Color matching at high illuminances: the color-match-area effect and photopigment bleaching

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We evaluated whether a self-screening hypothesis can account for changes in red–green color matches with changes in retinal illuminance and changes in the size of the matching field. The dependence of the color match on field size measured at moderate illuminances was not present at high illuminances. For color matches made with normal pupil entry, there was no need to postulate any factors other than self-screening to account for the changes with either illuminance or field size. The self-screening model allowed us to estimate the optical density of the foveal cones and the retinal illuminance that caused half of the photopigment to be bleached at equilibrium. These estimates were in quantitative agreement with previous estimates made using other techniques. We also found that the change in a color match with increasing illuminance was inconsistent with first-order kinetics.

INTRODUCTION

Normal human color vision is trichromatic at photopic luminances; any light can be exactly matched in color and luminance by a mixture of only three, suitably chosen, primaries.[1] It is generally accepted that trichromacy arises at the first stage of the visual process, at the photoreceptors. It is hypothesized that there are only three spectrally distinct photopigments, each localized to a specific class of photoreceptors, the long-wavelength-sensitive (LWS), the middle-wavelength-sensitive (MWS), and short-wavelength-sensitive (SWS) cones.[2] Because trichromacy occurs at the first stage of the visual system, color matches remain unchanged over a wide range of experimental conditions.

There are certain experimental manipulations that can cause color matches to change. Three such manipulations are (1) changing the field size or the retinal location of the matching lights, (2) increasing the retinal illuminance of the matching lights to levels that bleach an appreciable amount of photopigment, and (3) changing the point of entry of the matching lights in the pupil. Since a color match is established at the photoreceptor level, all three of these manipulations must alter the spectral sensitivity of the photoreceptors. One mechanism by which all these manipulations could produce such an alteration in the spectral sensitivities of the cones is self-screening.[3] Self-screening results from the dependence of the absorption spectrum of a photopigment on its optical density. The effect of self-screening is predicted by the Beer–Lambert equations (see Appendix A), which state that the absorption spectrum of a pigment in solution is dependent on the concentration of the pigment and the path length of light through the pigment. Self-screening was first hypothesized by Stiles[4] to affect human color vision. Since that time the dependence of color matching on field size,[5] retinal illuminance,[6–9] and pupil entry[8,10] have all been attributed to differences in optical density. Many of these studies have used the Rayleigh match to study the effect of these manipulations on color matching. In the Rayleigh match a mixture of a midwavelength (typically 546-nm) light and a long-wavelength (typically 670-nm) light are matched to a standard light (typically 589.6 nm). The advantages of this match are that it is easily instrumented, it is minimally affected by preretinal filters, and it is only minimally influenced by the SWS cone.

In this paper we discuss the effects of changing the size of the color-matching field (the color-match-area effect) and/or the retinal illuminance of the color-matching field (the color-match-illuminance effect) on a modified Rayleigh color match. Our hypothesis was that the effects of both area and illuminance can be quantitatively explained by self-screening. The role of self-screening in the color-match-illuminance effect has been evaluated extensively in recent years.[8,9] The color-match-illuminance effect when measured using a Rayleigh match consists of a shift of the color match starting at about 5000 Td such that increasing amounts of the long-wavelength primary are required.[6] The basic effect has been shown to be consistent with the self-screening hypothesis.[8,9] That is, as illuminance is increased, the concentration of the cone photopigments in the cones decreases, causing a decreased optical density of the photopigment and thus a shift in the color match. The color-match-area effect was studied recently by Smith and Pokorny.[5,11] The effect consists of an increased amount of the long-wavelength primary being required for a Rayleigh match as field size is increased from 0.5 to 10 deg. Since parafoveal cones are shorter than foveal cones[12] it has been hypothesized that differences in cone length across the retina cause changes in color matches owing to self-screening. Light follows a shorter path length through the parafoveal cones, which consequently have a lower optical density. At high illuminances, with substantial photopigment bleaching, the concentration of the photopigment in both the foveal and the parafoveal cones should be low. Thus, if both of these effects are due to self-screening, then the color-match-area effect should disappear at retinal illuminances high enough to bleach most of the cone photopigments.

