

Matching rod percepts with cone stimuli

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Abstract

Traditional methods for studying the effects of rod activity on color vision make it hard to assess the underlying physiological mechanisms. In this study, rod-mediated changes in color appearance were assessed by matching them with cone-mediated color changes. A four-primary photostimulator allowed independent control of rod and cone stimulation and identification of the cone types that generate color sensations equivalent to rod color sensations. The results showed that increases in rod stimulation required matches with cone stimuli that excited *M*-cones more than *L*-cones for all conditions. Matches for low-luminance conditions also required some *S*-cone stimulation. A subsidiary experiment showed that increases in rod modulation of an inducing field produced chromatic contrast effects like those produced by the *M*-cone system. The data are consistent with a hypothesis of perceptual normalization of scotopic vision to the chromatic appearance of objects under photopic conditions.

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1. Introduction

The traditional methods for studying rod influence on color vision assess changes in either color appearance or chromatic discrimination associated with variation in rod activation (reviewed by Buck, 2004), or to assess how color mixture data are altered by changes in rod activity (reviewed by Shapiro, Pokorny, & Smith, 1994). In this study we used a photostimulator with four primary lights that allowed independent control of the stimulation of the 4-receptor types in the human eye (Pokorny, Smithson, & Quinlan, 2004; Sun, Pokorny, & Smith, 2001a; Sun, Pokorny, & Smith, 2001b). Appearance changes associated with modulation of rod excitation with cone excitation held constant were matched by adjusting cone excitations with rod excitation held constant. This color-matching procedure equa-

ted the appearance of rod-mediated and cone-mediated color changes, but did not rely on how the stimuli looked.

1.1. Color percepts associated with rod activity

The color associated with rod stimulation varies with stimulus conditions. Nagel (1924) provides an elegant description of early experiments documenting that visual stimuli below cone threshold appear bluish. This has been confirmed in more recent work (Buck, 2004). When both rods and cones are active at mesopic light levels, rod activation has been reported to alter all three attributes of color perception; that is, hue, saturation and brightness. A consistent finding has been that rod stimulation enhances brightness (Benimoff, Schneider, & Hood, 1982; Ikeda & Shimozone, 1981) and decreases saturation of spectral lights (Buck, Knight, Fowler, & Hunt, 1998; Lythgoe, 1931; Nerger, Volbrecht, & Haase, 2003; Stabell & Stabell, 1975). Reports in the

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literature on the effect of rod stimulation on hue are less consistent and sometimes contradictory (reviewed by Buck, 2004).

The color percepts associated with rod stimulation have been studied by two methods, unique hue measurements and hue scaling. Differences in the wavelengths associated with the unique hues (red, green, blue and yellow) measured for dark-adapted and cone-plateau conditions or between foveal and parafoveal retinal locations have been used to characterize the modification in color appearance due to rod stimulation (Buck et al., 1998; Nerger, Volbrecht, & Ayde, 1995; Nerger, Volbrecht, Ayde, & Imhoff, 1998). The rationale for comparing the measured unique or scaled hues between the dark adapted and cone-plateau conditions is that rods are fully sensitive after 30 min dark adaptation but are insensitive following adaptation to a bright light. In a similar vein, unique hues have been measured in the parafovea where the density of rods is high and in the fovea where there are few or no rods. Hue and saturation scaling (Buck et al., 1998; Nerger et al., 2003) have been used as response measures with comparable manipulations of adaptation state or retinal locus.

While appearance studies offer important insights into the perceptual consequences of variation in rod input, these experimental designs do not yield results that can be readily understood in terms of underlying physiological mechanisms. Interpretation is complicated by the fact that single hue sensation may not be associated with a given cone type (Knoblauch & Shevell, 2001). For example, in a variety of stimulus situations, *M*-cone stimulation can yield a bluish perception (De Valois, De Valois, Switkes, & Mahon, 1997; Drum, 1989a, 1989b; Schirillo & Reeves, 2001). A change in hue percept accompanying a change in rod activation cannot readily be interpreted in terms of the rod signaling a chromatic percept associated with one or another of the cone types.

1.2. Alterations in color mixture data associated with rod activity

Grassmann (1853) outlined the conditions that allow treatment of color mixtures as a linear system. Foveal color matches of color-normal observers obey Grassmann's laws (additivity, scalar invariance and substitution of metamers), and can be characterized as being photopigment-limited. Dichromatic observers, however, can show similar trichromatic behavior. For large viewing fields and dim to moderate light levels, protanopes, deuteranopes and tritanopes all make unique trichromatic matches that are invariant with changes in light level. The matches are consistent with rods acting as a third, independent color vision mechanism (Pokorny, Smith, & Went, 1981; Smith & Pokorny, 1977). For the same stimulus conditions, color-normal observers

make trichromatic matches but the primary proportions change with changes in light level: a violation of Grassmann's scalar property. The changes in the primary proportions with variation in light level (Richards & Luria, 1964; Stiles, 1955) are consistent with rod signals adding to *S*-cone signals and, to a lesser extent, to *M*-cone signals.

