

Color matching at high illuminances: photopigment optical density and pupil entry

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Changes in the effective optical density of the cones are sufficient to explain changes in color matches with retinal illuminance and pupil entry. We performed three experiments. In the first experiment, six observers made color matches under both bleached and unbleached conditions to a series of six standard wavelengths. The effects of bleaching could be modeled by a decrease in optical density of the L and M cone photopigments. Slight spectral shifts in the peak wavelengths of the photopigments were required for different observers. In the second experiment we varied retinal illuminance of the color-matching field from 2.4 to 5.4 log Td for a series of long-wavelength primaries. The shape of the color match versus the intensity function was unchanged by the wavelength composition of the matching field. In the third experiment we measured the change in color match with retinal illuminance for different pupil entry positions. At low luminances there was a marked dependence of the color match on pupil entry positions. At high illuminance there was only a small dependence. The half-bleach illuminance values varied as expected from the Stiles-Crawford I effect. We conclude that for wavelengths >540 nm, changes in color matches with bleaching and pupil entry can be explained by changes in the effective optical density of the cones.

1. INTRODUCTION

By manipulating the intensity of three suitably chosen monochromatic lights, an observer can match a mixture of these three lights in luminance, color, and saturation to any other light of arbitrary spectral composition. This observation is the foundation of trichromatic theory. Once established, these physically different lights that are matched for the visual system (a color match) continue to appear to be the same to the visual system over a wide range of stimulus conditions. The generally accepted interpretation of trichromacy is that it is established at the first stage of the visual system, in the photoreceptors, and the visual system maintains a trichromatic organization at all subsequent levels. Thus two different light distributions that are a color match represent two physically different stimuli that cause identical quantal absorptions in the three cone photoreceptors. As a result, despite the physical difference between them, the two stimuli are physiologically identical. It is this strong link to photoreceptor responses that has made color matching a powerful technique for studying the spectra,¹⁻⁶ optical density,⁷⁻¹⁴ and regeneration kinetics^{11,12} of the cone photoreceptors. In recent years there has been an increasing interest in the use of color matching to study individual variations in the extinction spectra³⁻⁶ of the cone photopigments.

However, it is also known that there are stimulus conditions that cause changes in color matches. These conditions consist of changing the retinal position or field size of the color-matching field,^{7,10,15} changing the retinal illuminance of a test field,^{7,10,16-19} and changing the entry position of a test field through the pupil of the eye.^{9,20,21} There are a number of potential reasons for these stimulus-dependent changes in color matches, including differences in the optical density of the photopigments and preretinal filtering by the optic media and macular pigment. An ad-

ditional factor that was proposed²² but that did not receive widespread attention is the potential for variations in the waveguide properties of the cones to affect color matches. There is considerable evidence that cone orientation plays a role in the spectral sensitivity of the cones. It is well known that the color of a light changes with pupil entry, an effect known as the Stiles-Crawford II (SCII) effect.^{23,24} This color change is quantified by a change of the color-matching functions with pupil entry.^{22,24} Because there is a large degree of intraobserver variation in the location of the Stiles-Crawford (SC) peak,²⁵ contributions of spectral variation in waveguiding could also be a significant contributing factor to individual variability in color matching. In addition, it was proposed that the spectral waveguide properties of the cones change with retinal illuminance.^{26,27}

The size of any possible waveguide effects on spectral sensitivity is limited. Brindley and Rushton²⁸ showed that the change in color of monochromatic lights when the retina was transilluminated was of the same order as the SCII effect measured through the pupil. Miller⁸ and Starr²⁹ both showed that optical density was a major factor in determining the wavelength dependence of the directional sensitivity of the cones in dichromatic observers. Wyzecki and Stiles¹⁹ showed that, by assuming that the only factor changing with bleaching was the optical density of the cones, they could derive reasonable photopigment spectra, although the actual spectra at which they arrived are somewhat different from other estimates of photopigment spectra, a result reinforced by the analysis of MacLeod and Webster.⁶ Miller⁸ found that bleaching dichromats decreased the wavelength dependence of their Stiles-Crawford I (SCI) effect. Likewise, Alpern⁹ showed that bleaching the photopigments decreased the effect of pupil entry position as would be expected if the major portion of the SCII effect were due to changes in optical density with pupil entry. However, Alpern *et al.*²² later found that the

effects of changing pupil entry position on full-spectrum color matches in the unbleached state could not be attributed to self-screening alone. There is also indirect evidence that waveguides may not play a strong role in determining the absorption spectra of the cones. In patients with retinal diseases that severely affect the orientation and morphology of the cones, color matches are equivalent to those of a bleached normal observer.^{12,33} This result can also be seen by comparing the data of Smith *et al.*³⁴ with bleached color matches from the same laboratory.⁷

In this paper we describe experiments that test whether optical-density changes alone can account for the effect of changes in retinal illuminance and pupil entry. We take the experimental approach of directly manipulating the optical density of the cones by bleaching. All these experiments are performed at long wavelengths (>540 nm, called the Rayleigh region) for two reasons. First, this is the spectral region in which the simplifications and accuracy of a two-primary match are available. Matches must be precise to allow us to test for the presence of a factor other than optical density with reasonable power. Second, there are other factors adding to variability in the blue region of the spectrum, such as changes in absorption because of lens and macular pigmentation.