METHODS

Apparatus

To test this hypothesis, we constructed a high-illuminance, four-channel Maxwellian-view anomaloscope. Each channel had a 150-W tungsten–halogen light source (GE type FCS). To maximize the sensitivity of the color match to changes in

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optical density, it is desirable to use narrow-band primaries. We used fixed three-cavity interference filters (Ditric Optics) in each channel. To maximize the throughput of the system, all optical channels were combined by spectrally selective dichroic beam splitters (Optical Coating Laboratory, Inc.). Channels 1 and 2 provided 546- and 650-nm mixture primaries and were combined at a red–green beam splitter. Channel 3 was the standard channel. A front surface mirror was situated so that its edge bisected both Channel 3 and the combination of Channels 1 and 2, forming the bipartite field boundary. Channel 4 was a whole-field, 480-nm desaturant and was added to the other three channels at a blue–yellow beam splitter. All four channels were then brought to a common focus at a 2.1-mm circular aperture.[13] Located adjacent to this aperture were a circular neutral-density wedge (Kodak) and an achromatizing lens. A unit magnification of the aperture was focused in the plane of the observer's pupil. With this apparatus, we were able to obtain color matches with narrow-band primaries at illuminances as high as 600,000 Td.

All light sources except for the standard were controlled by linear light feedback circuits. The monitoring photocells (EG&G) were located after the interference filters to allow for accurate radiance control of the wavelength of interest. The light feedback circuits were controlled by two potentiometers. One potentiometer linearly controlled the ratio of red to green channels without appreciably affecting the illuminance, while the other controlled the illuminance of both the red and the green channels without affecting the ratio.[14] The potentiometer circuit either could control the individual lamps directly or could be monitored by a microcomputer, which then controlled the individual lamps. During the experiment the microcomputer continually monitored the potentiometer circuit and set the radiance of the red and green primaries. The computer also monitored a switch, controlled by the experimenter, that was used to signal that a match had been achieved. The computer saved the lamp settings for each match.

Calibrations

Each observer's color-matching data were calibrated immediately following the testing session. An EG&G Model 550 radiometer–photometer was mounted at the exit pupil, and the microcomputer reproduced the observer's settings for each illuminance. The microcomputer then recorded the photometer reading for each primary. We calculated the red-to-green (R/G) ratio as the ratio of the amount of "red" (650-nm) primary required to make a match divided by the amount of the "green" (546-nm) primary.[15]

Observers

Data were collected from 11 normal volunteers ranging in age from 23 to 47 years. Five of the observers were female; six were male. Each had a normal red–green color match, as ascertained in this experiment. In addition, all but three had previously had retinal exams and/or fundus photographs with no evidence of macular abnormalities. Two of the observers were the authors.

Stimuli

We used a bipartite field, with field sizes of 1, 2, 4, 8, and 10 deg. The standard hemifield contained a 589.6-nm light; the variable field contained a mixture of 650-nm (red) and 546-nm (green) lights. A 480-nm light masked the contribution of SWS cones at high illuminances and rods at low illuminances.[16] The 480-nm light was maintained at an illuminance 2 log photopic Td less than the standard.

Procedure

To make a color match, the experimenter set the standard to one of nine illuminances, beginning at 260 and ending at 260,000 Td. By turning a single knob, the observer could adjust the ratio of the "red" and "green" primaries at approximately constant retinal illuminance. A second knob was available to control the luminance of the mixture field.

Six observers participated in the study of field size conditions. At each retinal illuminance, the observers practiced matching a 10-deg field for 3 min.[17] Matches were then made in order from 8 to 2 deg. Observers SB and AE also made 1-deg matches. Matches were made in order of decreasing field size to ensure that the area of retina being tested was fully bleached without requiring a 3-min adaptation period at each field size. Typically each observer made three adjustments per condition. We report the median of the three R/G ratios.

Four other observers plus the two authors participated in a condition using only the 4-deg field size. The illuminances were the same as above. In this condition each observer made 10 matches at each illuminance, and the color match was computed as the average of the 10 individually computed R/G ratios.

