Cone-Specific Mediation of Rod Sensitivity in Trichromatic Observers

Arthur G. Shapiro

Purpose. The slope of the rod threshold versus the illuminance (TVI) function changes with the wavelength of the background light. This study was conducted to determine whether the changes in slope are due to the stimulation of specific cone classes.

Methods. An eight-channel optical system was used to generate lights that differed in cone and rod photoreceptor illuminance. Rod flicker TVI functions were measured in normal trichromatic observers at mesopic light levels. The independent variables were (1) the relative contribution of the short (S)- and long (L)- wavelength cones to the background light (i.e., the background lights varied along S-only and L-only lines), and (2) the temporal frequency of the flickering lights (4, 7.5, and 15 Hz).

Results. The 4-Hz rod flicker TVI function had a slope of 0.87 when measured near W (MacLeod-Boynton chromaticity of 0.66, 1.0). At 4 and 7.5 Hz, an increase in the relative L-cone illuminance steepened the slope of the rod-only TVI curve, but an increase in the relative S-cone illuminance had no effect. The slope of the 7.5-Hz TVI function decreased at higher illuminance levels. At 15 Hz, the thresholds could be measured over only a limited range.

Conclusions. The L-cone system contributes to the desensitization of the rod system at mesopic light levels, whereas, in the range of lights used in these experiments, the S-cone system apparently does not. The possibility that S-cone stimulation desensitizes the response to rod signals at higher levels of S-cone illumination cannot be eliminated. (*Invest Ophthalmol Vis Sci.* 2002;43:898–905)

The primate visual system operates over a range of 10 log units. This ability is due in part to the duplex retina in which scotopic (i.e., rod-dominated) vision operates at low light levels and photopic (i.e., cone-dominated) vision operates at high light levels. In several early studies, researchers proposed that these two systems behave independently of each other under many conditions,[1–4] but there is now clear evidence of the rods' influence on the cone systems and the cones' influence on the rod system.

Visual signals originating in the rod photoreceptors do not have their own pathway to the brain but instead combine with neural signals originating in the cone photoreceptors. Signals originating with the rod photoreceptors are transmitted to the retinal ganglion cells through at least two anatomic pathways. One pathway combines through second-order cells. Rod photoreceptors connect to rod bipolar cells, which in turn connect to rod (AII) amacrine cells. The rod amacrine cells have gap junction connections with on-center ganglion cells in sublamina *b* of the inner plexiform layer, and have inhibitory synapses with off-center ganglion cells in sublamina *a*. Rod signals may also enter the cone circuit through gap junctions between rod spherules and cone pedicles (see Refs. 5–7). There is also recent evidence in rodents of a third pathway connecting the rod photoreceptors directly to OFF cone bipolar cells.[8,9]

The general perceptual consequences of interaction between rods and cones have been documented extensively. We know, for instance, that the rod photoreceptor system influences cone-mediated sensitivity[10–13] and vice versa[14–18]; that interaction between the rod and cone systems is more evident with flashed lights than with steady lights[19]; and that location, spatial extent, and temporal frequency play an important role in determining the magnitude of rod and cone interaction.[17,20–24]

Rod–cone interaction (how rods influence cones) and cone–rod interaction (how cones influence rods) have become umbrella terms that characterize many classes of visual processing. One historical difficulty with experiments that investigate rod–cone (and cone–rod) interaction is that the narrow-bandwidth lights (i.e., lights of a few spectral wavelengths) used as experimental stimuli often stimulate more than one class of photoreceptor. These experiments therefore do not lend themselves as easily to physiological interpretation. Many previous researchers have addressed such topics by measuring rod sensitivity to lights to which the rod system is much more sensitive than the cone systems (e.g., Ref. 25) or by investigating the responses of monochromatic and dichromatic observers.[26–28]

To investigate questions concerned with cone–rod interaction, I used an approach based on the cone–rod photoreceptor space defined by Shapiro et al.[29] The cone–rod photoreceptor space permits the specification of lights so that the illuminance of the L-, medium-wavelength (M)-, and S-cone and rod photoreceptor classes can be manipulated independently of each other. It is therefore possible to specify lights that differ only in rod illumination. I will refer to such lights as rod-only lights. Such lights have the same chromaticity and photopic illuminance and therefore cannot be created with three-primary optical systems. To implement a cone–rod photoreceptor space, I used an eight-channel Maxwellian-view optical system that presents two light fields (a circular center and an annular surround). Each field was composed of four spectrally independent primaries and thus could be used to create rod-only lights. I measured an observer's sensitivity to rod-only lights against background lights that differ from each other in the excitation of a single cone photoreceptor class.

For this article, I examined rod TVI functions for 4-Hz flickering lights. Aguilar and Stiles[25] measured a rod TVI function by optimizing experimental parameters to isolate the rod system. One of these optimizations was to desensitize the cone systems with a long-wavelength adaptation light. They found that the slope of a major portion of the curve (i.e., when the adaptation light is between −2 and 2.2 log scotopic trolands [td]) is approximately 1.0. However, Sharpe et al.[26,27] and Shapiro et al[30] showed that the slope of the rod TVI function

From the Department of Psychology, Bucknell University, Lewisburg, Pennsylvania.

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Corresponding author: Arthur Shapiro, Department of Psychology, 4 Coleman Hall, Bucknell University, Lewisburg, PA 17837; shapiro@bucknell.edu.

for trichromatic observers is shallower when short-wavelength lights are used for the adaptation background. The slope of the curve is also shallower at all wavelengths for rod monochromatic observers. The implication is that the L-cone system inhibits rod detection.

I examined the effect that increasing the stimulation of the S and L cones has on rod sensitivity in trichromatic observers. I measured rod TVI functions from backgrounds that differ only in S-cone excitation and from backgrounds that differ only in L-cone excitation. The results agree with inferences made from field wavelength measurements in dichromatic observers (i.e., changes in S-cone illuminance of the background do not change the slope of the rod–TVI curve, but changes in L-cone illuminance of the background increase the slope of the function).