In experiment 1 we measure the variation in color matches in the Rayleigh region with variations of the standard wavelength and retinal illuminance for color-normal observers. We then ask whether a reasonable selection of photopigment spectra and optical densities can fit the effects of both changing the standard wavelength and bleaching the cones to a lower optical density. In experiment 2 we measure color matches as a function of retinal illuminance, keeping the standard constant but varying the mixture primaries. With this technique, the physiological stimulus (determined by the standard light) is held constant as the physical composition of the mixture field is varied by changing the wavelength of the red primary. This design tests whether the physical composition of a stimulus affects the change in color matches at high retinal illuminances. Experiment 3 directly compares the effects of changing pupil entry position under bleached and unbleached conditions.

2. METHODS

A. Subjects

A total of six observers participated in experiment 1. All were color normal, and they ranged in age from 28 to 41 yr. All observers except one of the authors were male. Only the two authors participated in experiment 2, which required highly experienced psychophysical observers. Four observers participated in experiment 3, the two authors and two other color-normal males. All observers had normal color vision and visual acuity corrected to 20/20. Informed consent was obtained from all observers. For experiment 3, 0.5% Mydracyl was used to dilate the observers' pupils.

B. Apparatus and Calibrations

The apparatus we used was the four-channel high-illuminance Maxwellian-view device under microcomputer control described previously.¹⁰ We used three-cavity interference filters (Ditric Optics) in each channel to control

the wavelength. All four channels were brought to a common focus at a 2.1-mm aperture. A unit magnification of this aperture was focused in the plane of the observer's pupil. During alignment to the apparatus and testing, we used infrared light-emitting diodes and a television camera to monitor the observer's pupil position and size; this ensures that all the light enters the eye through the appropriate portion of the pupil. The spectral distribution of the light produced by each filter was calibrated *in situ* at 1-nm intervals by a Princeton Applied Research spectroradiometer. The spectral sensitivity of the photometer was based on calibrations traceable to the National Bureau of Standards.

C. Color-Matching Technique

The observer continuously viewed a bipartite field. To make a color match, the observer turned one knob to adjust the color, i.e., the ratio of the long- and short-wavelength primaries in the mixture field. The observer turned another knob to adjust the luminance of the mixture field. Immediately after each session, the luminances of the long- and short-wavelength-mixture primaries were measured with an EG&G photometer under computer control. We report the color matches in terms of the log average ratio of the luminances of the long- and short-wavelength (red-to-green) primaries, the $\log(R/G)$, for the photometer. The actual sensitivity of the photometer was calibrated against a set of spectral lights of known radiance (traceable to the National Bureau of Standards).

D. Experiment 1

We measured Rayleigh color matches to a series of different wavelengths of the standard light (nominally 560, 570, 580, 590, 600, and 610 nm; see Fig. 1) for all six observers, using a 4-deg field. In a single session we measured ten color matches for each standard light, first at low retinal illuminance (2600 Td), then at high retinal illuminance (260,000 Td). The mixture primaries were nominally 546 and 650 nm. Subjects performed at least two separate runs for each condition. Standard wavelengths were varied in order of increasing wavelength.

1. Fitting Procedure

We fitted the extinction spectra of DeMarco *et al.*³² to the data, using a simplex³⁵ curve-fitting procedure to fit simultaneously both the bleached and the unbleached data. An optical density of 0.01 was used for both long-wavelength-sensitive (LWS) and middle-wavelength-sensitive (MWS) cones under the bleached conditions. We allowed the computer to adjust both the wavelength of peak sensitivity and the low-illuminance optical density of each photopigment (for a total of four parameters: LWS wavelength and optical density, MWS wavelength and optical density). The extinction spectra were shifted on a wavelength basis. We made exploratory fits by using different shifting metrics (i.e., wave number, etc.) and different bleached densities. The results reported are not sensitive to these details, and the values used were chosen for simplicity. The predicted $\log(R/G)$ ratio value was calculated for each trial fit. A least sum-squared-error (SSE) criterion was used to find the optimal fit. If the color matches could be well fitted by varying only the extinction spectra

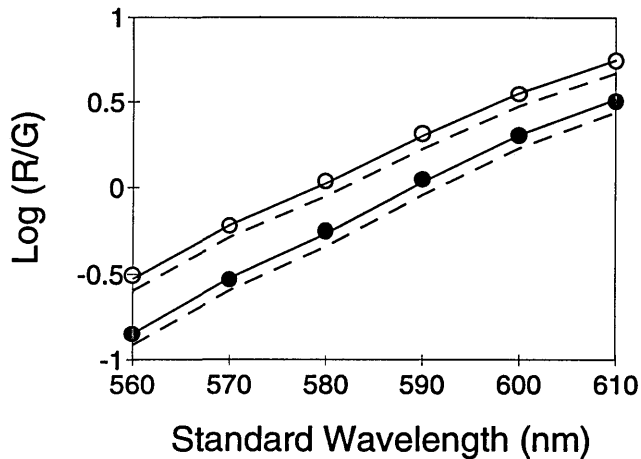


Fig. 1. Color matches as a function of standard wavelength at both low (filled symbols) and high (open symbols) retinal illuminances for one observer. Also shown are the fits for the unoptimized model (dashed curves) and the optimized model (solid curves). The wavelength axis indicates the nominal wavelength of each standard filter. Standard deviations for the matches are generally smaller than the symbol size.

and the optical density of the cone photopigments within a reasonable range, then we have no support for the hypothesis that there are important changes in waveguide properties at high retinal illuminances. That is, we asked whether a single set of photopigment extinction spectra could simultaneously fit both the bleached and the unbleached data. If individual observers with different cone orientations require only small differences in peak wavelength, then there is no compelling evidence that individual differences in waveguide properties contribute significantly to individual differences in Rayleigh matches. The fitting procedure was constrained such that there was a penalty for very large shifts in the peak wavelengths. The purpose of this constraint was to ensure that the program did not interchange the two pigments. Because the data were fitted to within experimental error with small shifts of the photopigment spectra, this constraint does not affect our conclusions (see below).

