

Control of the Modulation of Human Photoreceptors

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Abstract: Four primaries are required to modulate independently the three types of cone and the rod photoreceptors. In order to work in a 4-primary colorimetric system, it is necessary to have accurate estimates of an individual observer's receptor spectral sensitivities and prereceptor filtering. A technique to evaluate whether an individual observer's receptor sensitivities may be characterized as linear transforms of the Standard Observer's data for the colorimeter primaries is described. If the individual fulfills this prerequisite, the technique allows compensation for prereceptor filtering differences between the individual and the Standard Observer. For two observers who fulfilled this requirement, temporal contrast sensitivity functions for the three cone types and the rods were measured at different luminance levels using the method of silent substitution. Temporal contrast sensitivity functions for cones increased with luminance level from 0.5–50 photopic td. Temporal contrast sensitivity functions for rods increased with luminance level from 0.05 td (0.024 scotopic td) to 5 td (2.413 scotopic td), then decreased at 50 td (24.13 scotopic td). © 2000 John Wiley & Sons, Inc. *Col Res Appl*, 26, S69–S75, 2001

Key words: temporal contrast sensitivity; colorimeter; silent substitution; cone; rod

INTRODUCTION

For a visual system with only one type of photoreceptor, one primary is sufficient to control the activity of the photoreceptor. For a visual system with two types of photoreceptors, two primaries are needed for independent control of each photoreceptor. For the human visual system, four linearly independent primaries are required to modulate separately the four types of photoreceptors. Shapiro, Pokorny, and Smith¹ gave a theoretical introduction to a

four-primary colorimetric system. To use the 4-primary colorimetric system, it is necessary to have accurate estimates of an individual observer's receptor spectral sensitivities and prereceptor filtering. In Experiment 1, we evaluated whether an individual observer's receptor sensitivities could be characterized as linear transforms of Standard Observer data after correcting for prereceptor filtering variation. In Experiment 2, we used the 4-primary colorimetric system and the method of silent substitution to produce specific photoreceptor modulation. We then measured the temporal contrast sensitivity functions of the S, M, and L cones, and the rods.

METHODS

Apparatus

A Macintosh Quadra 950 and National Instrument interface boards controlled an 8-channel colorimeter (Fig. 1). The colorimeter presented a 6° circular center and a 16° annular surround. The center and the surround each consisted of 4 primary lights, 459, 516, 561, and 664 nm, with half-height bandwidths of 8–10 nm. LEDtronics manufactured the LEDs for the 459 and 664 nm primaries; the 516 and 561 nm primaries originated from Nichia LEDs. The LED output levels were controlled by a train of 2 μ s constant-amplitude pulses with varying density. Twelve-bit D/As fed the LED drivers.

For each channel, light from a LED (L1–L8) modified by an interference filter (IF) was collimated by a lens (L) and combined using a dichroic mirror (D), then focused on a 2 mm artificial pupil (AP) by a field lens (FL). Plastic diffusers (DF) placed in front of each LED provided uniform illumination at the artificial pupil. The center-surround field configuration was formed by a photometric cube (PC) and presented at optical infinity. Each observer's eye was 8 mm from the artificial pupil. The size of surround LED beam at this location, measured with an optical comparator, was 2.2 mm in diameter. This size was consistent with the calculated beam half-height width. The head of the observer was held

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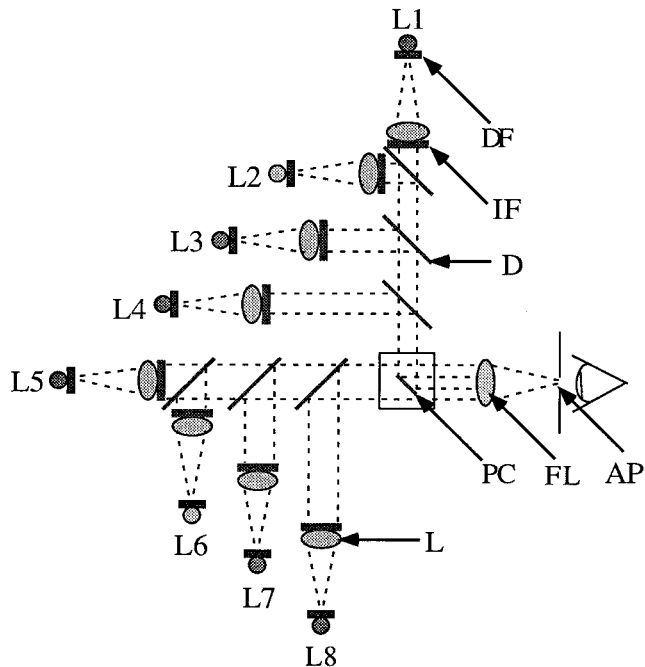