METHODS

Color Space

The cone–rod photoreceptor space of Shapiro et al.[29] can be used to create combinations of lights that, from any colored background, change the stimulation of the rod photoreceptor class and keep the stimulation of the cone photoreceptors constant. This type of silent substitution for the cone photoreceptors has been used previously, but only for a limited number of chromaticities.[31] The photoreceptor space of Shapiro et al.[29] is more general and can therefore be used to investigate rod system sensitivity while parametrically manipulating cone–photoreceptor illuminance. This cannot be accomplished within other photoreceptor spaces.[29,32,33]

The photoreceptor space of Shapiro et al.[29] is based on the linear transformation of four linearly independent primary lights with known spectral radiance distributions. The transformation creates a four-dimensional space in which each of the axes represents the excitation of one of the rod and cone photoreceptor classes. For example, let p1, p2, p3, and p4 represent coefficients that scale each of the four primary lights. When p1, p2, p3, or p4 equals 0, the corresponding primary emits no light; when the coefficient equals 1, the primary emits its maximum amount of light. If we let *S*, *M*, *L*, and *R* equal the quantal absorption per time unit of the S-, M-, and L-cone classes and of the rod photoreceptor class, respectively, a relationship between the quantal absorption of the photoreceptors and the energy produced by the phosphors can be expressed by the following equation

$$(\mathrm{S\ M\ L\ R}) = A[\mathrm{p1\ p2\ p3\ p4}]$$

where A is a 4×4 transformation matrix. A detailed derivation of A is given in Shapiro et al.,[29] but, in short, each element of A equals the spectral sensitivity of the receptors times the spectral energy of a primary times a constant, summed over each wavelength from 380 to 720 nm. Adjusting the values of p1, p2, p3, and p4 appropriately can create any particular value of S, M, L, and R. The proportion of the primaries required to manipulate the illuminance of any linear combination of the cone and rod photoreceptors can therefore be determined from the equation.

The Optical System

The data were collected using an eight-channel Maxwellian-view optical system, designed by Joel Pokorny at the University of Chicago and built with the assistance of Jules Quinlan. The system is depicted in the Figure 1A. The device contains two sets of four light channels. The light sources are LEDs, labeled R, G, C, and B for red, green, cyan, and blue, respectively. The peak wavelengths are 663, 561, 516, and 459 nm, respectively. The models and manufacturers of the LEDs are as follows: MT-5000-U (Marktech, Columbia, MD); EBG 5504S (Stanley, New Britain, CT); L200 CWGB6 (Ledtronics, Torrance, CA); and BP280 CWB1K (Ledtronics). The four lights are made spatially homogeneous by caps containing holographic diffusion filters. The lights are combined by dichroic filters placed in the light path at 45°. Dichroic filters

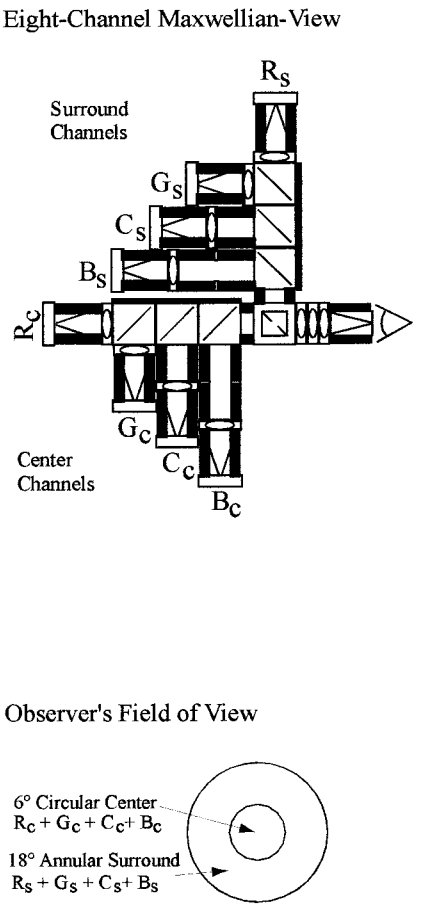

FIGURE 1. **(A)** Eight-channel Maxwellian-view optical system. The device contains two sets of four light channels. The light sources are LEDs, labeled R, G, C, and B for red, green, cyan, and blue. The lights are combined by dichroic filters placed in the light path at 45°. Dichroic filters transmit lights above a cutoff wavelength and reflect lights below that wavelength. The lights from the surround channels (indicated by subscript s) pass through a large aperture, and the lights from test channels (indicated by subscript c) pass through a small aperture. **(B)** The surround light produces an 18° annular field, the center lights produce a 6° circular field.

transmit lights with illuminances above a cutoff wavelength and reflect those with illuminances below that wavelength. The correct combination of dichroic filters ensures minimum light loss.

The lights from the surround channels (indicated by a subscript s) pass through a large aperture, and the lights from test channels (indicated by subscript c) pass through a small aperture, thus producing an 18° background field and a 6° test field (Fig. 1B). The two images are focused at the plane of the pupil.[34] A chin rest is used to maintain stable viewing. The absolute spectral energy distribution of the LEDs was measured with a scanning spectroradiometer. The energy calibrations for each LED were checked using a Spectroscan 650 (GretagMacbeth, New Windsor, NY). Conversion to photometric units (i.e., photopic and scotopic trolands) is based on standard colorimetric techniques.[35] The voltage output to the LEDs is generated by a digital-to-analog board (AO-10; National Instruments, Austin, TX) placed inside a computer (2000 Pentium; Gateway, Kansas City, MO). The board contains ten 12-bit digital-to-analog circuits. The voltage output was calibrated by the manufacturer and was checked after installation. The output from the board is then shaped by a pulse-density modulation driver circuit designed for color consistency and linearity.[36]

The chromaticity of each optical channel was chosen to produce a sizable area over which a reasonable amount of rod contrast can be achieved. Figure 2A shows a MacLeod-Boynton chromaticity diagram.[37] The points labeled B, C, G, and R are the chromaticities of the

four center channels of the eight-channel Maxwellian view. The dashed line defines the gamut of chromaticities that can be obtained from the system. Figure 2B shows a similar representation in a Commission Internationale de l'Eclairage (CIE) 10° chromaticity diagram.

