Chromatic perceptive field sizes change with retinal illuminance

Michael A. Pitts   Department of Psychology, Colorado State University, Fort Collins, CO, USA

Lucy J. Troup   Department of Psychology, Colorado State University, Fort Collins, CO, USA

Vicki J. Volbrecht   Department of Psychology, Colorado State University, Fort Collins, CO, USA

Janice L. Nerger   Department of Psychology, Colorado State University, Fort Collins, CO, USA

The effect of retinal illuminance (0.3–3.3 log td) on chromatic perceptive field size was investigated at 10° eccentricity along the horizontal meridian of the temporal retina. Using the 4+1 color-naming procedure, observers described the hue and saturation of a series of monochromatic stimuli (440–660 nm, in 10-nm steps) of various test sizes (.098-5°) after 30-min dark adaptation. Perceptive field sizes of the four elemental hues and the saturation component were estimated for each wavelength at each retinal illuminance. Results indicate that perceptive field sizes for blue, green, yellow, and saturation all decrease with increasing retinal illuminance; the perceptive field size for red is the smallest and invariant with intensity. The influence of rods on perceptive field size may account for some of the results; other factors are also considered.

Keywords: perceptive fields, retinal illuminance, color naming, peripheral color vision, rods, color vision

Introduction

Color perception in the peripheral retina has long been known to change as a function of stimulus size (e.g., Abramov, Gordon, & Chan, 1991, 1992; Gordon & Abramov, 1977; Johnson, 1986; Nagy & Doyal, 1993; Nerger, Volbrecht, Ayde, & Imhoff, 1998; Weitzman & Kinney, 1969). As the size of a chromatic stimulus is increased, color appearance initially changes rapidly and then decelerates to an asymptotic level. The critical size at which color appearance becomes stable with any further increases in test size can be measured psychophysically (Abramov et al., 1991) and can be conceptualized as filling a *chromatic perceptive field*.

Although achromatic perceptive fields have been measured in numerous studies (for reviews, see Ransom-Hogg & Spillmann, 1980; Troscianko, 1982), Abramov et al. (1991) were the first to measure perceptive field sizes for chromatic stimuli. By systematically manipulating the size of monochromatic stimuli, and having observers utilize the 4+1 color-naming technique, Abramov and colleagues determined that hue percentages increased to asymptotic levels. Interestingly, the perceptive field sizes measured by Abramov et al. (1991) were not the same for the four elemental hues; in general, green had the largest perceptive field and red the smallest. In a similar study, Angel (2004) measured chromatic perceptive fields under different adap-

tation states of the retina and reported that the sizes of perceptive fields were larger when measured under dark adaptation than under light adaptation conditions. In addition, Angel's measurements under dark adaptation were consistent with Abramov et al. (1991) (i.e., the perceptive field size of green was the largest and red was the smallest). Unfortunately, both of these studies only measured chromatic perceptive fields at one retinal illuminance, 1.3 log td; therefore, any effects of stimulus intensity could not be assessed.

Studies investigating Ricco's area after 30–45-min dark adaptation reported that Ricco's area decreased as background illuminance increased (Lelkens & Zuidema, 1983; Davila & Geisler, 1991; Glezer, 1965). In these studies, stimuli were chosen to elicit some rod input either by presenting blue-green stimuli and backgrounds (e.g., Lelkens & Zuidema, 1983; Davila & Geisler, 1991; Barlow, 1958) and/or with no background (e.g., Glezer, 1965; Davila & Geisler, 1991) or background levels ranging from scotopic to mesopic to photopic levels (e.g., Glezer, 1965; Lelkens & Zuidema, 1983).

While studies of chromatic perceptive fields (Angel, 2004) and Ricco's area (Lelkens & Zuidema, 1983; Davila & Geisler, 1991; Glezer, 1965, Barlow, 1958) have demonstrated changes in size and area under dark adaptation and light adaptation conditions, these studies have not examined how changing the intensity of a stimulus affects size or

area. The spatial summation studies are limited in this respect because they measure absolute and increment thresholds, but the studies that derive perceptive field size from color-naming functions offer a means by which to investigate changes in perceptive field size with changes in the retinal illuminance of a test stimulus. The goal of this study was to determine how changes in the retinal illuminance of a stimulus under dark-adapted conditions affected the sizes of chromatic perceptive fields. This information is particularly relevant given the use of color to convey information. If a stimulus is too small for the viewing conditions, the appropriate chromatic information will not be perceptible.

Methods

Observers

Two female observers, 28 and 46 years old, and one male observer, 24 years old, participated in the study. All were color-normal trichromats as assessed by the Farnsworth D-15, Farnsworth-Munsell 100-Hue, and Adams Desaturated D-15 panel tests and the Neitz OT-II anomaloscope. Observers were trained in the 4+1 color-naming technique, but were naïve with respect to their results and to the specific stimulus settings used in each experimental session.

Apparatus

Two channels of a conventional four-channel Maxwellian-view optical system were used. The common light source for both channels was a 300-W (5500 k) Xenon arc lamp (Model 66065, Oriel) regulated by a DC power supply (Model 68811, Oriel) at 290 W. Light leaving the two exit ports of the lamp housing passed through collimating lenses and infrared filters. In the test-stimulus channel, a beam splitter reflected light through a series of collimating and focusing lenses onto the entrance slit of a grating monochromator (Model H20, Instruments SA, Inc.; 4-nm half-amplitude bandpass). Upon exiting the monochromator, light passed through a neutral-density wedge, which was interfaced to a computer. A field stop was placed in a collimated portion of the channel to define the size and shape of the test stimulus. A shutter controlled by a driver system (Model T132, Uniblitz) exposed the test stimulus for 500 ms with an 18-s interstimulus interval (ISI).