2. Results and Discussion

The color matches of all observers in this study could be well fitted at both high and low retinal illuminances simultaneously with relatively minor parameter adjustments. Figure 1 shows the effect of the fitting procedure for one observer (AE). Color-matching data are indicated by the symbols; the model predictions are connected by the curves. For this observer, who had excellent color discrimination, the standard deviations of the matches are smaller than the size of the symbols, ranging from 0.002 to 0.02. For most observers color matches were most accurate at low retinal illuminances for the 570-, 580-, and 590-nm standards and least accurate for the high-illuminance 560-, 600-, and 610-nm standards. High-illuminance standard deviations were typically of the order of 0.01 to 0.03 $\log(R/G)$. The unadjusted primaries³² (dashed curves) do not describe this observer's color matches well. With relatively small adjustments, however, the data could be well fitted (solid curves). For all observers there were large changes between the low- and high-illuminance color matches. There were also consis-

tent differences among observers (Fig. 2) under both bleached and unbleached conditions. Despite these individual differences, the data of all observers could be well fitted with only small adjustments in the peak wavelengths of the photopigments. We could generally use the fitting procedure to fit a 1- to 3-nm range of peak wave-

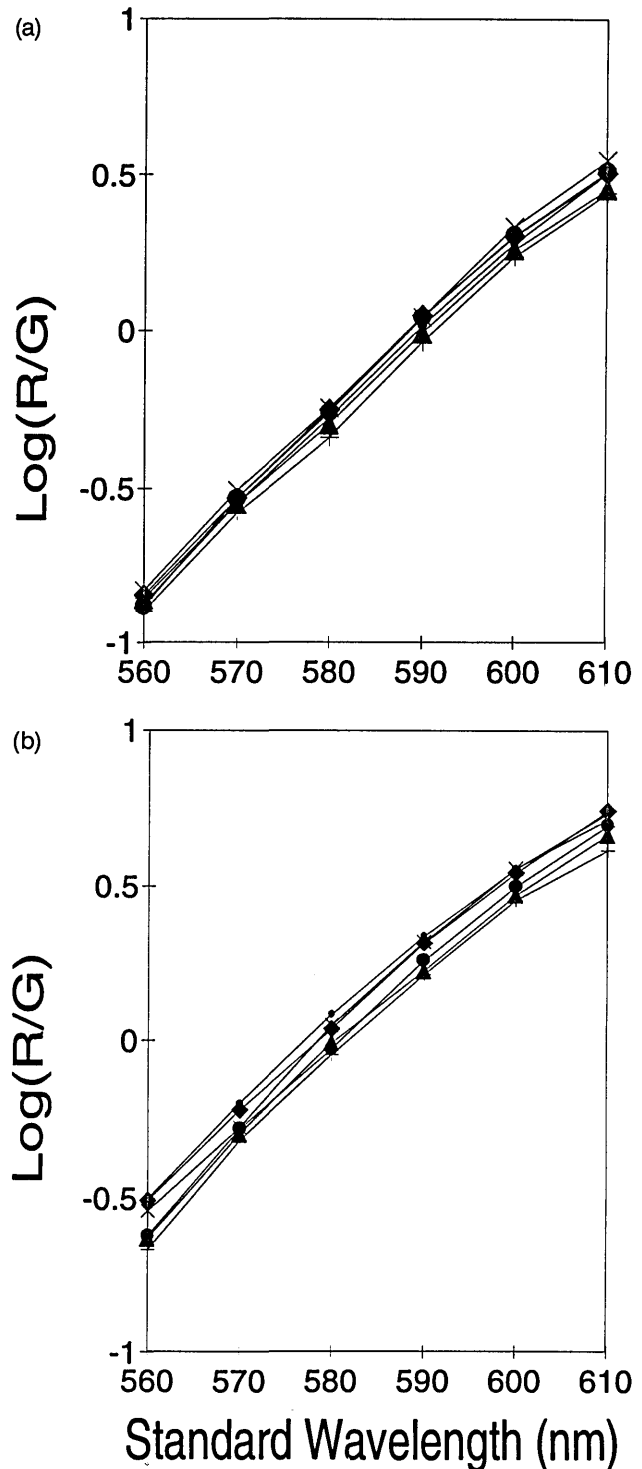


Fig. 2. Color matches for the six observers at (a) 3.4 log Td and (b) 5.4 log Td. Standard deviations vary for observer and condition. Generally, the lowest standard deviations are obtained for the 570- to 590-nm standard at low illuminances (from 0.004 to 0.02). The largest are obtained at high illuminances (0.008 to 0.03).