RESULTS

Results for four field sizes are shown for observer AE in Fig. 1. At low illuminances the color match depended on the size of the matching field, with larger field sizes requiring higher

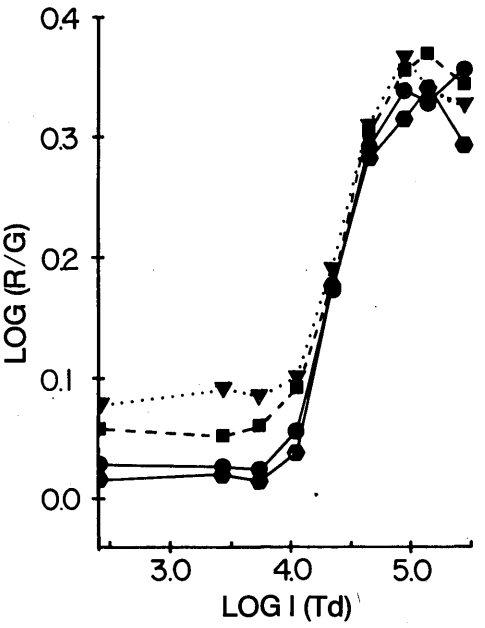

Fig. 1. Color-matching data for observer AE at four field sizes: 1 deg (hexagons), 2 deg (circles), 4 deg (squares), and 8 deg (triangles). The log(R/G) ratio is the log of the ratio of the amounts of the 650- and 546-nm primaries required to match a 589.6-nm standard.

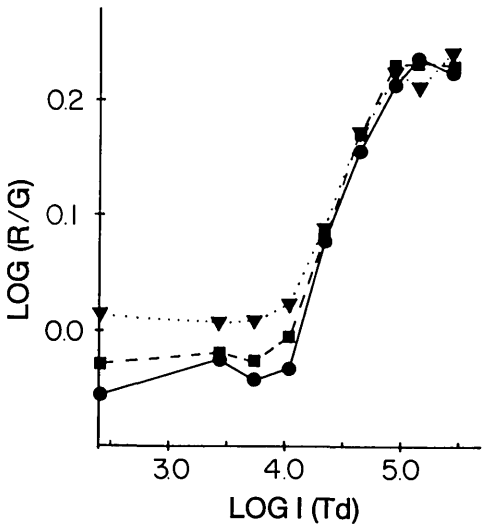

Fig. 2. Average color-match data for six observers at three field sizes. Symbols as in Fig. 1.

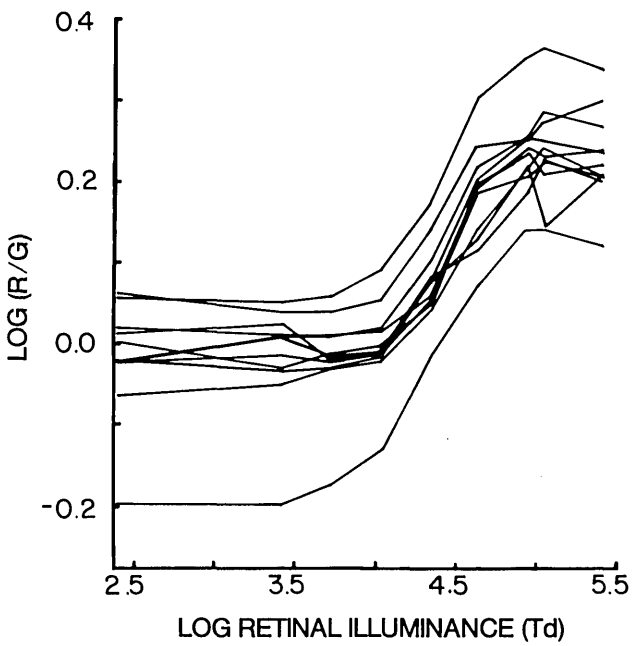

Fig. 3. Color-matching data for individual observers at the 4-deg field size.

R/G ratios, in agreement with the results of Pokorny and Smith.[5] From 260 to 5500 Td the color match did not depend on the retinal illuminance. As retinal illuminance increased above 5500 Td, the color match required progressively higher proportions of the 650-nm primary until, at about 90,000 Td, further increases in retinal illuminance caused no additional change in the color match.[18] At the high-illuminance asymptote, although the color match was more variable, there was no systematic effect of field size. This can be seen more clearly in Fig. 2, which shows results averaged for six observers at three field sizes.

Figure 3 shows the individual results for all of the observers for the 4-deg field size condition. This figure illustrates that there is considerable individual variability in the baseline color match and in the total size of the color-match-illuminance effect. It is of note that the illuminance at which the shift begins to occur is quite similar for all observers.

DISCUSSION

Theoretical Calculations of the Effects of Optical Density

To evaluate the data, we derived the relation between the results of these experiments [in log(R/G) ratio] and the optical density of the photopigments (see Appendix A). To make these derivations we had to assume that (1) all changes in the color match are due to changes in the optical density of the photopigments and (2) the extinction spectra for the photopigments could be approximated by those described by Smith *et al.*[19] The resulting predictions reflect the necessary effect of optical density on the color match that we employed.