In the fixation channel, a beam splitter reflected light through a series of collimating and focusing lenses and neutral density filters. Field stops defined the size, shape, and orientation of the fixation lights. A final beamsplitter combined the two channels into a common path. The final lens focused the light onto the plane of the observer's pupil. All lenses were doublet achromats, and mirrors were front-surfaced. A dental-impression bite-bar apparatus stabilized the observer's head and permitted adjustments for depth, height, and lateralization.

Stimuli

Test stimuli were presented along the horizontal meridian at 10° temporal retinal eccentricity. Measurements were taken at four stimulus intensities (0.3, 1.3, 2.3, and 3.3 log td), using six stimulus sizes at each retinal illuminance. The sizes were 0.25°, 0.5°, 1°, 2°, 3°, and 5° at 0.3 and 1.3 log td; 0.125°, 0.25°, 0.5°, 1°, 2°, and 3° at 2.3 log td; and 0.98°, 0.125°, 0.25°, 0.5°, 1°, and 2° at 3.3 log td. For each stimulus size at each retinal illuminance, 23 monochromatic stimuli (440-660 nm in 10 nm steps) were pseudo-randomly presented. Each stimulus was presented for 500 ms with an 18-s ISI.

A broadband (5500 K) fixation array consisting of two vertically displaced pinhole-size fixation points and a third horizontally displaced pinhole fixation point was used to ensure that the test stimulus was positioned at 10° temporal retinal eccentricity. Observers fixated on the horizontally displaced fixation point, while the test stimulus was centered between the two vertically displaced fixation points. To minimize adaptation effects (Jameson & Hurvich, 1967), the illuminance of the fixation points was adjusted to be just visible to the observer.

Calibrations

Radiometric measurements were made with an EG & G Gamma Scientific radiometer (Model DR-1500A). Photometric measurements using a Minolta Chroma Meter (Model CS-100) were made for a reference wavelength of 550 nm. Retinal illuminance values were determined using Westheimer's (1966) method. Neutral density filters and wedge positions were adjusted to maintain the desired retinal illuminance across wavelength. The neutral density filters and wedge were calibrated from 400-700 nm in 10-nm steps. The calibration of the monochromator was assessed at 632.8 nm with a helium-neon laser (Spectra Physics).

Procedure

All test sessions commenced after 30 min of dark adaptation. Observers were instructed to make hue and saturation judgments for each stimulus using the 4+1 color-naming technique (Gordon & Abramov, 1988; Gordon, Abramov, & Chan, 1994). Using this technique, observers described the appearance of each stimulus in terms of hue and saturation by first assigning percentages to one or two of the four elemental hues (blue, green, yellow, and red), always totaling 100%, and then assigning a percentage value to describe saturation, ranging from 0% (completely achromatic) to 100% (completely chromatic). Observers were asked to avoid using color-opponent pairs in their responses (i.e., blue-yellow and green-red), although all observers stated that these pairs were never perceived. If the observer could not make the hue and saturation judgments during the 18-s ISI, no values were recorded for that stimulus, and it was presented again later in the session.

Test sessions lasted approximately 2 hr. To obviate adaptation affects, only one retinal illuminance was tested per experimental session. Each observer completed 2-3 sessions at each illuminance level.

Results

Each hue response was transformed using an arcsine transformation to reduce effects of unequal variance (see Gordon, Abramov, & Chan, 1994). Using the method of analysis employed by Abramov et al. (1991), the transformed hue values were then scaled relative to the saturation rating, such that total hue equaled total saturation while maintaining the original hue ratio. Because the pattern of results was similar across observers, means were computed from the transformed values for each wavelength, stimulus size, and retinal illuminance across the three observers. It is the mean data based on the three observers that are reported here.

To estimate perceptive field sizes, the mean transformed values from the three observers were plotted as a function of stimulus size for every wavelength. Thus, these growth functions with the transformed values are defined by two factors: hue ratio and saturation. Because color appearance differed relative to size and intensity parameters, a criterion was employed to qualify data points for curve-fitting analysis. Of the six stimulus sizes presented at every wavelength for each illuminance level, responses to at least five stimuli had to exceed zero by the average of the standard error of the mean to be included in the analysis.

The Michaelis-Menten function was used to model hue responses and compute perceptive field sizes. Although this particular growth function is not necessarily physiologically relevant, it is useful to characterize mathematically asymptotic patterns (Abramov et al., 1991). An example of this analysis for each of the four hues at 1.3 log td is presented in Figure 1. In this figure, percent hue for each of the four hues increases as stimulus size increases. The stimulus size associated with 75% of the estimated asymptotic value was operationally defined as the *perceptive field size* (Abramov et al., 1991).

In Figure 2 and Figure 3, perceptive field sizes for each hue are plotted as a function of wavelength for each of the four retinal illuminances (a-d). Perceptive field sizes for "blue" and "yellow" are presented in Figure 2; results for "green" and "red" are displayed in Figure 3. For blue (Figure 2, ▲), yellow (Figure 2, ○), and green (Figure 3, △), perceptive field sizes decreased as retinal illuminance increased (i.e., the stimulus size associated with 75% of the asymptotic value was smaller for higher illuminance levels). With the exception of short-wavelength red, the perceptive field sizes for red remained essentially invariant across illuminance levels (Figure 3, ●). Also shown in Figure 2 and Figure 3 is the variation of perceptive field size for each hue across wavelength. This variability is greatest at the lowest

illuminance levels and is nearly imperceptible at the highest illuminance level.

