2002

Color vision sensitivity in normally dichromatic species and humans.

Richard Eugene Van Arsdel
University of Alabama at Birmingham

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

COLOR VISION SENSITIVITY IN NORMALLY DICHROMATIC SPECIES AND HUMANS

by

RICHARD E. VAN ARSDEL

A DISSERTATION

Submitted to the graduate faculty of The University of Alabama at Birmingham,
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy.

BIRMINGHAM, ALABAMA

2002

UMI Number: 3066350

UMI Microform 3066350

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

ABSTRACT OF DISSERTATION
GRADUATE SCHOOL, UNIVERSITY OF ALABAMA AT BIRMINGHAM

Degree Ph.D. Program Vision Science

Name of Candidate Richard E. Van Arsdel

Committee Chair Michael S. Loop

Title Color Vision Sensitivity in Normally Dichromatic Species and Humans

Spectral sensitivity functions for large, long-duration spectral stimuli presented on a photopic white background indicate that wavelength opponent mechanisms mediate detection of such stimuli in both normal and dichromatic humans. Normal humans detect the color of spectral flashes at detection threshold intensities, supporting the premise that wavelength opponent processes signal color. However, dichromatic humans do not see some colors at threshold; rather, they require stimuli up to about 0.4 log units above detection intensity. This suggests that dichromatic humans may have a defect in postreceptoral color processing. To test this, we determined color discrimination thresholds in normally occurring dichromats, including the chipmunk, the 13-lined ground squirrel, and the tree shrew.

Animals were trained with food to perform spatial two-choice discrimination tasks. Detection thresholds were first determined for white, 460-nm, 540-nm, 560-nm, 580-nm, 500-nm long-pass, and 500-nm short-pass increments on white backgrounds of 1.25 cd/m^2, 46 cd/m^2, and 130 cd/m^2. Animals were then trained to respond to the colored increments when paired with the white when both were at an intensity of 0.5 log units above each animal's detection threshold. Color discrimination thresholds were then determined by dimming stimulus pairs (colored vs. white) until the subjects could no longer make the discriminations.

Data indicate that the normally dichromatic species discriminated the color from the white stimuli at a mean intensity of 0.1 (± 0.1) log units above detection threshold in photopic conditions. The ability of normally dichromatic species to discriminate color near detection threshold intensity is consistent with increment spectral sensitivity functions that indicate detection by wavelength opponent mechanisms. This high color sensitivity of normal dichromats suggests that the low color vision sensitivity of dichromatic humans is an abnormal condition and indicates a possible defect in postreceptoral processing, but the specific nature of that dysfunction is open to speculation.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

Figure *Page*

INTRODUCTION

The phenomenon of color vision has fascinated people for centuries, and has served as a substrate for much conjecture. In ancient Greece, Plato remarked that the several colors can scarcely appear to a dog or to any animal as they appear to a human being; nor, indeed do they appear to one man as they do to another; or even to the same man at one time as they do at another (Beare, 1906). Today, the structure and function of systems mediating animal color vision remains the topic of research and debate for practical as well as scientific reasons. Much of our knowledge of color vision has come from a combination of anatomical, physiological, and psychophysical studies.

A good place to begin an overview of color vision is a consideration of photon capture by photoreceptors. The visual system of humans and macaque monkeys will be used as the model for the following synopsis, as most aspects of the macaque visual system have been shown to be physiologically and psychophysically indistinct from that of humans.

Photoreceptors

As light enters the eye, only a fraction of the photons reach the retina due to absorption and scatter; light of shorter wavelengths is particularly affected. Photoreceptors (rods and cones) absorb perhaps one half to two thirds of the light that reaches the retina. Cones are responsible for mediating color vision, and thus the rods will be excluded for the remainder of this discussion.

Each cone type has its own opsin and associated absorption maximum (λ_{max}). In humans with normal color vision, there are three cone types with peak absorptions located approximately at long (L) = 561 nm, medium (M) = 530 nm, and short (S) = 430 nm. Normalized photopigment absorptions for humans reported by Schnapf, Kraft, Nunn, and Baylor are shown in Figure 1. The presence of three photopigments is referred to as a state of trichromacy, whereas dichromatic individuals have two photopigments (thus two cone types), and monochromats have only one photopigment (thus one cone type).

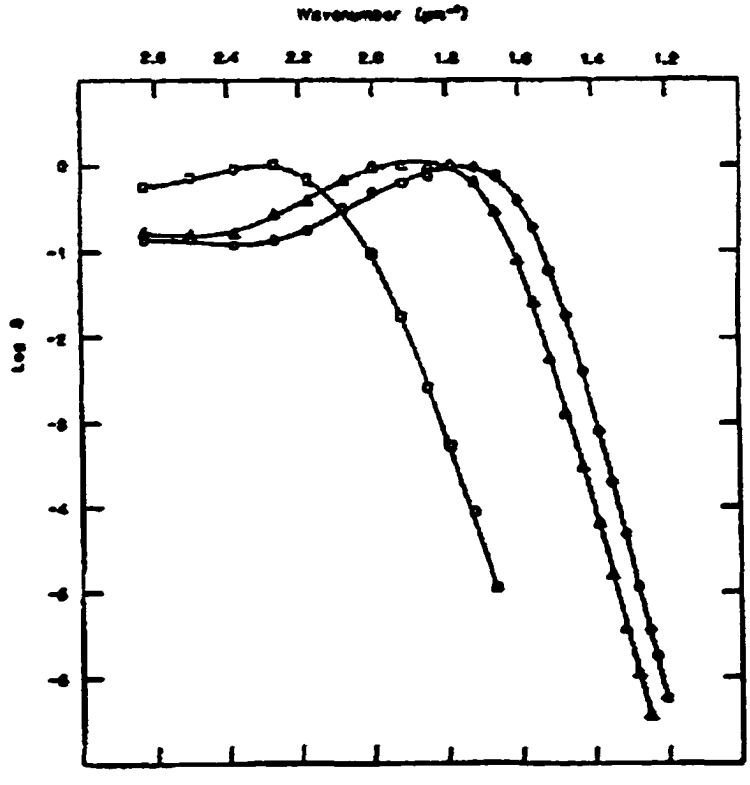

Figure 1. Photopigment absorption curves (λ_{max}) for humans.
Data for rod photopigments removed for clarity. Figure adapted from Schnapf, Kraft, Nunn, & Baylor, 1988.

The arrangement of S, M, and L cones in the living human eye has only recently been delineated. With the use of adaptive optics and retinal densitometry, it has been shown that the proportion of L to M cones is strikingly different between individuals with normal color vision, and that there are large patches of retina in which either M or L cones are missing (Roorda and Williams, 1999). Roorda and Williams speculate that the large individual differences in numbers and arrangement of cone classes indicate that evolution has not yet converged on an optimum proportion of M and L cones for the human eye, possibly because (a) red/green color vision is a relatively new feature of vision in old-world primates, or (b) the statistics of natural scenes, optical blurring, and "clever postreceptoral processing" make M and L cone topography unimportant for visual performance. In other words, if existing postreceptoral mechanisms are sufficient to process and interpret red/green color information from the environment such that an advantage is realized, then further refinement of that aspect of the visual system may not have occurred.

In his book on human color vision, Boynton (1979) discusses evolutionary aspects of photoreceptors in animals. He cites evidence from studies of genetic variation that the difference between the S and other cones is relatively ancient. However, the M and L pigments differ in structure by only 15 of the 364 amino acids, and it is estimated that the M and L cone differences arose only 30 million years ago.

Evolutionary concepts also apply to models of neural circuitry mediating various aspects of vision. With regard to color vision, multiple "opponent" pathways and circuits have evolved that exploit the differential absorption functions between cone types.

Opponency

An absorbed photon has the same effect on a photoreceptor regardless of wavelength. This direct correspondence describes the principle of univariance and implies that one photoreceptor cannot discriminate wavelengths to produce color vision. In order to produce color information, the difference in photon catch rate between cone types must be compared. It is generally agreed that spectrally opponent cells, referred to henceforth as color-opponent cells, make that comparison.

Ewald Hering was perhaps one of the earliest to propose an opponent theory, possibly inspired from his speculations on why one never sees reddish greens or yellowish blues. He suggested that the visual system might be capable of generating signals of two opposite kinds, depending upon wavelength. His theories were at odds with the much more popular trichromatic theory of Young and Helmholz, and decades passed before any physiological evidence supported his ideas (Svaetichin, 1953). Some of the most convincing physiological evidence came from studies by Wiesel and Hubel (1966) in the lateral geniculate body of the Rhesus monkey that led to a commonly used classification of three opponent cell types based on receptive field organizations, as shown in Figure 2. In the figure, "+" and "-" indicate increased and decreased responses, or spike frequencies. Type I and type III cells are shown as having centers with one characteristic response, and larger surrounds with different characteristic responses. Type II cells could be described as having centers and surrounds of the same size, or as having coincident receptive fields with different characteristics.

Whereas type III cells should be suited for responding to luminance contrast changes, type I cells should be suited for responding to both luminance and wavelength differences. Type II cells should be most effective in mediating color opponency, as

proposed by Rodieck (1991). As opposed to luminance contrast or acuity, which depend on differences in photon catch rates at different locations in space by photoreceptors, color vision depends on differences in photon catch rates in the same visual space by different photoreceptor types.

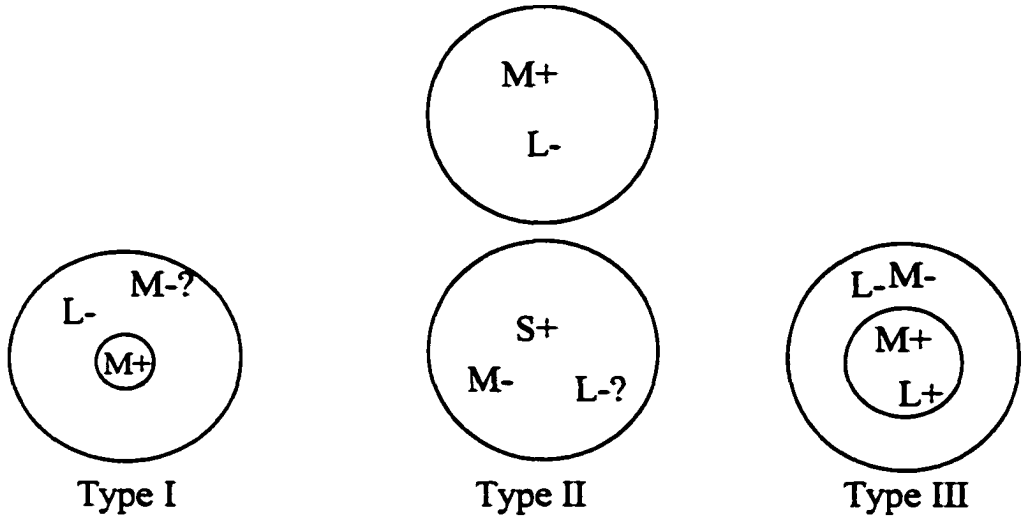

Figure 2. Opponent receptive fields of opponent cell types.
Figure interpreted from Wiesel and Hubel, 1966.

Type II cells constitute only about 6% of retinal ganglion cells (Rodieck, 1991). Nonetheless, they are good candidates for mediators of color opponency. In support of this concept, Curcio et al. (1991) reported that blue cones constitute only 8% of the cone population in the peripheral retina of humans, and further that no blue cones are found in the central retina. Yet blue hues elicit a strong color sensation in humans, as measured by colorimetric purity, and mediate increment-threshold spectral sensitivity for shorter wavelengths, as shown in Figures 5 through 7. Thus, a large population of photorecep-

tors or cells does not seem to be a requirement for good color vision or high sensitivity to spectral increments.

Another aspect of color vision concerns spatial interaction. Although type I cells could mediate color vision, a change in the size of a spectral stimulus, for example, increasing the stimulus size from an area smaller than the receptive field center to one that is larger, would change the relative balance of responses between the opposing center and surround receptive fields. This would cause a subsequent shift in perceived color, upsetting the principle of color constancy. Conversely, changing the stimulus size on a type II cell would increase or decrease stimulation of the opposing inputs by the same amount, maintaining color constancy.

Regardless of which cell type mediates color vision, most color vision models incorporate two color "channels" in humans, referred to as the Blue/Yellow (B/Y) channel and the Red/Green (R/G) channel. There is strong physiological evidence to support at least the B/Y portion of those models in human and primate trichromats. Specifically, the small bistratified ganglion cells are cited as the location where comparison of cone signals is made (Dacy & Lee, 1994). The pathway for the B/Y system is relatively well established, and can generally be modeled as illustrated in Figure 3.

The figure shows an S cone input to on-bipolar cells (On BP) that in turn synapse with a small bistratified ganglion cell (SBG) in the "on" sublayer of the inner synaptic layer. The M and L cones indiscriminately combine their outputs to the off-bipolar cells (Off BP) that in turn synapse with the SBG in the "off" sublayer. Thus, the M and L signals combine to form the "yellow" receptive field "surround," and the SBG cell can compare the relative input from different cone types and thus mediate B/Y color vision. The small bistratified ganglion cells do not show a significant surround component

(Rodieck, 1991), and that is consistent with the premise that type II cells are best suited for mediation of color opponency.

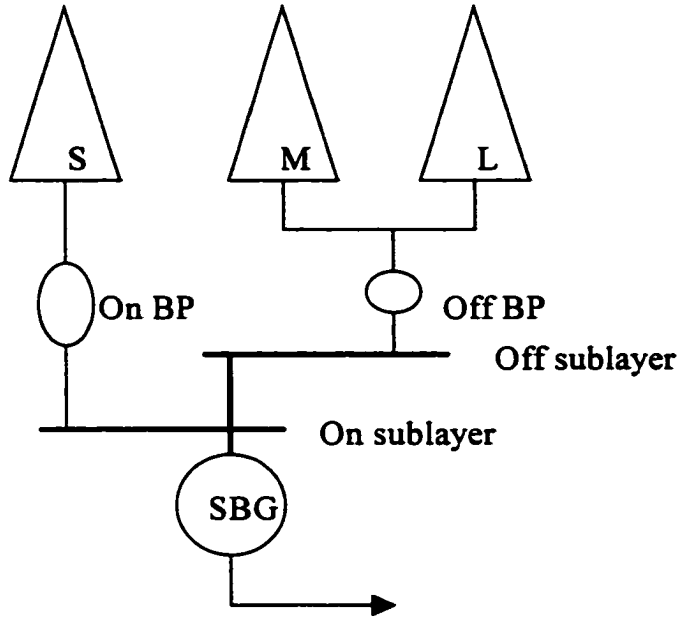

Figure 3. Schematic model of the B/Y system.
S, M, and L refer to short, medium, and long wavelength-sensitive photoreceptors. On BP and Off BP refer to on- and off- bipolar cells. SBG refers to a small bistratified ganglion cell that responds in an opponent fashion whereby (in this diagram) "S" signals "excite" and "M" and/or "L" signals "inhibit" the response from the SBG cell.

Thus the convergence of "on-S-cone" bipolar and "off-ML-cone" bipolar cells onto one small bistratified ganglion cell provides the neural mechanism for comparison and a locus for "B/Y" color vision channel. On the other hand, the retinal locus for comparison of R/G color vision where L and M cone signals are compared has remained elusive. Theories on the mechanism(s) mediating R/G color vision postulate various locations ranging from the retina to the striate cortex.

Physiological research has shown the presence of ganglion cells in the macaque retina whose receptive fields consist of two antagonistic center regions, one receiving

from L cones and the other from M cones, and which lack a surround (DeMonasterio, 1978). The composition of the surround in the R/G type I cell is also controversial: some contend that a R center has a G surround and vice versa (Reid & Shapley, 1992); others contend that either R or G centers have surrounds consisting of R+G input (Calkins & Sterling, 1999). The mechanism already exists whereby R+G contribute to the B/Y surround; so from an evolutionary perspective, it is not unreasonable to conjecture that this already existing mechanism might be exploited for use in a R/G color vision scheme.

Postretinal Pathways

Although beyond the scope of this paper, a brief introduction to the role of post-retinal processes in the mediation of color vision is of interest. Two major pathways have been described that carry information from the retina through the lateral geniculate nucleus (LGN) and to the visual cortex. The magnocellular (M cell) and parvocellular (P cell) pathways refer to groups of neurons whose cell bodies in the LGN are relatively large and small, respectively. The faster M pathway has been shown to convey information such as luminance changes, flicker, and movement. The slower P pathway exhibits longer integration times; it has been shown to mediate high-frequency spatial and perhaps color information (Livingston & Hubel, 1988). There is also some evidence that the koniocellular (K cells) found in the interlaminar LGN layers may carry color information from small bistratified ganglion cells to the "blob" areas in the striate cortex (Hendry & Reid, 2000).

The "blob" regions in layer 3 of the visual cortex have been shown to respond to color changes along both B/Y and R/G dimensions (Livingston & Hubel, 1984). They identified three main types of receptive fields, two of which they called "Double-

Opponent" fields for the R/G and B/Y dimensions, double in that they gave opposite responses to different parts of the spectrum in the center (for example, on to red and off to green). Interestingly, the Double-Opponent cells responded poorly or not at all to white light in any form.

Color vision processing has been shown in other higher level visual areas. There are color-coded thin stripes in visual area 2, and color-selective cells in visual area 4 (Shipp & Zeki, 1985). Even higher centers in the temporal cortex mediate what Ungerleider and Mishkin (1982) propose to be "what" information, as opposed to "where" information that is processed in the parietal region. Color vision information may contribute to their "what" functions of color and form.

Spectral Sensitivity of Normal Primates

Spectral sensitivity refers to the ability to detect light of various wavelengths and is usually determined with psychophysical techniques. Depending on the conditions of the experiment, three sensitivity curves can be produced, each shaped by cells constituting one or a combination of the M, K, and P pathways. The pathway used depends on which system is more sensitive for a given set of stimulus parameters. The three spectral sensitivity functions are usually referred to as the V_λ, V_λ', and increment-threshold spectral sensitivity (ITSS) functions.

V_λ refers to the photopic luminosity function that is determined by heterochromatic flicker fusion and other techniques (Wagner & Boynton, 1972). The function is one way to describe the effectiveness of photon catch and thus the visibility of light energy as a function of wavelength. V_λ is the basis for luminance units, and a representa-

tive curve is shown in Figure 4. The R and G cones mediate the V_λ function over most of its range.

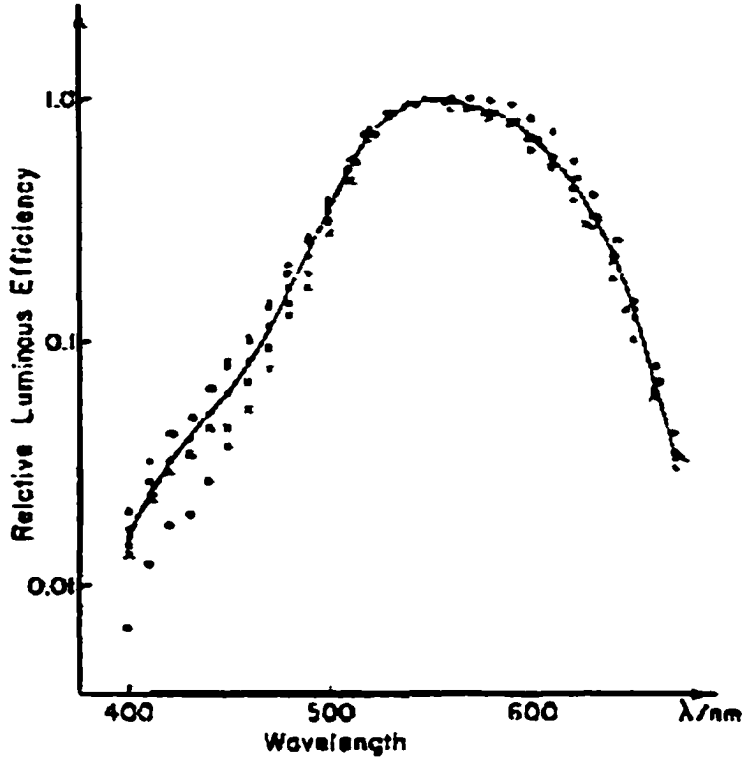

Figure 4. Typical human photopic luminosity function (V_λ).
Figure adapted from Wagner and Boynton, 1972.

In photopic increment-threshold conditions, spectral sensitivity functions take a different form. In studies on trichromatic humans and macaque monkeys, Sperling and Harwerth (1971) found that light-adapted subjects exhibited spectral sensitivity functions for increment flashes presented upon a white background with three distinct peaks as shown in Figure 5. The ITSS applies to large (1°), long (50 msec or more) flashes with background intensities of 1000 trolands or more.

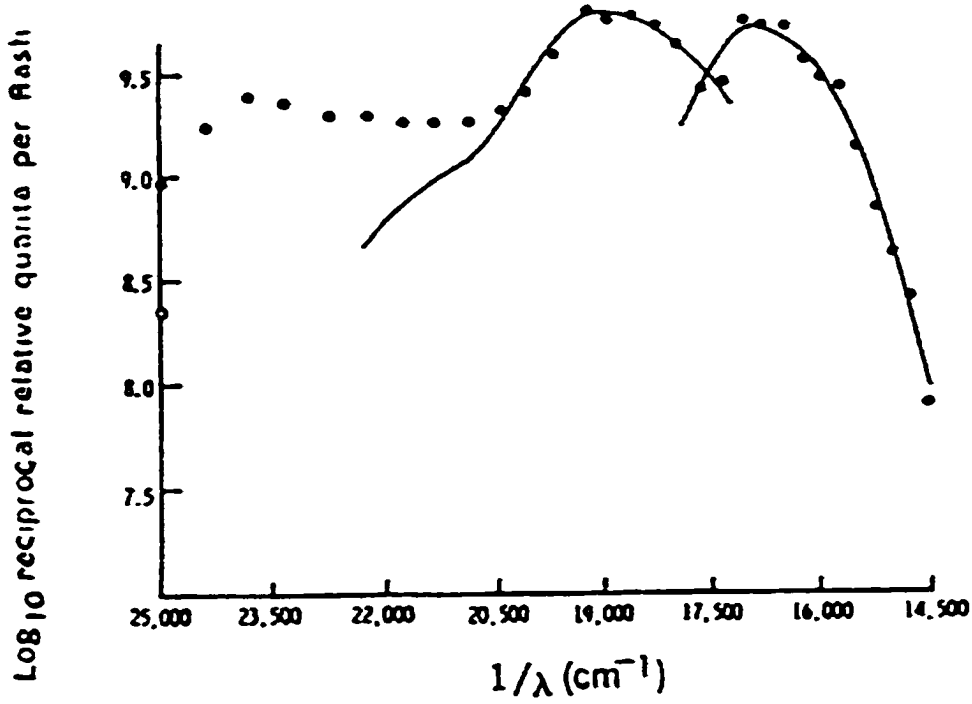

Figure 5. Sample ITSS for humans and macaques.

Data points represent sensitivity for flash (2°, 50 msec.) detection on an 18°, 1000-troland white background. Solid curves represent the best fit for linear subtractive interaction of the long wavelength sensitive cones and the middle wavelength sensitive cones. Figure adapted from Sperling and Harwerth, 1971.

The three peaks of the ITSS function are at about 445 nm, 535 nm, and 610 nm. The spectral locations of the three ITSS peaks are displaced from the locations of the absorption peaks of the underlying cone photopigments, as shown in Figure 6 (from Sperling & Harwerth, 1971). As a historical note, the minima are often called "Sloan notches," described during observations in brightness matching experiments (Sloan, 1928). Stiles and Crawford (1933) later observed the notching phenomenon as a minimum detection threshold on an achromatic adapting field.