1.3. Rod pathways

Anatomical and single-unit electrophysiological studies of the primate retina have shown that rods and cones do not have separate neural pathways to the brain; rather, they share the pathways with joint inputs to the retinal ganglion cells (literature reviewed by Sun et al., 2001b). The postreceptoral neurons conveying rod information have been ascribed to two primary pathways, one via ON rod bipolars, amacrine II cells, and ON and OFF cone bipolars, a high gain pathway hypothesized to mediate rod vision at low light levels. The second pathway transmits rod information via rod-cone gap junctions and ON and OFF cone bipolars, and is hypothesized to mediate rod vision at high scotopic and mesopic light levels (reviewed by Daw, Jensen, & Bunken, 1990; Sharpe & Stockman, 1999). Physiological recordings at mesopic light levels revealed strong rod inputs to the Magnocellular pathway, but weak rod inputs to the Parvocellular or Koniocellular pathways (Gouras & Link, 1966; Lee, Smith, Pokorny, & Kremers, 1997; Virsu & Lee, 1983; Virsu, Lee, & Creutzfeldt, 1987; Wiesel & Hubel, 1966).

1.4. Rationale of the study

For reasons outlined above, the classical methods used to study rod inputs to color vision do not yield results that are easily interpreted in terms of underlying physiological mechanisms. In this study, we matched the change in color appearance of a field associated with increased rod stimulation presented in one temporal epoch with changes in cone activations presented in a second epoch. We used two very different stimulus geometries, a parafoveal center-surround stimulus pattern for related colors (a stimulus field viewed in relation to other chromatic stimuli), and a foveally centered annulus pattern for unrelated colors (a stimulus field viewed completely in isolation). The shared attributes of the data likely reveal fundamental aspects of rod vision. We found that cone excitation stimuli matched to an increment in rod stimulation required more *M*-than *L*-cone excitation for all conditions tested. Under a limited set of conditions, matches also required more *S*-cone excitation.

The second purpose of this study was to study chromatic contrast with rod-inducing stimuli. We are not aware of any study investigating chromatic contrast

with rod-inducing stimuli. This is likely due to the limited ability of conventional methods to independently isolate or modulate each type of photoreceptor. For instance, scotopic contrast has been studied by measuring the color induced in a field that can be detected only by rods with chromatic cone inducing stimuli (e.g. Buck, 1997; McCann & Benton, 1969; McKee, McCann, & Benton, 1977; Stabell & Stabell, 1978; e.g. Willmer, 1949). Using the four-primary system, Sun et al. (2001a, 2001b) measured brightness induction from rods. It is of interest whether rod-inducing stimuli produce chromatic contrast. In the second experiment we measured the color appearance of a field using rod inducing stimuli.

The data reported here were collected using a four-primary photostimulator that allowed independent control of the stimulation of the rods and the three cone types. When changing chromaticity with monochromatic or three primary stimuli, it is possible to control either scotopic or photopic luminance but not both. The four-primary photostimulator overcomes this obstacle and allowed us to manipulate chromaticity while simultaneously controlling both rod and cone retinal illuminance levels.

2. Experiment 1

2.1. Methods

2.1.1. Apparatus

The photostimulator (Pokorny et al., 2004) was a colorimeter that used Light Emitting Diodes (LEDs), with light levels controlled by drivers that included voltage-to-frequency converters providing 1- μ s pulses at frequencies up to 250 kHz. The center and surround were each created with the combination of four primary channels, with light from four LEDs combined by use of a fiber optic assembly. Four fiber optic bundles were merged into a single bundle with the output fed into a spatial homogenizer terminated by a diffuser. Spectral composition was controlled by the LED spectra and interference filters sandwiched between each LED and the fiber optic bundle. The primary wavelengths for both center and surround were 460, 516, 558 and 660 nm, all with half-bandwidths of about 10 nm. Two camera lenses collimated light from the diffusers, one for the center and one for the surround. A photometric cube with a mirrored ellipse on the hypotenuse formed the center-surround field configuration. A field lens placed images of the diffusers in the plane of an artificial pupil for Maxwellian viewing. The field image was viewed at an apparent distance of one meter. A Macintosh Quadra 950 computer and four National Instruments (Austin, TX) interface boards provided 12 bit control of the photostimulator primaries.