Perceptive field sizes were also determined for saturation at each retinal illuminance. As shown in Figure 4, perceptive field sizes are larger in the short- and middle-wavelength regions of the spectrum compared to those of the longer wavelengths. As retinal illuminance increases, the perceptive fields for saturation decrease in size and become nearly invariant with respect to wavelength.

It is clear that perceptive field sizes of hue and saturation are influenced by retinal illuminance, and that the effects of illuminance are not uniform across the visual spectrum. To make comparisons of perceptive field size across hue, a single wavelength was chosen as representative of that hue (blue-460 nm; green-510 nm; yellow-580 nm; and red-650 nm) and is plotted in Figure 5. The representative wavelength was operationally defined for each hue as the wavelength that elicited the maximal hue response for that hue. To validate our choices, mean perceptive field size across all wavelengths that elicited the elemental hue response was also computed. Although absolute size of perceptive fields differed slightly, no differences in the pattern of perceptive field sizes were found for any of the four hue terms.
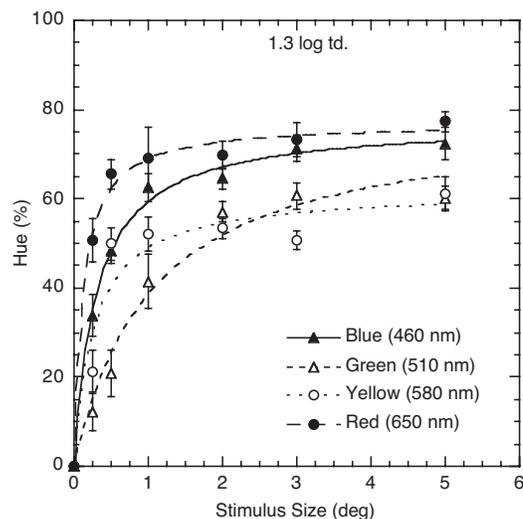

Figure 1. Mean transformed hue values plotted as a function of stimulus size and fitted with the Michaelis-Menten growth function. Error bars represent ±1 *SEM*.