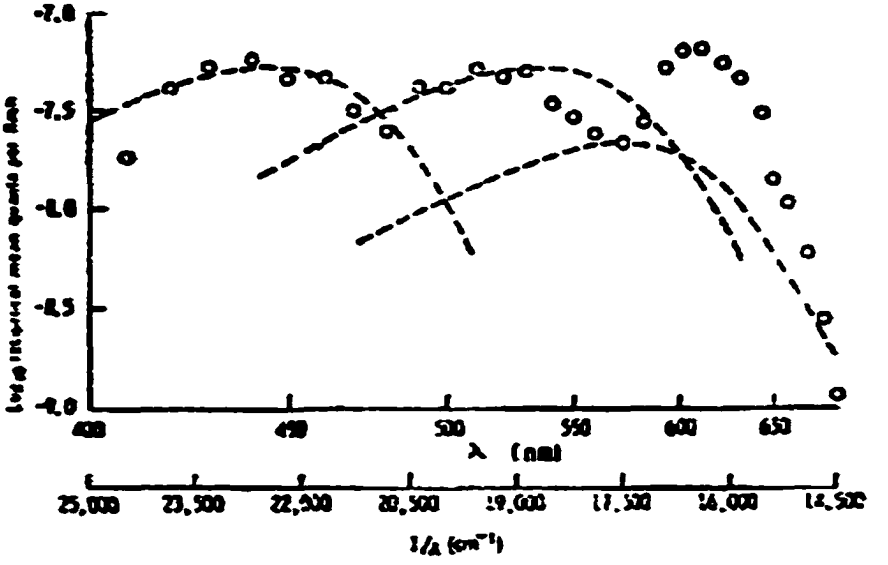

Figure 6. Photopigment (λ_{max}) absorption and the ITSS.

The data points (open circles) represent the measured ITSS. Dashed lines indicate λ_{max} pigment absorption peaks. Note that the 2nd (M) and third (L) photopigment peaks are shifted away from each other. Figure adapted from Sperling & Harwerth, 1971.

There is considerable evidence that wavelength-opponent mechanisms mediate the ITSS. The ITSS can be modeled by a subtractive interaction between the long and middle wavelength cones such that the middle and long wavelength peaks coincide with the observed ITSS (Sperling & Harwerth, 1971). Subtractive interaction was demonstrated directly by Guth, Donley, and Marrocco (1969) in color additivity experiments whereby *addition* of green light to a red test flash *raised* the detection threshold for that flash. Further, Dain and King-Smith (1981) reported that deuteranopic subjects have almost normal sensitivity to yellow flashes but significantly reduced sensitivity to red flashes on a white background, an event predicted by opponent models and subtractive interaction. Upon examination of Figure 6, one could deduce that lack of subtractive influence from the M cone would cause a relative "increase" in sensitivity to the middle

portion of the spectrum (although it is mediated by the L cone) and also the disappearance of the third peak of the ITSS (open circles). Thus, postreceptoral considerations such as the effect of cone type substitution on the effectiveness of red/green opponent cells may explain the decreased sensitivity of deuteranopes to red light.

There is general agreement that color vision is mediated by differential excitation or inhibition of wavelength opponent neurons by variable cone types. However, there is less agreement on the impact of this opponent mechanism on sensitivity to photopic increments. Kaplan, Lee, and Shapley (1990) and Jacobs (1993) propose that wavelength opponent neurons are less sensitive than nonwavelength-opponent neurons (i.e., neurons that are excited and inhibited by the same cone type). Conversely, Dain and King-Smith (1981) propose that wavelength opponency can enhance sensitivity to photopic increments compared to that of nonopponent neurons. This enhancement could derive from an excitation that is favored over inhibition for a particular wavelength opponent neuron when a spectral stimulus stimulates one cone type more than another, whereas for a nonwavelength-opponent cell (for example, a type III cell), the same stimulus would have less effect since stimulation of the surround would decrease the excitation from stimulation of the center.

High Color Vision Sensitivity

If wavelength-opponent mechanisms mediate the ITSS, one could predict that the color of increments should be identifiable at threshold intensities. King-Smith and Carden (1976) provided evidence supporting that prediction. They reported that trichromatic humans could discriminate spectral increments at detection threshold under photopic conditions, producing the ITSS function shown in Figure 7. They proposed that an

opponent color system makes the dominant contribution to visual detection in these conditions as the white adapting lights "selectively depress" the sensitivity of the luminance system, and that the color system is favored for mediating large (1+ degrees) and long (50+ msec) stimuli. In other words, the mechanism(s) mediating color discrimination may be the same mechanism(s) mediating detection thresholds for the increments in photopic conditions. This phenomenon, where color-opponent systems mediate the shape of detection threshold functions and the observer sees color at detection threshold, will be referred to henceforth as "high color sensitivity."

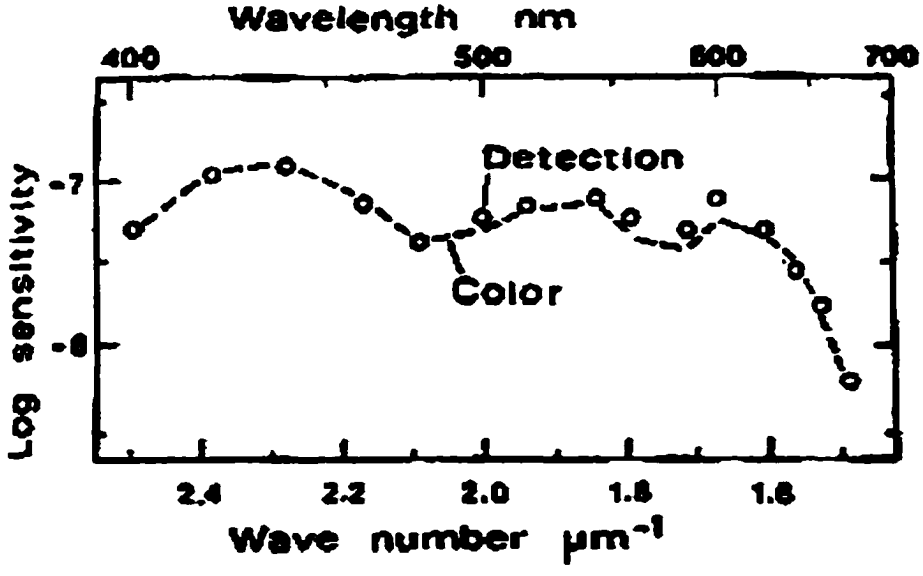

Figure 7. Color discrimination at detection.

Color discrimination (dashed lines) coincides with detection thresholds (open circles). Sensitivities were averaged for two observers and were for 1°, 200 msec test flashes on a 1000-troland background. Figure adapted from King-Smith and Carden, 1976.

The techniques used by King-Smith and Carden in that series of experiments are worth describing, as they form the basis for the techniques used in the experiments for this dissertation. Using a two-alternative forced choice procedure, they determined

whether spectral lights could be discriminated from white at threshold. Stimuli consisted of 1°, 200-msec flashes. White and spectral stimuli of equal detectability were presented in pairs separated by one second and the subject was forced to choose which was the spectral stimulus. The probability of a correct choice as a function of the stimulus intensity is shown in Figure 8. The bottom half shows three pairs of stimuli: red-white (R/W), blue-white (B/W), and yellow-white (Y/W). The upper half shows control data for discrimination of white and spectral stimuli from a blank (no stimulus). In other words, it shows the detection thresholds. In each case, the spectral and white stimuli are equally detectable, ruling out intensity as a cue for discrimination between the white and spectral stimuli.

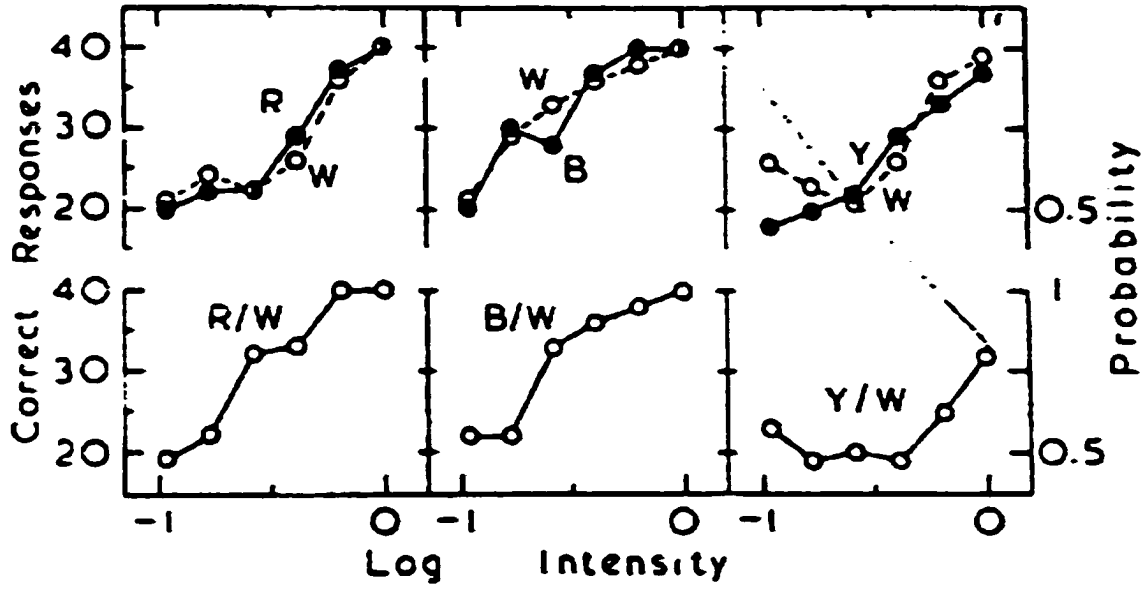

Figure 8. Discrimination of spectral colors from white.

Upper panels are controls showing equal detectability for white and spectral stimuli. Lower panels show the probability of correctly identifying (equally detectable) spectral vs. white stimuli as a function of intensity related to threshold. Stimuli were 1°, 200-msec test flashes on a 1000-troland white background. Figure adapted from King-Smith and Carden, 1976.

Figure 8 shows that red (664 nm) and blue (463 nm) test stimuli can be discriminated from white as easily as they can be detected, that is, the color of the red and blue test stimuli was recognized at detection threshold, supporting the theory that wavelength-opponent systems mediate detection under these conditions. The figure also shows that discrimination of yellow (584 nm) from white was not made at threshold, suggesting that the wavelength-opponent system does not mediate detection of the yellow test flashes.

High color vision sensitivity was later demonstrated in macaques (Loop & Crossman, 2000). They used a two-alternative forced choice procedure to determine detection thresholds for white and for spectral stimuli. They then increased the intensity of paired white and spectral stimuli by 1 log unit above their respective detection thresholds and presented them with various levels of attenuation. They found that trichromatic macaques could discriminate spectral increments from a white increment at detection thresholds, indicated by the horizontal line in Figure 9 where log attenuation equals 1.0. Roberts and Loop (1999) also reported that goldfish demonstrated high color vision sensitivity, lending support to the concept of an evolutionary advantage to color vision in that color vision enhances the ability to detect stimuli in a photopic environment.

High color vision sensitivity can be predicted from analysis of color-opponent cell types. Dain and King-Smith (1981) proposed that color-opponent cells should be more sensitive than noncolor-opponent cells to spectral increments in light-adapted subjects. They argued that for color-opponent cells (type I or II), there is some wavelength range that will favor excitation over inhibition (or will favor one antagonistic response over another). There is no such wavelength range for noncolor-opponent cells, for example, type III cells in Figure 2, because the same photoreceptors provide input for both excitation and inhibition. This wavelength-balanced cancellation may account for that which

King-Smith and Carden (1976) referred to as selective depression of the luminance system by white light, and for the more recent finding that the "best detected" colored increment was seen 3-9 times better than the best-detected luminance increment (Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993).

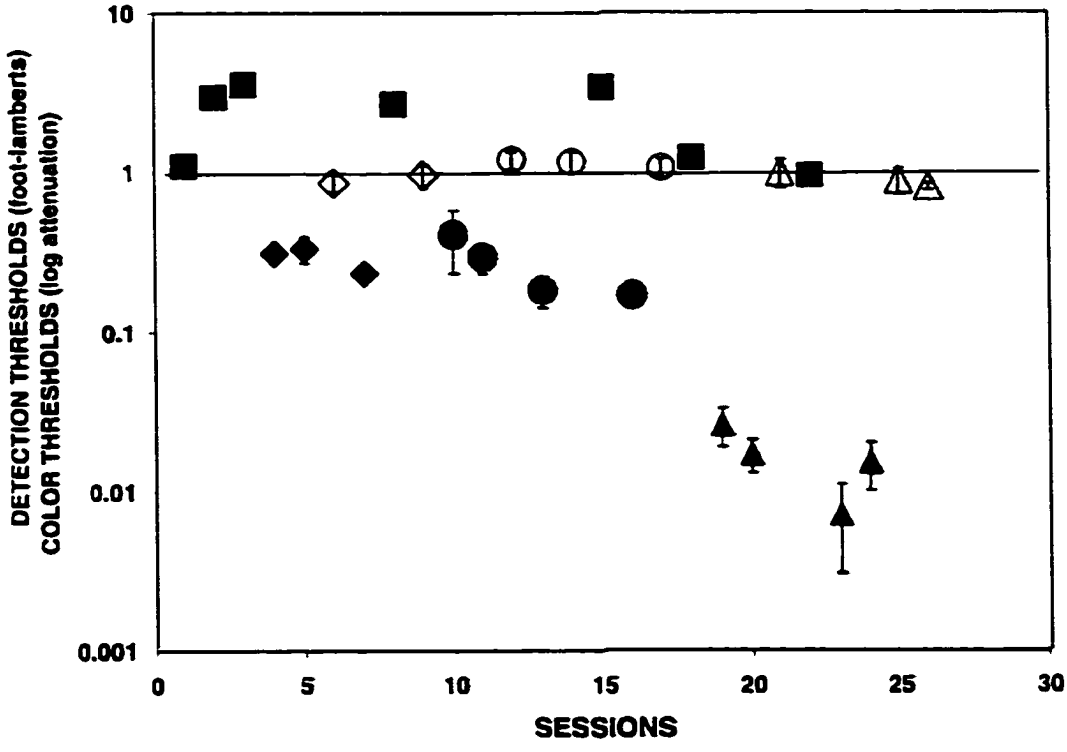

Figure 9. Color discrimination at detection thresholds for the macaque.

Solid symbols are detection thresholds (squares = white, diamonds = 618 nm, circles = 516 nm, triangles = 456 nm). Open symbols are color discrimination thresholds (diamonds = white vs. 618 nm, circles = white vs. 516 nm, triangles = white vs. 456 nm). Horizontal line denotes color discrimination thresholds of 1.0 log attenuation where color discrimination threshold equals detection threshold. Stimuli were 2°, 500 msec on a white background at 60 Foot-Lamberts. Figure adapted from Loop & Crossman, 2000.

Color Vision Sensitivity in Human Dichromats

Human dichromats have been shown to lack a photopigment, and thus lack one photoreceptor type. More specifically, protanopes lack the L photopigment/cone type,

and deuteranopes lack the M pigment/cone type. Tritanopes lack the S pigment/cone type, but that is a rare occurrence that will not be addressed in this dissertation. There has been debate as to whether a remaining cone type substitutes for the lacking cone type or if the lacking cone type "disappears" altogether. However, the limiting factor for spatial acuity in healthy human eyes is the granularity of the photoreceptor mosaic, and color defective individuals exhibit normal spatial vision (Fletcher & Voke, 1985), supporting the theory that cone types are substituted rather than omitted (Boynton, 1979).

Lack of a cone type is a basic feature of human dichromacy and results in alteration of V_λ for dichromats. Pokorny, Smith, and Verriest (1979) compared V_λ for normal trichromats to that of protanopes and deuteranopes, as displayed in Figure 10. The figure shows that protanopes have a "luminosity loss" in the "red" and deuteranopes have a slight "luminosity" loss in the "green" and "blue" portions of the spectrum.

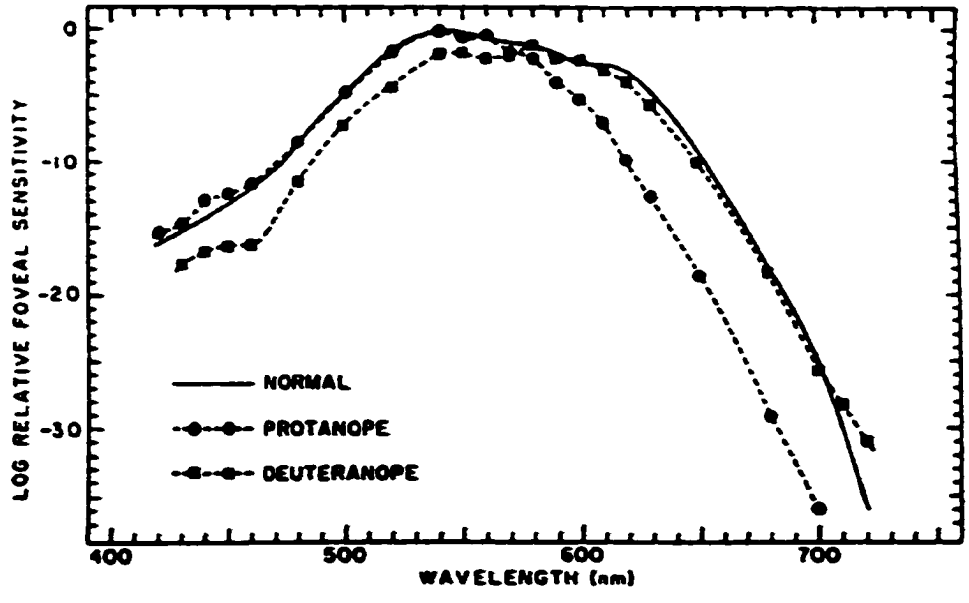

Figure 10. Spectral sensitivity (V_λ) for trichromats and dichromats. Figure adapted from Pokorny, Smith, & Verriest, 1979.

For long-duration photopic stimuli, the ITSS of human dichromats can be modeled by a subtractive interaction as it was for normal trichromats. Miyahara, Pokorny, and Smith (1996) detailed this aspect of dichromacy. The authors in that study report that dichromatic subjects as well as normal subjects demonstrated sensitivities predicted by opponent (subtractive) systems but not predicted by luminance (additive) systems. Specifically, the opponent-system-mediated sensitivities were greater at 540-nm and longer wavelengths and on each side of the Sloan notch than were the luminance system mediated sensitivities. Figure 11 shows their data points for dichromats falling on predicted lines, but does not show the predicted sensitivities for the "additive" system that did not contain the data points. Further, Miyahara et al. also propose that the subtractive interaction between the short wavelength cone type and the remaining longer wavelength (M or L) cone type in dichromats occurs over a wider range than for trichromats. In summary, their findings indicate that dichromatic human ITSS functions are mediated by wavelength opponent mechanisms, as is the case for trichromats.

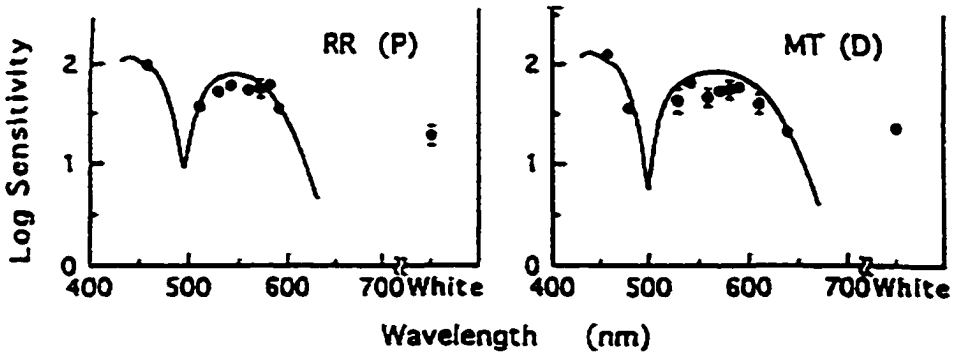

Figure 11. ITSS for dichromats.

The solid line is the prediction based on a subtractive interaction between B and G cones for protanopes, and between B and R cones for deuteranopes. Stimuli were 2° test flashes on a white pedestal (800 trolands) and a 19° background (200 trolands). Figure adapted from Miyahara et al., 1996.

A more illustrative account with more data points describing the ITSS function for human trichromats and dichromats is shown in Figure 12 (Schwartz, 1994). In that figure, Sloan notches are evident for trichromats, protanopes, and deuteranopes, indicating detection by wavelength opponent systems.

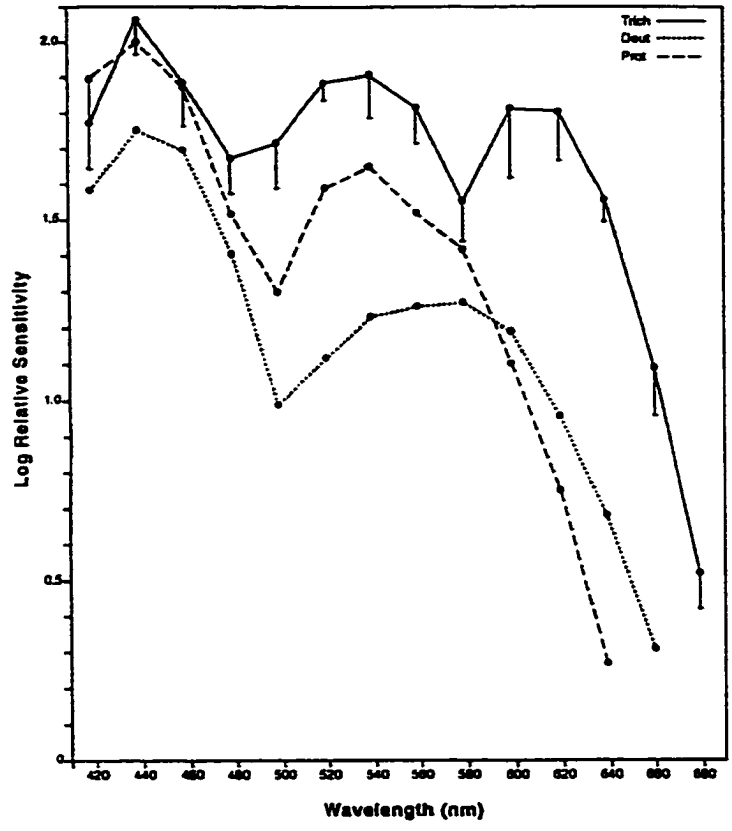

Figure 12. Increment spectral sensitivity functions for dichromats and trichromats. Functions for trichromats, protanopes, and deuteranopes are represented by the solid, dashed, and dotted curves respectively. Figure adapted from Schwartz, 1994.

Some perceptual phenomena in dichromats require consideration of alterations in postreceptoral processes such as opponent or other mechanisms. Hurvich and Jameson (1955) suggested that dichromats lack a R/G opponent color system, and this suggestion is supported by the following findings: Deuteranopes are less sensitive to red light than

normal trichromats, particularly for longer duration stimuli (Dain & King-Smith, 1981); and dichromats do not see some colors at increment detection thresholds (Kuyk & Loop, 1998).