Table 1. Results of Applying the Fitting Procedure to the Color Matches of Each of the Six Observers

Subject	LWS Optical Density	MWS Optical Density	LWS Peak Wavelength (nm)	MWS Peak Wavelength (nm)	SSE	Distance of SC Peak from Pupil Center (mm)
AE	0.51	0.28	568.9	543.6	0.0014	1.5
SB	0.56	0.15	564.3	548	0.0066	1.8
DG	0.55	0.34	569	542.8	0.003	
YC	0.4	0.34	569	548.9	0.0102	0.6
MK	0.36	0.28	567.4	547.6	0.0074	2.3
GS	0.51	0.24	565.1	545.9	0.0075	

lengths of one pigment by varying the other three parameters appropriately. The two parameters, peak wavelength and optical density, are shown for each pigment in Table 1. The unshifted values for these photopigment spectra, expressed on an energy basis at the cornea, are 543 nm for the MWS pigment and 566 nm for the LWS pigment. The model fit to the data has a strong covariance between parameters, and thus Table 1 should be considered as an indication that the data can be well fitted by a simple model. Figure 3 demonstrates the effects of the covariance between parameters. Figure 3(a) shows error contours for observer AE on a peak-wavelength grid. To generate Fig. 3 we combined a grid search procedure with an optimization procedure. Thus, for a grid of peak wavelengths of the LWS and MWS photopigments, we found the best-fitting optical densities of the LWS and MWS photopigments by using the simplex procedure. We plotted the log SSE contours at each point on the grid and constructed the contours from these values. Successive contours are separated by a factor of 2 in total error, with the central, minimal contour at an SSE of 0.0025. This is equivalent to an error of 0.014 log(R/G) per match. Thus we see that for observer AE the computer found an optimum fit with MWS peaking at 543.6 nm and LWS at 568.9 nm, but the fits at 545 and 565 nm are essentially equivalent. Figure 3(b) shows similar contours, but here they are generated for an optical-density grid for the same observer. Figure 3(c) shows an optical-density grid that was generated for observer SB, who had an unusually asymmetric balance of densities (see Table 1). From these plots it is clear that we can find nearly equivalent fits to the data that use slightly different parameter values.³⁰ We can also see that, although observer SB has a very high ratio of LWS to MWS optical densities, a slightly worse-fitting set of parameters gives a more evenly balanced estimate of the optical densities. This change is within the error bounds estimated for the data.

We also measured the alignment of the cones to the pupil³⁶ for four of these observers. The distance from the center of the pupil (where the color-matching measurements were made) to the SC maximum is shown for these observers in the rightmost column of Table 1. This distance did not affect the color-matching data as would be expected with a strong spectral-dependent waveguide effect. We also found, as did previous authors,² that we required higher densities in the LWS cones than in the MWS cones. This is a consistent result across all observers and was checked by single runs as well as by the average data. The fits were the same. This is a result that is apparent in Miller's data from dichromats,⁸ in the full-spectrum data of both Wyszecki and Stiles¹⁹ and Alpern *et al.*,²² and in the derivation of fundamentals from the

color-matching data of dichromats.² The source of this inequality is not known; the error could be due to differences in the cones or in the photopigments, or it could be due to a systematic error in the estimates of photopigment extinction spectra. Such an error would suggest a systematic bias in the estimates of the cone photopigment spectra. The spectra used in the current study agree with both direct estimates from outer segment current recording³¹ and the iodopsin extinction spectrum^{3,32} and are linear transformations of color-matching functions, suggesting that the higher optical density determined for the LWS cones is a true property of the cone photoreceptors and not an error. In conclusion, there is no need to invoke any additional factors beyond optical density and small differences in the photopigments to account for the color matches of individual observers in experiment 1.

E. Experiment 2: Determining Color-Match Illuminance Effect

Color matches change when the cone photopigments are bleached^{10,17,18} (the color-match illuminance effect). If there are illuminance-dependent changes in waveguide properties of the cones,^{26,27} then the shape of the color-match-illuminance effect might be wavelength dependent. The design for this experiment features fixed standard and short-wavelength primaries, but there is also a long-wavelength primary that varied across sessions. This design has two advantages. First, the physiological (and psychological) stimulus varies only in retinal illuminance despite different long-wavelength primaries because an equal quantum match must always be made to the 560-nm standard. Second, altering the long-wavelength primary alters the relative importance of both self-screening and possible changes in waveguides with retinal illuminance, unless the two mechanisms have identical dependence on wavelength. For instance, as wavelength increases, the ratio of the cone diameter to wavelength decreases, which should affect waveguide properties.^{29,37} If the only factor causing the change in the color matches from low to high illuminances is self-screening, then the shape of the change in log(R/G) versus luminance will be independent of wavelength because the percent bleach is nearly linearly related to log(R/G).^{10,26,27} If both self-screening and illuminance-dependent changes in waveguide properties are important but are present in differing amounts as a function of the wavelength of the long-wavelength primary, then the shape of the color-match illuminance effect should be wavelength dependent.

1. Methods

To test for the effect of wavelength composition on the size and shape of the color-match illuminance effect, we