All rod-only lights have the same 10° chromaticity and photopic illuminance; hence, these lights are considered metameric with standard photometric procedures. Figure 2C shows a zoom-in view of a MacLeod-Boynton chromaticity diagram. The numbers inside the diagram indicate the maximum percent of rod contrast when the photopic illuminance is set to 1500 td. Rod contrast is greatest near midwhite (0.66, 1.0) and decreases farther away. The values vary, depending on photopic illuminance and the relative maximum emission of the LEDs. At the level shown, the maximum attainable contrast level is 38.2%; at 1200 photopic td, a maximum of 41% can be achieved at a slightly lower luminance. I was able to obtain more than a 50% contrast when the illuminance of the G LED was higher relative to the illuminance of the R LED; such an adjustment created a lower maximal illumination.

Procedure

After the observer dark adapted for 30 minutes, he or she adapted for 3 minutes to a steady uniform field. Both the center and surround fields were set to the same S, M, L, and R illuminance levels. The observer fixated on the center of the central field. Peripheral presentation would have achieved optimal stimulation of the rods; however, the photoreceptor space was based on a transformation of 10° color-matching functions measured with central fixation. A comparison of thresholds measured on this device yielded approximately a 0.3-log-unit threshold difference between central and 9° eccentricity at scotopic light levels. This is consistent with Shapiro et al.,[29] who showed that for large test lights, rod thresholds differ only minimally when presented centrally or peripherally.

In each trial, the center field was modulated sinusoidally along a line in the four-dimensional receptor space. The dependent variable was the amplitude of the modulation at observer threshold. In each session, thresholds were measured at up to four illuminance levels. A neutral-density filter (2.5 in.; Reynard Corp., San Clemente, CA) positioned behind the exit pupil of the optical system controlled the absolute illuminance level. The lights in the center and surround fields were set to the same chromaticity. The observer started with the darkest filter level. After the thresholds were measured at that level, the filter level was increased, and the observer adapted for 3 minutes to the new level.

Thresholds were measured by either a method-of-adjustment or a staircase procedure. For the method-of-adjustment procedure, the observer set the amplitude of the modulation until flicker was just detectable. The test light was presented for 0.5 seconds (two cycles at 4 Hz), followed by 2 seconds of readaptation. For the method-of-adjustment procedure, the threshold equals the mean of five adjustment settings. Directions at each stage of the experiment (e.g., "starting trial," "out-of-range," "one-minute of adaptation remaining") were delivered through audio files (.wav) played on the computer's speaker system. The observer had control over two buttons and the joystick lever: One button changed the lights ±0.1 of the operating range and the other ±0.01 of the operating range, and the forward–backward movement of the joystick was used to make still finer adjustments. Each time the observer adjusted the control, the program updated the output waveform-array and swapped the array into the output buffer. The result was a smooth transition from one output buffer to another. The action of the analog output board (as well as the timing of the waveforms) was checked by viewing the output of the light with a photocell connected to an oscilloscope. When the thresholds were measured by a staircase procedure, the experiment had the same time course, except that the observer pressed buttons on the joystick to indicate whether he or she saw the flickering light. A modified binary search (MOBS) staircase[38] manipulated amplitude of the flickering light. Threshold was the average of five sessions.