Deuteranopes are less sensitive to red light. Since the absorption curves of L and M cones overlap over most of their ranges, one would expect that replacement of the M cones with L cones should result in little if any loss of sensitivity in the middle range of the visible spectrum, as is the case. The L cones do, however, support the visible range at longer wavelengths. One might expect that the additional L cones in deuteranopes would result in at least the same or even increased sensitivity to red light. However, Dain and King-Smith (1981) showed that the opposite occurs; that is, they showed that deuteranopes are less sensitive to longer wavelengths than trichromats.

Dichromats do not see some colors at threshold. Kuyk and Loop demonstrated that dichromats require up to 6 times more light to discriminate the color of some spectral lights than they need to detect those stimuli (Kuyk & Loop, 1998). This "low color sensitivity" was demonstrated in a subsequent experiment by Loop, Shows, Mangel, and Kuyk (2002). In that study, normal observers were able to discriminate white and spectral stimuli at intensities near detection thresholds, but color-deficient humans required suprathreshold stimulus intensities to discriminate the white and spectral flashes, as shown in *Figure 13* (Loop et al., 2002).

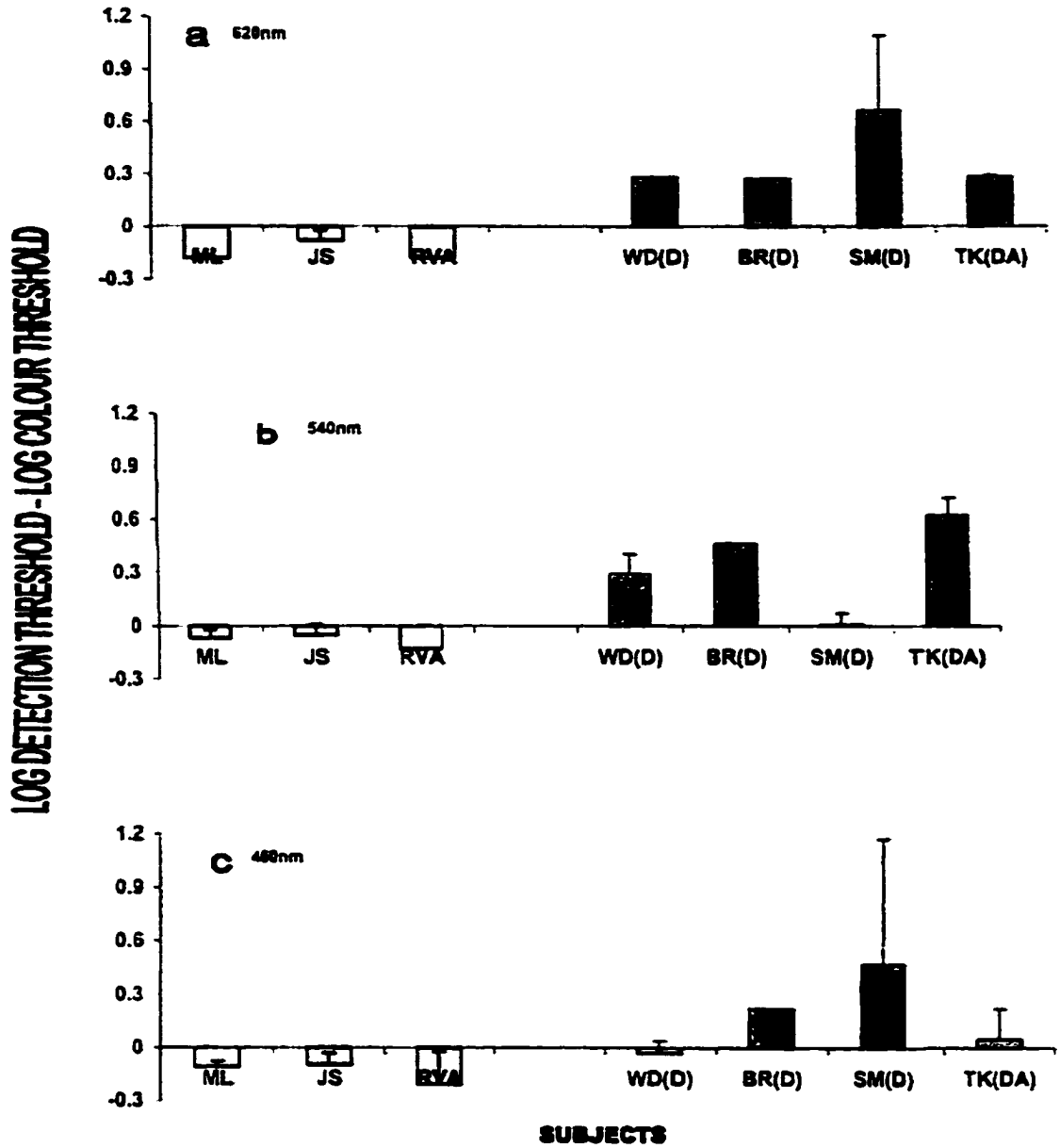

Figure 13. Color thresholds for color-normal and color-abnormal humans.

Open figures indicate normal trichromats. (D) indicates dichromat, (DA) indicates deuteranomalous. A difference of zero indicates that the flash color could be discriminated at the same intensity that the flash could be detected. Positive values indicate that color discrimination required a higher flash intensity than simple detection, while negative values indicate that color discrimination required a lower flash intensity than detection. Test stimuli were 2°, 200-msec increments on a white 1000-troland background. Figure adapted from Loop et al., 2002.

These findings call for further consideration of cone types and associated opponent mechanisms. Assuming that one remaining cone type substitutes for another, for example, that L cone types substitute for M cone types in deuteranopes, the receptive fields of type I, II, and III cells would be altered, as shown in Figure 14.

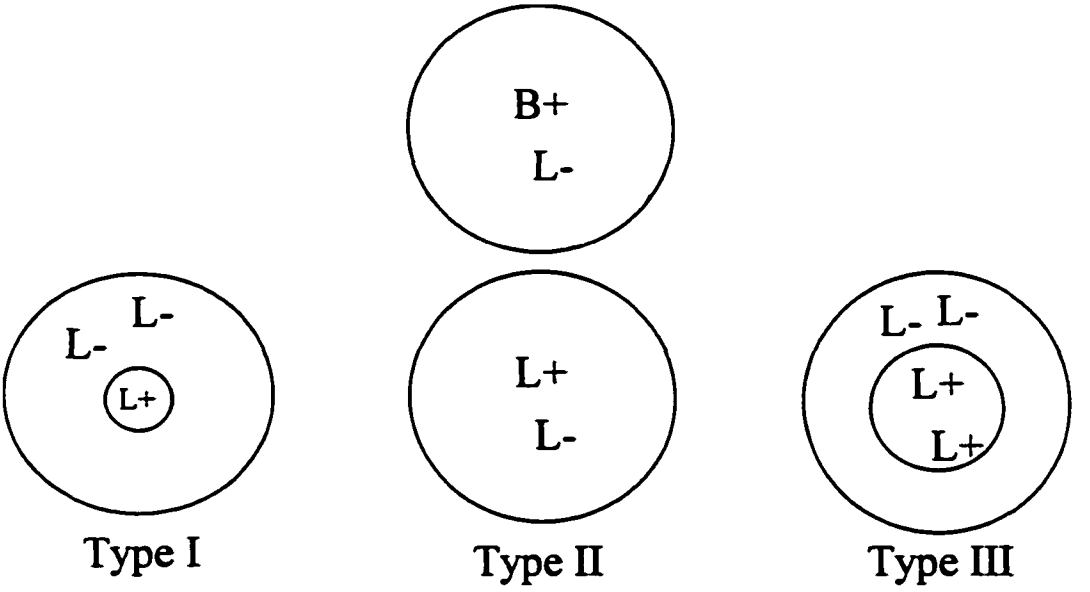

Figure 14. Hypothetical opponent receptive fields for dichromats.
Shows replacement of (M) type photoreceptor by (L) type, mapped to the cell types shown in Figure 2.

In this model, the type I cell could still mediate luminance contrast and acuity, but color opponency would be lost, since the surround that was mediated by M (or M+L) cones in normal trichromats would be mediated only by L cones in the deuteranope. Thus, there would be increased inhibition for long wavelength stimuli in the type I cell, and that sensitivity should be reduced (for stimuli larger than the center of the receptive field), as is the case. The type III cells, which originally received input from both M and

L cones in their centers as well as their surrounds, should be relatively unaffected. The resulting luminance contrast and temporal characteristics of vision should be relatively unaffected in the deuteranope, as is the case. Significantly, the model predicts that the L-M type II cell should be severely affected, in that the spatially coincident excitatory and antagonistic responses for any wavelength cancel. Such a cell would essentially be useless, with little to no activity or useful information for further processing.

These foreseeable rearrangements of the receptive fields in a human deuteranope, whereby the L-M opponent system no longer exists, explain their inability to discriminate amongst middle to long wavelength stimuli, and their detection insensitivity to long wavelengths. However, their B-L neurons remain wavelength opponent despite the "loss" of input from the "M" cone type. Since these color-opponent neurons appear to mediate detection of spectral increments (Figures 11 and 12), it is hard to understand why dichromats do not see color at detection threshold.

Considering the above models of altered opponent mechanisms in dichromats, two possible explanations are proposed for the failure of color-abnormal subjects to discriminate color at detection threshold: (a) detection is mediated by a luminance mechanism, or (b) there is a postreceptoral defect in color processing.

A growing body of evidence contradicts alternative (a). Color-opponent models describe increment-threshold spectral sensitivity functions in normal humans and in dichromatic humans, whereas luminance functions do not (Miyahara et al., 1996; Schwartz, 1994). Further, several characteristics of normal human detection of spectral increments indicate mediation by opponent neural pathways. For example, psychophysical measurements of human dichromats to colored stimuli indicate long temporal integration (King-Smith & Carden, 1976), slow and sustained threshold reaction times

(Schwartz & Loop, 1982), and a sluggish temporal appearance (Schwartz & Loop, 1983). Further, using spatially coincident increments and background, VanVeen (2000) found a unimodal distribution of long-duration threshold reaction times to spectral increments in both normal and color-abnormal subjects, whereas detection of stimuli by the luminance system results in a bimodal distribution of short reaction times, one peak occurring at stimulus onset and one peak occurring at stimulus offset. These reaction time findings suggest that both color-normal and color-abnormal humans detect spectral increments with a sustained response mechanism thought to be typical of color-opponent neural mechanisms (Schwartz, 1992; Schwartz & Loop, 1982).

Alternative (b) proposes that humans with abnormal color vision exhibit defective postreceptoral processing. This alternative can be investigated through an experiment that asks the following question: is the low color sensitivity of human dichromats due to (a) a general feature of dichromacy across species or (b) an abnormal physiological condition in humans? The former assertion infers that normally occurring dichromats (i.e., most mammals) should exhibit low color vision sensitivity. The latter assertion predicts that normally occurring dichromats exhibit high color vision sensitivity, and carries the implication that color defective humans may have altered postreceptoral (opponent and/or other) processing mechanisms in addition to lacking a cone type. In other words, if the low color sensitivity in human dichromats reflects a defect in central mechanisms as a result of defective wavelength opponent input (i.e., input being nonwavelength-opponent due to pigment replacement), then no such deficit should exist in normally dichromatic species.

Color Vision in Normal (Nonhuman) Dichromats

Fortunately, certain characteristics of visual systems have been conserved across vertebrate species, and this provides opportunities for comparative studies. A survey of a wide variety of mammals has led to the conjecture that the most common form of mammalian color vision is dichromacy, in that most possess two cone types sensitive to wavelengths at opposite ends of the visual spectrum (Jacobs, 1993). These may be designated as "S" and "LM" cones with peak sensitivities to shorter and longer wavelengths, respectively. The "S" photopigment generally has a peak absorbance at about 420 nm-450 nm and the "ML" at about 500 nm or longer. Rodieck (1998) compiled generalized photopigment absorption curves of nonprimate and primate cones, as shown in Figure 15.

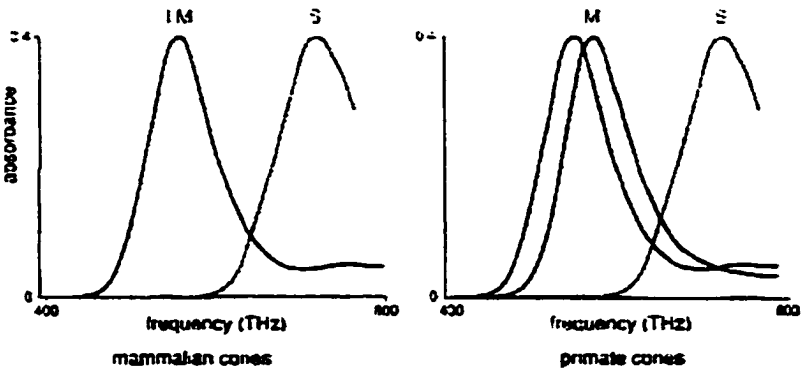

Figure 15. Cone absorption curves of mammals and primates.
Note that spectral distribution is expressed in frequency units rather than traditional wavelength units, thus reversing the relative positions of the S and ML pigments on the abscissa. Figure adapted from Rodieck, 1998.

The λ_{max} function has been determined for a number of animals. Jacobs (1993) provides λ_{max} functions for species grouped as primates, carnivores, and rodents, as shown in Figures 16-18.

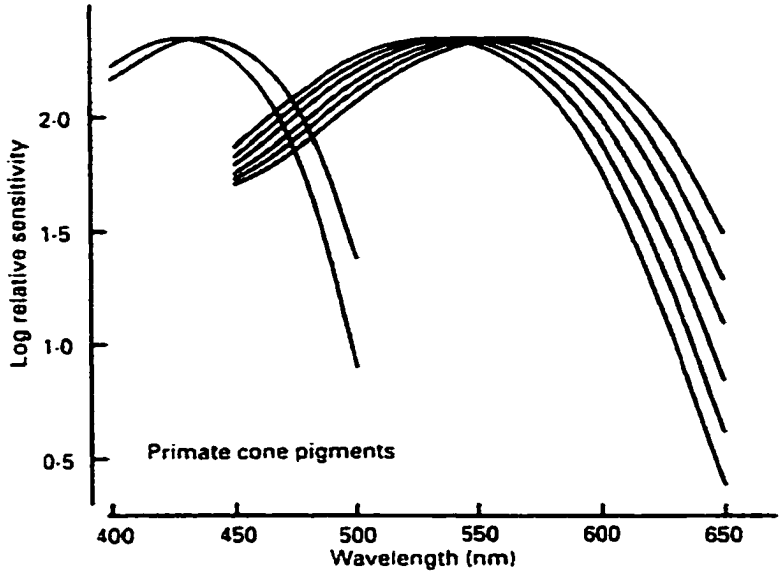

Figure 16. λ_{max} for primates.
Figure adapted from Jacobs, 1993.

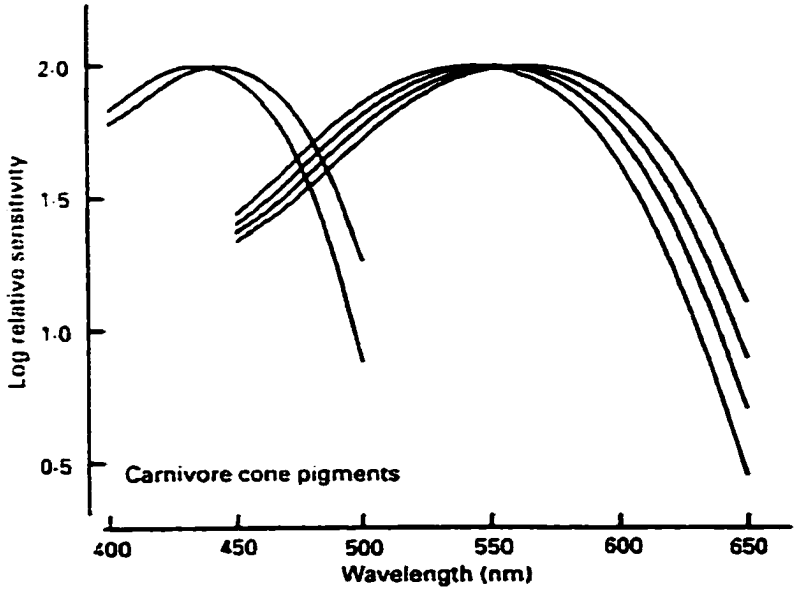

Figure 17. λ_{max} for carnivores.
Figure adapted from Jacobs, 1993.

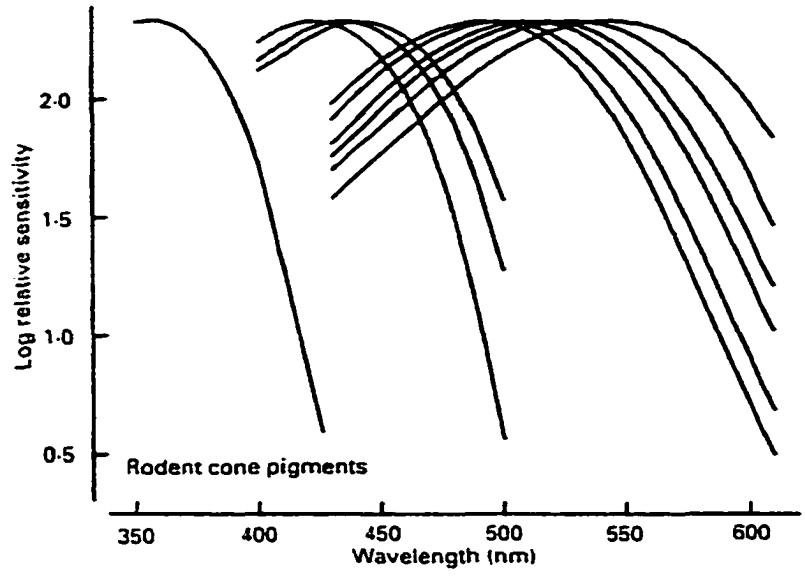

Figure 18. λ_{max} for rodents.
Figure adapted from Jacobs, 1993.

With consideration of photopigment genes and physiological evidence from rods and cones, Jacobs further suggested that the earliest mammals had retinas containing cones and two types of cone photopigment; and this is part of his argument that the base-line condition for mammalian color vision is dichromacy. In further support of this concept, he and others have determined ITSS functions for several species, including the 13-lined ground squirrel (*Citellus tridecemlineatus*) and the tree shrew (*Tupaia glis*).

Ground squirrels are diurnal rodents with photoreceptors resembling rods and two types of cones with photopigment. The Golden Manteled ground squirrel (*C. lateralis*) has λ_{max} values of about 500 nm (rod), short wavelength cone S = 436 nm, and medium-long wavelength cone ML = 518 nm (long cone) (Kraft, 1988). Thirteen-lined ground squirrels have also been characterized as dichromats with well-defined neutral points (Anderson & Jacobs, 1972). Further, some of their color discriminating abilities are similar to those of dichromatic humans (Jacobs & Yolton, 1971). The ITSS for the 13-

lined ground squirrel is shown in Figure 19 (Jacobs, 1993). To illustrate the similarity across species, the ITSS functions of the domestic dog (Jacobs, 1993) and the tree shrew (Jacobs & Neitz, 1986) are shown in Figures 20 and 21, respectively.

Although these ITSS functions have been determined for these normally dichromatic species, high color vision sensitivity has not been determined in any of these animals. Demonstration of high color vision sensitivity in these animals would support the theory that this phenomenon is a normal feature of dichromacy, and that the lack of this phenomenon in dichromatic humans may indicate a deficiency in postreceptoral processing mechanisms in addition to lacking a cone type.

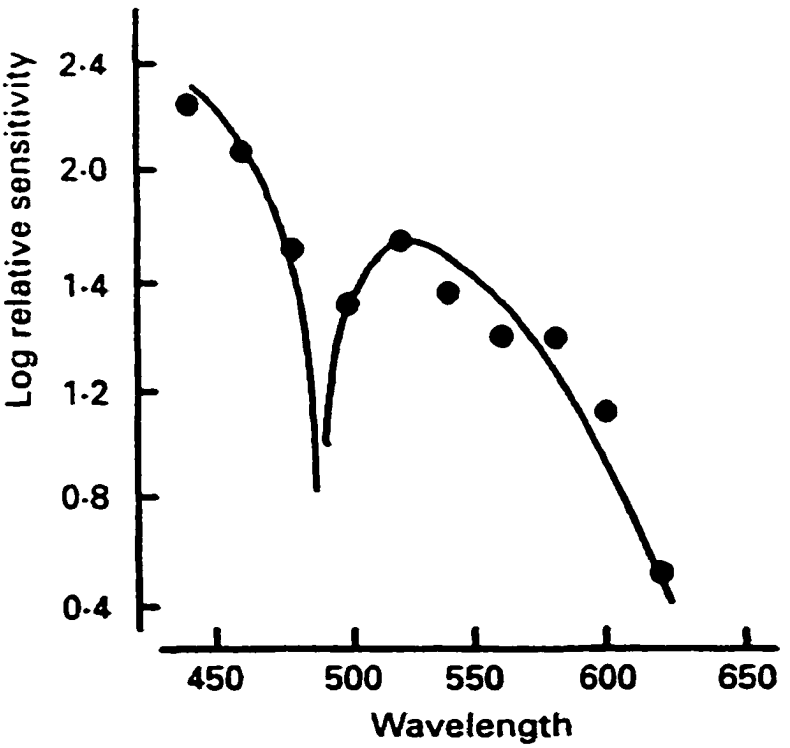

Figure 19. ITSS for the 13-lined ground squirrel.
Solid line indicates prediction by subtractive combination of cone pigments. Figure adapted from Jacobs, 1993.

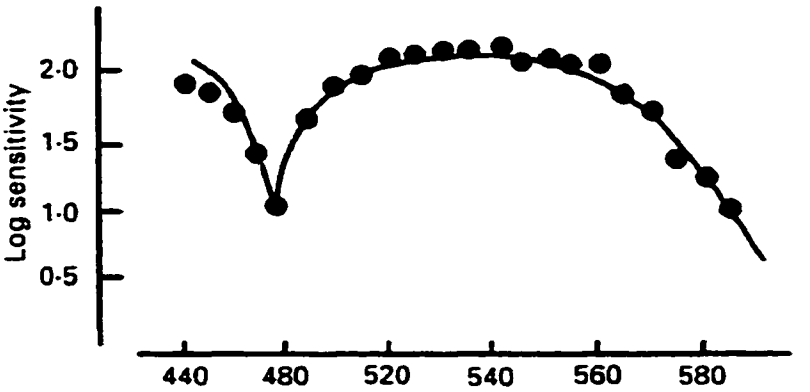

Figure 20. ITSS for the domestic dog.

Solid line indicates prediction by subtractive combination of cone pigments. Figure adapted from Jacobs, 1993.

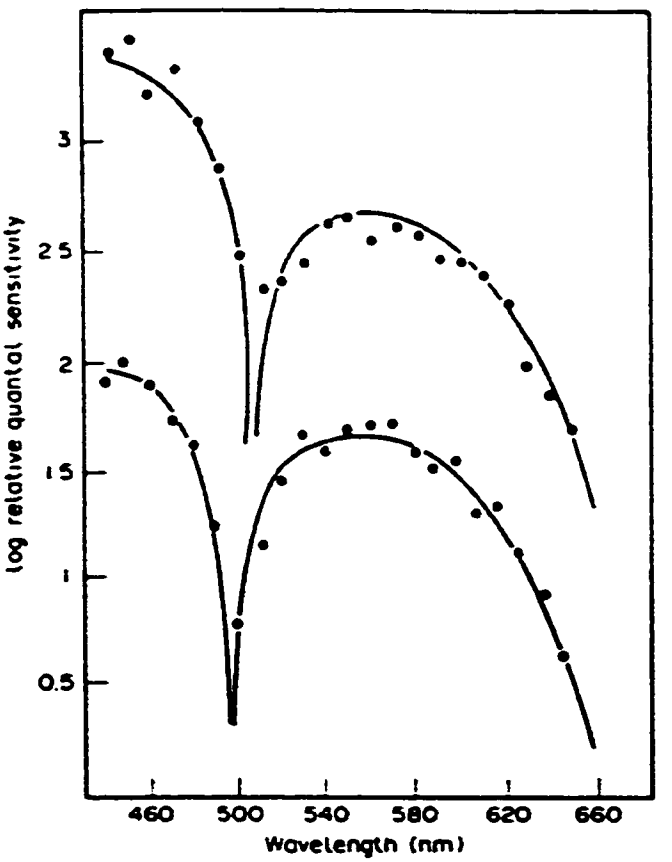

Figure 21. ITSS for the tree shrew.