2.1.2. Observer calibration

The cone stimuli were specified in a relative cone-rod space (Smith & Pokorny, 1996) based on the 10° Standard Observer (Shapiro, Pokorny, & Smith, 1996). To use the Standard Observer defined receptor sensitivities for an individual observer we employed an observer calibration procedure that compensated for pre-receptor filtering differences between the observer and the Standard observer as well as correcting for variation in color-normal observer receptor spectral sensitivity (Pokorny et al., 2004; Sun et al., 2001a, 2001b). At the same peripheral location of the central field as for the main experiments, the observer made a photopic color match between two successively presented displays, one containing a mixture of the 460 and 558-nm lights, the other a mixture of the 516 and 660-nm lights. The 558-nm primary served as the reference, and the observer made a match by varying three parameters; the luminance of the 460-nm light, the luminance ratio of the 516 and 660-nm lights, and the combined luminance of the 516 and 660-nm lights. By comparing the relative radiances of the four lights required by the individual with the values theoretically required by the CIE (1964) 10° Standard Observer, the difference in sensitivity between the individual and the Standard Observer at the wavelengths of our primaries could be estimated. This method assumes that an individual observer's spectral sensitivities at the primary wavelengths do not differ significantly from linear transforms of the Standard Observer color matching functions. Pokorny et al. (2004) showed by calculation that the variation in spectral location of the L-cone spectral sensitivity associated with the common L-cone (A180) and (S180) polymorphism (Sharpe et al., 1998) results in error in receptor isolation of less than 2%. Thus the Observer Calibration Procedure can compensate for receptor spectral sensitivity variation as well as correcting for individual pre-receptor differences.

2.1.3. Stimuli

We evaluated the effect of increased rod excitation on field appearance for two stimulus situations, one for related colors (a stimulus field viewed in relation to other chromatic stimuli) and the second for unrelated colors (a stimulus field viewed completely in isolation). A center-surround pattern (Fig. 1, upper left panel) was used for related colors; an annulus pattern (Fig. 1, lower left) for unrelated colors.

The center-surround pattern consisted of a 2° circular central field within a 10° annular surround. The observer fixated on a small, dimly-illuminated achromatic appearing spot placed at 6° in the temporal retina. The cone excitations in the center and surround were kept identical, with the rod signal in the center being incremented in a 1-Hz temporal square-wave function. The temporal profile of the rod modulation

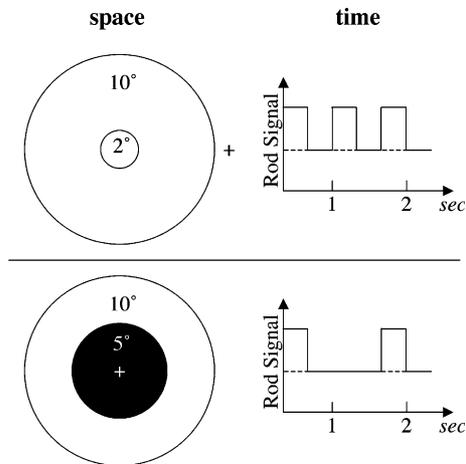


Fig. 1. The spatial structures and temporal profiles of the center-surround pattern (upper) for related colors and the annulus pattern (lower) for unrelated colors. The “+” sign indicates the location of the fixation point in each pattern.

with the center-surround pattern is shown in the upper right panel in Fig. 1. During the half-cycle with high rod modulation the center field differed in appearance from the surround; while during the half-cycle with low rod modulation (with no difference in rod excitations between the center and surround) the center and surround combined to produce a large uniform appearing field.

For the 5–10° annulus pattern, the fixation point was presented at the center. The rod signal was modulated as a step function, with a cycle of 2 s with the rod signal incremented during the first 0.5 s. The temporal profile of the rod modulation is shown in the lower right panel in Fig. 1.

For both stimulus patterns, data were collected for six cone chromaticities at 7 retinal illuminances: 1, 2, 10, 20, 40, 80 and 160 photopic Td. For all chromaticities and light levels, the baseline rod trolands (Shapiro et al., 1996) maintained a constant relationship to the cone trolands:

$$\text{Rod Td} = 0.85(\text{Cone Td})$$

Fig. 2 shows the cone chromaticities in the relative cone-troland space. The dashed lines enclose the gamut of photostimulator chromaticities with at least 50% Weber rod contrast. For all stimulus conditions the rod increment was set to a 35.3% Weber rod contrast [Weber contrast = $(1.15 - 0.85)/0.85 = 35.3\%$]. The rod contrast was restricted to 35.3% so that the adjustments required for the cone matches remained within the photostimulator gamut.

In a separate control experiment we evaluated the adequacy of rod isolation by viewing the stimulus field following 2 min of light adaptation to an 80,000 Td broadband light. For both stimulus patterns, 40% rod modulation was not visible in the first 4–5 min following

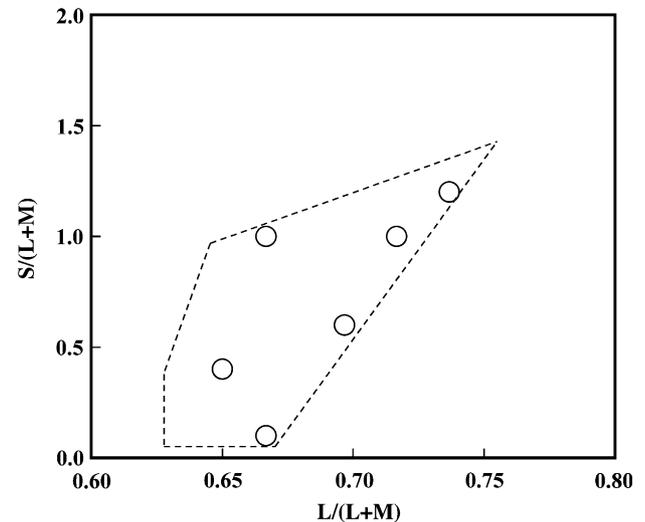


Fig. 2. The stimulus chromaticities in the relative cone-troland space. Dashed lines indicate the gamut of 50% Weber rod contrast within the four-primary colorimetric system.

extinction of the adaptation light, confirming rod isolation.