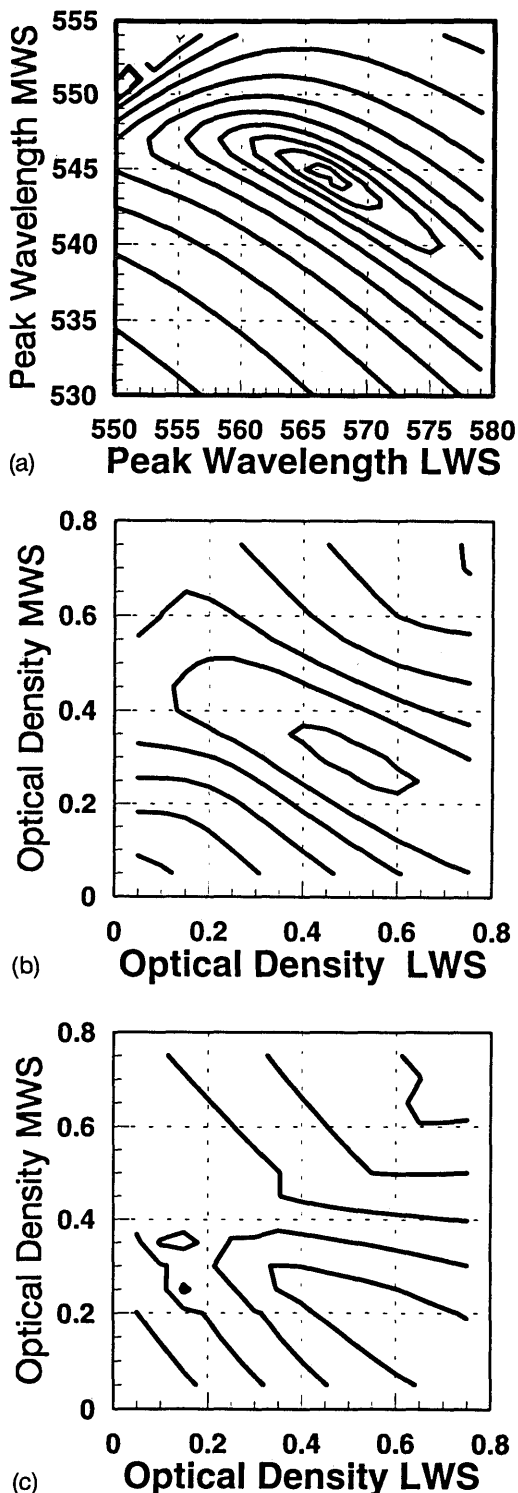


Fig. 3. Error contours generated by using a combined grid search and optimization technique. (a) The best-fit error as a function of the peak wavelength of the LWS and MWS photopigments for observer AE. (b) Error contours as a function of optical density for the two photopigments for observer AE. Thus these two panels represent the projection of the minimum error surface onto two planes of the parameter space for AE. We generated the contours by using a simplex routine to compute the best-fitting combination of the other two parameters for grid points and then by using the resulting SSE's to generate a contour map. The innermost contour on all plots is for an SSE of 0.0025, representing an average deviation of the model from the data of $\sim 0.014 \log(R/G)$. Each successive contour line represents a doubling of the SSE. (c) A contour plot on an optical-density grid for observer SB.

made a series of color matches to a 560-nm standard, using a 2-deg bipartite field. The long-wavelength primary, fixed for a given session, was 570, 589.6, 610, or 650 nm. The short-wavelength primary was 546 nm, and a dim 480-nm light overlaid the entire field to minimize contributions to the color match from short-wavelength-sensitive (SWS) cones or rods. Illuminance was varied from 3.4 to 5.4 log Td in 15 steps, with 10 color matches made by using the method of adjustment at each illuminance. To ensure that a steady state of photopigment concentration and neural adaptation for all retinal illuminances $>3.8 \log \text{ Td}$ was reached, the observer made matches for 3 min before any were collected as data. In a pilot study we determined that an adaptation period at lower illuminances had no effect on the data.

2. Results and Discussion

The shape of the curve relating color matches to retinal illuminance was independent of the long-wavelength primary. The color-matching data are plotted for each observer as symbols in Fig. 4. As the long-wavelength primary was increased from 570 to 650 nm, the color-match illuminance effect increased in size. That is, the change with illuminance in the $\log(R/G)$ increased as the wavelength of the long-wavelength primary increased. The solid curves in Fig. 3 are the same line for each condition, with only a change in the relative height and a vertical translation. Thus there is no systematic change in the shape of the color-match-illuminance effect with wavelength. This supports the idea that for the range of light levels tested there are no physical changes in cone morphology such that there are changes in spectral properties of waveguiding. If such changes are occurring, they must either be small or follow the same wavelength dependence as the optical density of the photopigments.

F. Experiment 3: Effect of Pupil Entry and Bleaching on Rayleigh Matches

To test directly or the effect of pupil entry on color matches, we varied the entry position of the color-matching field along a vertical axis. We were restricted to a vertical axis by the need to maintain the optical quality of the bipartite-field boundary⁹ (which was oriented vertically). Matches were made in one of two types of experimental session. In an illuminance session the Maxwellian-entry position was fixed, and color matches were made at a series of nine retinal illuminances ranging from 2.4 to 5.4 log Td. The observer made ten settings of the matching field at each retinal illuminance. In a pupil session the retinal illuminance was fixed at either 3.4 or 5.4 log Td, and the entry positions of the Maxwellian-view system were varied in the plane of the pupil. At 5.4 log Td, the entry position was alternated from a central (or, if possible, peak) entry position to a more peripheral entry position. This was done to maintain the retina in as bleached a state as possible because, for the entry positions far from the SCI peak, the maximum luminance of the color-matching apparatus was insufficient to maintain a full bleach (see Subsection F.1 below). It was not possible to change the entry position rapidly between individual settings because the bite bar positioner had to be moved while the pupillary image was compared with a calibration grid. The position of each observer's SC peak was estimated in two ways. First, we