Position on vertical axis (sensitivity) reflects background luminance level. Figure adapted from Jacobs and Neitz, 1986.

Helmholtz-Kohlrausch Effect

The high color sensitivity of normal humans and macaques and the low color sensitivity of dichromatic humans are also reflected in their detection thresholds for colored lights. This is actually a variant of the Helmholtz-Kohlrausch Effect, whereby color adds to the apparent brightness of a stimulus. The incorporation of color along with luminance on the apparent brightness of visual stimuli has been extensively studied and eloquently modeled (Guth, 1991).

More recently, Loop and Crossman demonstrated the Helmholtz-Kohlrausch effect at threshold levels, as shown in Figure 22. In the figure, solid bars indicate white increment-thresholds, and open bars indicate the relative attenuation needed to reach threshold for the same increment but with a red filter placed in the path of the light.

In that experiment, Loop and Crossman found that a broadband long wavelength filter (Kodak #25) lowered detection thresholds for trichromatic humans and macaques. Interestingly, the same filter increased detection thresholds for dichromatic humans. Their results are consistent with studies demonstrating the ability to discriminate color at detection threshold by trichromatic humans (King-Smith & Carden, 1976) and macaques (Loop & Crossman, 2000) and the lack of that ability by human dichromats (Kuyk & Loop, 1998; Kuyk, Shows, Van Arsdel, & Loop, 2000). This effect has not been shown at threshold levels for normally occurring dichromats, and thus was included in this experiment in order to substantiate (or refute) the presence of high color vision sensitivity in those animals.

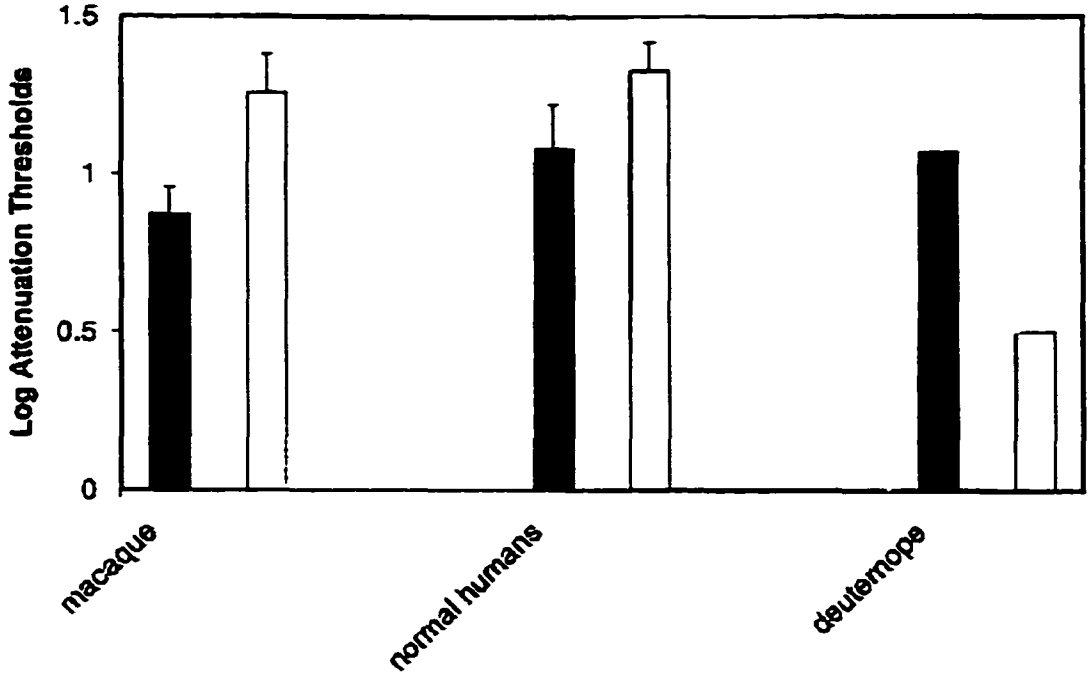

Figure 22. Detection thresholds with and without red filter for macaque and human. Solid bars indicate white increment-thresholds, and open bars show change in detectability with addition of a Kodak #25 red filter to the same increment. Figure adapted from Loop and Crossman, 2000.

METHODS

Subjects

Animal subjects included a 13-lined ground squirrel (*C. tridecemlineatus*), chipmunk (*T. strictus*), and tree shrews (*Tupaia*) that were individually housed, trained, and tested at 85% free-food body weight. They had free access to water and were maintained in a room with a 16:8 light-dark cycle.

Human subjects included a dichromat (deuteranope), a deuteranomalous trichromat, and two normal trichromats recruited from the campus at the University of Alabama at Birmingham. Color vision function was assessed with the Nagel anomaloscope and the Farnsworth D-15 test.

The Institutional Animal Care and Use Committee and the Institutional Review Board for Human Use at the University of Alabama at Birmingham granted approval for use of animal and human subjects in this study (Appendix).

Apparatus

Light from two Kodak slide projectors was directed through two different channels, each containing a condensing lens, aperture, interference filter, neutral density filters (or gray lexan filters or a counter-rotating neutral density wedge filter), and projection lens as shown in Figure 23. The light paths were combined at a common beam splitter, shuttered, and projected on a screen. The large plate beam splitter was mounted on a galvanometer such that the spectral increment was projected to the opposite side

(L or R) from the white increment. Subjects viewed the stimuli through two clear Plexi-glas windows, and those windows served as keys for animal resonses.

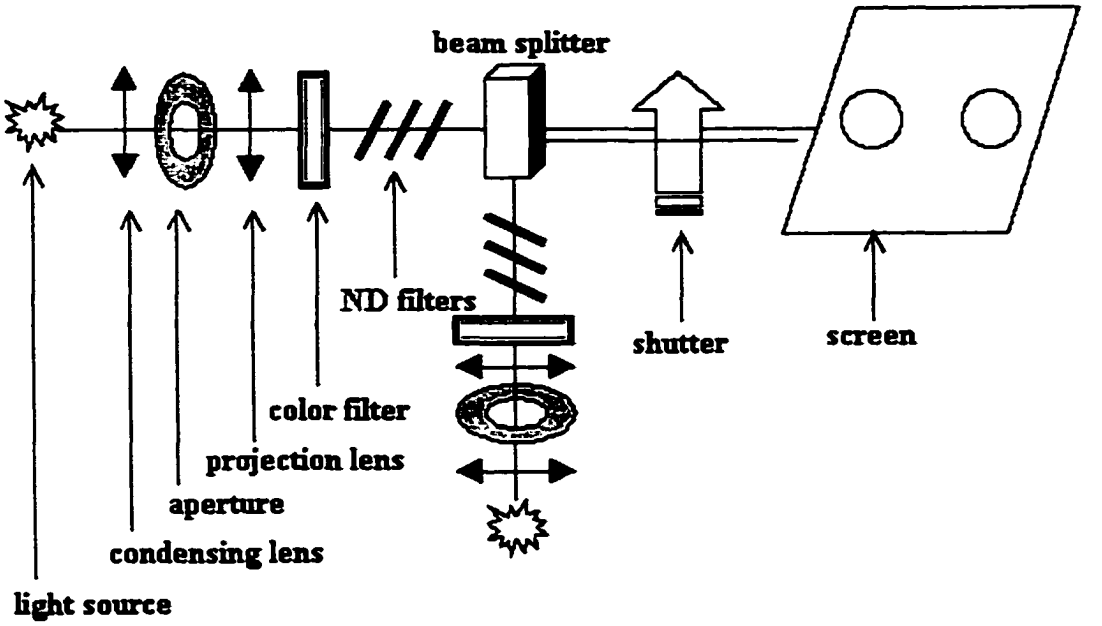

Figure 23. Optical apparatus.
See text for details.

Background and Stimuli

A fluorescent tube illuminated a translucent white plastic screen to produce a white background of 3000° K. The background source was shielded with cardboard in various configurations to produce background levels of 1.25 cd/m^2, 46 cd/m^2, and 135 cd/m^2. White stimuli were produced with Kodak slide projectors and adjusted with various Kodak broadband filters and neutral density filters to obtain a color temperature of 3,000° K. Spectral stimuli were produced with interference filters to present narrow bandwidth stimuli centered on 480-nm, 540-nm, 560-nm, and 580-nm wavelengths. Colored broadband stimuli were produced with a 500-nm short-pass filter, a 500-nm

long-pass filter, and a Kodak #21 broadband filter with transmission above 540 nm. Transmission characteristics of those filters are shown in Figures 24-26. Note that 100% transmission is at the top of the graphs in Figures 24 and 25, but at the bottom of the graphs (reversed) in Figure 26.

White, spectral, and broadband filtered light was projected on the translucent white screen to produce circular test spots one inch in diameter. The position of the spots varied up to 2 mm in all directions from center, helping to reduce possible localization cues. The borders of the circular test fields were slightly defocused to reduce extraneous spatial cues.

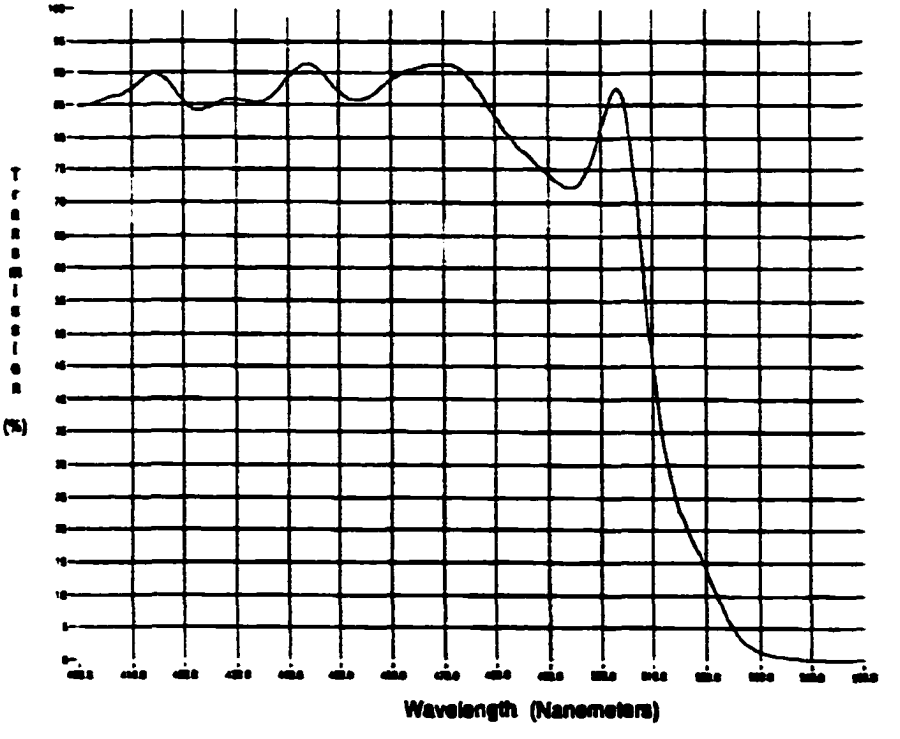

Figure 24. Transmission of 500-nm short-pass filter.
Figure provided by Oriel Corporation.

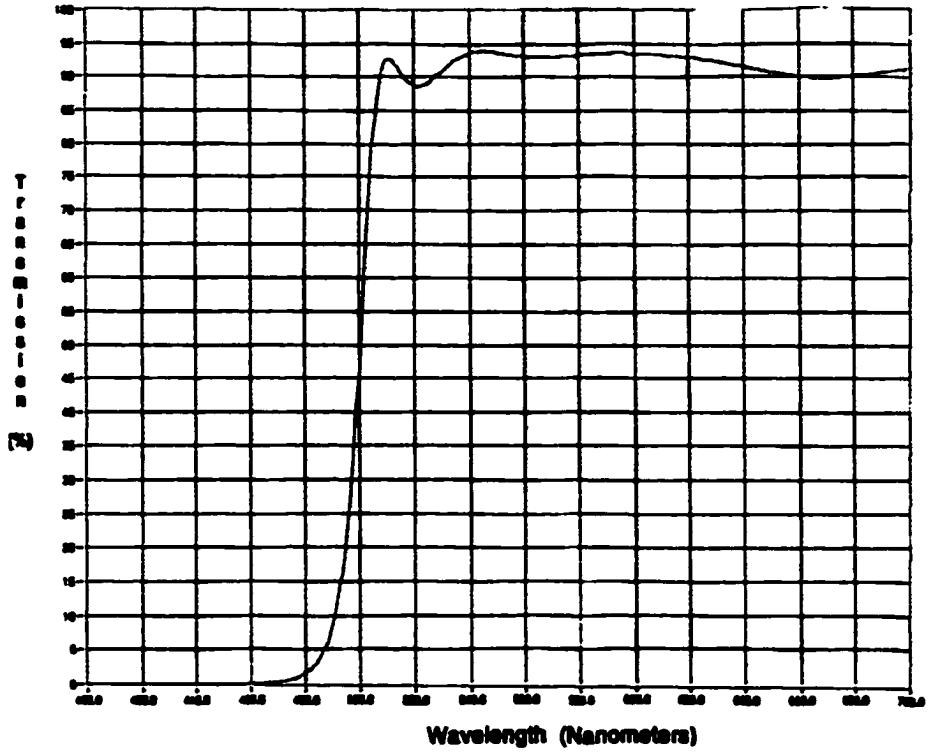

Figure 25. Transmission of 500-nm long-pass filter.
Figure provided by Oriel Corporation.

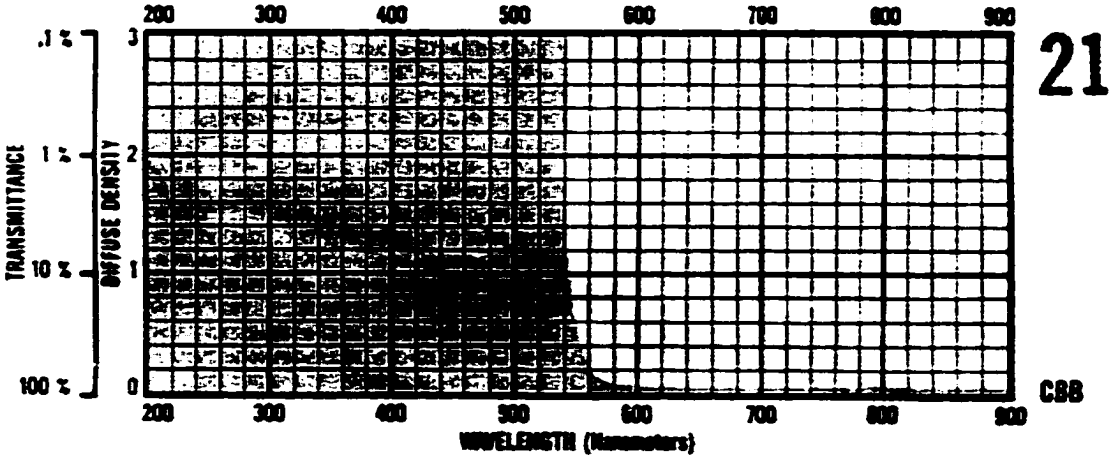

Figure 26. Transmission of Kodak #21 broadband Filter.
Figure provided by Kodak Corporation.

Calibrations

Stimulus intensity, as interpreted by Cornsweet (1970)[1], was measured with a Tektronix J-16 photometer and an 8° or 1° luminance probe. Light sources were set to a specified starting intensity 5 minutes after they were turned on and whenever stimulus parameters changed, and were thus calibrated frequently.

Kodak neutral density filters used in this experiment have a flat spectral transmission for visible light. Lexan gray filters, used in the white light channel, were calibrated with results shown in Figure 27. Above 490 nm these filters exhibited an optical density very close to 0.29; below 490 nm the density was more variable but varied less than 0.1 density units from the value of 0.29. The figure also shows the density for double density lexan filters, which showed similar characteristics and had an optical density of 0.58.

The counter-rotating neutral density wedge, used in the color channel, was calibrated for five stimuli as shown in Figure 28. The figure shows that the neutral density wedge provided a consistent optical density for light of all wavelengths used in this experiment.

---

[1] "The names and classes of photometric units (units describing amounts of light) have grown over the years into an unbelievably confusing jumble. There are few among even the most scholarly who can tell you how many nits (sic) there are in an apostilb, or even whether or not there are any. (There are either $1/\pi$ or $1.018/\pi$, depending upon whether in the book I am referring to, cd stands for candle or candela; or maybe there are $1.10/\pi$ if the apostilbs are in German [Hefner] units.) Worse yet, a few words that have useful and unambiguous meanings to the typical speaker of English have been assigned specific definitions, so that it is now improper to use those terms to refer to what they used to refer to. The difficulties involved in correctly using photometric units are further compounded in a book of this kind because the meanings of most units depend upon certain optical and perceptual concepts and facts with which the reader is not yet acquainted. The term 'intensity" is improperly used throughout this book. Technically, it applies only to point sources of light; it is not proper, for example, to say anything about the intensity of light falling on a surface, or the intensity of the stimulus (unless it happens to be a point source). Nevertheless, it is probably better, pedagogically, to use the word "intensity" improperly. When used in this book, it means just what you think it means."

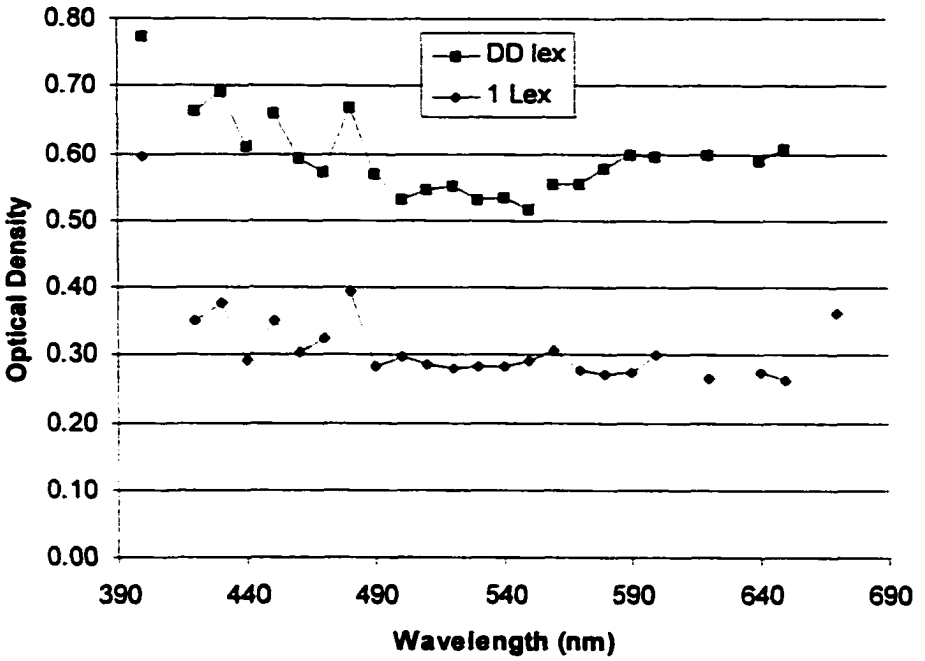

Figure 27. Optical density of lexan filters.
DD indicates double density lexan filter.

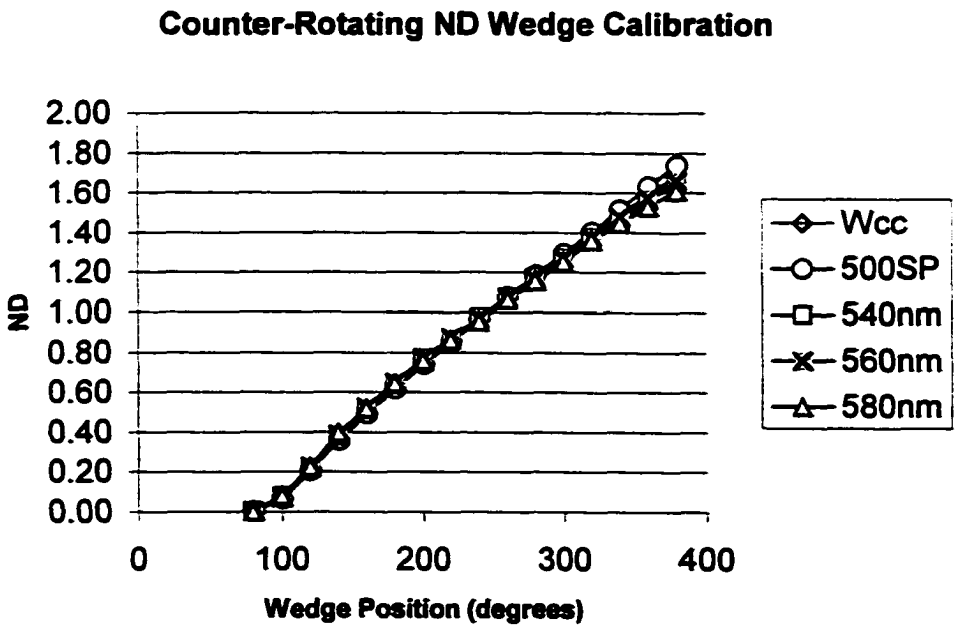

Figure 28. Counter-rotating neutral density wedge calibration.

Procedures

Training consisted of classical and operant conditioning. Food reward was given for desired behavior coupled with a tone played over a speaker. Desired behavior was shaped such that the animal (a) located the food source; (b) associated the delivery of reward with a tone (classical conditioning); (c) responded to the presence of a stimulus (by pressing the proper key); (d) exhibited a detection threshold for a white stimulus; (e) exhibited a detection threshold for spectral stimuli; and (f) exhibited a discrimination threshold for a white vs. spectral stimulus.

Psychophysical experiments consisted of spatial two-choice visual discrimination tasks for food reward. A flowchart of the automated cascade of events is presented in Figure 29. The flowchart illustrates that once a stimulus was presented the apparatus verified that the clear Plexiglas keys were released (open), allowing the subject to respond. Correct responses resulted in a reward coupled with a tone, followed by an inter-trial interval (ITI) of 2.0 s, while incorrect responses were followed by an ITI of 2.0-4.5 s with no food reward or tone. The longer ITI served to slow the animal down and helped to maximize the percentage of correct responses. Left, right, correct, and incorrect responses were counted as well as the number of trials. When the number of trials reached 10, the trial block ended, allowing for recording of data and preparation of the next stimulus.

During training, position habits, that is, a tendency to favor either (L) or (R) keys, triggered a correction procedure, depicted in the gray areas in the flowchart. If an animal pressed the same key four times, the correction procedure maintained the correct stimulus on the "unfavored" key and required that the animal press that key in order to proceed.