2.1.4. Procedure

In a single session, the observer first dark-adapted for 30 min. Then matches were made for one stimulus pattern and one light level. Each of the six chromaticities was presented twice using a random presentation order. For the center-surround pattern, the change in color appearance of the center was characterized by a temporal matching technique, in which the observer adjusted the cone signals $[L/(L + M), S/(L + M)$ and $(L + M)]$ of the center during the matching epoch to equate the rod percept seen during a stimulus epoch. The observer could toggle freely between the stimulus epoch, in which rod signal was modulated in a 1-Hz square-wave, and the matching epoch, in which the cone signals were modulated in a 1-Hz square-wave with observer control of the cone modulation depths. There was no cone modulation during the stimulus epoch, and no rod modulation during the matching epoch. For the annulus pattern, the first 0.5 s served as the stimulus epoch in which the rod signal was incremented; the following 1.5 s served as the matching epoch in which the observer adjusted cone excitations to match the color appearance of the annulus in the stimulus epoch. For both patterns, the observer could adjust the cone stimuli during the matching epoch with a joystick. The joystick was programmed so that control was analogous to orthogonal directions in a MacLeod–Boynton type chromaticity diagram: Horizontal manipulations varied $L/(L + M)$; vertical manipulations varied $S/(L + M)$, all at a constant illuminance. Retinal illuminance could be adjusted using a pair of switches on the joystick. A confirmation button signaled a satisfactory match, followed by the

next chromaticity. Each session was replicated three times on different days. The mean and standard error over the three days for each chromaticity and light level were calculated.

2.1.5. Observers

The observers were two authors, *DC* and *JP*, both experienced psychophysical observers with normal color vision (assessed by the Neitz OT anomaloscope and Farnsworth–Munsell 100-hue test). No measurements were made at 1 Td for *JP* because rod modulation did not alter the test field appearance at this light level.

2.2. Results

2.2.1. The center-surround pattern for related colors

The matching results in the relative cone-troland space with the center-surround pattern at 2 and 10 Td for both observers are shown in Fig. 3. In this Figure, open circles represent the stimulus chromaticities and solid circles represent the matching chromaticities. The arrows connect the stimulus chromaticities and their corresponding matching chromaticities. To provide the reader with an idea of the gamut of chromaticities employed in this experiment, we present the data on a cone chromaticity diagram that includes the regions covered

by eight basic colors: red, green, blue, yellow, orange, pink, purple and white (Cao, Pokorny, & Smith, in press). Each region was defined by the centroid OSA-UCS L, j, g values for each non-dark appearing basic color from Boynton and Olson (1987) and is represented by an ellipse with a fill color representative of its basic color.

At 2 Td (Fig. 3, left panels), increased rod excitation shifted the matching chromaticities to the upper left relative to the stimulus chromaticities in the diagram. The chromaticity shifts caused by the incremental rod excitations were relatively small: no shifts were across color categories. At 10 Td (right panels), the shifts were toward left. The magnitudes of the shifts at 10 Td were smaller than those at 2 Td.

To characterize the effect of rod stimulation on the L/M -cone channel and S -cone channel separately, we plotted the matching $L/(L+M)$ versus the stimulus $L/(L+M)$ (Fig. 4, left panels) and the matching $S/(L+M)$ versus the stimulus $S/(L+M)$ separately (right panels). The data on Fig. 4 are the matching results at 2 Td. In each panel, a 45-deg dashed line indicates no effect of rod stimulation. The matching $L/(L+M)$ was smaller than, but linearly related to the stimulus $L/(L+M)$. A regression line was fitted for the matching $L/(L+M)$ on the stimulus $L/(L+M)$. For