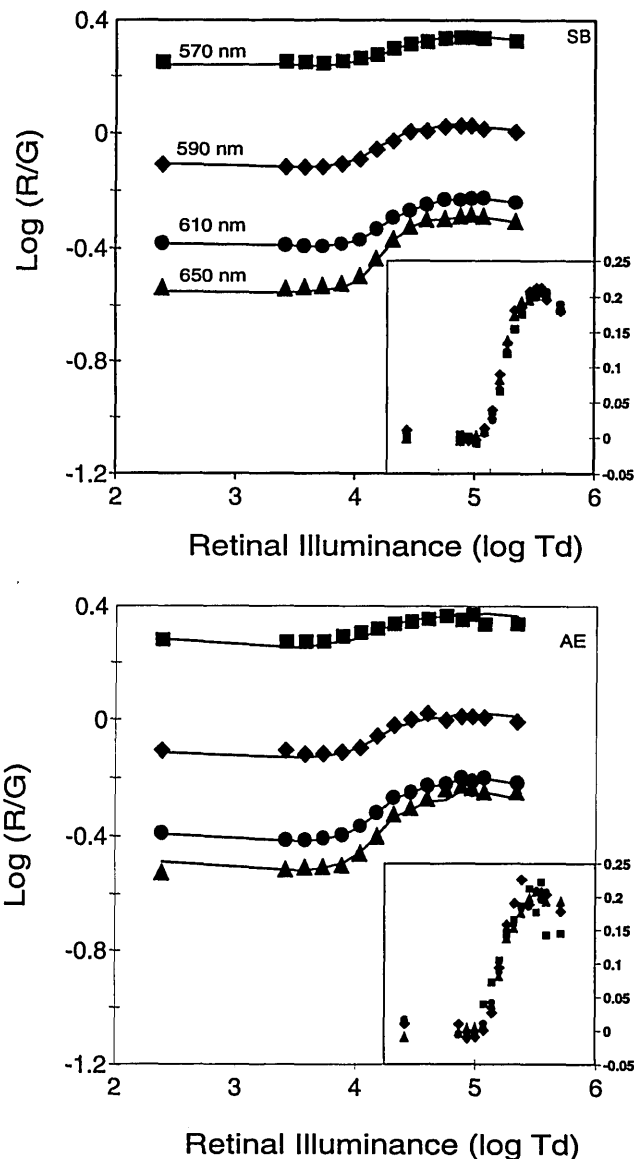


Fig. 4. Color matches for two observers as a function of retinal illuminance. All matches are to a 560-nm standard. The green primary was 546 nm, and the long-wavelength primary was 570 nm (squares), 590 nm (diamonds), 610 nm (circles), or 650 nm (triangles). The solid curves are the same curve scaled and drawn through the data for each wavelength (see text). The inset curves show the same data, except here the data have been scaled.

used a reflectometer capable of scanning the pupil³⁸ to determine the location of peak retinal reflectance.^{39,40} Second, each observer reported where he or she believed the vertical position of greatest luminosity was for the entry beam of the Maxwellian-view system. The two techniques agreed well. We also measured the SC effect of the first kind for two of the observers (SB and YC) over their entire pupils. The peak measured in this way agreed to within 0.5 mm with the peak position determined by using the reflectometric technique.³⁶

1. Results and Discussion

Changes in pupil entry had a significant effect on color matches at low but not high retinal illuminances. In the intensity runs, the half-bleach illuminance was lowest and the optical density highest when the matching fields entered near the peak of the SC effect (Fig. 5). For eccen-

tric pupil entry, as opposed to more central or peak entries, there is a high half-bleach illuminance and less effect of bleaching. The curves tend to converge for all pupil entries at high retinal illuminances. This is seen more clearly in Fig. 6, which shows data for four observers when the pupil position is varied within a session. At low retinal illuminances the color matches show a strong dependence on pupil entry position. However, at high retinal illuminances there is much less dependence on pupil position, with the curves being essentially flat except at the margins of the pupil. The data for these extreme pupil entry positions require relatively more green than red primary. This is the opposite result from that obtained at the low retinal illuminances. Perhaps full bleaching at extreme pupil entry positions did not occur. This possibility is supported by the data from the intensity runs, which show that the observers have not reached a high-illuminance asymptote at the eccentric pupil positions.

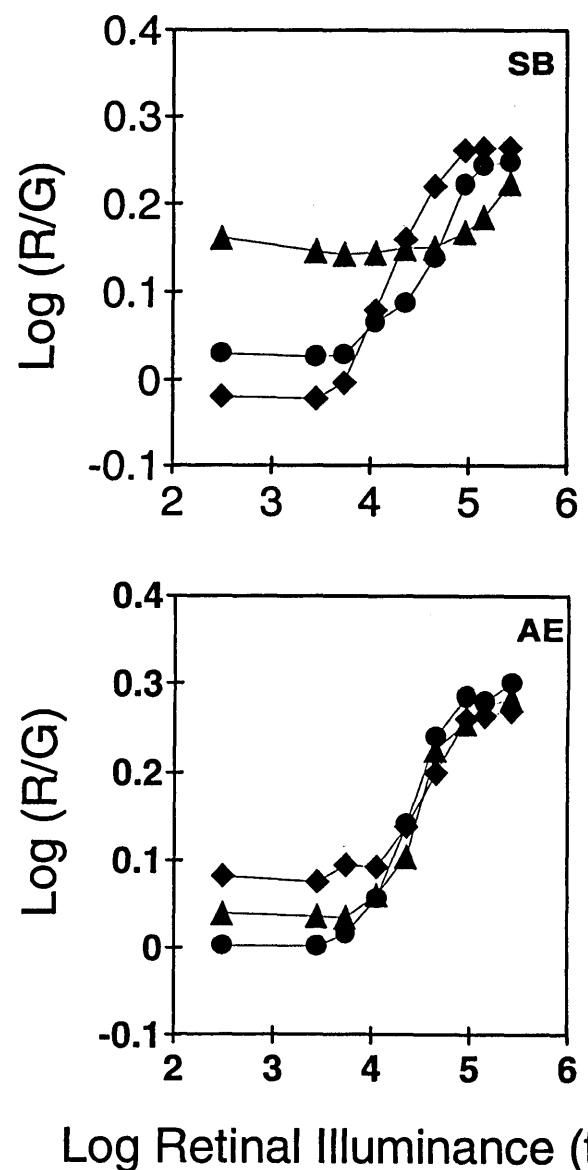


Fig. 5. Color matches as a function of retinal illuminance for two observers at three different pupil entry positions. Positions are 2 mm below the center of the dilated pupil (diamonds), in the center of the dilated pupil (circles), or 2 mm above the center of the dilated pupil (triangles). The two observers have different locations for their SC peaks.