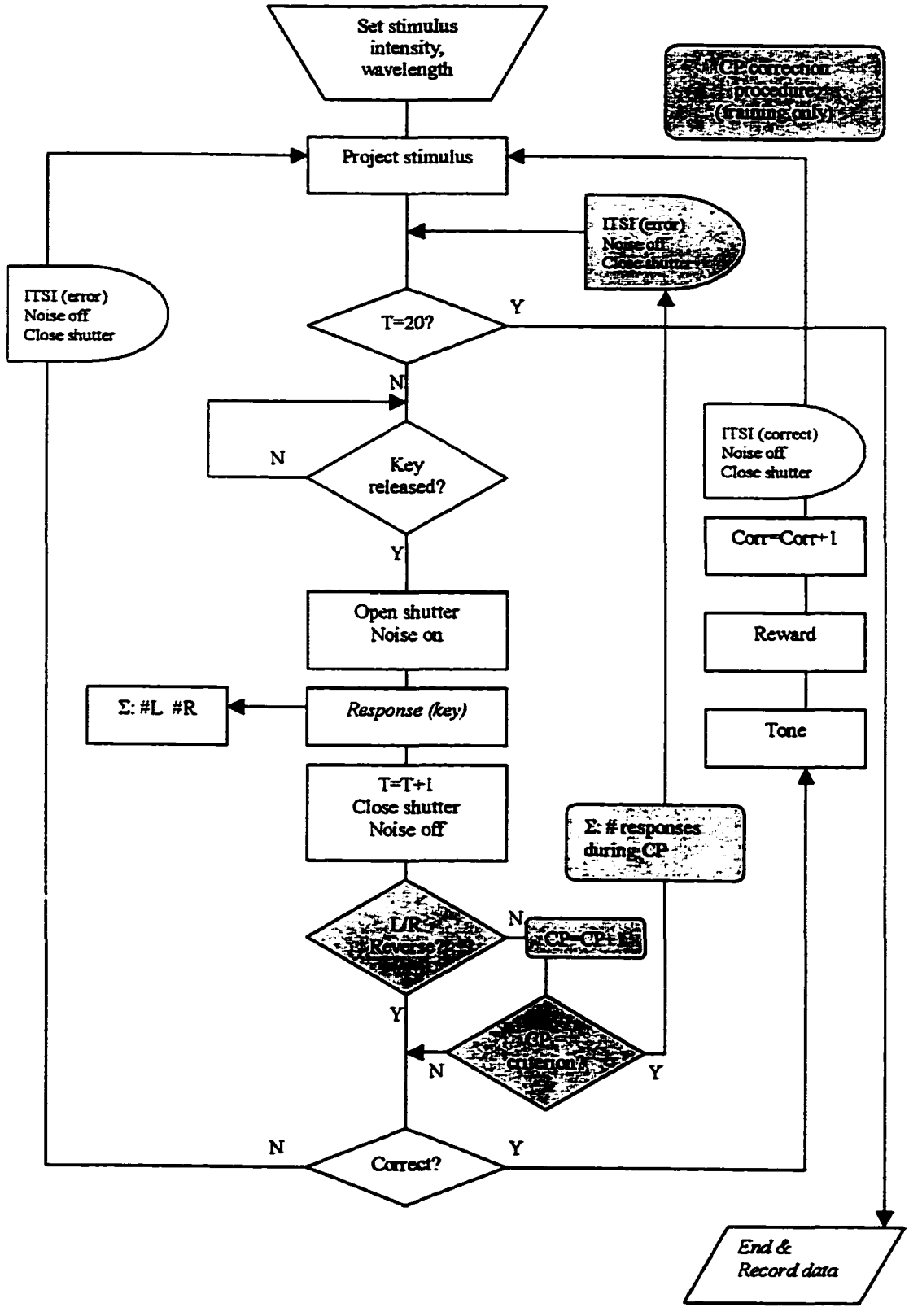

Figure 29. **Trial block flowchart.**

For detection threshold testing, white, broadband color, and spectral increments were presented to the left (L) or right (R) side of the display. Order of L/R presentation was arranged according to the rules as specified in the Gellerman series (Gellerman, 1933). This series was designed as a means to maximize a probable chance score of 50% in procedures incorporating alternating position and animal subjects. Use of the Gellerman series avoids such problems as long strings of one-sided choices or inadvertent patterns that can lead to position habits and other confounding behaviors. The series includes such requirements as an even number of L/R presentations, an equal probability of L/R reversals and nonreversals, and a maximum of three presentations of the same stimulus in a row (LLL). An example Gellerman series is as follows:

L R R L R R L L L R L R L R R L R L L R

Detection thresholds were determined over several days for white and colored increments. The animal was rewarded for pressing the window through which the increment was visible. Testing consisted of 10-trial blocks starting at a stimulus luminance of about 1.0 log units above detection threshold. The stimulus luminance was decreased 0.3 log units on subsequent blocks of trials until the stimulus elicited a correct response rate below 70%. Detection thresholds were established as the intensity associated with a 75% correct response rate.

One or two final blocks of trials were then run at the starting intensity to determine if any nonstimulus variable such as fatigue or satiation could account for declining performance. This also provided a criterion for acceptance of data for a block of trials that was independent of the threshold measurement. The criterion for data acceptance was that the animals return to a level of 80% correct within two blocks of trials run at the starting intensity. A level of 80% was chosen because it was above the 75% threshold

but below 90%. A requirement of 90% correct would have been a stringent criterion for a block of 10 trials, in that it would have allowed only one error after a series of difficult discriminations and would have resulted in rejection of a large portion of the data.

For color discrimination threshold testing, white and spectral increments were presented simultaneously to either side of the display, again arranged as specified in the Gellerman series. The animal was rewarded for pressing the window through which the spectral increment was visible. The white and all spectral increments were presented at starting intensities of 0.5 log units above an individual animal's detection thresholds. In cases where the discrimination could not be made, the increments were presented at starting intensities of 1.0 log units above detection threshold. Once color discrimination was established, color thresholds were determined by reducing luminance of both white and spectral increments 0.3 log units for each subsequent block of trials, as was done with the detection threshold testing. Again, a final block of trials was then run at the starting intensity to determine if any nonstimulus variable such as fatigue or satiation could account for declining performance. Color discrimination thresholds were established as the increment intensities associated with a 75% correct response rate. To rule out extraneous variables caused by channel configuration, the white and color channels were reversed, (i.e., the filters were physically moved to the opposite channels) and all stimuli were recalibrated in the reversed configuration for some of the color discrimination trial blocks.

The same apparatus was used for human testing with the following exceptions: (a) the viewing distance was 24 in. in order that subjects could look through the animal chamber, producing a stimulus size of 2°, and (b) responses were made on handheld right and left buttons instead of the keys pressed by the animals. Procedures were the same for

humans, with the following exceptions: (a) humans were tested only with the 500-nm long-pass and 500-nm short-pass stimuli at a background intensity of 130 cd/m^2, (b) stimuli were presented in one block of 40 trials instead of six blocks of 10 trials, and (c) no food reward was incorporated.

Threshold Helmholtz-Kohlraush Effects testing was conducted in the same manner as the increment detection trials, with the following exception: upon determination of the detection threshold for a white stimulus, that stimulus was set at 0.5 log units above those detection levels and a color filter was placed in the light beam of that same stimulus. Detection thresholds were again determined for the colored stimulus, allowing direct measurement of the effect of color on the detectability of that stimulus.

RESULTS

Data are grouped under five headings. A sample of raw data illustrating actual responses and frequency of seeing curves without analysis are presented first. Secondly, data for individual normal dichromatic subjects at various background intensities are presented. This is followed by a comparison of normally dichromatic species for a given stimulus and background intensity. Then data are presented by visual function category, that is, normal dichromats vs. normal humans vs. dichromatic humans. Finally, data are presented for the Helmholz-Kohlrausch experiments.

Sample Responses and Raw Data

Detection thresholds and color discrimination thresholds were determined for all subjects. An illustrative account of all data collection trials for one animal is displayed in sequential array in Figure 30. The figure depicts the entire sequence of trial blocks from start to finish for that animal, starting with determination of detection thresholds for the white stimulus. That was followed by determination of detection thresholds for a 540-nm stimulus, then by determination of color discrimination thresholds for that 540-nm stimulus paired with the white stimulus, and so on for the remaining stimuli.

The white and color channel reversals are also depicted in Figure 30, where "N" indicates the normal configuration and "R" indicates the reversed configuration. There was no statistically significant difference in the means for all conditions where channels were reversed (mean difference = 0.03 log attenuation, $t = 0.557, p = 0.583$).

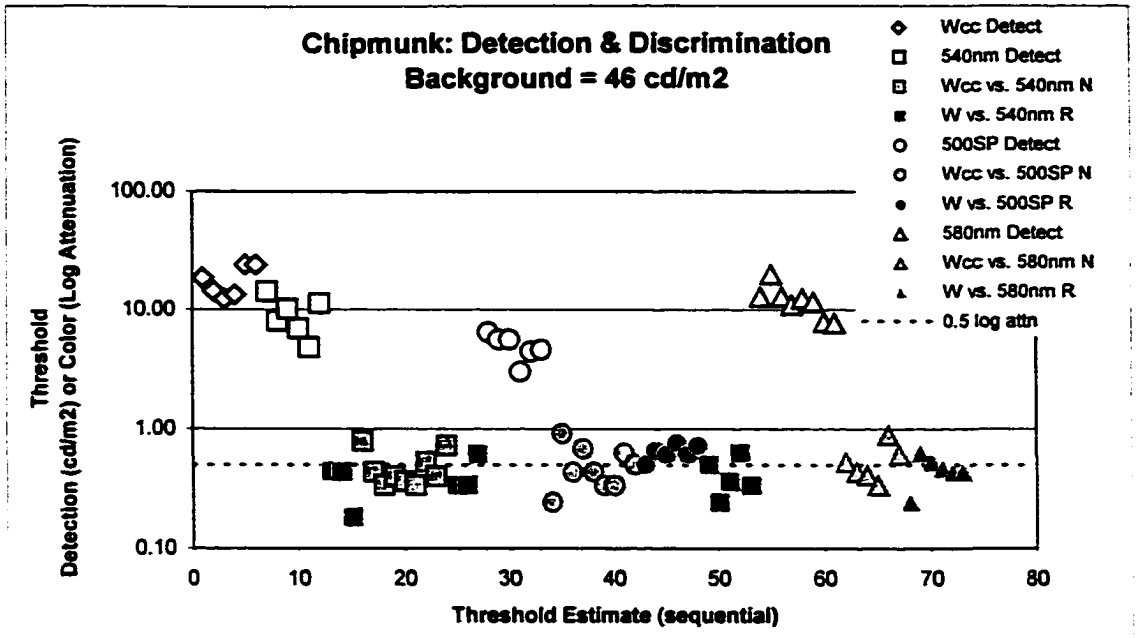

Figure 30. Sequential detection and discrimination trials for the chipmunk. Open symbols in indicate detection thresholds in cd/m^2. Closed symbols indicate color discrimination thresholds in log attenuation from a starting intensity of 0.5 log units above detection threshold. The dotted line indicates a color discrimination threshold of 0.5 log units (i.e., detection and color discrimination thresholds of equal intensity). Reverse-pattern shapes indicate trials where stimulus channels were reversed. In this example, the closed symbols are clustered about the dotted line, indicating that color discrimination occurred at detection threshold intensities for all stimuli, including conditions where the channels were reversed.

A sample collection of frequency of seeing curves is displayed in Figures 31 and 32. Figure 31 shows that as the stimuli are attenuated, the animal's ability to respond correctly deteriorates. Threshold estimates, defined as 75% correct response rates, were calculated from these curves using the least squares method. Figure 32 isolates one frequency of seeing curve to illustrate response variability. Variability was generally low for easily detectable stimuli where responses were approximately 100%. Variability increased as the stimuli became more difficult to detect, then decreased again below threshold where responses of approximately 50% correct occurred by chance.

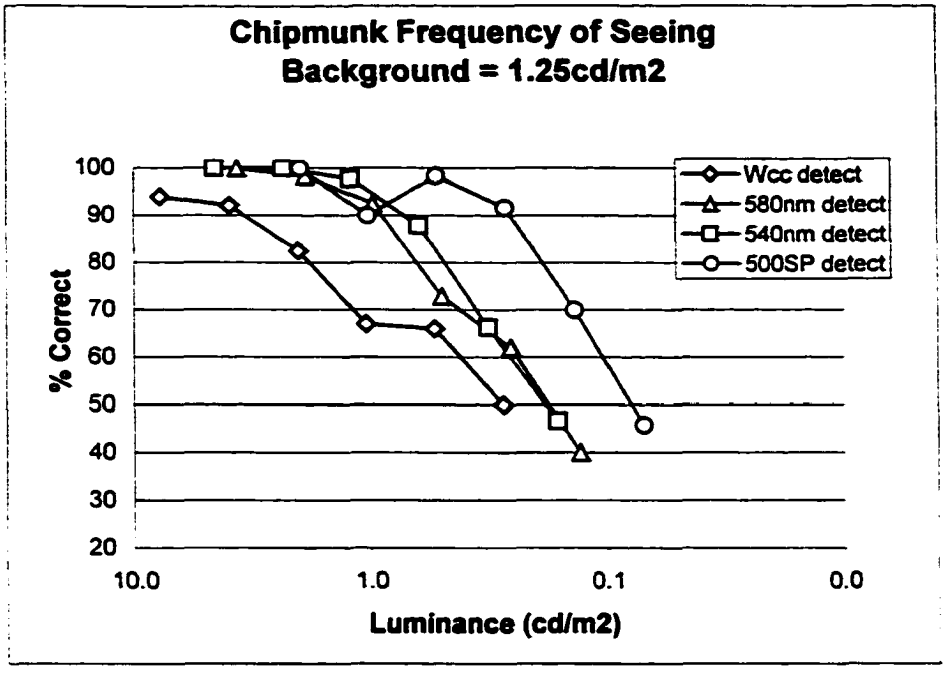

Figure 31. Sample frequency of seeing curves.

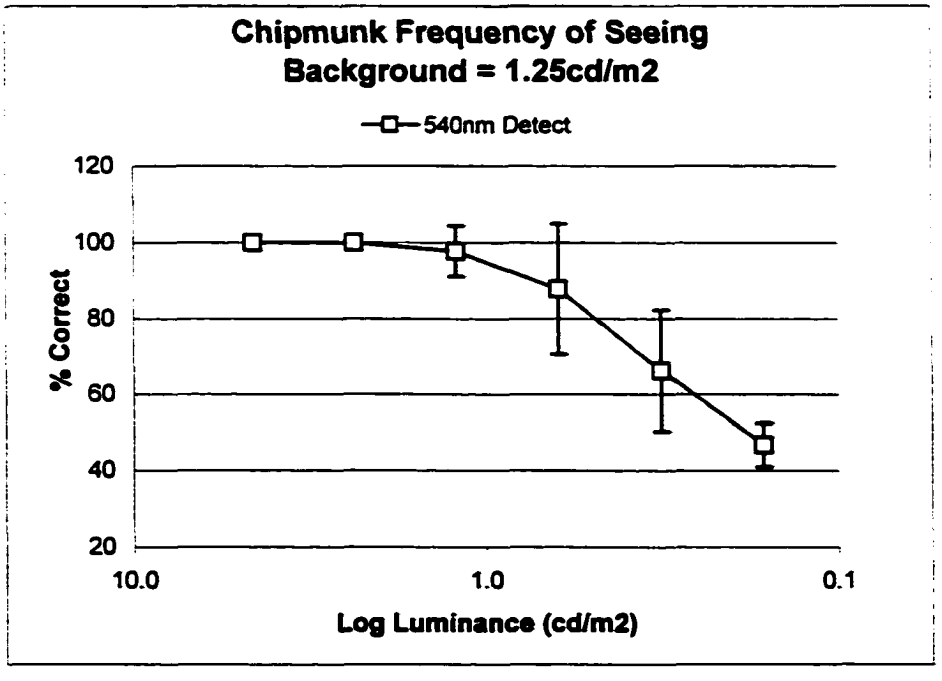

Figure 32. Sample response variability.
Error bars indicate standard deviation.

Thresholds of Individual Normal Dichromats

Figures 33 through 36 illustrate detection and color discrimination thresholds for each animal, presented with various stimuli at three background levels. The ordinate in the figures indicates the difference between detection and discrimination thresholds measured as log attenuation from the starting intensity. A value above zero indicates that log attenuation for color discrimination was less than that needed for detection (i.e., more light was needed to identify color than to detect it). A value of zero indicates that log attenuation for discrimination was the same as that for detection (i.e., color was identified at detection threshold). Error bars indicate standard deviations. Mean values in log units above threshold with SD for Figures 33 through 36 are shown in Table 1.

Table 1

Color Thresholds vs. Background Level

Subject – Background Level	500SP	500LP	540/560 nm	580 nm	Mean	SD
CM-1.25	0.43	-	0.65	0.43	0.51	0.14
GS-1.25	0.06	-	0.68	0.86	0.77	0.20
CM-46	-0.06	-	0.06	0.00	0.00	0.18
GS-46	-0.01	-	0.07	0.12	0.06	0.16
TS1-46	0.19	-	0.25	-0.02	0.14	0.16
TS2-46	0.25	-	0.26	0.12	0.21	0.20
CM-130	0.06	-0.01	-	-	0.03	0.12
GS-130	-0.02	0.08	-	-	0.03	0.15
TS1-130	0.29	0.17	-	-	0.23	0.13
TS2-130	0.01	0.29	-	-	0.15	0.17

CM = chipmunk; GS = ground squirrel; TS = tree shrew. Stimuli included 500 nm short pass, 500 nm long pass, 540 nm spectral (chipmunk & ground squirrel), 560 nm spectral (tree shrew), and 580 nm spectral. Background levels are in cd/m^2.

Figure 33 shows that the chipmunk did not exhibit color discrimination at detection thresholds with a low background intensity of 1.25 cd/m^2. However, at moderate (46 cd/m^2) and bright (130 cd/m^2) background intensities the chipmunk was able to discriminate color at detection threshold intensities. Figure 34 shows that the ground squirrel performed similarly to the chipmunk, in that it was also able to discriminate color at or near detection threshold intensities. In addition, the ground squirrel was able to discriminate the 500-nm short-pass stimulus at the low background intensity.

The tree shrews were not tested at the low background level, but were tested at the medium and high background intensities. Figure 35 shows that tree shrew #1 was able to discriminate color within 0.3 log units of its detection threshold, and was able to discriminate the 580-nm stimulus at detection threshold on the 46-cd/m^2 background. Similarly, Figure 36 shows that tree shrew #2 also discriminated color within 0.3 log units of detection threshold intensities, and was additionally able to discriminate the 500-nm short-pass stimulus at detection threshold intensities.

Figure 37 displays averaged data for all normal dichromats, including the chipmunk, ground squirrel, and tree shrews. These results indicate that, in general, color cannot be discriminated at detection thresholds for low background intensities, but that color discrimination occurs close to detection thresholds at higher background intensities.

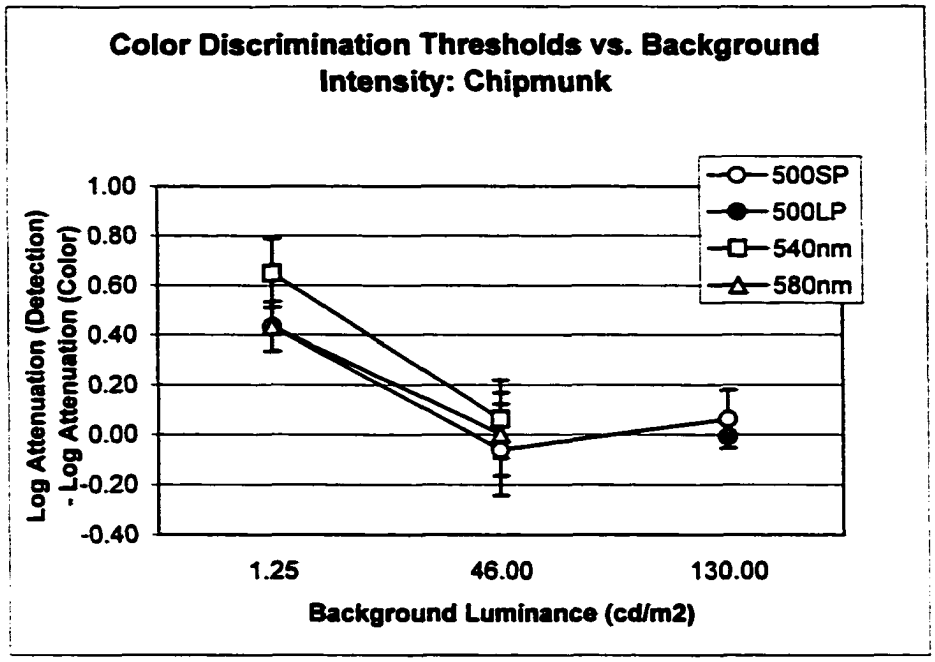

Figure 33. Color thresholds vs. background intensity for the chipmunk.

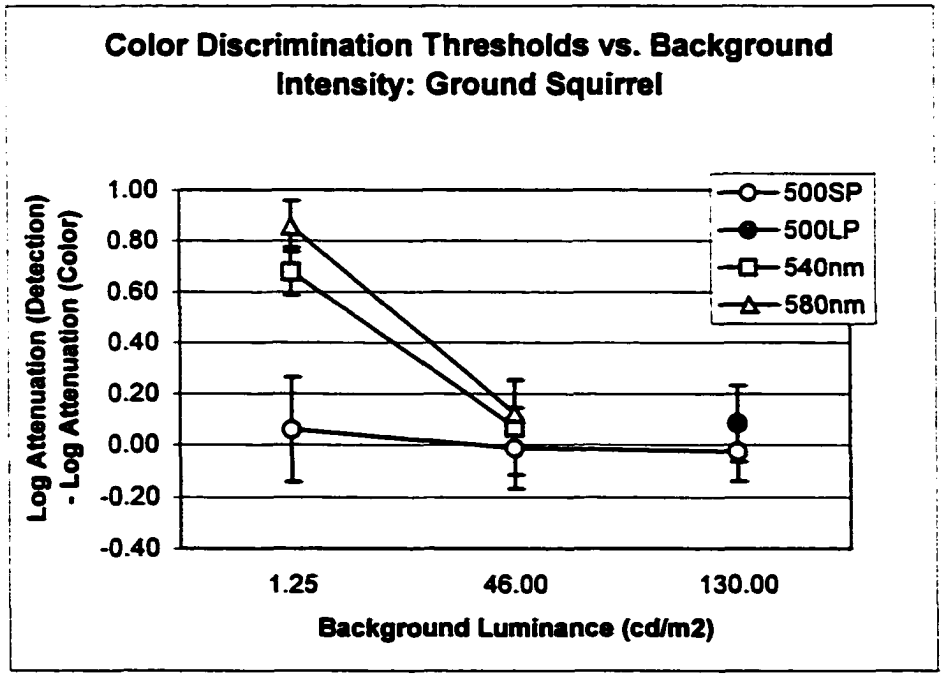

Figure 34. Color thresholds vs. background intensity for the ground squirrel.