Figure 4 illustrates the fact that as the optical density of the photopigments increases, the Rayleigh match shifts, requiring a higher proportion of the green primary. To facilitate comparison with the data we plot the predictions in terms of the log(R/G) ratio.[20] The two curves of Fig. 4 are predictions for different ratios of optical densities in the LWS and MWS cones. This choice of ordinate scale also has the important advantage of being almost linearly related to optical density.[21] This linear relation simplifies interpretation of the data. For instance, for any starting density, bleaching half of the remaining photopigments will move the match halfway along the curve toward the color match at a density of 0.0. Thus the color match is proportional to the amount of photopigment bleached.

Effect of Bleaching

At low illuminances, the color match depends on the size of the matching field, a result consistent with the effective optical density of the parafoveal cones being lower than that of the foveal cones. At high illuminances and low photopigment concentrations, there is no field size effect. This supports the

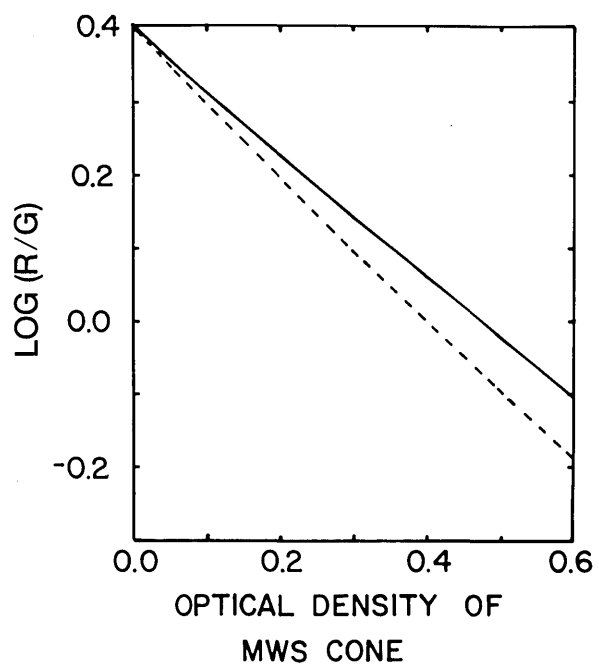

Fig. 4. Effect of optical density on log(R/G). The log(R/G) values are predicted from Beer's law (see Appendix A). The two curves represent different ratios of the densities of photopigment in the LWS and MWS cones. The solid line is based on equal densities in the two cones; the dashed lines show the prediction if the LWS density is 1.5 times the MWS density.

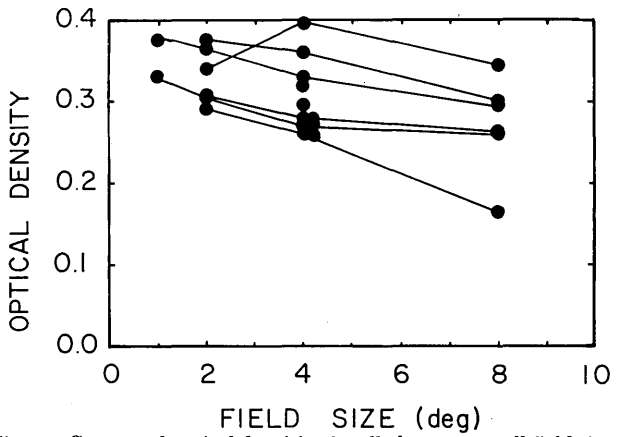

Fig. 5. Computed optical densities for all observers at all field sizes. Points from the same observer are connected by solid lines. These values were computed assuming that the peak optical densities of the LWS and MWS cones were equal. If it were assumed that the LWS cone density were 1.3 times that of the MWS cone, the optical densities would be scaled by a factor of 1.2 (see Fig. 4).