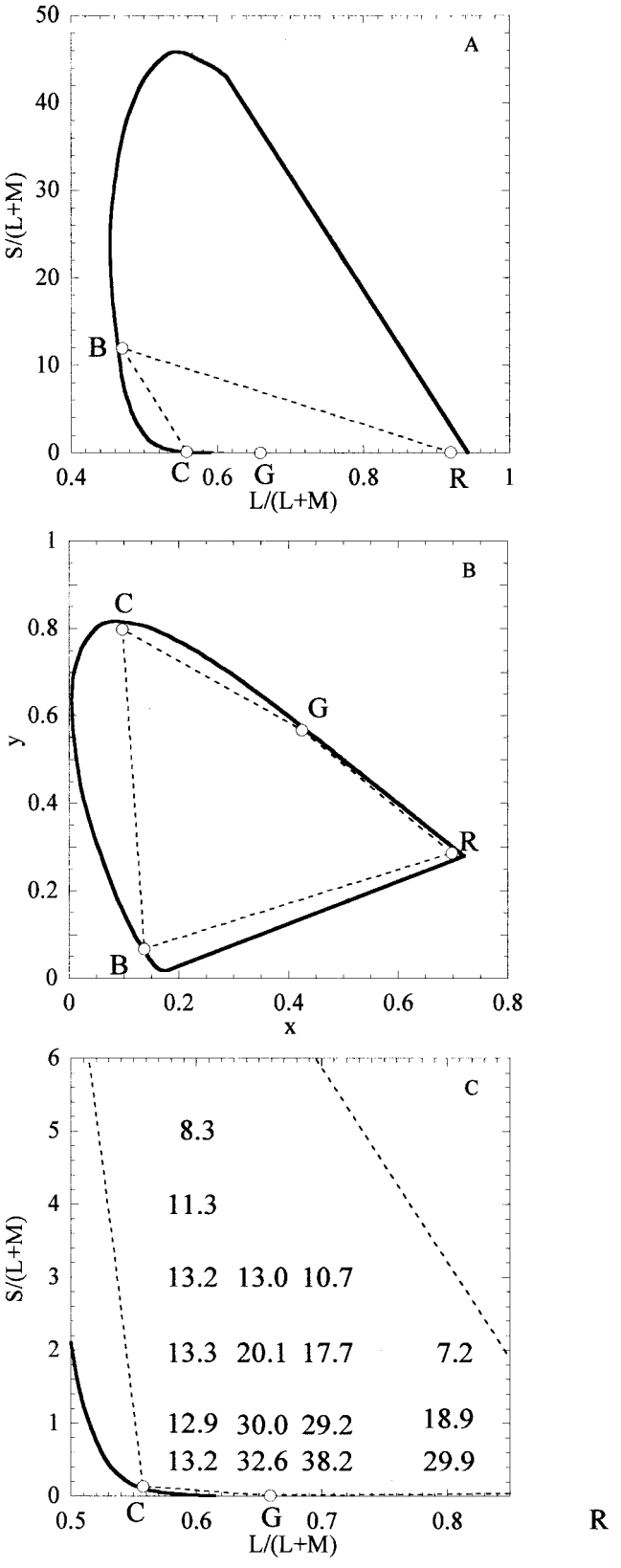

FIGURE 2. (A) MacLeod-Boynton chromaticity diagram[37] depicting the chromaticity of the B, C, G, and R LEDs. *Dashed line* defines the gamut of chromaticities that can be obtained from the system. (**B**) The same representation in a CIE 10° chromaticity diagram. (**C**) Numbers inside the diagram indicate the maximum percentage of rod contrast when the photopic illuminance is set to 1500 td. The maximum scotopic contrasts depend on photopic illuminance and the relative maximum emission of the LEDs.

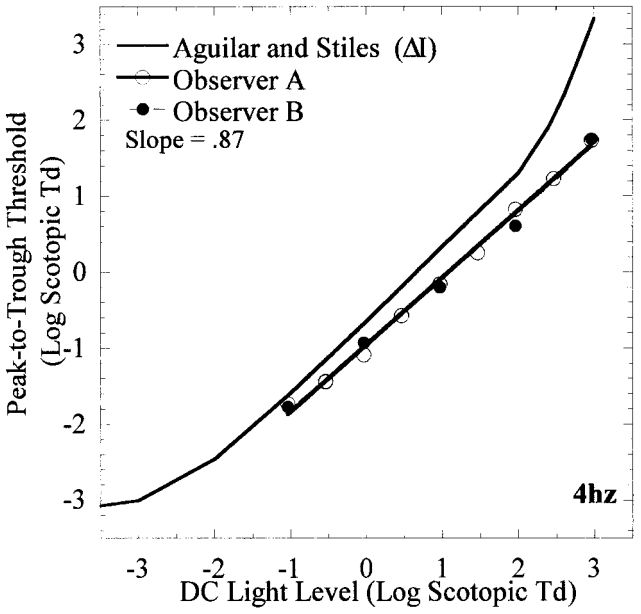

FIGURE 3. A TVI function for 4-Hz rod-only flickering lights. The peak-to-trough threshold amplitude at threshold is plotted versus the DC illuminance of the background. The McLeod-Boynton chromaticity of the light was 0.66, 1.0.

Observers

There were two female observers and one male observer, aged 20 to 22 years. All three had color normal vision, as assessed by the Farnsworth-Munsell (FM) 100-hue test. The male subject had a Rayleigh match within the normal range. The study complied with the tenets of the Declaration of Helsinki and was approved by the institutional experimentation committee, with all observers giving informed consent before participation.

RESULTS

Measurement of the Rod TVI Function

A typical rod-flicker TVI function is shown in Figure 3: the peak-to-trough amplitude of the 4-Hz flickering light at threshold is plotted versus the DC illuminance of the background. The MacLeod-Boynton chromaticity of the light was (0.66, 1.0). The photopic illuminance equaled the mean rod illuminance at the direct-current (DC) level. The threshold Weber contrast at illuminance levels below −2 log scotopic td is greater than 1.0[25] and cannot be created by sinusoidal stimuli. The higher range is limited by the amount of light that can be produced by the optical system.

For comparison, I have included a function fit to the classic Aguilar and Stiles[25] rod TVI data (dashed line). The thresholds from both observers for the flicker TVI are in the same range as those of Aguilar and Stiles, but the curve is shallower. A line fit to the flicker TVI data has a slope of 0.87 compared with a slope of 1.0. The curve also saturates at a higher illuminance level. The results are therefore consistent with those of Sharpe et al.,[27] who found a shallower slope in a rod monochromat. Normal observers also have a shallower rod TVI curve when measured on short-wavelength instead of long-wavelength backgrounds.[26,30] It therefore appears that, under many viewing conditions, the rod system is more sensitive at higher illuminance levels than previously indicated.

Effect of Rod-Only Lights on the Rod System in Individual Observers

Photoreceptor spaces, whether for cones only or for rods and cones, are calculated from a transformation of standardized color-matching data, which are the average data from many observers collected under specific conditions. Many physiological factors can affect an individual's color-matching settings, thereby making a photoreceptor space based on standardized color-matching data unsuitable for isolating a physiological mechanism for that individual. Some of the most common sources of individual variation are the transmission properties of the prereceptoral media (e.g., macular pigment, lens, cornea), variations in illuminance created by changes in pupil size, and nonstandard cone photoreceptor pigments.[39]

To test for isolation of the rod system, I compared TVI functions for test lights containing varying amounts of cone-photoreceptor illuminance. At higher illuminance levels, cone systems are more sensitive than the rod system. Therefore, if I have successfully isolated the rod system, thresholds should be maximal along the rod-only line. I measured the threshold amplitude of a test light modulated sinusoidally along four different lines in the rod (R)/L-cone (L) color plane defined by the vectors (L = 0, R = 1), (L = 0.1, R = 1), (L = 0.5, R = 1), (L = 1, R = 1). The vector (L = 0, R = 1) defines a line that has no L-cone modulation; the vector (L = 0.1, R = 1) defines a line whose ratio of rod trolands to L-cone trolands is 10:1, and so on. The center of modulation for all four lines had a chromaticity near mid white.