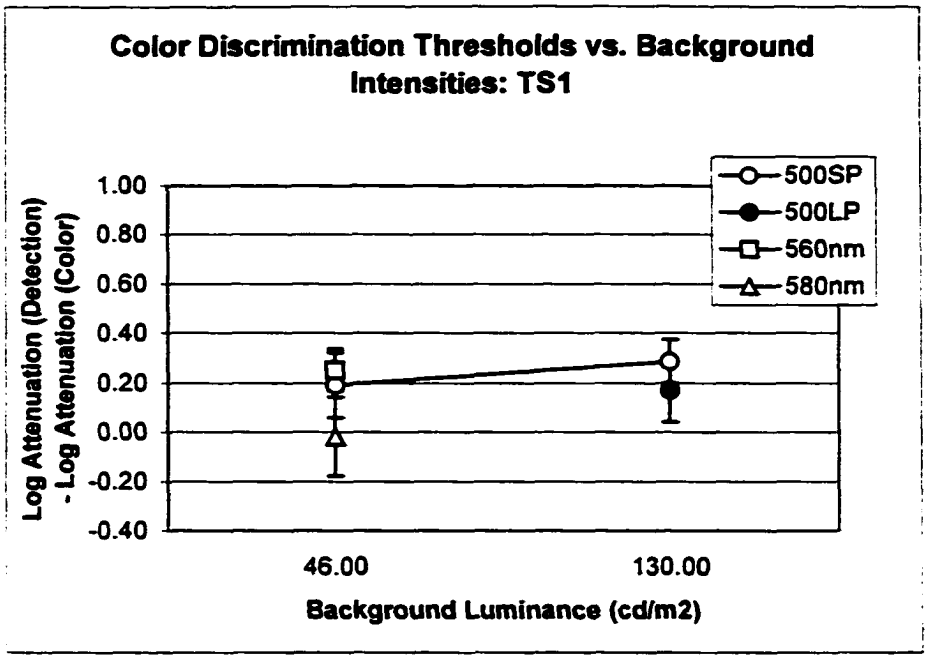

Figure 35. Color thresholds vs. background intensity for tree shrew #1.

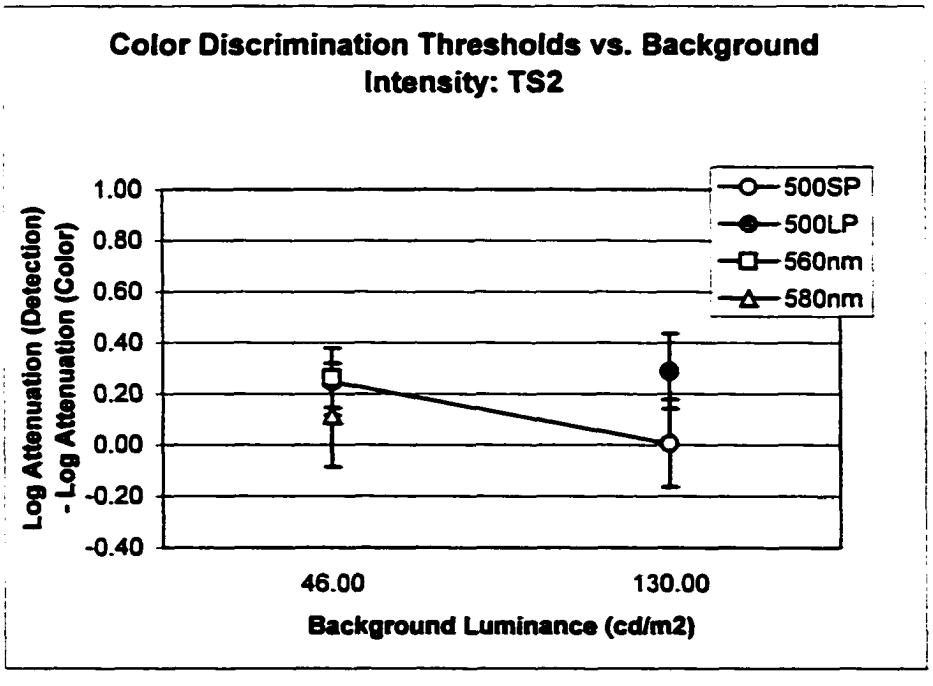

Figure 36. Color thresholds vs. background intensity for tree shrew #2.

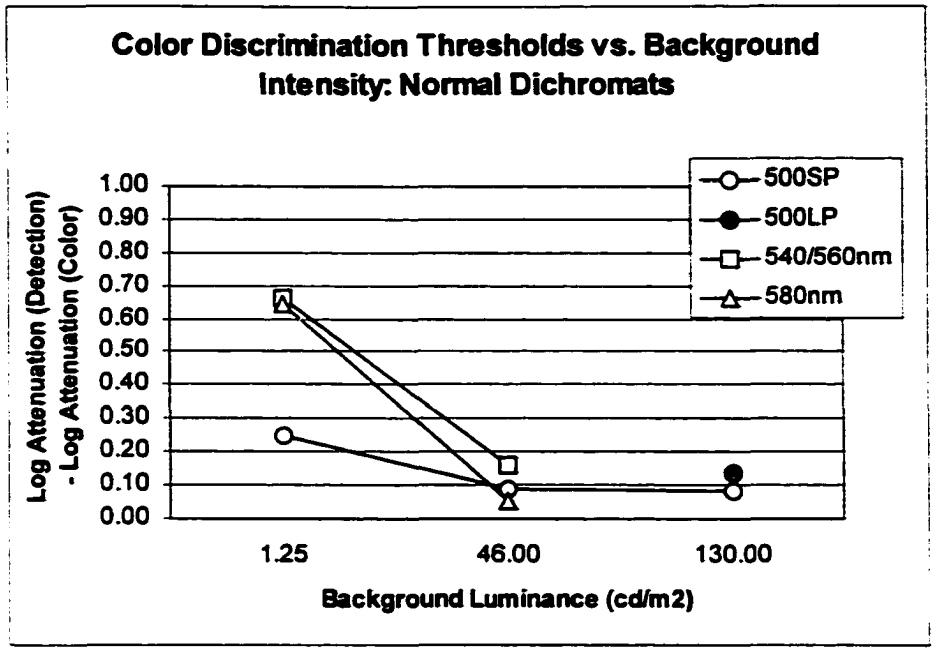

Figure 37. Color thresholds vs. background intensity for normal dichromats.

Comparison of Normally Dichromatic Species.

The next series of figures display the data listed in Table 1 to compare normally dichromatic species for a given stimulus and background level. Figure 38 shows that the chipmunk and ground squirrel discriminated the color of the 500-nm short-pass stimulus on the medium intensity background at or slightly below the detection threshold, and that the tree shrews required higher intensities to discriminate the color. Figure 39 shows that the chipmunk and ground squirrel discriminated the 540-nm stimulus on the medium background within 0.1 log units of detection threshold, and that the tree shrews discriminated the 560-nm stimulus within 0.3 log units of detection. Figure 40 illustrates some variability across and within species with the 580-nm stimulus on the medium background. However, in this condition, all of the normal dichromats identified the stimulus color within 0.12 log units of detection threshold.

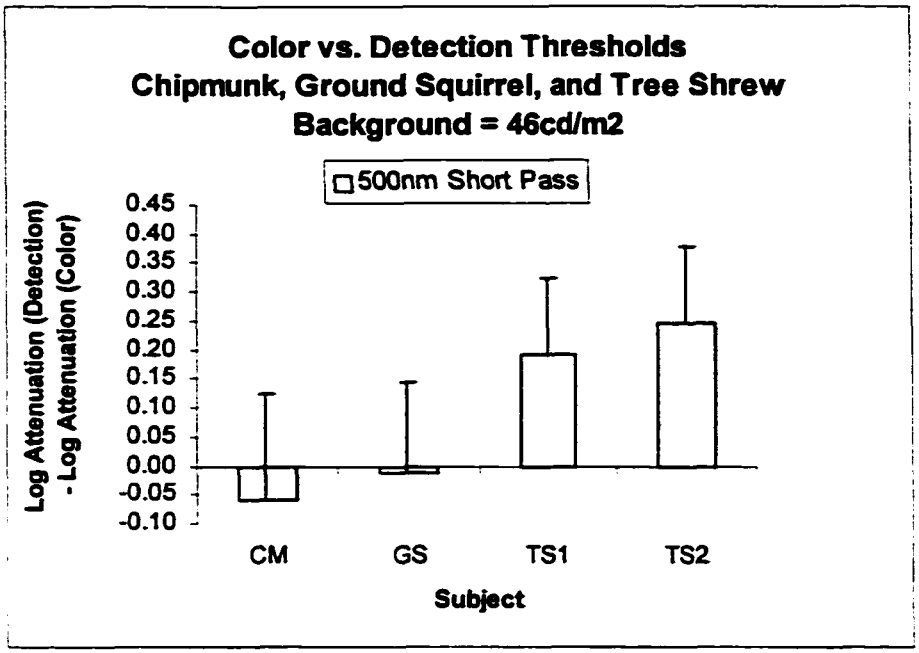

Figure 38. Detection vs. color thresholds for normal dichromats 1.

Stimulus = 500 nm short pass. Background = 46 cd/m^2. Error bars indicate standard deviation.

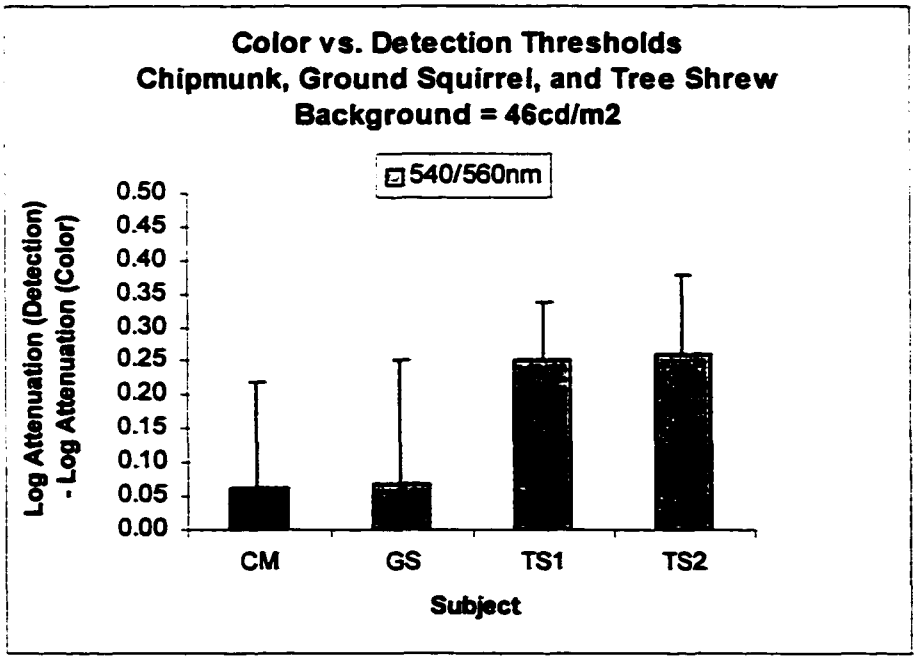

Figure 39. Detection vs. color thresholds for normal dichromats 2.

Stimulus = 540 nm spectral for the tree shrews and 560 nm spectral for the chipmunk and ground squirrel. Background = 46 cd/m^2. Error bars indicate standard deviation.

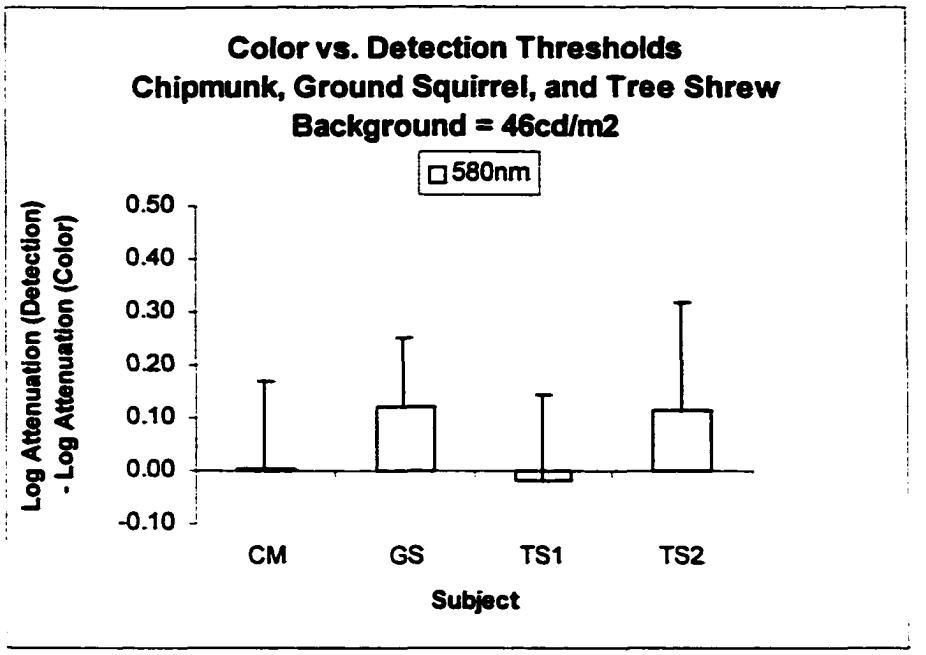

Figure 40. Detection vs. color thresholds for normal dichromats 3. Stimulus = 580 nm spectral. Background = 46cd/m^2. Error bars indicate standard deviation.

Figure 41 again shows some variability between and within species for the 500-nm short-pass stimulus on a bright background. However, three of the normal dichromats discriminated the stimulus within 0.1 log units of detection threshold, and the remaining tree shrew discriminated the stimulus within 0.3 log units of detection threshold. Although the tree shrews exhibited considerable variability between subjects, TS2 was able to discriminate color from white at detection threshold in this condition.

Figure 42 shows that for the 500-nm long-pass stimulus on the bright background, the chipmunk identified color at detection threshold, the ground squirrel identified color within 0.1 log units of detection threshold, and the tree shrews did so within 0.3 log units of detection threshold.

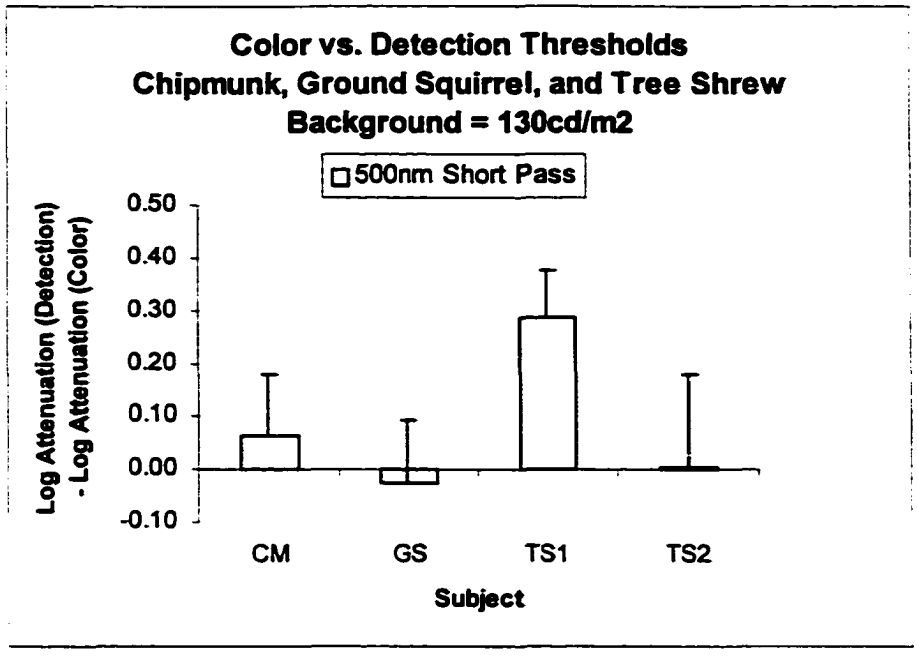

Figure 41. Detection vs. color thresholds for normal dichromats 4.

Stimulus = 500 nm short pass. Background = 130 cd/m^2. Error bars indicate standard deviation.

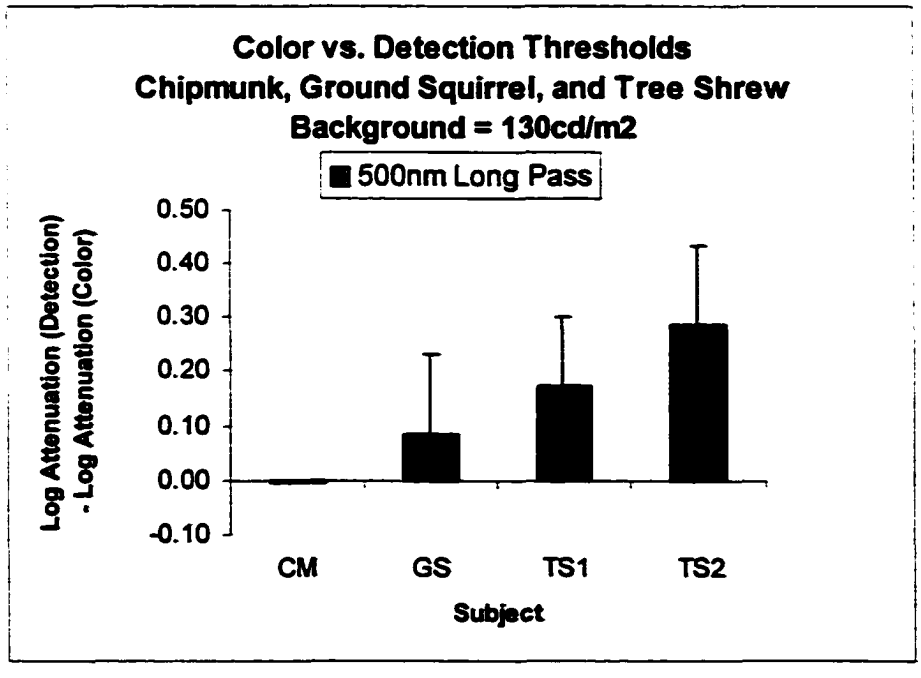

Figure 42. Detection vs. color thresholds for normal dichromats 5.

Stimulus = 500 nm long pass. Background = 130cd/m^2. Error bars indicate standard deviation.

Comparison by Visual Function Category

The following figures display data grouped by visual function category in Table 2. Visual function categories include normally dichromatic species (ND), normal trichromatic humans (NH), and dichromatic and deuteranomalous humans (DH). The deuteranomalous trichromat exhibited detection sensitivity and color discrimination sensitivities similar to the dichromatic human in this study; therefore, those two subjects were grouped into one visual function category (DH).

Table 2
Color Thresholds by Vision Function Category

Vision Function Category and Background Level	540/560 nm	580 nm	Short Pass	Long Pass
ND – 1.25	0.66	0.65	0.25	-
ND – 46	0.16	0.06	0.09	-
ND – 130	-	-	0.08	0.13
NH – 130	-	-	-0.21	0.09
DH – 130	-	-	-0.08	0.49

ND = normal dichromats; NH = normal humans; DH = dichromatic humans. Background levels are in cd/m^2.

Figure 43 shows averaged data for normal dichromats for all stimuli at all three background intensities. At low background illumination, these subjects required more than 0.6 log units of additional light to discriminate the 540-nm, 560-nm, and 580-nm stimuli, but performed better with the 500-nm short-pass stimulus. At the brighter background levels of 46 cd/m^2 and 130 cd/m^2 the subjects consistently discriminated color within about 0.1 log unit of their detection thresholds. The 500-nm long-pass stimulus

was used instead of the 540/560-nm and 580-nm spectral stimuli on the 130-cd/m^2 background in order to produce stimuli of sufficient intensity.

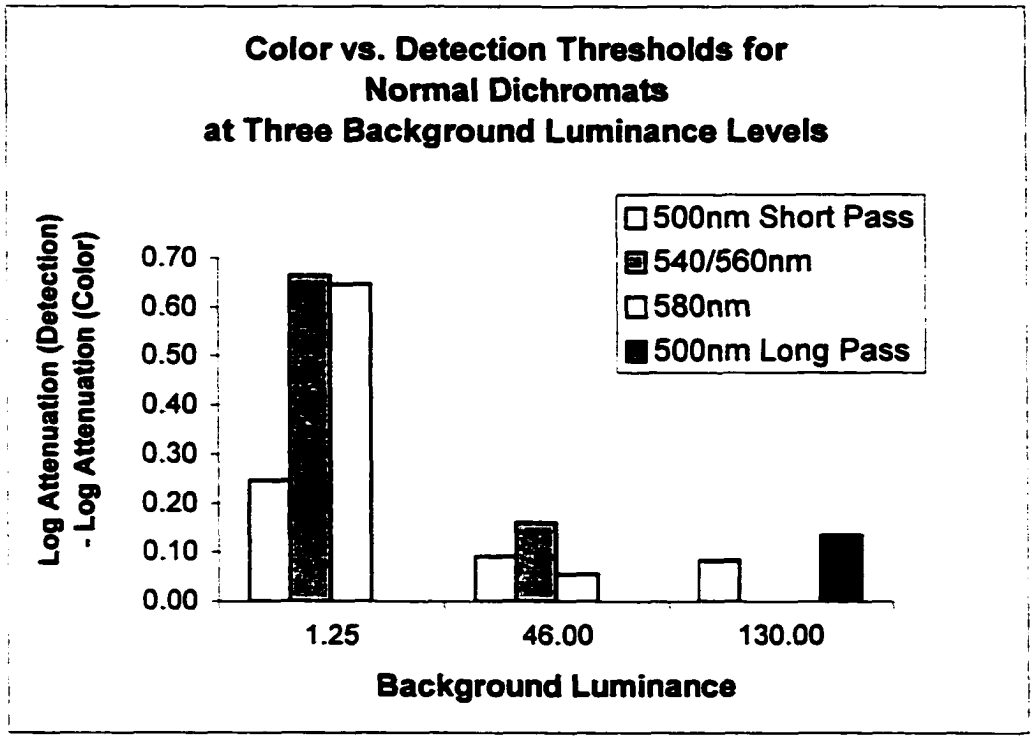

Figure 43. Color discrimination by normal dichromats at three background intensities. A 500-nm long-pass stimulus was used instead of the 540/560-nm spectral and 580-nm spectral stimuli on the 130-cd/m^2 background.

Figure 44 illustrates a comparison of normal dichromats, normal humans, and dichromatic humans at the brightest background level. The figure shows that subjects in all categories were able to identify the 500-nm short-pass stimulus within 0.1 log units of threshold intensities. However, whereas normal dichromats could discriminate the long-pass stimulus from white within about 0.1 log units of detection threshold, dichromatic humans (with a similar ITSS) required an increase of about 0.5 log units above threshold intensity. This difference between normal dichromats and dichromatic humans for the

long-pass stimulus is statistically significant ($t = 4.47, p = 0.01$). The figure also shows that normal humans identified the color of a Kodak #21 long-pass stimulus within 0.09 log units of detection threshold. There was no statistically significant difference between the normal humans and the normal dichromats for the long-pass stimuli ($t = 0.68, p = 0.54$).