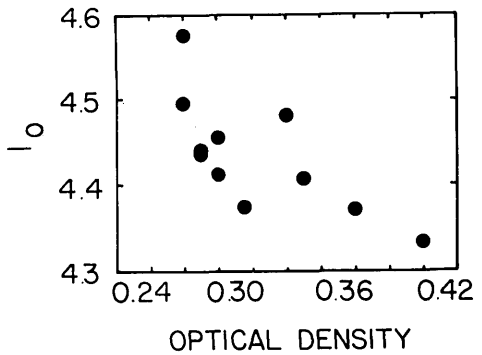

Fig. 6. Comparison of the half-bleach illuminance (I_0) values as a function of optical density for all observers at 4 deg.

hypothesis that at long wavelengths, where macular pigment is not a factor, the major difference between large and small field color matches is due to differences in optical density and not to other factors.

If self-screening is the only factor causing the changes in color matches, then the relation between photopigment density and the log(R/G) ratio of Fig. 4 permits estimation of a number of parameters. If we assume a relation between the optical density of the LWS and MWS photopigment, then the size of the bleaching-induced shift in the color match tells us what the initial low-illuminance optical density was. For the purposes of this paper we will treat the LWS and MWS cones as having identical optical densities,[22] although there is some evidence[23,24] that suggests that the ratio is more nearly 1.3. Likewise, since the relation between the log(R/G) ratio and optical density is nearly linear, the illuminance at which half of the color-match shift has occurred should be the illuminance at which half of the photopigment is bleached (the half-bleach illuminance, I_0). Comparison of these parameters with published values obtained using other techniques provides a test of the hypothesis that optical-density changes alone can account for the change in the color match with illuminance.[25]

To obtain estimates of optical density and I_0, a cumulative normal distribution was fitted to the color-match-illuminance data. Using the cumulative normal distribution allowed an arbitrarily steep function to be fitted to the data. From these fits only two parameters were considered, the difference between the low-illuminance and the high-illuminance asymptotes (the size of the shift in the color match), and the mean of the distribution (I_0).[26] The optical-density change was computed from the Beer–Lambert equations (see Appendix A).

Figure 5 shows the estimated optical density for each field size.[27] Note that the larger field sizes have a somewhat smaller optical density; this is a restatement of the field size effect. The average calculated density for the 2-deg field size is 0.33. This figure is in agreement with recent estimates based on psychophysics,[8,9,23,24] retinal densitometry,[28] and microspectrophotometry.[22]

Figure 6 shows the estimated half-bleach illuminances as a function of optical density for the 4-deg field size. The correlation between the half-bleach illuminance and optical density is $r = 0.61$.[29] The mean of the half-bleach illuminances for all observers was 4.4 log Td. This number is in excellent agreement with estimates made by several investigators using retinal densitometry[30–32] and psychophysics.[8]

Figure 7 compares a prediction of the color-match-illuminance effect based on first-order kinetics[31] with the 4-deg data of one of our observers. At low retinal illuminances the data fell below the prediction, whereas at high illuminances the data were above the prediction.[33] Since the steady-state optical density is an equilibrium between the bleaching rate and the regeneration rate, we must conclude that the regeneration process is not described by first-order kinetics. At low illuminances, regeneration is faster than that predicted by first-order kinetics. At higher illuminances the regeneration rate is slower than that predicted by first-order kinetics. The plateau in color matching is reached at illuminances that should bleach only 80–85% of the pigment. This is similar to results that have been reported using retinal densitometry for both human cones[35] and cat rods.[36] The steepness in the color-match-illuminance shift is also evident in the data of Alpern[8] and Wyszecki.[34] We conclude that the bleaching curve for the human retina is steeper than predicted by first-order kinetics.

These results provide strong support for the self-screening hypothesis. If changes in waveguide effects[21,25] were signif-

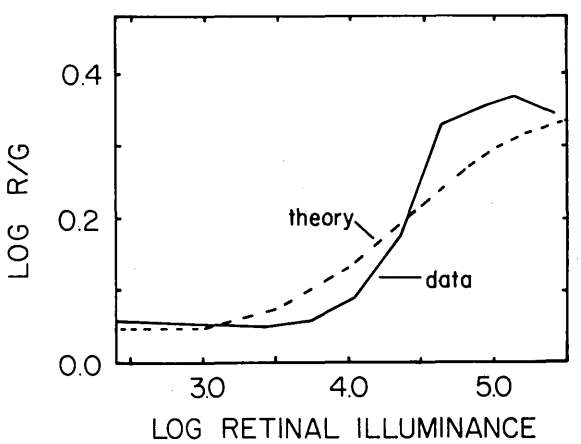

Fig. 7. Comparison of the observed dependence of the color match on retinal illuminance (solid line) with the predictions of the first-order kinetic equation (dashed line) for one observer. Results are similar for all observers.[33]

icant for our test conditions, we might expect a high-illuminance color-match-area effect because the morphology of the cones changes from the central fovea to the near periphery.[12] We found no area effect at high illuminances. Although there is evidence[21,25] that there are illuminance-dependent changes in waveguide effects for eccentric pupil entry, we find no need to invoke such changes for our conditions. One of the major differences between our analysis and that of others[21,25] is the assumed nature of human photopigment kinetics. We argue that if kinetics is not first order, then self-screening alone can account for changes in the color match with both illuminance and field size.