Figures 4 (observers A and B) show the TVI functions using lights modulated along these lines. The 95% confidence limits for each point are smaller than the data symbol. I am encouraged by these results, because the observer was least sensitive to rod-only lights (filled circles). At higher illuminance levels (>0 log scotopic td), the observer's sensitivity increased as the L-cone component increased. If the best rod isolation direction were something other than L = 0, R = 1, I would expect higher thresholds for lights modulated in other directions, and I would expect the thresholds not to decrease, as was the case with the thresholds for lights modulated along L = 0.5, R = 1 and along L = 1, R = 1. Similar results have been obtained in one other observer. Additionally, lights modulated along cone isolation lines at scotopic levels could not be detected. The slopes of the L = 0, R = 1 line in Figure 4 (top and bottom) are 0.92 and 0.93. The slopes are steeper than those in Figure 3, because the L/(L + M) chromaticity for the lights in Figure 4 was 0.73 (see Fig. 6).

Although these results are encouraging, this method of identifying rod isolation is clearly indirect. Sun et al.[40] have now developed a technique for normalizing an individual observer into a four-primary CIE 10° colorimetric system for calibration of the eight-channel Maxwellian view. The observers first make settings for scotopic matches, equating three of the LEDs individually to the Y LED. This allows for the adjustment of individual differences in prereceptoral filters. Sun et al. compared these weights to photopic luminance matches made by adjusting the R (664 nm) primary. They found that observers could make the photopic matches and that receptoral spectral sensitivities could be approximated by linear transformations of the CIE 10° standard observer.

Effect of Changing the Adaptation Level of the L and S Cones

To examine the extent that S-cone adaptation mediates the sensitivity of the rod system, I measured rod threshold at adaptation chromaticities that varied along the S-cone line. Thus, at any level of scotopic illuminance, all background lights differed only in S-cone illumination. If the S-cone system does not affect the rod system, then these backgrounds should not change rod threshold.

Figure 5 shows the TVI function for observer A, measured from the four S-cone chromaticities. The rod thresholds are approximately the same in all conditions. The amount of S-

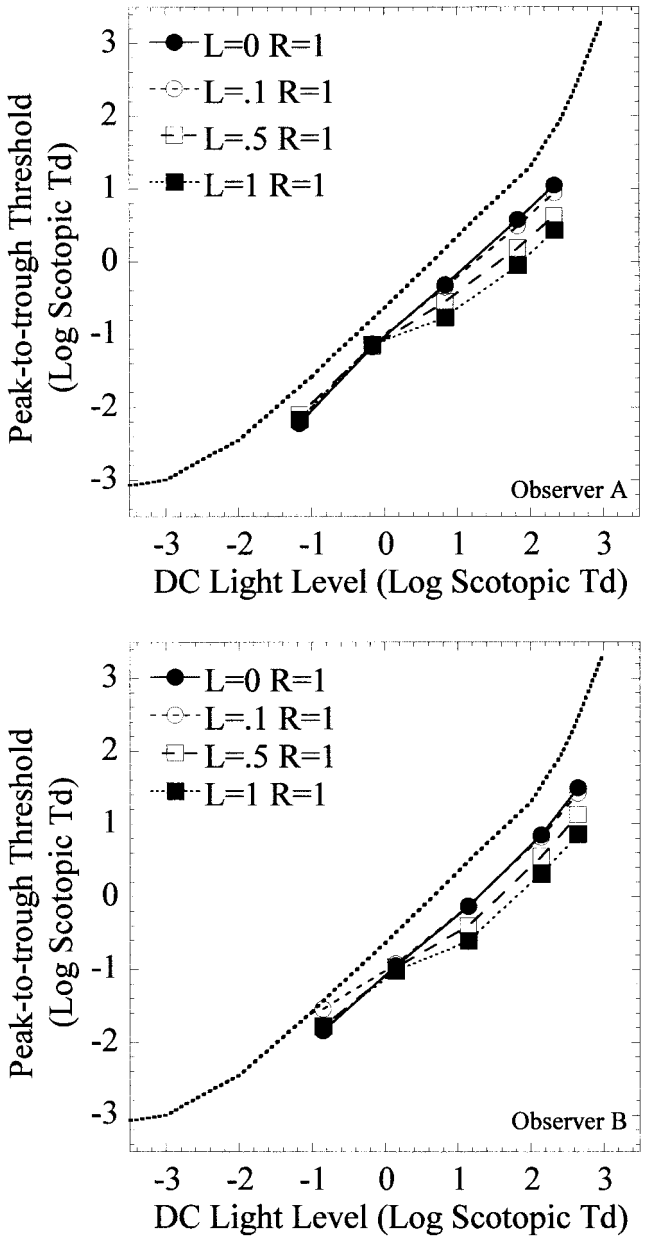

FIGURE 4. TVI functions for test lights containing varying amounts of L-cone photoreceptor illuminance. The center of modulation had a chromaticity of 0.66, 1.0.

cone excitation in the background has no effect on the slope of the TVI curve. The L/(L + M) chromaticity was 0.73, which is greater than that in Figure 3. The average slope of the four curves was 0.91, higher than the slope in Figure 3 (Fig. 6).

Figure 5 also shows the rod thresholds versus S-cone background measured with the staircase procedure for observer B. I measured rod thresholds at two illuminance levels at which cone rod interaction would be likely to occur: 0.8 and 1.81 log scotopic td at 9-second cone chromaticities. The thresholds are in the same range as those found with the method-of-adjustment procedure shown for observer A. More important, there is no change in rod threshold as a function of S-cone excitation. It therefore appears that under steady adaptation, the S-cone system does not affect the sensitivity of the rods.

Similar measurements were made on the effect of the L-cone system on rod sensitivity. Figure 6 shows 4-Hz rod-only TVI curves in the data from observer A for three steady backgrounds that differ in the ratio of L-cone–rod illumination. At any scotopic illuminance level (axis) these backgrounds differed from each other only in L-cone illumination. The three conditions are identified by the L/(L + M) chromaticities shown. These lights differ in photopic illuminance (L + M), and therefore differ in their y coordinate S/(L + M), even though they do not differ in the ratio of rod-to-S-cone illumination. The 95% confidence interval for all points is approximately the same size as the data symbol, except at the lowest illuminance level. The function produced by the backgrounds with the highest L-cone ratio had a slope of 0.98, and the function produced by backgrounds with the lowest L-cone ratio had a slope of 0.80. Increases in the L-cone adaptation level desensitized the rod system.