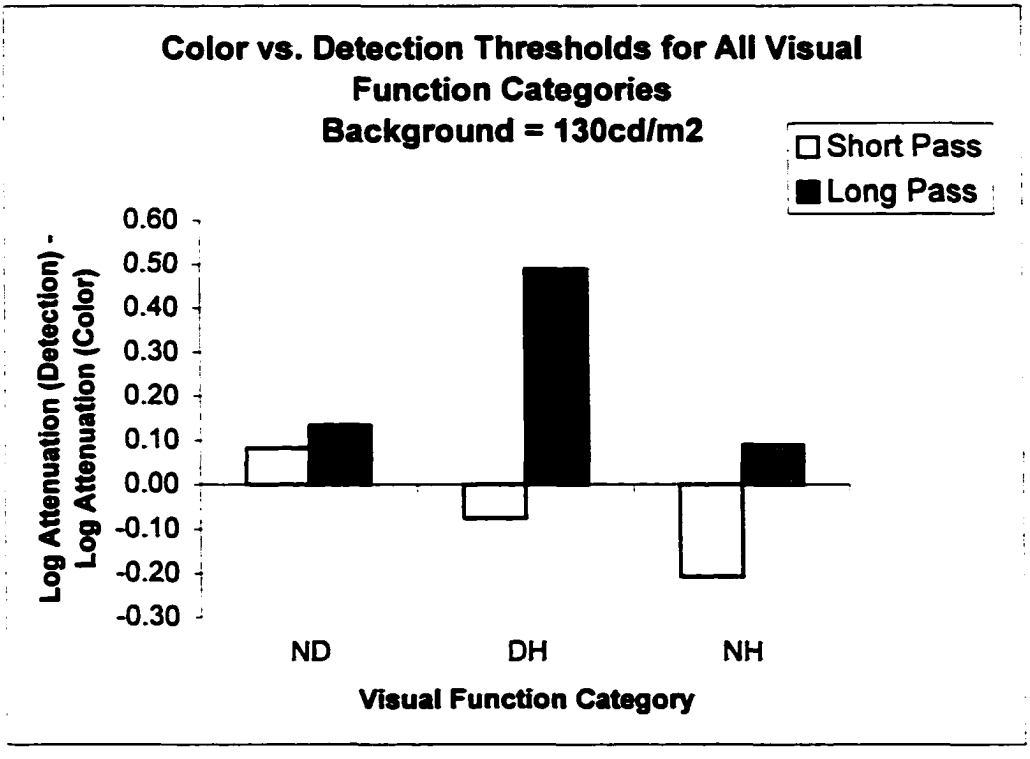

Figure 44. Color discrimination for all visual function categories.
Stimuli = 500 nm short pass (all subjects), 500 nm long pass (ND & DH), and Kodak #21 Red Filtered (NH). Background = 130 cd/m^2.

It is worth noting that color discrimination thresholds are often below detection thresholds, as shown in Figure 44 where the humans viewed the 500-nm short-pass stimulus. This phenomenon was noted by King-Smith and Carden (1976) and can be attributed to the fact that in the detection task only one stimulus is presented, but on the

discrimination task two stimuli are presented. Thus, there are two opportunities for the subject to make an assessment as to the nature of the stimulus: if one stimulus is not detected, the other might still be detected and identified.

Helmholz-Kohlrausch Experiment

Results of the experiment on the threshold Helmholz-Kohlrausch effect are shown in Figure 45. These results support earlier findings from Loop and Crossman (2000) for normal humans and macaques, shown earlier in Figure 22. In Figure 45, white detection thresholds are set at 0.0 log attenuation by definition, and the detection thresholds for the colored stimuli are plotted relative to the white thresholds, since they were produced by placing a filter in the same channel with the same starting intensity. When the 500-nm short-pass filter was placed in the channel, the animals required more light to detect the stimulus. However, when the 500-nm long-pass filter was placed into the channel, each of the normal dichromats consistently detected the stimulus more readily although there was physically less light in the channel. The enhanced detectability was statistically reliable ($t = 2.68$, $p = 0.009$).

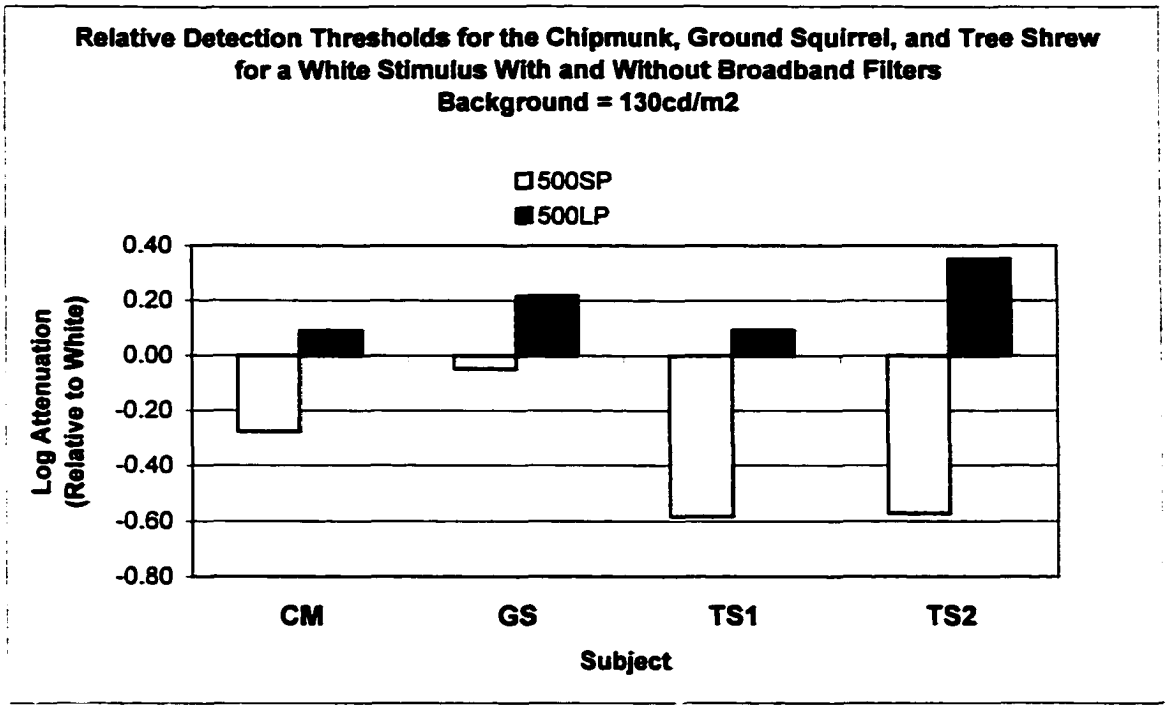

Figure 45. Threshold Helmholz-Kohlrausch Effect for normal dichromats.

White detection thresholds are at 0.0 log attenuation. Color detection thresholds are plotted relative to the white thresholds.

DISCUSSION

Interpretation of Results

Results indicate that normally occurring dichromats can discriminate color from white at or near detection thresholds in photopic conditions. This enhanced photopic detection sensitivity in normal animals, as mediated by wavelength opponency in the form of high color vision, appears to be a feature of normal color vision, whether it is dichromatic (per this study), trichromatic (King-Smith & Carden, 1976; Loop & Crossman, 2000), or based on more cone types (Roberts & Loop, 1999). On the other hand, color-abnormal humans require higher intensities to see the color of an increment than to detect it (Loop et al., 2002).

The difference between normal dichromats and human dichromats becomes even more apparent when the data for the 500-nm short-pass filter are removed and the medium and bright background are combined (i.e., if data are combined for the longer wavelength stimuli on a photopic background). That combination includes the (a) normal dichromats viewing the 540-nm, 560-nm, and 580-nm stimuli on the 46-cd/m^2 background, (b) normal dichromats viewing the 500-nm long-pass stimulus on the 130-cd/m^2 background, and (c) the humans viewing the long-pass stimuli on the 130-cd/m^2 background. Compilation of that data with data from the Loop study (Loop et al., 2002), where human subjects viewed 540-nm and 620-nm stimuli on a 1000-troland background, results in a clear distinction between normal dichromats and human dichromats, as shown in Figure 46. That set of data indicates that normal dichromats discriminate

color at 0.12 +/- 0.08 log units above detection threshold, dichromatic humans at 0.40 +/- 0.08 log units above detection threshold, and normal humans at 0.03 +/- 0.12 log units below detection threshold. The difference between the normal dichromats and the normal humans is not quite statistically significant ($t = 2.32$, $p = 0.054$). More interestingly, the difference between the normal dichromats and the dichromatic humans is highly statistically significant ($t = 5.2$, $p = 0.001$).

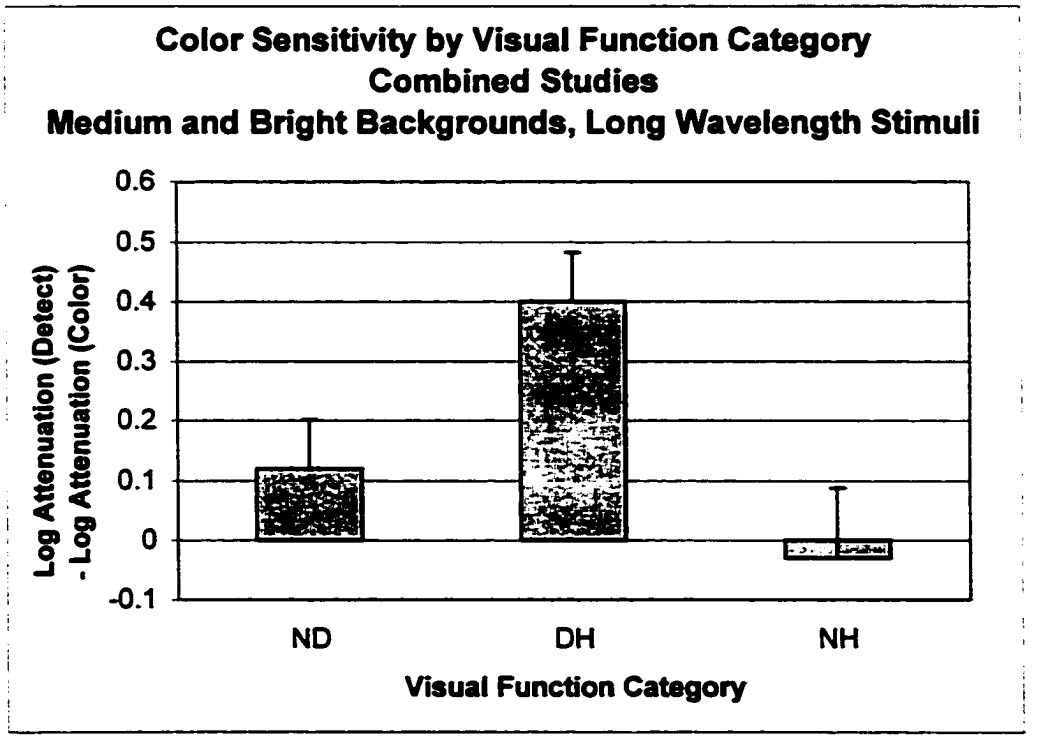

Figure 46. Color sensitivity by visual function category – combined studies. Error bars indicate one standard deviation.

The validity of the assessment that the normal dichromats see color at threshold is bolstered by the findings that at low background intensity (i.e., at 1.25 cd/m^2), the normal dichromats' ability to discriminate color deteriorated. As is found in normal human trichromats (King-Smith & Carden, 1976), the luminance system mediates detection at

low light levels where the color system is at a disadvantage. This double dissociation reduces concerns over possible systematic errors in the apparatus, methods, training, and animal behavior that could confound results.

Since red/green dichromats and anomalous trichromats appear to detect large, long-duration spectral increments with color-opponent mechanisms under light adapted conditions (Miyahara et al., 1996; Schwartz, 1994), they should be able to discriminate the color of a visual stimulus at detection threshold. The lack of high color vision sensitivity in human dichromats, coupled with the presence of high color vision in normally occurring dichromats, supports the hypothesis that dichromacy in humans affects postreceptoral opponent processing mechanisms, and thus that inputs to central color processing mechanisms are abnormal.

There is additional evidence supporting the hypotheses that dichromacy in humans affects postreceptoral opponent processing mechanisms. Regan, Reffin, and Mollon (1994) recently studied the discrimination ability of color-deficient individuals, and found that R/G dichromats have elevated color discrimination thresholds on the *tritan* (B/Y) axis. That was an unexpected finding, since variation of colors along the tritan axis alters the ratio of input from the S/M or S/L cone types for the protanopes and deuteranope, respectively. In other words, the intact B/Y opponent system of R/G human dichromats should enable normal discrimination of those stimuli. They assert that it is "commonly assumed that these ratios are extracted by a phylogenetically ancient subsystem that remains unimpaired in red-green colour blindness." Regan et al. subsequently propose that the "opposed inputs to the residual colour channel of the dichromat might be less well balanced" in human protanopes and deuteranopes than in normal trichromats.

Alterations in postreceptoral processes of human dichromats may be manifest further along the visual pathway. Many contend that color perception, particularly red/green color vision, is normally multiplexed out of the parvocellular pathway. This is entirely feasible from a physiological standpoint; about 80% of normal human retinocortical systems are comprised of the parvocellular pathway whose neurons are wavelength opponent (Lee, 1996). Since human dichromats have been shown to have normal acuity, the parvocellular pathway is presumably functioning normally with regard to spatial function. Whether the cells that mediate red/green color-opponent functions are absent, silent, or used for other functions is open to speculation.

If the opponent function in the color vision pathway were altered, the central color processing mechanisms of dichromatic humans would be confronted with abnormal input. For instance, one could speculate that Livingston and Hubel's double-opponent cortical cells do not receive proper red/green opponent information from the parvocellular pathway, and thus cannot signal the recognition of those colors. Again, whether such cells degenerate during developmental stages due to lack of activity, remain silent, or are recruited to perform other tasks is open to speculation.

Ancillary Observations

All animals used in this study demonstrated higher detection thresholds for all stimuli than did humans, particularly for the white and long-pass stimuli, as shown in Figure 47. This finding is predicted by the contrast sensitivity functions of various animals, as compiled by Petry, Fox, and Casagrande (1984) in Figure 48. In that figure the ground squirrel and tree shrew are shown to be about ten times less sensitive than humans to contrast at all spatial frequencies. The dichromatic humans and normal humans did

not show a statistically significant difference in their thresholds for the white stimulus used in this study ($t = 1.05$, $p = 0.4$) or others (Kuyk et al., 2000).

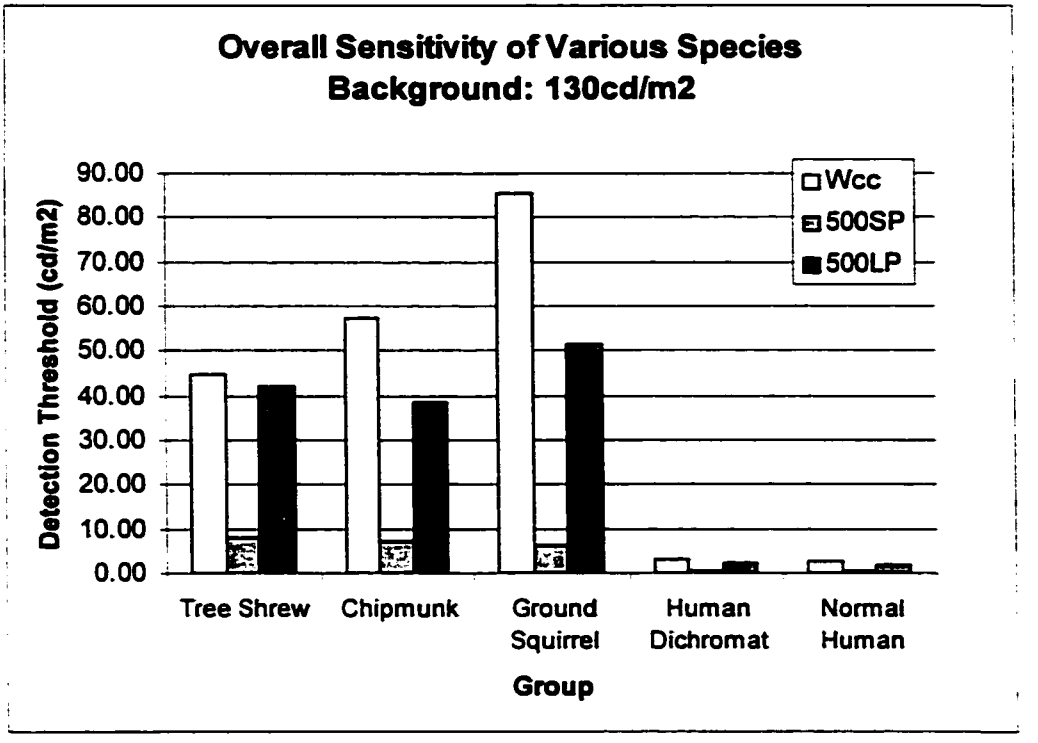

Figure 47. Overall sensitivity of various species.
Stimuli included color-corrected white (Wcc), 500 nm short pass (500SP), and 500 nm long pass (500LP).

Human subjects described the appearance of the blue stimulus at threshold as having a gradual onset, unclear borders (often described as a faint "smudge"), and persistent visibility once its presence was realized. This indicates in a conscious sense that faint blue increments are detected by the blue-yellow wavelength-opponent parvocellular system, since that system has a sparse representation in the retinal photoreceptor mosaic and exhibits relatively extensive spatial and temporal integration. It is interesting to reflect upon how that system can mediate such a strong color sensation (i.e., have such a

highly saturated appearance) when there are so few "blue" cone types in the retina and, indeed, when none exist in the central fovea (Roorda & Williams, 1999).

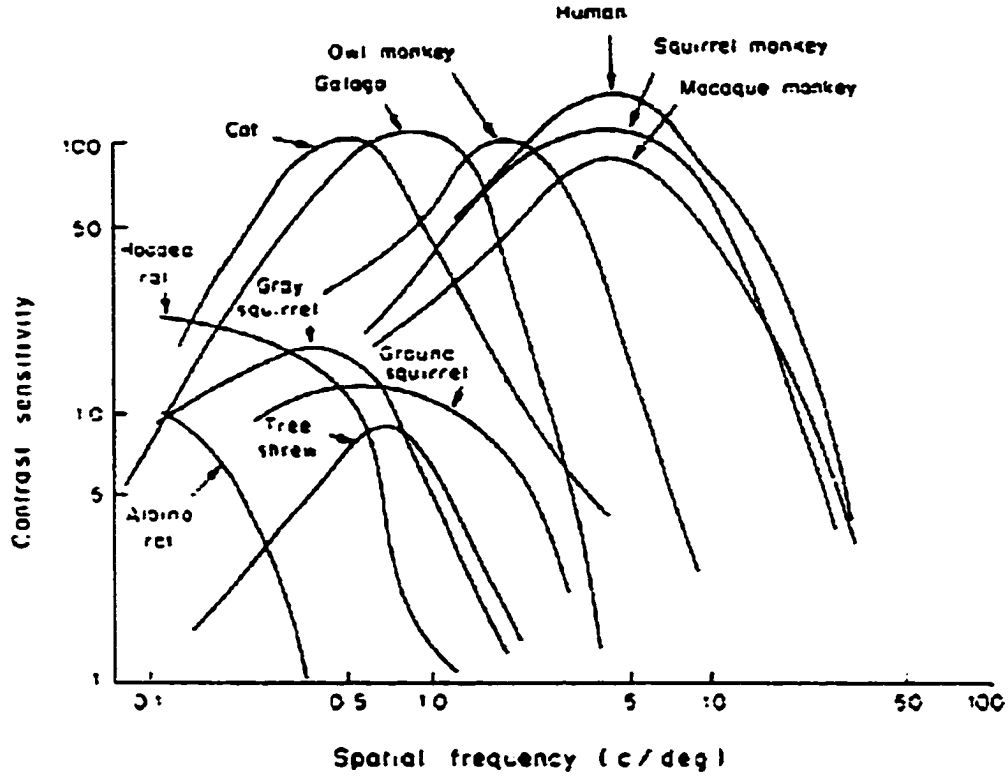

Figure 48. Spatial contrast sensitivity for various animals.
Figure adapted from Petry, Fox, and Casagrande (1984).

The human dichromats in this study commented that when asked to discriminate colors from white, the long-pass stimulus appeared somehow "different" but not really different in color. The human dichromats could have observed subtle qualitative differences between the stimuli not noticed by the trichromats, since color is such a strong identifying characteristic for the latter subjects. As an aside, subtle differences between stimuli tend to be amplified when working at threshold levels, a phenomenon that is almost universally noticed by subjects in such experiments. This can be compared to the discrimination task commonly given to patients during a refraction, whereby they are

asked, "which is better, one or two?" for a pair of stimuli that differ only slightly in their amount of distortion and blur. In particular, the end point for the Jackson Crossed Cylinder clinical test is when two distorted and blurred stimuli are "about the same," or equally blurred/distorted. That threshold discrimination task is often stressful to observant patients, who often notice differences they can't quite "put a finger on" and who often ask for the stimuli to be presented multiple times.

Experimental Design Considerations

For this experiment, use of luminance units was valid despite the fact that different species have different spectral sensitivity (V_λ and ITSS) functions. This is because color discrimination thresholds were determined as attenuation from intensity settings based on a given animal's detection threshold; therefore, the units used to measure light levels in this experiment are relative, and any unit could have been chosen. As an aside, the human V_λ function does not accurately depict sensitivity to spectral increments on a photopic white background. This is apparent upon examination of Figure 9, in which detection threshold values differ according to wavelength. In other words, equally detectable stimuli should all have the same luminance (Foot-Lamberts in that figure), but they do not. This is again apparent in Figure 30, in which equally detectable stimuli have a wide range of luminance values (cd/m^2 in that figure). This discrepancy is due to the fact that luminance values are derived with flicker photometry. In order to accurately reflect sensitivity to colored stimuli under nonflicker conditions, a new set of units would have to be devised that incorporates the ITSS function of humans. That issue is beyond the scope of this paper, but may be of concern to those working in environmental vision

and to industries that seek to standardize measures to more accurately specify the visibility or appearance of colored surfaces.

Viewing conditions for animals and humans differed in that humans viewed stimuli through the animal chamber at a distance of 24 in., such that the spots subtended an angle of 2°. For the animals, viewing distance was about one inch, making the visual angle subtended by the stimulus larger. However, humans have a higher spatial acuity than the animals used in this study. That fact and a host of other spatial and temporal differences between the species make efforts to construe equivalent tasks across species problematic. However, this viewing distance issue is mitigated by the fact that the ITSS for normal and dichromatic humans has been shown to be relatively invariant for stimulus sizes between 2° and 10° (Miyahara et al., 1996).

Task equivalence was also an issue for human dichromats and trichromats with respect to longer wavelength colored stimuli. Five hundred-nanometer short-pass and 500-nm long-pass filters were chosen, since 500 nm is the location of the Sloan notch (neutral point) for the animals used in this study, as well as for human dichromats. However, for normal humans, the 500-nm long-pass filter encompasses a second Sloan notch that negates output from the R/G channel, thus favoring detection by the luminance system. This is supported by earlier investigation of spectral increment-thresholds whereby the opponent color system did not contribute to detection of a 577-nm stimulus, even when the luminance system was depressed in that region (Mullen, 1987). This effect can be seen by examination of Figure 6, in which the human trichromat ITSS curve exhibits a minimum, and the medium-wavelength photopigment absorption curve exhibits a maximum, over the range of 540 nm to 580 nm. Therefore, to present a commensurate task to the normal humans in this experiment, a Kodak #21 filter was chosen because

it essentially acts as a long-pass filter that transmits wavelengths above about 540 nm, the approximate location of the second (longer wavelength) Sloan notch for normal humans.

The background levels proved to be adequate for the purposes of this experiment. The medium (46 cd/m^2) and high (130 cd/m^2) background levels were of sufficient intensity to favor detection by the color system in all the normal dichromats (i.e., the background and stimuli were in the photopic range of vision). The low background level (1.25 cd/m^2) was included for the chipmunk and the ground squirrel to demonstrate a breakdown of high color vision (i.e., that the color system is at a disadvantage in scotopic conditions).