SUMMARY

The assumption that the differences between our 5000- and 90,000-Td color matches are due to changes in optical density leads us to

(1) Estimate the optical density of the cones as being between 0.3 and 0.5,

(2) Estimate that the illuminance at which half of the cone photopigments are bleached is 4.4 log Td, and

(3) Conclude that the kinetics of cone photopigment regeneration cannot be described by the first-order kinetic equation. Regeneration rates at moderate retinal illuminances must be faster than predicted by first-order kinetics.

These conclusions are in quantitative agreement with conclusions based on other techniques, such as retinal densitometry. We interpret this agreement as failing to reject the hypothesis that the only factor causing differences between 1000- and 100,000-Td color matches, given normal pupil entry, is the change in optical density that is due to bleaching. For our stimulus conditions there is no evidence of the failure of the self-screening hypothesis that has been found for peripheral pupil entry.[25] The change in the color match as a function of retinal illuminance is a powerful technique for studying the processes of photopigment bleaching and regeneration.

APPENDIX A: THE DERIVATION OF THE SELF-SCREENING MODEL

In this appendix we derive the relation between the Rayleigh match and the optical density of the photopigments. The assumption underlying the following discussion is that there are three cone photopigments. There is a SWS pigment with an extinction spectrum α_S contained in SWS cones, a MWS pigment with extinction spectrum α_M contained in MWS cones, and a LWS pigment with extinction spectrum α_L contained in LWS cones. The extinction spectra are obtained from the fundamentals of Smith *et al.*,[37] although results would be similar for most reasonable sets of primaries. The absorption spectra of the photopigments depend on the extinction spectra, the concentration, and the path length of light through the photopigment.

The equal-quantum-match condition can be stated formally as follows: Let $L(\lambda)$, $M(\lambda)$, and $S(\lambda)$ represent the quantal absorption spectra of the three cones. Let $Q1(\lambda)$ and $Q2(\lambda)$ be two lights of arbitrary spectral distribution. These two lights are said to match if each class of cone has the same number of photoabsorptions on each side of the field, that is, if

$$\int_\lambda L(\lambda)Q1(\lambda)d\lambda = \int_\lambda L(\lambda)Q2(\lambda)d\lambda, \quad \text{(A1.a)}$$

and if

$$\int_\lambda M(\lambda)Q1(\lambda)d\lambda = \int_\lambda M(\lambda)Q2(\lambda)d\lambda, \quad \text{(A1.b)}$$

and if

$$\int_\lambda S(\lambda)Q1(\lambda)d\lambda = \int_\lambda S(\lambda)Q2(\lambda)d\lambda. \quad \text{(A1.c)}$$

From these relations it is clear that the equal quantum condition depends only on the absorption spectra of the cones and not on the actual number of photoreceptors present.

Using the Beer–Lambert relation, we describe the dependence of the absorption spectra on the concentration and path length for a pigment in solution as

$$F(\lambda) = 1 - \exp[-\alpha(\lambda)cl], \quad \text{(A2)}$$

where $F(\lambda)$ is the fraction of light absorbed, $\alpha(\lambda)$ is the extinction spectrum of the pigment, c is the chromophore concentration of the photopigment, and l is the path length of light through the pigment (see also Ref. 38).

For the color match used in this paper, a mixture of "red" (650-nm) and "green" (546-nm) primaries is matched to an "orange" (589.6-nm) primary. Ignoring the contribution of the SWS cones[16] results in

$$Q(590)L(590) = Q(546)L(546) + Q(650)L(650) \quad \text{(A3.a)}$$

and

$$Q(590)M(590) = Q(546)M(546) + Q(650)M(650), \quad \text{(A3.b)}$$

where

$Q(\lambda)$ is the amount of light required for a color match,

$M(\lambda)$ is the sensitivity of the MWS cone,

$L(\lambda)$ is the sensitivity of the LWS cone.