Figure 6 (bottom) shows a similar set of measurements in observer C, made with a finer set of chromaticities and plotted in a manner similar to Figure 5 (bottom). I measured thresholds for rod-only lights as a function of L-cone illumination at five scotopic illuminance levels, using the staircase procedure. Data from two chromaticities at the end of the line were eliminated from the study before the data were examined, because the observer stated that the surround did not match the center. At higher illuminance levels there was a clear increase in rod threshold as a function of L-cone illumination.

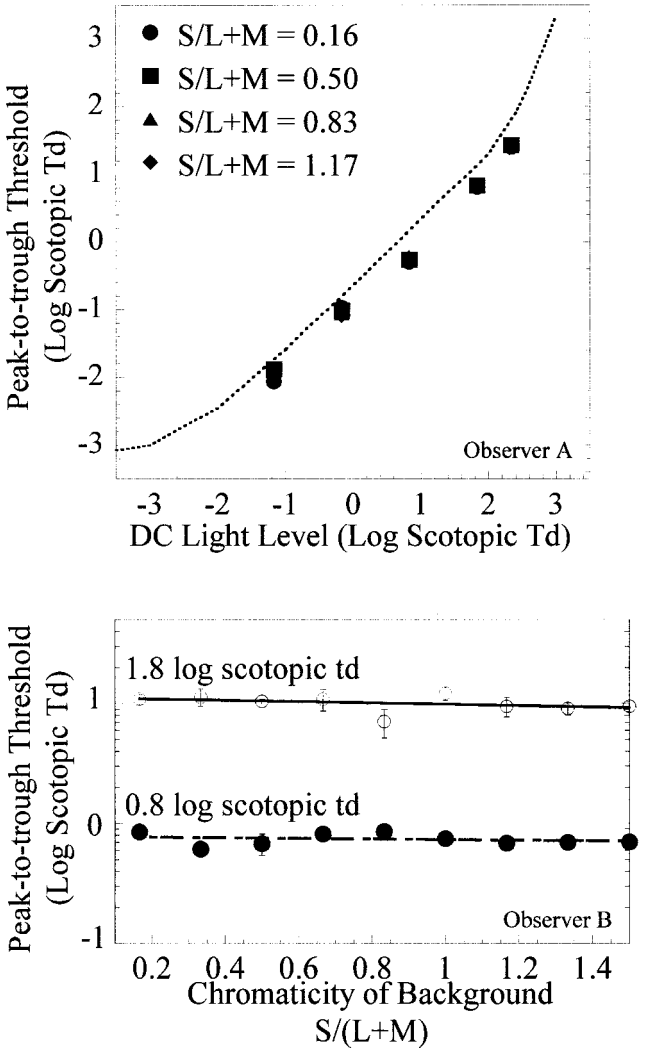

FIGURE 5. *Top*: TVI function for observer A, from the four S-cone chromaticities (*upper left*). The L/(L + M) chromaticity was 0.73. *Bottom*: Rod thresholds versus S-cone background in observer B at two scotopic illuminance levels: 0.8 log scotopic td and 1.81 log scotopic td.

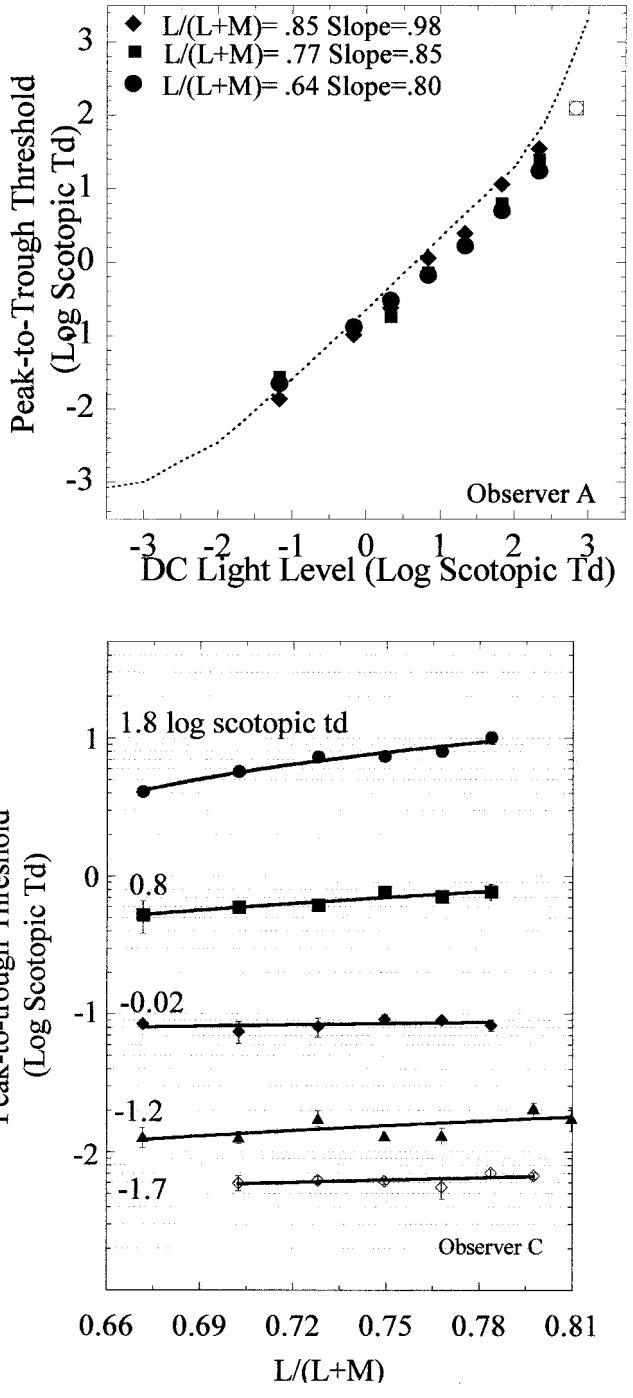

Figure 6. *Top*: Four-Hz rod-only TVI curves in observer A for three steady backgrounds that differ in the ratio of L-cone–rod illumination. The lights are identified by the L/(L + M) chromaticity (*upper left*). The 95% confidence interval for all points is approximately the same size as the data symbol, except at the lowest luminance level. *Bottom*: A similar set of measurements on observer C, made with a finer set of chromaticities and plotted versus the chromaticity of the background.