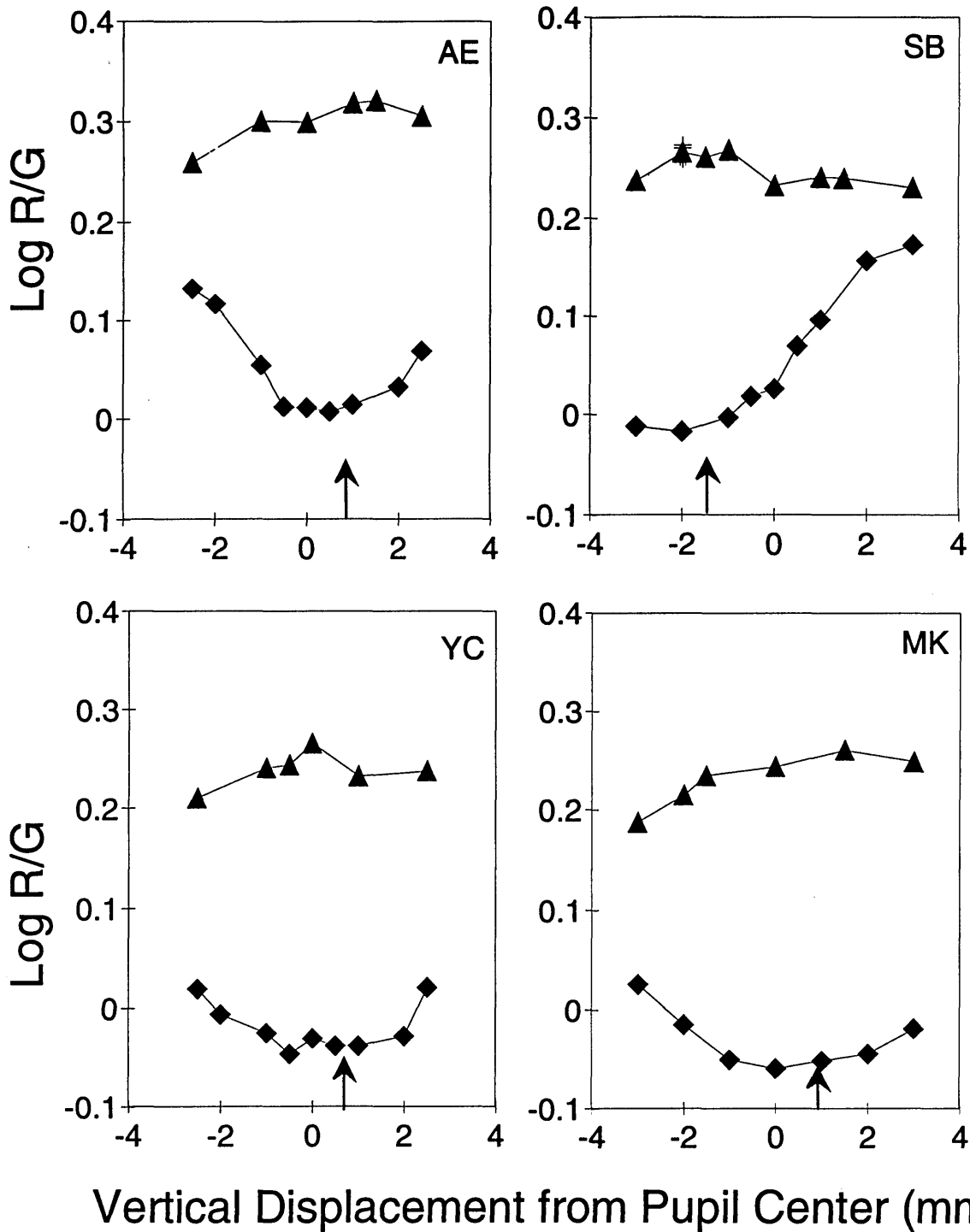


Fig. 6. Color matches as a function of pupil entry position along a vertical traverse of the pupil for four observers. Matches were made at either 3.4 log Td (diamonds) or 5.4 log Td (triangles). Arrows indicate the location of the peak of the SCI function along the vertical traverse as described in the text.

However, the intensity runs (Fig. 5) also show a slight tendency not to converge at high retinal illuminances. Thus there could be a slight SCII effect at high illuminances; however, it is small and of opposite effect from the low-illuminance SCII effect.

3. DISCUSSION

In experiment 1 we showed that the change in color matches that occurs with bleaching could be modeled by

only a change in the optical density of the photopigments. In addition, we showed that the differences between the normal observers can be modeled with only changes in optical density and slight shifts of the photopigment spectral sensitivities.^{3,4,13} In experiment 2 we showed that the shape of the change in color matches with retinal illuminance depends only on the physiological response of the retina to light (bleaching) and not on the physical composition of the stimulus. We previously showed that some of the details of this illuminance-dependent change are

consistent with densitometric measures of photopigment bleaching.^{10,12} In experiment 3 we showed that bleaching greatly reduces the size of the SCII effect. Taken together, these results support the idea that stimulus conditions that cause changes in color matches in the long- (>540 nm) wavelength portion of the visible spectrum do so by changing the effective optical density of the cone photopigments. That is, changes in Rayleigh color matches with changes of retinal illuminance, pupil entry, and field size¹⁰ occur because of changes in optical density. Thus one can adequately model color matches by applying Beer's law to suitable photopigment extinction spectra.