Figure 5 illustrates the effect of retinal illuminance on perceptive field size and the differences in perceptive field size among the hues with retinal illuminance. The largest differences are found at the lowest illuminance, and become smaller as retinal illuminance is increased. At the highest illuminance level (3.3 log td), little or no differences were found in perceptive field size among the four hues. At the three lower retinal illuminances, the perceptive field of green was clearly the largest, followed by yellow and blue.
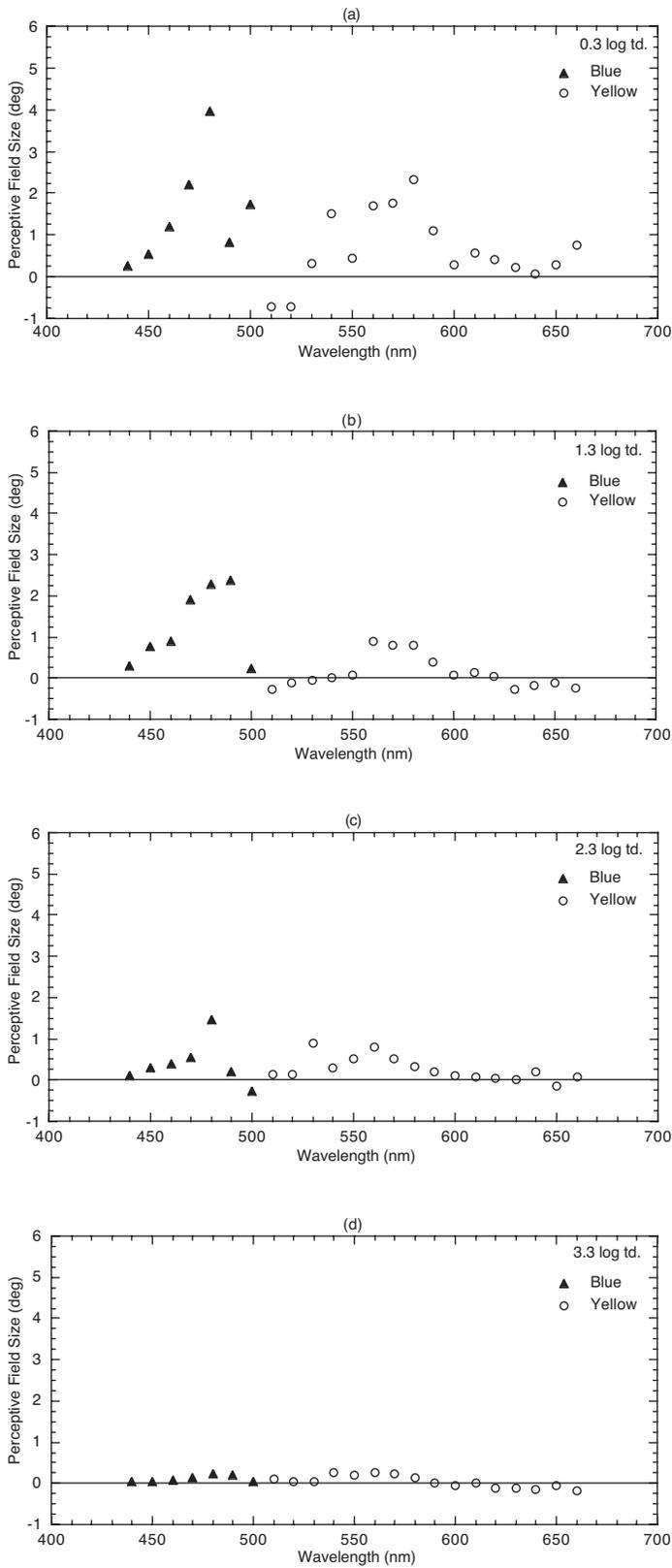
Figure 2. Perceptive field sizes of blue and yellow as a function of wavelength for a series of retinal illuminances.
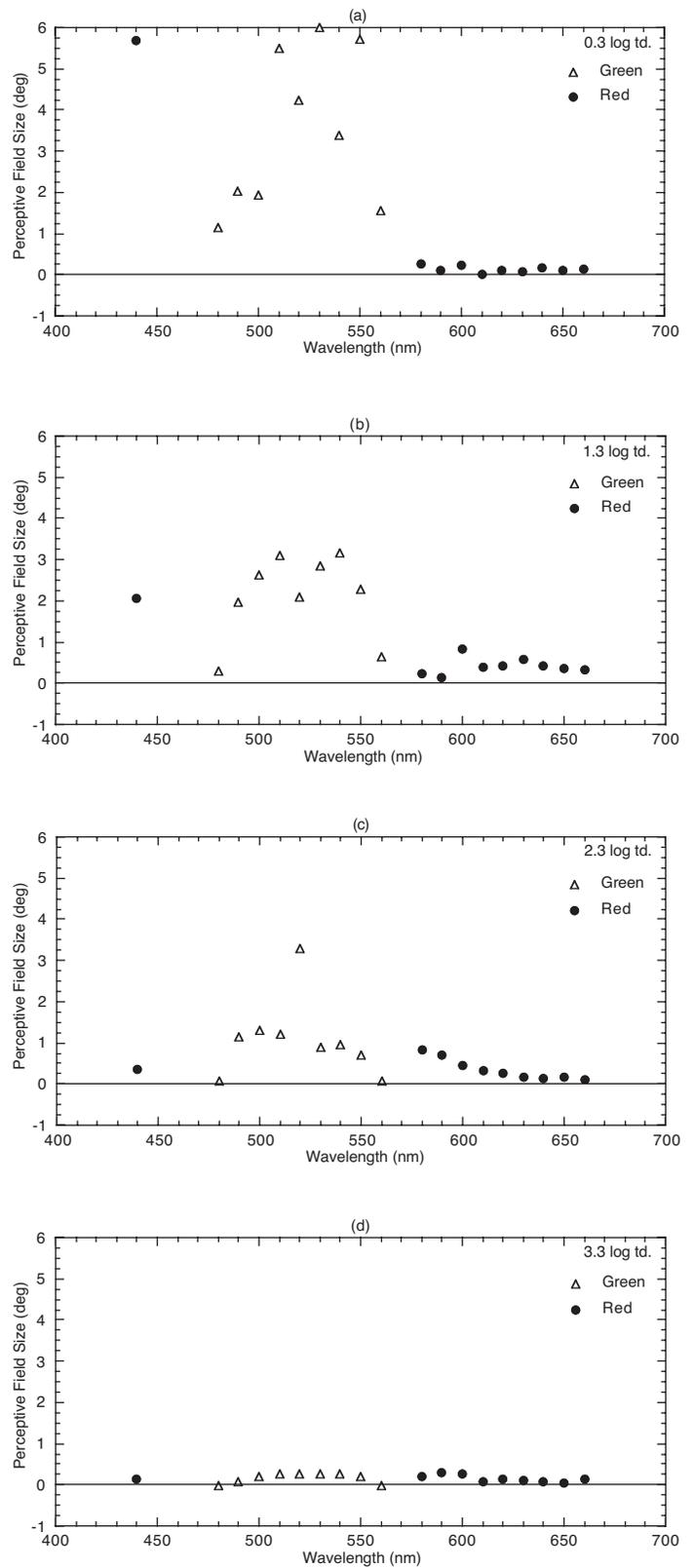
Figure 3. Perceptive field sizes of green and red as a function of wavelength for a series of retinal illuminances.
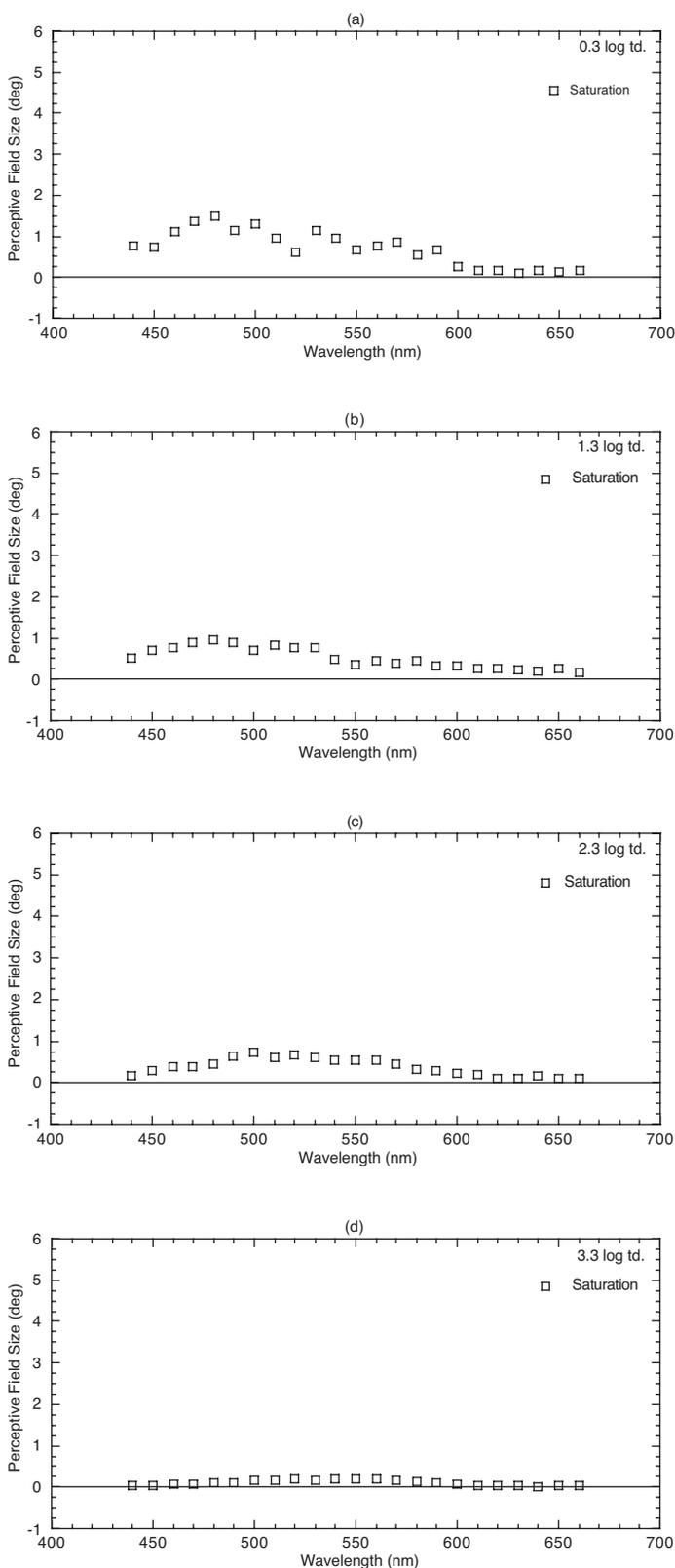
Figure 4. Perceptive field sizes of saturation as a function of wavelength for a series of retinal illuminances.

