathematical models by Enroth-Cugell and Robson (1966, 1984) and Krantz (2000), the model utilized in this study had to be altered to analyze color stimuli. This was achieved by adding a series of "color filters" to the existing Krantz program. Three filters were used to change computer pixel information into color-opponency data. The validity of these filters was tested through a full-field stimulation assessment. The model replicated the spectral sensitivity curves of the three cone systems with remarkable accuracy, and comparisons to past physiological findings yielded correlation coefficients at or near 1.00 (Stockman, Sharpe, & Fache, 1999; Stockman & Sharpe, 2000). The opponency system analysis showed trends that were also similar to accepted physiological data. The color-inclusive model was further verified through a behavioral experiment. A set of eight simultaneous color contrast stimuli were designed and presented to both the model and human participants. The participants performed a color-matching task and recorded their results. The participants' results were highly correlated to the results obtained from the model. These findings mean that the color-inclusive model can simulate the visual processes responsible for simultaneous color contrast with a fair amount of accuracy. Due to the fact that the model is only composed of receptive fields, the results also show that simultaneous color contrast processing begins in the ganglionic receptive fields and appears to be the result of lateral inhibition. Furthermore, the magnitude of the correlation indicates that the color-opponent receptive fields in the retina are the primary units of color opponency in the visual system. The results of this study are very promising and indicate that computer modeling is a viable and accurate way to study sensory processing in a quantitative manner. In future studies, the color-inclusive model could be utilized to investigate the physiological processes underlying a wide variety of other color phenomenon. The model could also be expanded to included motion analysis and temporal components. The addition of such features would add even greater realism to the model and may eventually lead to the creation of a fully functioning computerized retina. Nonetheless,

this study has several limitations that should be addressed in future research efforts. First, it was not possible to find physiological data that assessed all three channels of opponency information simultaneously: achromatic, red-green, and blue-yellow. Consequently, conglomerations of physiological findings were utilized to evaluate the model's color-opponent outputs. The data sets showed similar trends, but were far from being a perfect match. Thus, every effort should be made to locate physiological data or collect physiological data on all three channels so that the reliability of the final filter can assessed. However, this lack of similar color-opponency data may indicate that the final filter needs to be adjusted or replaced. Another shortcoming of the study was the narrow scope of the behavioral testing. The psychophysical data was collected from two participants who only performed a small number of trials on a set of eight stimuli. More participants, more trials, and more simultaneous color contrast stimuli should be utilized in any future psychophysical testing. Finally, this model only replicates the responses of the retinal receptive fields. It is well known that stimuli at this stage in the visual system are only perceived as edges. Humans do not perceive the surrounding world as a collection of edges and lines; we see whole forms and solid figures. The solid nature of an object is not added until the cortical processing levels. Consequently, a model of the retina alone will never be able to account for all visual processes and perceptual phenomenon. It will eventually be necessary to create cortical models and models of the LGN to obtain a truly accurate and realistic view of the visual system.

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