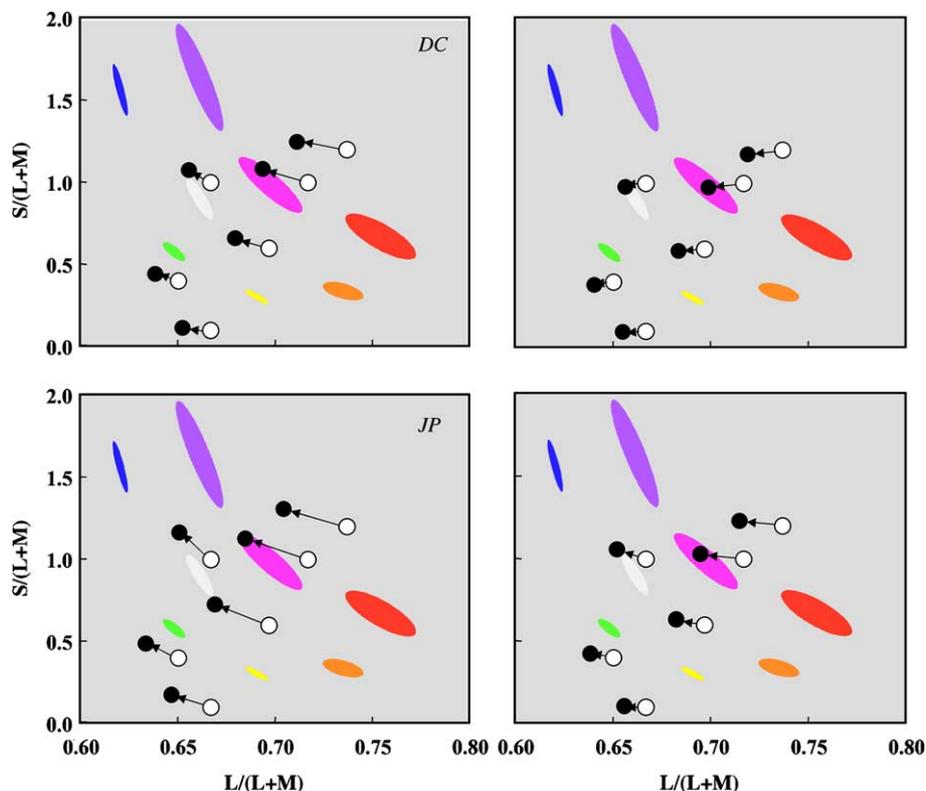


Fig. 3. The matching results at 2 Td (left column) and 10 Td (right column) with the center-surround pattern. The ellipses show the regions of eight non-dark appearing basic colors in the cone chromaticity space defined by the centroid L, j, g values of the basic colors from Boynton and Olson (1987) (see text for details). Upper: for *DC*. Lower: for *JP*.

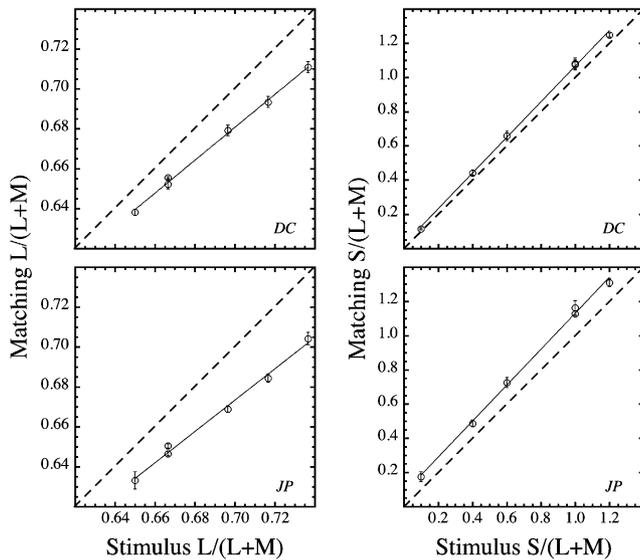


Fig. 4. The matching $L/(L + M)$ versus the stimulus $L/(L + M)$ (left column) and the matching $S/(L + M)$ versus the stimulus $S/(L + M)$ (right column) at 2 Td with the center-surround pattern. Upper: for DC. Lower: for JP.

the regression, the $L/(L + M)$ chromaticity of the EES (0.667) was subtracted from the matching or stimulus $L/(L + M)$. The fitted intercept and slope at 2 Td was -0.013 and 0.825 for DC, or -0.019 and 0.785 for JP, respectively. At 2 Td, the matching $S/(L + M)$ was larger than, and was linearly related to the stimulus $S/(L + M)$. The fitted intercept and slope of the matching $S/(L + M)$ on the stimulus $S/(L + M)$ was 0.023 and 1.043 for DC, and 0.077 and 1.053 for JP, respectively.

The fitted intercepts and slopes of the matching $L/(L + M)$ [or $S/(L + M)$] on the stimulus $L/(L + M)$ [or $S/(L + M)$] at all light levels are shown in Fig. 5. In the Figure, the left and right columns show the fitted parameters for $L/(L + M)$ and $S/(L + M)$, respectively. In each panel, the left and right ordinates represent the fitted intercepts and slopes respectively. A positive intercept and a slope larger than or equal to one indicate that the matching value is larger than the stimulus value. On the other hand, a negative intercept and a slope less than or equal to one indicate the matching value is less than the stimulus value. Left- and right-dashed arrows in the Figure indicate a zero intercept and a unit slope, respectively. For $L/(L + M)$, the fitted intercepts were always negative while the fitted slopes were less than one for both observers, indicating that the matching $L/(L + M)$ is less than the stimulus $L/(L + M)$ at all light levels. Secondly, with an increase in light level, the fitted intercept was closer to zero and the fitted slope was closer to one, indicating decreasing shifts with increasing light level. For the $S/(L + M)$, the fitted intercept was positive and the fitted slope was larger than one only at 1 or 2 Td, indicating that the matching $S/(L + M)$ is larger than the stimulus $S/(L + M)$ only at 1 or 2 Td.