Discussion

The results of this experiment indicate that chromatic perceptive field sizes are dependent on retinal illuminance. In general, perceptive fields are larger at lower illuminance levels, and decrease in size as retinal illuminance is increased (Figure 2 and Figure 3). With the exception of the highest retinal illuminance, the perceptive field of green was the largest of the four hues, and that of red was the smallest (Figure 5). This finding is consistent with previous measurements taken at the same retinal location and at 1.3 log td (Abramov et al., 1991; Angel, 2004).
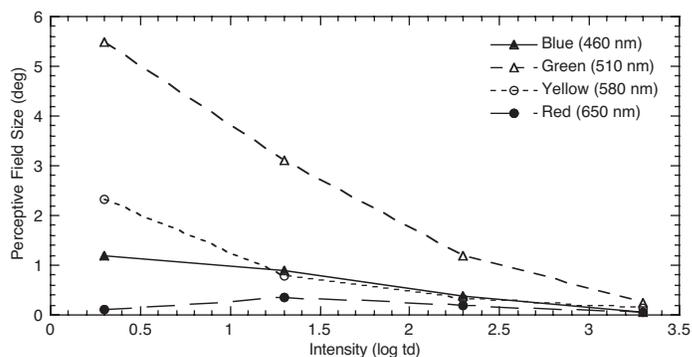

Figure 5. Perceptive field sizes of the four elemental hues are plotted as a function of retinal illuminance.

Saturation

One might expect that perceptive field size for hue would be the same as perceptive field size for saturation. If only one and the same hue term was used to describe a monochromatic stimulus at each size, then the perceptive field size for the elemental hue and saturation would indeed be the same. Because most stimuli, however, are described with two hue terms, and the hue ratio is not constant with stimulus size, the perceptive field size values for hue are not the same as those for saturation.

Results from this study demonstrate that the perceptive field size estimates for saturation were smaller than those at comparable retinal illuminances for the four elemental hues (Figure 4 versus Figure 2 and Figure 3), especially at the three lower retinal illuminances. As stimulus size increased, perceived saturation (chromatic versus achromatic content) stabilized at a smaller stimulus size than the perceived hue ratio. In other words, the critical size at which maximal chromaticity is reached can be smaller than the critical size for a particular maximal hue. This difference provides evidence that variation in perceptive field size among the four elemental hues cannot be due to variation in saturation.

Furthermore, the middle wavelengths of the visible spectrum are known for appearing less saturated than the short and long wavelengths. The middle wavelengths have larger perceptive field sizes, but at the lower retinal illumi-

nances, the shorter wavelengths also have larger perceptive fields than the longer wavelengths. When comparing saturation perceptive field sizes to blue and green perceptive field sizes, the blue and green perceptive field sizes are again larger than saturation. For example, at 0.3 log td, the largest perceptive field size for saturation is less than 2°, yet the perceptive field sizes in the short- and middle-wavelength regions of the spectrum are generally larger than 2°. If the variations in perceptive field size for the elemental hues were completely mediated by saturation, then the chromatic and saturation field sizes should be the same.

Role of rods

Because all sessions were run after 30-min dark adaptation, it is possible that not only cones but also rods affected color appearance at the lower retinal illuminances. Numerous studies have provided support for a rod influence on color perception by reporting unique hue shifts (e.g., Buck, Knight, & Bechtold, 2000; Nerger, Volbrecht, & Ayde, 1995; Nerger et al., 1998), color discrimination differences (e.g., Nagy & Doyal, 1993; Stabell & Stabell, 1977), and successive scotopic contrast effects (e.g., Buck, 1997) under conditions known to elicit neural activity from the rods. If rod activation influences these various aspects of color perception, it seems likely that rods also influence measurements of chromatic perceptive fields and, thus, contribute to the larger perceptive field sizes.