A. Stiles-Crawford II Effect

We find that the bleached peripheral pupil entry color matches require slightly less red light than do the central entry matches. Although we cannot rule out the possibility that this residual SCII effect is due to incomplete bleaching, a reverse SCII effect under bleached conditions agrees with some theoretical predictions of the SCII effect.²⁹ Thus there is a possibility that the residual dependence of color matches on pupil entry position is a true measure of wavelength-dependent waveguiding. The size of the effect is small compared with the variability of matching under these conditions. This residual SCII effect at high illuminances might explain the difference between our conclusions and those of Alpern *et al.*²² These authors performed full-spectrum color matches with different pupil entry positions for lights that did not bleach appreciable photopigment. They then evaluated the ability of self-screening models to describe the data. They rejected the self-screening model for a number of different choices of photopigment spectra. If there is a small residual waveguide effect under bleached conditions together with waveguide effects at shorter wavelengths, this could explain the difference between our conclusions and those of Alpern *et al.* It is not possible to determine the size of the discrepancy between the studies because their matches included short-wavelength components. It is possible that their effects are due to changes in waveguiding at short wavelengths. Combined with our results, this suggests that there may be spectral effects of waveguiding either at shorter wavelengths for the L and M cones or for the SWS cone in particular. Alternatively, Walraven⁴¹ has argued that the SCII effect at short wavelengths can be attributed to the scarcity of SWS cones because a smaller proportion of peripherally entering light will be caught by neighboring SWS cones.⁴²

B. Relation of Stiles-Crawford I and II Effects

Because the major source of change in color matches with pupil entry is changes in the effective optical density of the cones, a first-order model predicts that the change in optical density should predict the change in the SCI effect. That is, sensitivity and the effective optical density should be closely linked. The logic of this argument is that we see only the photons that are absorbed, and the number of these photons is determined by the effective optical density. This model predicts that, if an experimental manipulation changes the density of the photopigments from 0.3 to 0.15, the total quantal absorption will decrease from 50% ($10^{-0.3}$) to 30% ($10^{-0.15}$). The SCI effect actually measured is considerably larger than

that predicted from a change in optical density (see Fig. 5). Thus this simplistic model can be ruled out. A more realistic model must incorporate the fact that a psychophysical density estimate is an estimate of the average amount of pigment seen by the photoreceptors. If most of the light escapes the cones at the inner segment and is not seen by neighboring cones, then the optical-density estimate from psychophysics would not change. This model does not account for the data and disagrees with other studies.⁴² We find that the bleaching induces a change in $\log(R/G)$, from ~ 0.3 to ~ 0.06 with changes in pupil entry. This corresponds to a density decrease from 0.33 to 0.07⁴³ and requires a change of the half-bleach illuminance of 0.56 log unit. However, the half-bleach illuminance actually increases by 1.0 log unit. This implies that for peripheral pupil entry either a significant percentage of the light exits the cones and is not reabsorbed elsewhere or the light exits the inner segment before absorption. This result is complementary to the results of Chen and Makous,⁴² who showed that roughly half of the visually effective light for peripheral pupil entry positions is absorbed after leaving one cone and entering a neighbor.

C. Individual Differences in Optical Density

Several studies have reported that individuals vary in the optical density of their cone photopigments.^{5,10,14,30,44} Webster and MacLeod¹⁴ calculated that the optical density of all three cone photopigments covaried. Whereas our data do not test this notion directly (the fits from experiment 1 are not adequately constrained, and the number of observers is limited), the large effect of pupil-entrance position on optical density measured in experiment 3 suggests that individual variability in pupil entry could be a major factor contributing to individual variability in optical density.

D. Photopigment Extinction Spectra and Cone Absorption Spectra

A remaining question is whether waveguide effects are in any way involved in determining the spectral sensitivity of the LWS and MWS cones. That is, are the spectral sensitivities of the cones different from the density-corrected extinction spectra of the photopigments? The analysis of MacLeod and Webster⁶ supports the idea that they may be different. They propose that physiological techniques such as outer-segment recording³¹ and changes in color matches^{6,16,19} give a measure of the photopigment spectra (as opposed to the photoreceptor spectra) and produce spectral sensitivities shifted to slightly longer wavelengths than do more-classic psychophysical techniques. The current study cannot directly address this issue because we make a limited number of comparisons across conditions that change the spectral sensitivities of the cones. Trial research with the Wyszecki-Stiles fundamentals indicates that the fundamentals of DeMarco *et al.*³² fit our data slightly better, but the difference is not striking.

In addition, the analysis of DeMarco *et al.* indicates that their fundamentals are well fitted by the Schnapf *et al.*³¹ cone photopigment nomograms with only a slight shift in peak wavelength. Thus, whereas this experiment cannot rule out a role for the alteration of the cone spectral sensitivities by waveguiding, there is no evidence that there are large changes in spectral waveguiding over the range of

pupil entry positions and retinal illuminances used in this study.

4. CONCLUSIONS

In conclusion, we find that in the Rayleigh region of the spectrum changes in color matches with changes in retinal illuminance and with pupil entry can be accurately modeled as changes in the effective optical density of the cones. In addition, we find that differences in color matches between color-normal observers can be adequately modeled as differences in both optical density and wavelength of peak sensitivity of the LWS and MWS cone photopigments.

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