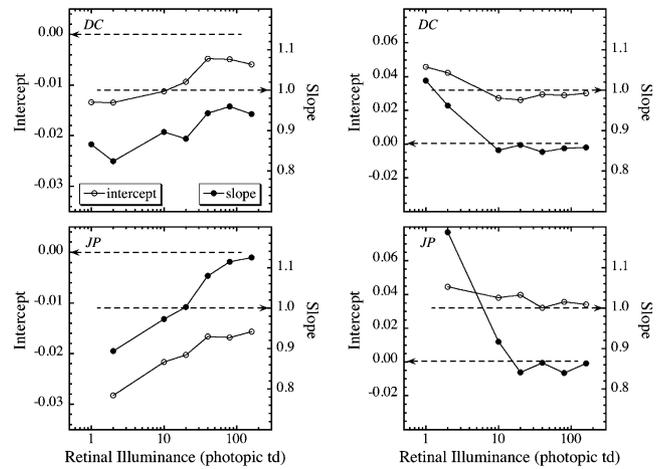


Fig. 5. The fitted intercepts and slopes at different light levels with the center-surround pattern. In each panel, the intercepts and slopes are represented by the left and right vertical axes, respectively. Left and right dashed arrows indicate a zero intercept and a unit slope. The results for $L/(L + M)$ are shown in the left column and for $S/(L + M)$ in the right column. Upper: for DC. Lower: for JP.

At light levels higher than 2 Td, the fitted intercept was close to zero and the fitted slope was close to one, indicating no difference between the matching $S/(L + M)$ and the stimulus $S/(L + M)$.

Since the matching cone Weber contrast [(matching illuminance – stimulus illuminance)/stimulus illuminance] was similar for all of the cone chromaticities at each light level, average cone Weber contrasts are shown in Fig. 6. At 2 Td, the average matching cone Weber contrast was 11% to match the 35.3% rod Weber contrast for DC, and was 24% for JP. For both observers, the matching cone Weber contrasts decreased exponentially with the light level.

2.2.2. The annulus pattern for unrelated colors

Fig. 7 shows the annulus pattern fitted intercepts and slopes at various light levels. Similar to the results with the center-surround pattern, the fitted intercept of the

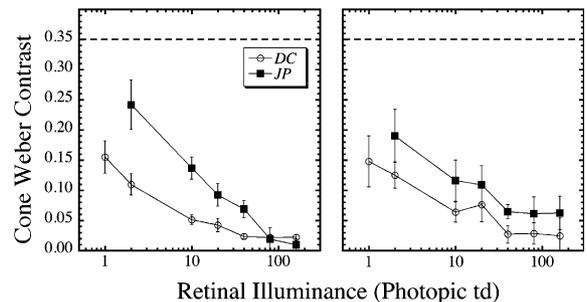


Fig. 6. The cone Weber contrast [(matching illuminance–stimulus illuminance)/stimulus illuminance] required to match a 35.3% rod Weber contrast (indicated by the dashed lines) with variation in light level. The left panel shows the results for the center-surround pattern and the right panel for the annulus pattern.

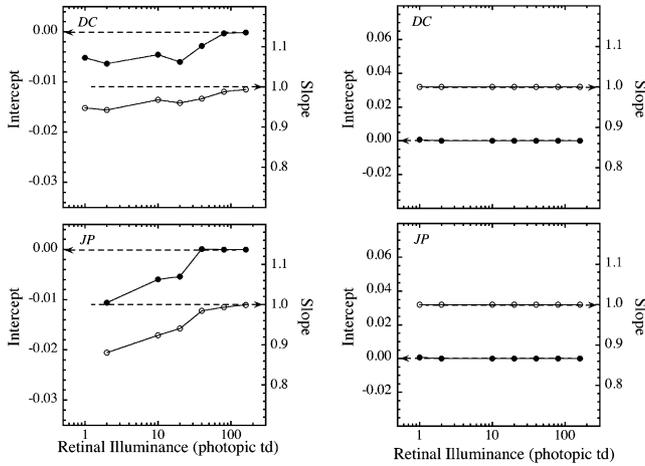


Fig. 7. Same as Fig. 5, with the annulus pattern.

relative matching $L/(L + M)$ on the relative stimulus $L/(L + M)$ was negative while the fitted slope was less than one, indicating that the matching $L/(L + M)$ was smaller than the stimulus $L/(L + M)$ at all light levels. The shift in $L/(L + M)$ decreased with increasing light level. Compared with the results with the center-surround pattern, the fitted intercept was closer to zero and the fitted slope was closer to one at the same light level, indicating the shift in $L/(L + M)$ was weaker with the annulus pattern. The fitted intercept of the matching $S/(L + M)$ on the stimulus $S/(L + M)$ was close to zero and the fitted slope was close to one, indicating a negligible shift in $S/(L + M)$ at all light levels.