Taking the ratios of each side and substituting from Eq. (A2), we find that

$$\frac{\{1-\exp[-\alpha_L(590)c_Ll_L(f_L)]\}}{\{1-\exp[-\alpha_M(590)c_Ml_M(f_M)]\}} = \frac{X\{1-\exp[-\alpha_L(546)c_Ll_L(f_L)]\} + \{1-\exp[-\alpha_L(650)c_Ll_L(f_L)]\}}{X\{1-\exp[-\alpha_M(546)c_Ml_M(f_M)]\} + \{1-\exp[-\alpha_M(650)c_Ml_M(f_M)]\}}$$

where

$\alpha_L(\lambda)$ is the extinction spectrum of the LWS pigment,
$\alpha_M(\lambda)$ is the extinction spectrum of the MWS pigment,
c_L and c_M are the dark-adapted chromophore concentrations of the LWS and MWS pigments, respectively,
l_L and l_M are the path lengths of light through the LWS and MWS pigments, respectively,
f_L and f_M are the fractions of the LWS and MWS pigments unbleached, and
X is the R/G ratio, or $X = Q(650)/Q(546)$.

If this equation is solved for representative choices of initial ratios of the LWS and MWS photopigments, the effect of optical density on the color match can be predicted. The results of these predictions are plotted in Fig. 4. By using the Rushton–Dowling equation,[28] $I/(I + I_0)$ for f_L and f_M, the predicted effect of bleaching on the color match can be determined.

ACKNOWLEDGMENT

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13. A 2.1-mm aperture permits both high retinal illuminances and homogeneous appearing matching fields. We monitored the size and the position of the pupils of all except four of the observers using an infrared TV system. The natural pupil was never smaller than 2.1 mm, even at the highest illuminances.
14. This configuration allowed us to use a fixed standard and thus to specify uniquely the retinal illuminance.
15. The log(R/G) ratio values are expressed in terms of the photocell's "photopic" spectral sensitivity.
16. To determine whether the 480-nm desaturant had any effect on the R/G ratio, observer SB performed complete trichromatic matches of the 589.6-nm standard plus a 480-nm primary to the mixture of the 650- and 546-nm primaries. When the log(R/G) ratios from the control experiment were compared with data from the main experiment, we found no reliable difference in the measured R/G ratios. We also made a series of dichromatic matches, varying the relative amount of the whole-field 480-nm desaturant. There was no reliable effect of the 480-nm desaturant on log(R/G).
17. To determine the appropriate adaptation period we performed control experiments in which the color match was measured as a function of time following exposure to each retinal illuminance. For all illuminances except 11,200 Td the bleaching-induced shift in the color match was complete within 3 min. At 11,200 Td there was a very slow bleaching effect that could take up to 15 min to reach asymptote. However, the total error that this slow shift could account for is of the order of 0.02 log unit. The 10-deg matches were made to ensure an adaptation period at each retinal illuminance. Data obtained at this field size were not recorded.
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25. Wooten[21] and Fuld *et al.* [K. Fuld, B. R. Wooten, and L. Katz, "The Stiles–Crawford hue shift following photopigment depletion," Nature **279,** 152–154, 1979)] have argued that self-screening cannot account for the total change in the color match at high illuminance. Their argument is based on the failure of the color-match data to fall on a straight line when plotted against percent pigment bleached as computed from first-order kinetics.
26. Rms errors were between 0.001 and 0.052.
27. There were no reliable evidence of a systematic effect of field size on the half-bleach illuminance for our six observers. The two observers with the largest effects were our most variable observers and have the lowest reliability in the estimate of their half-bleach illuminance.
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29. This correlation (although statistically significant) is not stressed since if the two extreme points are omitted the correlation coefficient drops to 0.2.
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33. We have normalized these curves at the half-bleach illuminance value. That is, we assumed that our estimate of the half-bleach illuminance was accurate and then used that estimate as a parameter for the first order prediction. This assumption does not affect the difference in shape between the data and the theoretical prediction. We show the data of only one observer, although similar deviations from the first-order predictions are evident for

all observers. In addition, the data of Wyszecki[34] and Alpern[8] also show the same trend. Wyszecki and Stiles[9] have shown that complete sets of color-matching functions obtained at high illuminances are compatible with the self-screening hypothesis.
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