All stimuli in the Abramov et al. (1991) study were presented following 10-min dark adaptation, and at a retinal illuminance of 1.3 log td. Although these conditions favor stimulus absorption by cones, rod signals may not have been completely eliminated. Angel (2004) investigated a rod-based explanation for the Abramov et al. (1991) results. In her study, color judgments were made during the time associated with the cone plateau or with the rod plateau, manipulated by rod-bleach versus dark-adapted conditions, respectively. Angel (2004) reported that perceptive field sizes were larger when conditions were optimized for rod input. Angel (2004) found, however, that the perceptive fields of green and yellow were still larger than those of red, even when conditions limited rod input. It seems that rod signals can influence the size of perceptive fields, but cannot completely account for the different perceptive field sizes among the four elemental hues.

With increases in retinal illuminance, the influence of rods would be expected to decrease. Indeed, our results show smaller perceptive fields with increases in retinal illuminance. This finding is consistent with previous work on Ricco's area for achromatic and blue/green stimuli. These studies demonstrated that as rod input was minimized with increases in background illuminance, Ricco's area decreased (Lelkens & Zuidema, 1983; Davila & Geisler, 1991; Glezer, 1965; Barlow, 1958).

Other neural mechanisms

At all retinal illuminances, the perceptive field size for red was the smallest. Anatomical (Ahnelt, Kolb, & Pflug, 1987; Curcio, Sloan, Kalina, & Hendrickson, 1990) and psychophysical (Nerger & Cicerone, 1992; Vimal, Pokorny, Smith, & Shevell, 1989; Williams, MacLeod, & Hayhoe, 1981; Roorda & Williams, 1999) studies have demonstrated unequal distributions and densities of the three cone types. A number of studies conclude that the L:M cone ratio is approximately 2:1, though some have suggested large variability among observers (e.g., Brainard et al., 2000; Vimal et al., 1989). In addition, genetic research suggests this L:M ratio becomes larger at more eccentric locations (Hagstrom, Neitz, & Neitz, 1998). Farther along the retinal pathway, there are more red/green opponent ganglion cells (Calkins, Tsukamoto, & Sterling, 1998; Dacey, 1993, 1994) than yellow/blue cells, and this difference continues to the cortical level where there are again more red/green opponent cells than yellow/blue cells (Johnson, Hawken, & Shapley, 2004; Thorell, DeValois, & Albrecht, 1984; Michael, 1978a, 1978b). It is possible that these inequalities contribute to differences in chromatic perceptive field sizes. Although an argument could be made to account for the small perceptive field size of red, it is unclear how these physiological findings could provide an explanation for the sizes of the blue, green, and yellow perceptive fields.

Abramov et al. (1991) compared perceptive field sizes to known sizes of receptive fields in the retina, V1, and V4 and concluded that perceptive fields are not determined at the level of the retina. It is now clear that such a comparison is largely dependent on the retinal illuminance. If the perceptive field sizes measured in the current study are compared to receptive field sizes at several levels along the visual pathway, different correlations could be made between receptive and perceptive fields. For example, if the sizes measured at 3.3 log td are compared to various receptive field sizes, an argument for a retinal origin could be made. If, on the other hand, the sizes measured at 0.3 log td are used as a basis for comparison, area V4 becomes the most likely candidate for the processing of perceptive fields. Because it is unlikely that the neural origin of perceptive fields depends on stimulus intensity, this type of comparison is unlikely to be productive.

Of course, such a comparison does raise an interesting proposition: Do receptive fields change in size with stimulus intensity? If the chromatic perceptive field sizes are so variable, is it a problem with the method or is there a physiological substrate to support such variability. Early studies in the cat retina (Clelland & Enroth-Cugell, 1968; Enroth-Cugell, Hertz, & Lennie, 1977a, 1977b) and monkey lateral geniculate nucleus (Wiesel & Hubel, 1966) suggest that receptive field sizes are not affected by changes in stimulus intensity; however, a more recent study (Sceniak, Ringach, Hawken, & Shapley, 1999) has demonstrated that as contrast increases, receptive fields in the primate visual

cortex become smaller. It thus seems plausible that chromatic perceptive fields could also be represented by an underlying physiological flexibility in cortical receptive fields.

Possible limitations of methodology

In both of the previous chromatic perceptive field size studies (Abramov et al., 1991; Angel, 2004), as well as in the current study, estimates of perceptive field sizes at some wavelengths and retinal illuminances resulted in negative values (see Figure 2 and Figure 3). Abramov and colleagues (1991) postulated that the negative values for blue indicated the presence of a second sub-mechanism, tritan-B. Although our data show some negative values for blue, there are more negative values for yellow at the lower retinal illuminances (Figure 2). Abramov et al. (1991) also obtained negative values for yellow but only at the longer wavelengths rather than both the middle and long wavelengths (Figure 2). It may be the case that the negative values do not represent a second neural mechanism but rather represent the limitations of the particular analysis developed to ascertain perceptive field size and the change in hue ratio with stimulus size. For example, a 510-nm, 0.5° stimulus presented at 0.3 log td appeared more yellow than green to all observers. As stimulus size increased, however, the hue ratio changed and the 510-nm stimulus appeared more green than yellow. In this particular example, a decay function instead of a growth function exists for yellow, resulting in a negative k-value.