The cone Weber contrast data for the annulus pattern were very similar to those with the center-surround stimulus pattern (Fig. 6). That is, for both stimulus configurations, the matching cone Weber contrast decreased exponentially with increasing illuminance level.

3. Experiment 2

3.1. Methods

Experiment 2 employed the same center-surround pattern as in Experiment 1 but here the rod excitation in the surround field rather than the center field was modulated in a 1-Hz square wave function. The color appearance of the center was matched with variation in the center field cone excitations using the same technique as in Experiment 1, i.e. the temporal matching, which allowed the observer to toggle between the stimulus and matching epochs freely. Data are reported for two (or three) retinal illuminances: 2, 10 and 20 Td. Observer JP reported a reddish center in the stimulus epoch at 2 Td, but he could not make satisfactory matches due to the gamut limit of the photostimulator. No color changes were seen above 20 Td.

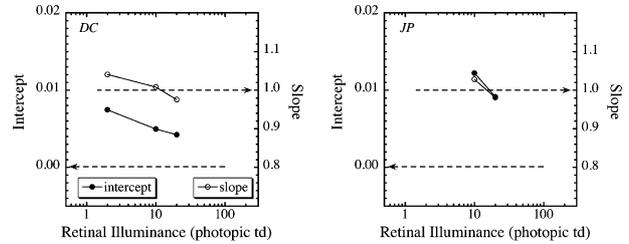


Fig. 8. Intercepts and slopes for $L/(L + M)$ for Experiment 2. Data format is the same as for Fig. 5.

3.2. Results

The fitted intercepts and slopes of the matching $L/(L + M)$ on the stimulus $S/(L + M)$ at 2, 10, and 20 Td are shown in Fig. 8. The matching $L/(L + M)$ was always larger than the stimulus $L/(L + M)$ at all light levels. Further, the higher the light level, the weaker the shift in $L/(L + M)$ caused by rod inducing stimuli. Neither observer needed to change $S/(L + M)$ to make the matches (data are not plotted). Finally, the matching illuminance was always lower than the stimulus illuminance, indicating that the rod-inducing stimuli made the center appear darker. For DC, the relative decrements in illuminance [(matching illuminance – stimulus illuminance)/stimulus illuminance] were 9%, 4% and 2% at 2, 10 and 20 Td, respectively. For JP, the relative decrements in illuminance were 13% and 10% at 10 and 20 Td, respectively.

4. Discussion

For both stimulus patterns in Experiment 1, the matching $L/(L + M)$ was smaller than the stimulus $L/(L + M)$. This finding indicated that rod signals were interpreted as M -cone signals. Schirillo and Reeves (2001) reviewed studies that show that, depending on stimulus conditions, M cone activity may be associated with both “green” and “blue” percepts. The rod contribution to a “green” percept is consistent with unique yellow and hue scaling data (Buck, Knight, & Bechtold, 2000; Nerger et al., 1998).

In a context different from ours, McCann and Benton (1969) reported data on matching rod percepts with cone stimuli. They found that a variety of color sensations can be achieved under conditions in which only the rods and the long-wave cones are responding. A complex multicolored scene was illuminated with 546 and 656 nm lights, with the radiance of 546 nm light set so that it was above threshold for only the rods. The 656 nm light was above threshold for the L -cones and the rods. The colors seen were reds, yellows, blue-greens and grays. They asked observers to alternate eyes to compare rod-cone colors with cone-cone colors, and

searched for the cone stimuli that yielded the same color percepts equal as seen in the rod-cone condition. McCann and Benton reported the color sensations produced by rods and long wavelength cones were comparable to those produced by 656 and 495 ± 4 nm lights. In the cone excitation diagram, 495 nm plots on the spectrum locus just above the abscissa. A line connecting 656 and 495 nm is only slightly inclined from horizontal, a result, concordant with the present findings (the expectation from the rod signal being interpreted as an *M*-cone stimulus is a horizontal line).

For both stimulus patterns, the rod contribution to both the *M*-cone system and brightness decreased with increases in light level. There were likely two mechanisms contributing to this, one concerning the adaptational state of the two systems and the second via an interactive process. Over the majority of the range of light levels employed here, the rod system exhibits Weber adaptation (Aguilar & Stiles, 1954) while the cone system shows sub-Weber behavior (Mueller, 1951). At mesopic light levels cone stimulation can inactivate the rod system (Shapiro, 2002; Stabell & Stabell, 1996; Stabell & Stabell, 1975).

There were two differences in the results for the annulus and center-surround stimulus patterns. First, the shifts in $L/(L + M)$ with the annulus pattern for unrelated colors were smaller than those with the center-surround pattern for related colors. Second, the matches required higher $S/(L + M)$ at 1–2 Td only with the center-surround pattern, but not for the annulus pattern. The characteristics of the stimuli at the endpoints for the two paradigms are quite different. For the related colors, the observer toggled between two temporally modulated stimuli, one with rod contrast, the second with cone contrast. Thus the match was made under conditions where spatial and temporal contrasts were present. For the unrelated colors, the observer adjusted the cone stimulus with the objective of producing a steady appearing field with no temporal alternation. The differences in spatio-temporal contrast between the two patterns may be related to the observation that in detection experiments, rod-cone interactions can be greater for transient than for steady conditions (e.g. Buck, Stefurak, Moss, & Regal, 1984; Ingling, Lewis, Loose, & Myers, 1977).