As with Figure 6 (top), the threshold difference was greater at 1.8 log scotopic td than at 0.8 log scotopic td. At −1.7 and −0.02 log scotopic td the threshold curves were flat. The trends are the same as those seen in observer A. Rod thresholds increase as a function of L-cone illumination. The one exception is at −1.2 log scotopic td, at which there appears to be a slight change in threshold as a function of L-cone illumination.

Effect of Temporal Frequency at on the Rod TVI Curve

There is considerable evidence for multiple rod temporal-frequency channels.[6,41–43] Connor and MacLeod[42] showed that, below 0 log scotopic td, the critical flicker frequency (CFF) for rod-only lights is determined by the rod slow pathway and has a maximum of 6 to 10 Hz. At higher than 0 log scotopic td, the CFF is determined by the rod fast pathway and is above 25 Hz. The slow pathway presumably arises from signals that travel along the rod→rod bipolar→AII amacrine cell anatomic pathway before interaction with the cone pathway. The rod fast pathway presumably originates in rod signals entering the cone system through gap junctions at the rod–cone receptor level, or possibly, through a direct rod-off bipolar pathway. It is therefore reasonable to suppose that the effect of cone-only backgrounds may be different for low and high frequency rod-only flicker.

I repeated the experiments in Figures 5 and 6 for observer A for 7.5- and 15-Hz rod-only flickering lights. Figure 7 shows the effect in observer A of changing the S-cone illumination of the background. At 7.5 Hz, the rod-only thresholds could be measured for the same range as at 4 Hz. There was a clear dip in the curve, starting at 0 log scotopic td. This dip was also found in the 7.5-Hz rod flicker TVI curve of Sharpe et al.[44] and indicates detection by a second mechanism, presumably the rod fast pathway. The rod thresholds were not affected by the S-cone chromaticity of the backgrounds. The slope of the curve between 0.3 and 2.3 log scotopic td was 0.87, which is in the same range as measured previously. At 15 Hz, thresholds could be measured only at two illuminance levels. S-cone chromaticity did not affect discrimination. Figure 7 (bottom) shows the effect of changing the L-cone illumination. At 7.5 Hz there was a small change in the slope of the curve at different L-cone illuminations (slope = 0.88 vs 0.83). At 15 Hz, thresholds could be measured only at 2.3-log-scotopic-td backgrounds. The illuminances at the two chromaticities were 1.5 and 1.3 log scotopic td.

Discussion

In this study, I examined whether signals that originate in S cones and L cones influence rod sensitivity in trichromatic observers. The general conclusions are the following: (1) The slope of the rod TVI curve is shallower than that proposed by Aguilar and Stiles[25] under most adaptation conditions; (2) S-cone backgrounds, in the range of lights used, do not affect the slope of the TVI curve; and (3) an increase in the L-cone illuminance of the background increases the slope of the rod-TVI function. These conclusions agree with other TVI data in the literature, based mostly on dichromatic observers and rod monochromatic observers. Rod and cone interactions manifest themselves differently depending on the specific stimulus conditions and on the observer's task. For instance, under many conditions rod signals appear to shift the appearance of lights toward bluish. By making standard linking assumptions between intensity of the bluish hue and the S-cone pathway, many researchers have concluded that signals originating in the rods travel, in part, through the S-cone pathway, albeit nonlinearly.[44–47] In contrast, the results in the current study indicate that changes in the S-cone adaptation level, which substantially alter observer sensitivity to signals originating in the S cones, do not affect an observer's sensitivity to signals originating in the rods (a result that is consistent with the TVI curves measured in S-cone monochromats).[27] Rod signals may or may not share pathways with the S-cones, but S-cone signals do not appear to regulate rod sensitivity. It is, however, entirely conceivable that the change in sensitivity is the result of complete adaptation that occurs during the presence of the