The results shown in Figures 2-4 indicate that perceptive field sizes approach 0° as retinal illuminance increases. This may seem counterintuitive, especially if the perceptive field sizes measured at high intensities are smaller than retinal receptive field sizes. It is the case, however, that very small stimuli have been shown to appear supersaturated at high intensities (e.g., Cicerone & Nerger, 1989; Krauskopf, 1964). In addition, these studies have demonstrated that for very small, intense stimuli, the same physical wavelength can lead to disparate hue sensations from one instance to the next. It is possible, that with very tiny stimuli, perception is cone limited, and the size of the perceptive field is defined by this limitation for the highest retinal illuminance but not for the three lower illuminance levels. The supersaturation of small stimuli at high intensities is consistent with the results for saturation shown in Figure 4. The perceptive field sizes for saturation become increasingly small with increases in retinal illuminance.

Bezold-Brücke hue shift

The Bezold-Brücke effect is a perceptible change in color appearance with increasing retinal illuminance (i.e., the stimulus appears more blue or yellow). For the purposes of calculating perceptive field size, it might be expected then, that as retinal illuminance is increased, the perceptive field size of yellow and blue should decrease, whereas that

of red and green should increase. This is not what was seen in the data of this experiment where the perceptive field size of all four elemental hues decreased with increases in retinal illuminance.

The results from this study on peripheral perceptive field sizes may, however, be relevant to previous Bezold-Brücke hue-shift experiments (Imhoff, Volbrecht, & Nerger, 2004; Stabell & Stabell, 1979, 1982) conducted in the peripheral retina. Bezold-Brücke experiments usually use one stimulus size for all luminance levels. Because retinal illuminance has been shown to alter perceptive field sizes, it is possible that perceptive fields for some of the elemental hues are being filled while perceptive fields for the other hues are not being filled in the Bezold-Brücke experiments. This may potentially explain some discrepant findings between foveal studies (e.g., Boynton & Gordon, 1965; Cohen, 1975; Luria, 1967; Purdy, 1931, 1937) and peripheral studies on the Bezold-Brücke hue shift (Imhoff et al., 2004; Stabell & Stabell, 1979, 1982).

Conclusion

Perceptive field sizes of the four elemental hues and saturation were estimated at 10° temporal retinal eccentricity at various retinal illuminances for a series of wavelengths across the visible spectrum. Perceptive field sizes for blue, green, yellow, and saturation decreased with increasing retinal illuminance; the perceptive field size for red was the smallest of the four hues and showed little change with retinal illuminance. Thus, the differences among the perceptive field sizes of the four hues were larger at lower luminance levels, and negligible at higher luminance levels.

Acknowledgments

References

Abramov, I., Gordon, J., & Chan, H. (1991). Color appearance in the peripheral retina: Effects of stimulus size. *Journal of the Optical Society of America*, 8, 404-414. [PubMed]

Abramov, I., Gordon, J., & Chan, H. (1992). Color appearance across the retina: Effects of a white surround. *Journal of the Optical Society of America*, 9, 195-202. [PubMed]

Ahnelt, P., Kolb, H., & Pflug, R. (1987). Identification of a subtype of cone photoreceptor, likely to be blue sensitive, in the human retina. *Journal of Comparative Neurology*, *255*, 18-34. [PubMed]

Angel, C. (2004). *The effect of rods on perceptive field size at 10 degrees eccentricity in the four retinal quadrants.* Unpublished doctoral dissertation, Colorado State University, Colorado.

Barlow, H. B. (1958). Temporal and spatial summation in human vision at different background intensities. *Journal of Physiology*, *141*, 337-350. [PubMed]

Boynton, R., & Gordon, J. (1965). Bezold-Brücke hue shift measured by color-naming technique. *Journal of the Optical Society of America*, *55*, 78-86.

Brainard, D., Roorda, A., Yamauchi, Y., Calderone, J., Metha, A., Neitz, M. (2000). Functional consequences of the relative numbers of L and M cones. *Journal of the Optical Society of America*, *17*, 607-614. [PubMed]

Buck, S. (1997). Influence of rod signals on hue perception. *Vision Research*, *37*, 1295-1301. [PubMed]

Buck, S., Knight, R., & Bechtold, J. (2000). Opponent-color models and the influence of rod signals on the loci of unique hues. *Vision Research*, *40*, 3333-3344. [PubMed]

Calkins, D., Tsukamoto, Y., & Sterling, P. (1998). Microcircuitry and mosaic of a blue-yellow ganglion cell in the primate retina. *Journal of Neuroscience*, *18*, 3373-3385. [PubMed]

Cicerone, C., & Nerger, J. (1989). The relative numbers of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea centralis. *Vision Research*, *29*, 115-128. [PubMed]

Clelland, B. G., & Enroth-Cugell, C. (1968). Quantitative aspects of sensitivity and summation in the cat retina. *Journal of Physiology*, *198*, 17-38. [PubMed]

Cohen, J. (1975). Temporal independence of the Bezold-Brücke hue shift. *Vision Research*, *15*, 341-351. [PubMed]

Curcio, C., Sloan, K., Kalina, R., & Hendrickson, A. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, *292*, 497-523. [PubMed]

Dacey, D. (1993). Morphology of a small-field bistratified ganglion cell type in the macaque and human retina. *Visual Neuroscience*, *10*, 1081-1098. [PubMed]

Dacey, D. (1994). Physiology, morphology and spatial densities of identified ganglion cell types in primate retina. In G. Bock & J. Goode (Eds.), *Higher-order processing in the visual system* (pp. 12-34). New York: Wiley.