The results in Experiment 2 indicated the rod hue in the annulus could produce chromatic contrast in the center. Rod inducing stimuli caused the test field to appear darker, and required more *L*- than *M*-cone excitation. This indicated that the rod contribution to the chromatic signals occurred before the neural locus of chromatic contrast. Although we can infer the sequence of processing rod input and induction, our results do not offer insight as to the locus of chromatic contrast.

The mechanism by which rod stimulation contributes more to the *M*-cone system than the *L*-cone system is

unclear. The data of this study were collected at mesopic light levels where rod information has been hypothesized to be conveyed by the rod-cone gap junction pathway (Daw et al., 1990; Sharpe & Stockman, 1999). Assuming rods have input to both *M*- and *L*-cones via gap junctions, then the average *L/M* ratio of about 2:1 might bias the rod weighting in chromatic opponent receptive fields. To test this possibility, we located individuals with unbiased *L/M* cone ratios and measured their cone matches to rod increments. Using heterochromatic modulation photometry (Pokorny, Smith, & Lutze, 1989), we identified two observers with *L/M* cone ratios that differed from the observers in Experiment 1. Observer *ML* (female) had *L/M* cone ratio of 0.58. Observer *PL* (male) had a *L/M* cone ratio of 1.28. Observers *DC* and *JP*, the authors, had *L/M* cone ratios of 2.42 and 2.28, respectively. The differences in these estimated *L/M* ratios are of sufficient magnitude that the second-order variation in cone ratio estimation associated with photopigment polymorphism and other prereceptoral and receptor factors (<19% of the flicker photometric variance, Pokorny, Smith, & Wesner, 1991) would not alter the conclusion that one of the observers has a preponderance of *M*-cones (Observer *ML*), two had a preponderance of *L*-cones (Observers *DC* and *JP*) and the fourth a more nearly balanced *L/M* ratio (Observer *PL*). We measured cone matches to rod modulation with the center-surround pattern at 10 Td for *ML* and *PL*, using the same stimulus chromaticities as in Experiment 1. The matching results for these observers were comparable to those reported earlier for the other two observers: the matching $L/(L + M)$ was smaller than the stimulus $L/(L + M)$; and the matching $S/(L + M)$ was very close to the stimulus $S/(L + M)$. The fitted intercept and slope of the matching $L/(L + M)$ on the stimulus $L/(L + M)$ were -0.010 and 0.852 for *ML*, -0.009 and 0.906 for *PL*, -0.011 and 0.897 for *DC*, and -0.013 and 0.867 for *JP*, respectively. In other words, the cone chromaticity matched to rod modulation did not depend on the observer's *L/M* cone ratio. Thus, we ruled out the possibility that the source of selective *M*-cone input from rod activation arose from the biased *L/M* cone ratios.

4.1. A hypotheses based upon perceptual normalization

With decreasing light level, human vision maintains a perceptual stability through the transition between daylight and twilight conditions. Real world objects, with broad reflectance spectra, do not abruptly change color with diminution in light level, rather there is a gradual decrease in saturation and color gamut. Several studies demonstrate rudimentary color vision for colored papers under scotopic illumination conditions (Ishida, 2002; Middleton & Mayo, 1952; Schneider & von Campenhausen, 1998; Shin, Yaguchi, & Shioiri, 2004). "Scotopic color vision" arises because the photochromatic

interval is small to non-existent for long wavelength lights, even at threshold (Wald, 1945). Objects in the natural environment have broad spectral reflectance functions and may be distinguished by differences in rod and L -cone activation.

As previously noted, at mesopic light levels rod signals are hypothesized to be conveyed through cone pathways via the rod-cone gap junctions. Thus rods feed indiscriminately into the centers and surrounds of M – L and L – M receptive fields. Under dim light conditions where the M -cone is below threshold, for broadband stimuli, the rods signal greenness in M – L units and combine with L -cone activity signaling redness in L – M units. If the visual system normalizes responses to maintain a chromatic gamut congruous with what is seen under photopic conditions, then rod signals would be interpreted as including some greenness. The mechanisms responsible for the normalization may be comparable to the chromatic red–green normalization of observers with very different ratios of L - to M -cones. The wavelength of unique yellow varies only slightly between observers (Brainard et al., 2000; Pokorny et al., 1991). The perceptual normalization hypothesis maintains that the spectral position of unique yellow is the wavelength that produces the same relative quantum catch in the L and M cones as does the average environmental illuminant (Mollon, 1982; Pokorny & Smith, 1977). In a parallel manner, rod stimulation may assume a chromatic appearance mimicking the M -cone, maintaining some distinction between long and short wavelength color appearance.

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