The configuration of the background is a variable that might have been further optimized. The color system could have been further isolated with a "pedestal" configuration whereby the stimulus is superimposed on a background of the same size. This condition has been shown to favor detection by the color system over the luminance system (Snelgar, Foster, & Scase, 1987).

In future experiments, animals might be trained to execute an "orienting" response, whereby they are temporarily diverted from the stimulus at the instant it is presented and then required to approach the stimuli for each trial. This procedure should help to slow the animals down, possibly cause them to be more deliberate, and reduce the tendency to respond with a position habit. In addition, this procedure might further isolate the color system by eliminating transient "on" cues presented at stimulus onset (for example, when a shutter opens) that are mediated by luminance system detection.

The finding that color discrimination thresholds were occasionally lower than their detection thresholds merits comment. This phenomenon has been noted previously (King-Smith & Carden, 1976, Kuyk et al., 2000), and may be attributed to the fact that

there is a greater likelihood of detecting a stimulus in the discrimination task, since there are two stimuli in the discrimination task vs. one stimulus in the detection task. Further, color discrimination may be made either by recognizing the color in the colored stimulus or by recognizing a lack of color in the white stimulus. Thus, discrimination thresholds are likely to be manifest slightly below detection thresholds in these experimental conditions even if the thresholds are psychophysically or physiologically equal.

CONCLUSIONS AND RECOMMENDATIONS

Human Dichromats Exhibit Postreceptoral Abnormalities

Normally occurring dichromats are able to discriminate colors near detection thresholds. Human dichromats, even though they demonstrate similar increment-threshold spectral sensitivity functions, and even though they appear to detect those increments with a color-opponent system, cannot discriminate some colors at detection threshold. These findings indicate that in addition to lack of a cone type, dichromatic humans may exhibit a postreceptoral processing dysfunction that is not a feature of normal dichromacy. The specific nature of the processing dysfunction in human dichromats is open to speculation, and further research is required to address that mystery.

Recommendations for Further Study

Although time-intensive, it would be of benefit to further define color discrimination curves with more background intensities, and/or to vary stimulus sizes to observe the effect on color discrimination ability. This might allow comparison across species as to where the mesopic range of vision occurs, that is, the ambient light levels where color-opponent systems start functioning to enhance detection of colored stimuli in the environment.

For this experiment, animals with cone-dominated retinas were chosen in order that comparisons could be made to human foveal data. In future studies, addition of animals with rod-dominated retinas, such as canine species, might highlight aspects of

interaction between color-opponent and luminance systems, or might help to determine if the presence of high color vision sensitivity is a function of the proportion of cones vs. rods. Also, investigation of primates with a mixed population of trichromats and dichromats could lead to research on the physiological basis for the effects of dichromacy on humans.

Implications for Occupational Vision

The findings from this study have implications for occupational vision, particularly with regard to color vision testing. In the occupational setting, the low color sensitivity of human dichromats and some anomalous trichromats can jeopardize effectiveness and safety in the workplace. The ability to discriminate colors or to discriminate a colored object from a background is essential for certain jobs, such as an electrician or one who prepares custom paint mixtures. To manage this problem, an effort to develop standards and job classifications was undertaken during World War II, resulting in a system with seven job categories adopted by industry and the military (Thompson, 1993). "Normal" color vision is recommended for five of those seven categories.

In the military, several thousand jobs are specifically characterized with detailed functional requirements, including color vision. Identification and assessment of color-deficient individuals is a problematic aspect of job placement. Because of the highly variable types of color deficiency, particularly in the case of anomalous trichromats, numerous tests of color vision have been devised, each addressing particular aspects of color vision and each with drawbacks. The following list includes some commonly used tests:

1. The Nagel anomaloscope. Often referred to as the gold standard for diagnosing vision defects, this test of color matching can identify and quantify all types of color deficiencies. However, it is expensive and requires considerable training to administer the test and to interpret results.

2. Pseudoisochromatic plates. These plates are used to screen for R/G anomalies only. Technically, it requires "northern daylight" illumination or a Macbeth Illuminant C, a light source that is expensive and often not available. Varieties include the Ishihara plates, Dvorine plates, and American Optical H-R-R plates.

3. Ishihara plates. This widely used test has been cited as the most sensitive for quickly identifying individuals with all levels of color deficiency, the most impervious to changes in viewing conditions, and the most popular of all the color vision screening devices in use today (Johnson, 1992).

4. Dvorine plates. Similar to pseudoisochromatic plates.

5. American Optical Hardy-Rand-Rittler (H-R-R) plates also screen for B/Y anomalies but no longer available.

6. Farnsworth-Munsell 100-hue test. This color discrimination test enables detection and quantification of R/G and B/Y anomalies. Purportedly it may be used to separate individuals into classes of "superior, average, and low color discrimination" and to measure the zones of color confusion of color defective people (Farnsworth, 1957). The test requires considerable time and concentration, and a thorough understanding of the testing procedure, on the part of the subjects and administrators.

7. Farnsworth D-15 "dichotomous" test is a condensed version of the 100-hue test. It is clinically useful in identifying patients who might have problems with color vision, but may not distinguish protanomalous from deuteranomalous individuals.

8. Farnsworth Lantern (FALANT). This rather old test is still used as an alternative color vision test by the U.S. Navy (Hackman & Holtzman, 1992). Equipment cannot be calibrated and is not generally available. The test is not effective in identifying some color defective individuals, and is no longer accepted by the U.S. Air Force for color vision testing.

All of these color vision tests require training to administer, produce variable results, and are difficult to interpret and standardize. In addition, none of these tests are suitable for use on very young children or infants because of their complexity. On the other hand, as the various tests measure color vision in slightly different ways, the availability of this battery of tests may help to make more certain diagnoses when necessary (Lakowski, 1969).

Results from this experiment could have clinical value in the form of a new color vision test exploiting the low color sensitivity of dichromats and some anomalous trichromats and the high color sensitivity of normal trichromats. The elegance of the tHKe experiment demonstrated the conceptual simplicity and operational utility for such a test that could be conducted on a standard computer. The detection and selection of a broadband long-wavelength stimulus set just below the threshold for a white stimulus in a multiple forced choice test on a computer screen could simplify administration and interpretation of tests for R/G color deficiency. This could enable faster and easier identification of dichromatic and anomalous trichromatic individuals that exhibit low color sensitivity. Further, such a test might be adapted for use in infant color vision assessment in that preferential viewing techniques could be incorporated.

This experiment has longer-term implications. Research on dichromacy has long furthered understanding of color vision processing mechanisms at all levels, from the

photoreceptor to the visual cortex and beyond. Continued basic research may lead to applied clinical research on color deficiencies, enhanced knowledge of underlying physiological mechanisms, and opportunities for eventual treatment and/or management of such conditions.

REFERENCES

Anderson, D. H., & Jacobs, G. H. (1972). Color vision and visual sensitivity in the California ground squirrel (Citellus Beecheyi). *Vision Research, 12,* 1995-2004.

Beare, J. I. (1906). *Greek theories of elementary cognition from Alcmaeon to Aristotle* (p. 55). Oxford: Clarendon Press.

Boynton, R. M. (1979). *Human Color Vision.* New York: Holt.

Calkins, D. J., & Sterling, P. (1999). Evidence that circuits for spatial and color vision segregate at the first retinal synapse. *Neuron, 24,* 313-321.

Chaparro, A., Stromeyer, C. F., Huang, E. P., Kronauer, R. E., & Eskew, R. (1993). Colour is what the eye sees best. *Nature, 361,* 348-50.

Cornsweet, T. (1970). *Visual Perception.* New York and London: Academic Press, 7.

Curcio, C. A., Allen, K. A., Sloan, K. R., Lerea, C. L., Hurley, J. B., Block, I. B., et al. (1991). Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *Journal of Comparative Neurology, 312,* 610-624.

Dacy, D. M., & Lee, B. B. (1994). The 'blue-on' opponent pathway in primate retinal originates from a distinct bistratified ganglion cell type. *Nature, 367,* 731-735.

Dain, S. J., & King-Smith, P. E. (1981). Visual thresholds in dichromats and normals; the importance of post-receptoral processes. *Vision Research, 21,* 573-580.

DeMonasterio, F. M. (1978). Properties of ganglion cells with atypical receptive-field organization in retina of maaques. *Journal of Neurophysiology, 41*(6), 1435-1449.

Farnsworth, D. (1957). The Farnsworth-Munsell 100-Hue Test for the examination of color discrimination. Manual for test administration. Munsell Color Company, Inc., Baltimore, MD.

Fletcher, R., & Voke, J. (1985). *Defective colour vision: fundamentals, diagnosis and management.* Bristol: Adam Hilger Ltd.

Gellerman, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *Journal of Genetic Psychology, 42,* 206-8.

Guth, S. L., Donley, N. J., & Marrocco, R. T. (1969). On luminance additivity and related topics. *Vision Research, 9,* 537-575.

Guth, S. L. (1991). Model for color vision and light adaptation. *Journal of the Optical Society of America 8*(6), 976-993

Hackman, R. J., & Holtzman, G. L. (1992). Color vision testing for the U.S. Naval Academy. *Military Medicine, 157*(December), 651-7.

Hendry, S. H., & Reid, R. C. (2000). The koniocellular pathway in primate vision. *Annual Review of Neuroscience, 23,* 127-53.

Hurvich, L. M., & Jameson, D. (1955). Some quantitative aspects of an opponent-colors theory-II. Brightness, saturation, and hue in normal and dichromatic vision. *Journal of the Optical Society of America, 45,* 602-616.

Jacobs, G. H. (1993). The distribution and nature of colour vision among mammals. *Biological Reviews, 68,* 413-471

Jacobs, G. H., & Neitz, J. (1986). Spectral mechanisms and color vision in the tree shrew (Tapaia Belangeri). *Vision Research, 26*(2), 291-298.

Jacobs, G. H., & Yolton, R. L. (1971). Visual sensitivity and color vision in ground squirrels. *Vision Research, 11,* 511-537.

Johnson, D. D. (1992). The Ishihara Test: on the prevention of job discrimination. *Journal of the American Optometric Association, 63*(5), 352-360

Kaplan, E., Lee, B. B., & Shapley, R. M. (1990). New views of primate retinal function. *Progress in Retinal Research, 9,* 273-336.

King-Smith, P. E., & Carden, D. (1976). Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration. *Journal of the Optical Society of America, 66*(7), 709-717.

Kraft, T. W. (1988). Photocurrents of cone photoreceptors of the golden-mantled ground squirrel. *Journal of Physiology, 404,* 190-213.

Kuyk, T. K., & Loop, M. S. (1998). Color thresholds in human dichromats. *Investigative Ophthalmology and Visual Science, 39*(4), S614.

Kuyk, T. K., Shows, J. F., Van Arsdel, R. E., & Loop, M. S. (2000). Color vision in human dichromats. *Investigative Ophthalmology and Visual Science, 41*(4), S807.

Lakowski, R. (1969). Theory and practice of colour vision testing: A review Part 1. *British Journal of Industrial Medicine, 26,* 173-189.

Lee, B. B. (1996). Receptive field structure in the primate: Minireview. *Vision Research, 36,* 631-655.

Livingston, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science, 240,* 740-9.

Livingston, M., & Hubel, D. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience, 4*(1), 309-356.

Loop, M. S., & Crossman, D. K. (2000). High color vision sensitivity in macaque and humans. *Visual Neuroscience, 17,* 119-125.

Loop, M. S., Shows, J. F., Mangel, S. C., & Kuyk, T. K. (2002). *Colour Thresholds in dichromats and normals.* Manuscript submitted for publication.

Miyahara, E., Pokorny, J., & Smith, V. (1996). Increment threshold and purity discrimination spectral sensitivities of X-chromosome-linked color-defective observers. *Vision Research, 36*(11), 1597-1613.

Mullen, K. T. (1987). Spatial influences on colour opponent contributions to pattern detection. *Vision Research, 27,* 829-839.

Petry, H. M., Fox, R., & Casagrande, V. A. (1984). Spatial contrast sensitivity of the tree shrew. *Vision Research, 24*(9), 1037-42.

Pokorny, J., Smith, V. C., & Verriest, G. (1979). *Current Ophthalmology Monographs.* New York: Grune & Stratton, Inc.

Regan, B. C., Reffin, J. P., & Mollon, J. D. (1994). Luminance noise and the rapid determination of discrimination ellipses in colour deficiency. *Vision Research, 34*(10), 1279-1299.

Reid, R. C., & Shapley, R. M. (1992). Spatial structure of cone inputs to receptive fields in primate lateral geniculate nucleus. *Nature, 356,* 716-718.

Roberts, C. M., & Loop, M. S. (1999). Color vision thresholds in goldfish (Carassius auratus). *Journal of the Alabama Academy of Sciences, 70*(1-2), 16.

Rodieck, R. W. (1991). Which cells code for color? In Valberg, A. & Lee, B.B. (Eds.), *From Pigments to Perception.* New York: Plenum Press, 83-93.

Rodieck, R. W. (1998). *The First Steps in Seeing.* Sunderland, MA: Sinauer Associates, Inc.

Roorda, A., & Williams, D. R. (1999). The arrangement of the three cone classes in the living human eye. *Nature, 397,* 520-522.

Schnapf, J. L., Kraft, T. W., Nunn, B. J., & Baylor, D. A. (1988). Spectral sensitivity of primate photoreceptors. *Visual Neuroscience, 1,* 255-261.

Schwartz, S. H. (1992). Reaction time distributions and their relationship to the transient/sustained nature of the neural discharge. *Vision Research, 32,* 2087-2092.

Schwartz, S. H. (1994). Spectral sensitivity of dichromats: role of postreceptoral processes. *Vision Research, 34*(22), 2983-2990.

Schwartz, S. H., & Loop, M. L. (1982). Evidence for transient luminance and quasi-sustained color mechanisms. *Vision Research, 22,* 445-447.

Schwartz, S. H., & Loop, M. L. (1983). Difference in temporal appearance associated with activity in the chromatic and achromatic systems. *Perception & Psychophysics, 33,* 388-390.

Shipp, S., & Zeki, S. (1985). Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature, 315,* 322-5.

Sloan, L. L. (1928). The effect of intensity of light, state of adaptation of the eye, and size of photometric field on the visibility curve. *Psychological Monographs, 38,* 1-87.

Snelgar, R. S., Foster, D. H., & Scase, M. O. (1987). Isolation of opponent-colour mechanisms at increment threshold. *Vision Research, 27,* 1017-1027.

Sperling, H. G., & Harwerth, R. S. (1971). Red-green cone interactions in the increment threshold spectral sensitivity of primates. *Science, 172,* 180-4.

Stiles, W. S., & Crawford, B. H. (1933). The luminal brightness increment as a function of wave-length for different conditions of the foveal and parafoveal retina. *Proceedings of the Royal Society (London) B, 113* (pp.496-530).

Svaetichin, G. (1953). The cone action potential. *Acta Physiologica Scandinavica, 29,* 565-600.

Thompson, A. K. (1993). Conserving Vision. In R. Zajtchuk et al. (Eds.), *Textbook of Military Medicine* (Part III, Volume 2, Chapter 8, pp.253-304). Washington, DC: Office of The Surgeon General, Department of the Army, United States of America.

Ungerleider, L. G., & Mishkin, M. (1982). In D. J. Ingle, M. A. Goodale, R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549-586). Cambridge, MA: MIT Press.

VanVeen, D. P. (2000). *The reaction time of dichromatic observers to spectral increments, evidence for use of a color-opponent mechanism.* Unpublished master's thesis, University of Alabama, Birmingham, Alabama.

Wagner, G., & Boynton, R. M. (1972). Comparison of four methods of heterochromatic photometry. *Journal of the Optical Society of America, 62*(12), 1508-15.

Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the Rhesus monkey. *Journal of Neurophysiology, 29*, 1115-56.

APPENDIX

INSTITUTIONAL APPROVAL LETTERS

UAB THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Institutional Review Board for Human Use

Form 4: IRB Approval Form
Identification and Certification of Research Projects Involving Human Subjects

The Institutional Review Board for Human Use (IRB) has an approved Multiple Project Assurance with the Department of Health and Human Services and is in compliance with 21 CFR Parts 50 and 56 and ICH GCP Guidelines. The Assurance became effective on January 1, 1999 and the approval period is for five years. The Assurance number is M-1149, identification number 01.

Principal Investigator:	RICHARD E. VANARSDEL
Protocol Number:	X000309001
Protocol Title:	Studies of Vision Sensation and Perception

The IRB reviewed and approved the above named project on 5/11/00. The review was conducted in accordance with UAB's Assurance of Compliance approved by the Department of Health and Human Services. This Project will be subject to Annual continuing review as provided in that Assurance.

This project received **EXPEDITED** review.

IRB Approval Date: 5-11-00

Date IRB Approval Issued: 5/11/00

Marilyn Doss

Marilyn Doss, M.A.
Vice Chair of the Institutional Review Board for Human Use (IRB)

Date IRB Approval Issued: 5/11/00

Investigators please note:

The IRB approved consent form used in the study must contain the IRB approval date and expiration date.

IRB approval is given for one year unless otherwise noted. For projects subject to annual review research activities may not continue past the one year anniversary of the IRB approval date.

Any modifications in the study methodology, protocol and/or consent form must be submitted for review and approval to the IRB prior to implementation.

Adverse Events and/or unanticipated risks to subjects or others at UAB or other participating institutions must be reported promptly to the IRB.

1120 Administration Building
701 20th Street South
934-3789
Fax 934-1301
irb@uab.edu

The University of
Alabama at Birmingham
Mailing Address:
AB 1120
1530 3RD AVE S
BIRMINGHAM AL 35294-0111

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Office of the Provost

NOTICE OF APPROVAL

DATE: January 31, 2000

TO: Michael S. Loop, PhD
WORB-610 4390
FAX: 934-5725

FROM: Clinton J. Grubbs, PhD, Chairman CJG
Institutional Animal Care and Use Committee

SUBJECT: Color Vision Thresholds in Ground Squirrels (NSF) 000105114

On January 26, 2000, the University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) reviewed the animal use proposed in the above referenced application. It approved the use of the following species and numbers of animals:

Species	Use Category	Number in Category
Squirrels	B	6

Animal use is scheduled for review one year from January 26, 2000. Approval from the IACUC must be obtained before implementing any changes or modifications in the approved animal use.

Please keep this record for your files, and forward the attached letter to the appropriate granting agency.

Refer to Animal Protocol Number (APN) 000105114 when ordering animals or in any correspondence with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns or questions regarding this notice, please call the IACUC office at 934-7692.

Institutional Animal Care and Use Committee
B10 Volker Hall
1717 7th Avenue South
205.934.7692 • Fax 205.934.1188
iacuc@uab.edu
www.uab.edu/uabrs/iacuc

The University of
Alabama at Birmingham
Mailing Address:
VH B10
1530 3RD AVE S
BIRMINGHAM AL 35294-0019

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM
Office of the Provost

NOTICE OF APPROVAL WITH STIPULATIONS

DATE: November 15, 2000

TO: Michael S. Loop, Ph.D.
WORB-610 4390
FAX: 934-5725

FROM: Clinton J. Grubbs, PhD, Chairman
Institutional Animal Care and Use Committee

SUBJECT: Color Vision Thresholds in Ground Squirrels (NSF) 000105114

On October 25, 2000, the University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) reviewed the animal use proposed in the above referenced application. It approved the use of the following species and numbers of animals:

Species	Use Category	Number in Category
Chipmunks	A	3

Approval is granted with the following stipulations:

principal investigator will provide personnel training for handling, care and use of chipmunks and squirrels.

Animal use is scheduled for review one year from October 25, 2000. Approval from the IACUC must be obtained before implementing any changes or modifications in the approved animal use.

Please keep this record for your files, and forward the attached letter to the appropriate granting agency.

Refer to Animal Protocol Number (APN) 000105114 when ordering animals or in any correspondance with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns or questions regarding this notice, please call the IACUC office at 934-7692.

Institutional Animal Care and Use Committee
B10 Volker Hall
1717 7th Avenue South
205.934.7692 • Fax 205.934.1186
iacuc@uab.edu
www.uab.edu/uabrs/iacuc

The University of
Alabama at Birmingham
Mailing Address:
VH B10
1530 3RD AVE S
BIRMINGHAM AL 35294-0019

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Office of the Provost

NOTICE OF APPROVAL

DATE: January 16, 2001

TO: Michael S. Loop, Ph.D.
WORB-610 4390
FAX: 934-5725

FROM: Clinton J. Grubbs, Ph.D., Chairman C-J-G
Institutional Animal Care and Use Committee

SUBJECT: Modification of Color Vision Thresholds in Ground Squirrels (NSF) 000105114

On January 3, 2001, the University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) reviewed the animal use proposed in the above referenced application. It approved the modification as described: addition of treeshrews. The following species and numbers of animals reflect this modification.

Species	Use Category	Number in Category
Tree Shrews	A	3

Animal use is scheduled for review on 1/31/01. Approval from the IACUC must be obtained before implementing any changes or modifications in the approved animal use.

Please keep this record for your files.

Refer to Animal Protocol Number (APN) 000105114 when ordering animals or in any correspondance with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns or questions regarding this notice, please call the IACUC office at 934-7692.

Institutional Animal Care and Use Committee
B10 Volker Hall
1717 7th Avenue South
205.934.7692 • Fax 205.934.1188
iacuc@uab.edu
www.uab.edu/iacuc

The University of
Alabama at Birmingham
Mailing Address:
VH B10
1530 3RD AVE S
BIRMINGHAM AL 35294-0019

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Office of the Provost

NOTICE OF APPROVAL

DATE: February 13, 2001

TO: Michael S. Loop, Ph.D.
WORB-610 4390
FAX: 934-5725

FROM: Clinton J. Grubbs, Ph.D., Chairman
Institutional Animal Care and Use Committee

SUBJECT: Color Vision Thresholds in Ground Squirrels (NSF) 010205114

On February 11, 2001, the University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) reviewed the animal use proposed in the above referenced application. It approved the use of the following species and numbers of animals:

Species	Use Category	Number in Category
Chipmunks	B	3
Ground Squirrels	B	5
Tree Shrews	B	3

Animal use is scheduled for review one year from February 11, 2001. Approval from the IACUC must be obtained before implementing any changes or modifications in the approved animal use.

Please keep this record for your files, and forward the attached letter to the appropriate granting agency.

Refer to Animal Protocol Number (APN) 010205114 when ordering animals or in any correspondence with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns or questions regarding this notice, please call the IACUC office at 934-7692.

Institutional Animal Care and Use Committee
B10 Volker Hall
1717 7th Avenue South
205.934.7692 • Fax 205.934.1188
iacuc@uab.edu
www.uab.edu/iacuc

The University of
Alabama at Birmingham
Mailing Address:
VH B10
1530 3RD AVE S
BIRMINGHAM AL 35294-0019

GRADUATE SCHOOL
UNIVERSITY OF ALABAMA AT BIRMINGHAM
DISSERTATION APPROVAL FORM
DOCTOR OF PHILOSOPHY

Name of Candidate Richard E. Van Arsdel

Graduate Program Vision Science

Title of Dissertation Color Vision Sensitivity in Normally Dichromatic Species and Humans

I certify that I have read this document and examined the student regarding its content. In my opinion, this dissertation conforms to acceptable standards of scholarly presentation and is adequate in scope and quality, and the attainments of this student are such that he may be recommended for the degree of Doctor of Philosophy.

Dissertation Committee:

Name	Signature
Michael S. Loop, **Chair**	
Roderick J. Fullard	
Timothy W. Kraft	
Thomas K. Kuyk	
Stuart Mangel	

Director of Graduate Program

Dean, UAB Graduate School

Date 8/24/02