Davila, K. D., & Geisler, W. S. (1991). The relative contribution of pre-neural and neural factors to areal summation in the fovea. *Vision Research*, *31*, 1369-1380. [PubMed]

Enroth-Cugell, C., Hertz, B. G., & Lennie, P. (1977a). Cone signals in the cat's retina. *Journal of Physiology*, *269*, 273-295. [PubMed]

Enroth-Cugell, C., Hertz, B. G., & Lennie, P. (1977b). Convergence of rod and cone signals in the cat's retina. *Journal of Physiology*, *269*, 297-318. [PubMed]

Glezer, V. D. (1965). The receptive fields of the retina. *Vision Research*, *5*, 497-525. [PubMed]

Gordon, J., & Abramov, I. (1977). Color vision in the peripheral retina. II. Hue and saturation. *Journal of the Optical Society of America*, *67*, 202-207. [PubMed]

Gordon, J., & Abramov, I. (1988). Scaling procedures for specifying color appearance. *Color Research and Application*, *13*, 146-152.

Gordon, J., Abramov, I., & Chan, H. (1994). Describing color appearance: Hue and saturation scaling. *Perception & Psychophysics*, *56*, 27-41. [PubMed]

Hagstrom, S., Neitz, J., & Neitz, M. (1998). Variations in cone populations for red-green color vision examined by analysis of mRNA. *Neuroreport*, *9*, 1963-1967. [PubMed]

Imhoff, S., Volbrecht, V., & Nerger, J. (2004). A new look at the Bezold-Brücke hue shift in the peripheral retina. *Vision Research*, *44*, 1891-1906. [PubMed]

Jameson, D., & Hurvich, L. M. (1967). Fixation-light bias: An unwanted by-product of fixation control. *Vision Research*, *7*, 805-809. [PubMed]

Johnson, E. N., Hawken, M. J., & Shapley, R. (2004). Cone inputs in macaque primary visual cortex. *Journal of Neurophysiology*, *91*, 2501-2514. [PubMed]

Johnson, M. (1986). Color vision in the peripheral retina. *American Journal of Optometry and Physiological Optics*, *63*, 97-103. [PubMed]

Krauskopf, J. (1964). Color appearance of small stimuli and the spatial distribution of color receptors. *Journal of the Optical Society of America*, *54*, 1171.

Lelkens, A. M. M., & Zuidema, P. (1983). Increment thresholds with various low background intensities at different locations in the peripheral retina. *Journal of the Optical Society of America*, *73*, 1372-1378. [PubMed]

Luria, S. (1967). Color-name as a function of stimulus-intensity and duration. *American Journal of Psychology*, *80*, 14-27. [PubMed]

Michael, C. R. (1978a). Color vision mechanisms in monkey striate cortex: Dual-opponent cells with concentric receptive fields. *Journal of Neurophysiology*, *41*, 572-588. [PubMed]

Michael, C. R. (1978b). Color vision mechanisms in monkey striate cortex: Simple cells with dual opponent-color receptive fields. *Journal of Neurophysiology*, *41*, 1233-1249. [PubMed]

Nagy, A., & Doyal, J. (1993). Red-green color discrimination as a function of stimulus field size in peripheral vision. *Journal of the Optical Society of America*, *10*, 1147-1156. [PubMed]

Nerger, J., & Cicerone, C. (1992). The ratio of L cones to M cones in the human parafoveal retina. *Vision Research*, *32*, 879-888. [PubMed]

Nerger, J., Volbrecht, V., & Ayde, C. (1995). Unique hue judgements as a function of test size in the fovea and at 20-deg temporal eccentricity. *Journal of the Optical Society of America*, *12*, 1225-1232. [PubMed]

Nerger, J., Volbrecht, V., Ayde, C., & Imhoff, S. (1998). Effect of the S-cone mosaic and rods on red/green equilibria. *Journal of the Optical Society of America*, *15*, 2816-2826. [PubMed]

Purdy, D. (1931). Spectral hue as a function of intensity. *American Journal of Psychology*, *43*, 541-559.

Purdy, D. (1937). The Bezold-Brücke phenomenon and contours for constant hue. *American Journal of Psychology*, *49*, 313-315.

Ransom-Hogg, A., & Spillmann, L. (1980). Perceptive field size in fovea and periphery of the light- and dark-adapted retina. *Vision Research*, 20, 221-228. [PubMed]

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

Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience*, *2*, 733-739. [PubMed]

Stabell, B., & Stabell, U. (1982). Bezold-Brücke phenomenon of the far peripheral retina. *Vision Research*, *22*, 845-849. [PubMed]

Stabell, U., & Stabell, B. (1977). Wavelength discrimination of peripheral cones and its change with rod intrusion. *Vision Research*, *17*, 423-426. [PubMed]

Stabell, U., & Stabell, B. (1979). Bezold-Brücke phenomenon of the extrafoveal retina. *Journal of the Optical Society of America*, *69*, 1648-1652. [PubMed]

Thorell, L. G., DeValois, R. L., & Albrecht, D. G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research*, *24*, 751-769. [PubMed]

Troscianko, T. (1982). A given visual field location has a wide range of perceptive field sizes. *Vision Research*, *22*, 1363-1369. [PubMed]

Vimal, R., Pokorny, J., Smith, V., & Shevell, S. (1989). Foveal cone thresholds. *Vision Research*, *29*, 61-78. [PubMed]

Weitzman, D. O., & Kinney, J. S. (1969). Effect of stimulus size, duration, and retinal location upon the appearance of color. *Journal of the Optical Society of America*, *59*, 640-643. [PubMed]

Westheimer, G. (1966). The Maxwellian view. *Vision Research*, *6*, 669-682. [PubMed]

Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the Rhesus monkey. *Journal of Neurophysiology*, *29*, 1115-1156. [PubMed]

Williams, D., MacLeod, D., & Hayhoe, M. (1981). Punctate sensitivity of the blue-sensitive mechanism. *Vision Research*, *21*, 1357-1375. [PubMed]