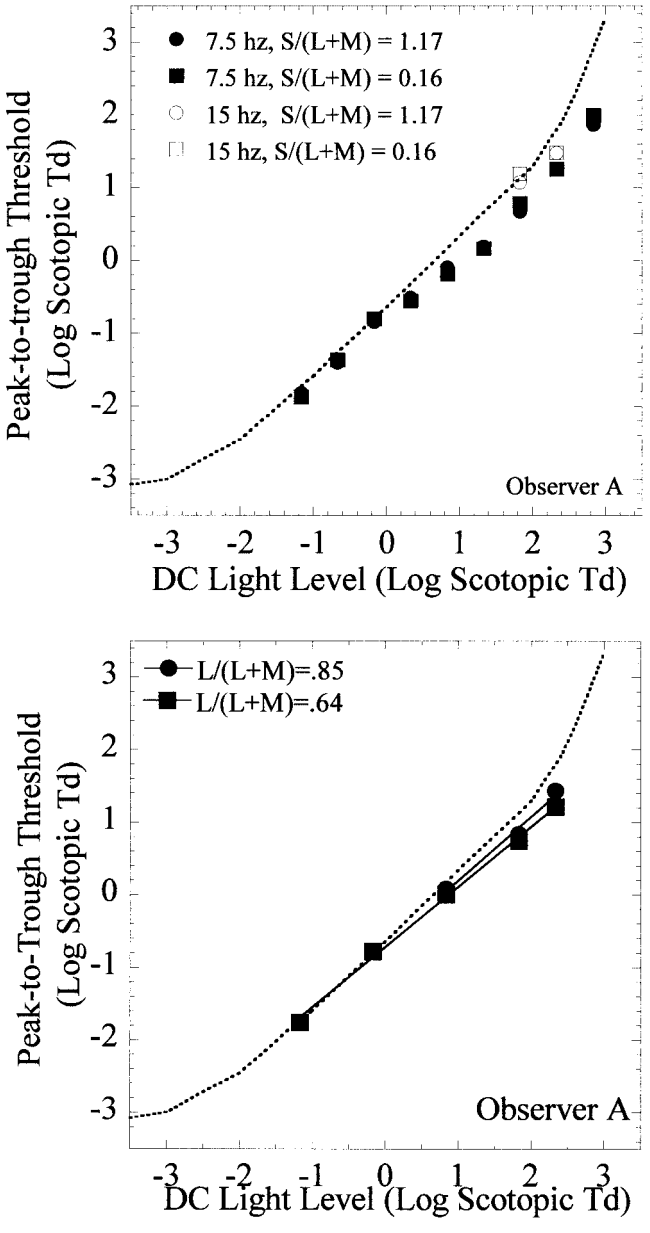

FIGURE 7. *Top*: TVI curve from two S-cone chromaticities. The rod-only test light flickered at 7.5 Hz (*filled symbols*) and 15 Hz (*open symbols*). *Bottom*: TVI curve from two L-cone chromaticities. The test light frequency equaled 7.5 Hz. Thresholds for 15 Hz could be measured only at the highest illuminance level.

steady field. A distinction has to be made between rod influences on color perception, rod and cone detection, and the influence of cone adaptation on rod gain control.

It is also possible that the effects found along the L-cone line were not found along the S-cone line because of the comparative range of the adaptation lights: At 2 log scotopic td, a 460-nm light produces 7.86 log quanta/sec·deg^2 and a 663-nm light produces 11.2 log quanta/sec·deg^2. The π_1 field point (the radiance at which the S-cone threshold is raised by a factor of 10) is 8.73, and the π_5 field point is 9.31. Because the radiance from a 460-nm light is below the field point and the radiance for a 663-nm light is above the field point, the potential threshold elevation for the L-cone system is much greater than for the S-cone system (using Stiles' standard template,[35] this equals a threshold elevation of approximately 0.46 log units for the S cones and well above 2 log units for the L cones). The lights along the L-cone line are at a much higher point on the L-cone TVI function than the S-cone lights are on the S-cone TVI function.

However, because of the limitations posed by the high value of rod contrast at threshold, the actual range of the lights used in the experiment was far less than the potential at the end-point chromaticities. I measured the S- and the L-cone thresholds on the respective cone isolation lines at a fixed scotopic illuminance. The S-cone thresholds were measured before the experiments and over a smaller range of chromaticities, whereas the L-cone thresholds were measured at the same time as the rod thresholds on L backgrounds and at the same chromaticities. At 1.8 log scotopic td, the threshold elevation for the S cones was approximately 0.20 log units (with a slope quite similar to that found by Zaidi et al., 1992).[48] Along the L-cone line, the L-cone threshold elevation was approximately 0.25 log units. At 1.8 log scotopic td the S-cone backgrounds covered 53 just-noticeable differences (JNDs), and the L-cone backgrounds covered approximately 90 JNDs. Thus, the range of lights used for the L-cone system was only slightly greater than that for the S-cone system.

Because of the limitation in stimulation range, this study cannot rule out the possibility that the S-cone signals would affect rod discrimination at a higher S-cone illuminance. Indeed, Sharpe et al.[27] noted that in the blue-cone monochromat S-cone thresholds on a 450-nm field do not increase until after rods saturate. It may therefore be impossible to generate lights that are equated for the S and L field elevations at low enough scotopic levels.

Rod signals predominate in magnocellular pathway ganglion cells at and below 20 td, and can be found in parvocellular pathway cells below 2 td.[49] Thus, it is likely that in this study L-cone mediation reduced the significance of rod signals in the magnocellular pathway. The range of lights that could effectively isolate the M-cone was limited by the maximum illuminance of the G LED, and I will not speculate on the effect of M-cone changes on rod sensitivity. I also did not address whether changes along L–M lines (L + M equals a constant) and photopic-luminance-only (L + M + S) lines elevate rod thresholds as much as equivalent changes in L-cone illumination alone. The results of such an experiment will presumably indicate a cone-level or postreceptoral locus for the elimination of rod signals at higher illuminance levels. It may be of importance that L-cone interaction was most evident at higher illuminance levels, a finding that may indicate cone-specific interaction with the fast-rod pathway. However, I think it unlikely that a steady state change in adaptation level would have a large effect on a processing stage that passes high temporal frequencies.

An important as yet unanswered question concerns how rod signals are eliminated from vision at higher light levels. Do they shut down passively through a system of saturation, or are the signals actively suppressed by other mechanisms? The results of the experiments in this study argue that signals from the L-cone system either directly or indirectly (through luminance or chromatic pathways) contribute to saturation of the rod system at higher light levels. One possibility is that the L-cone system actively inhibits rod function through a system of neural gain control, possibly through feedback from amacrine cells.[50] It is also possible that rod desensitization occurs as rod and L-cone signals compete for the same postreceptoral pathways. At higher illuminance levels, the increase in L-cone signals effectively masks the rod signal, thus driving up the rod threshold. The experiments described in this article did not differentiate between these two hypotheses.

Finally, it is clear from this study and other investigations into the scotopic TVI function that under many conditions, the rod system remains active at a higher illuminance than was previously thought. This may be important in situations that require a silent rod system, such as colorimetric specification,

color-matching predictions, and cone-specific sensitivity measurements. Stiles[51] and Shapiro et al.[52] have suggested that a good metric for identifying conditions under which the rod system may intrude is to divide the scotopic difference between two fields by the rod threshold at mean scotopic illuminance levels. The data presented herein suggest that the Aguilar and Stiles function[25] leads to underestimating the significance of rod contribution in many test conditions.

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