FIG. 1. 8-channel colorimeter diagram. L1 to L4 are center LEDs; L5 to L8 are surround LEDs. Light from each LED passed through plastic diffusers DF before being collimated by a lens L, and passed through an interference filter IF. The LED/filter combinations produced primaries with dominant wavelengths of 459, 516, 561, and 664 nm. Lights within the center and the surround pathways were combined using dichroic mirrors D. The center-surround field configuration was formed by a photometric cube PC with a mirrored ellipse on the hypotenuse. A field lens FL focused the LED images on the 2-mm artificial pupil AP, producing a field image at optical infinity.

stable by a chin-rest, with the superciliary ridge of the viewing eye resting against the AP mounting. L had a 76 mm focal length; FL had a focal length of 60 mm. The optical pathlengths from the LEDs to the artificial pupil were identical for all channels.

Inconel neutral density filters, calibrated for each primary, were placed in the final common pathway to control the average light level. A fixation point allowed the stimulus to be viewed at 10° in the temporal retina.

Calibration

The spectral distributions and the radiant outputs of the primaries were measured at the eyepiece. The spectral output of each channel was measured at the maximum LED output with an Optronics OL754 spectroradiometer at 2 nm intervals. While the pulse-frequency modulation technique offers high LED output linearity over a 3 log unit range for modulation around a mean level,² we observed small but systematic deviations from linearity with variation in steady light level. These deviations are presumably caused by thermal effects associated with changes of current in the diode junction.³ Linearization of each LED output was attained with three linear equations for the ranges of 0.1–1, 0.01–0.1, 0.001–0.01 of the maximum

LED output. The maximum photopic illuminance output of the center 561 nm LED was measured with an EG&G 550 Radiometer/Photometer and used as a reference to calculate the illuminances of the other LEDs.

Observers

Two observers, HS (one of the authors) and HH (naive observer), participated in the experiment. Both are normal trichromats as assessed with Ishihara pseudoisochromatic plates and the Neitz OT anomaloscope. Both observers gave Farnsworth–Munsell 100-Hue error scores of four. HS is myopic (-5.5) and wore a nontinted contact lens. HH is also myopic (-2.5) and did not wear a corrective lens during the experiment. Although the center-surround field was presented at optical infinity, the 2-mm AP provided sufficient depth of the field so that this observer did not require a corrective lens during the experiment.

EXPERIMENT 1

Rationale

The CIE scotopic luminosity function $V'(\lambda)$ can be decomposed into two components to separate the spectral sensitivity of the photoreceptor and the spectral transmittance spectrum of the prereceptor filtering:

$$V'(\lambda) = W'(\lambda) F_s(\lambda), \quad (1)$$

where $W'(\lambda)$ represents the CIE $V'(\lambda)$ expressed at the retinal level and $F_s(\lambda)$ represents the prereceptor filter transmittance associated with Standard Observer for scotopic photometry. The $W'(\lambda)$ is based on the absorption spectrum of rhodopsin adjusted for physiological optical density. We assume $W'(\lambda)$ is invariant across observers, because no rhodopsin polymorphisms have been reported for normal human observers.⁴ The values of the prereceptor filter transmittance $F(\lambda)$ are known to vary among observers. For a scotopic luminance match between a reference light $P_{ref}(\lambda)$ and a test light $P_{test}(\lambda)$, the Standard Observer match is given by:

$$P_{ref}(\lambda) W'(\lambda) F_s(\lambda) = a_s P_{test}(\lambda) W'(\lambda) F_s(\lambda), \quad (2)$$

where a_s is calculated based on $V'(\lambda)$. For a scotopic match made by an individual observer:

$$P_{ref}(\lambda) W'(\lambda) F_o(\lambda) = a_o P_{test}(\lambda) W'(\lambda) F_o(\lambda), \quad (3)$$

where $F_o(\lambda)$ is the prereceptor filter transmittance for the individual observer, and a_o is set by the individual observer. The ratio a_s/a_o represents the difference in prereceptor filtering between the Standard Observer and the individual observer. This method of scotopic luminance matching can be used to calibrate the individual prereceptor difference, and equate the scotopic luminances of the primaries 459, 516, and 561 nm.

At long wavelengths, the cones and the rods have similar sensitivities, mitigating against use of the scotopic luminance match to calibrate the individual prereceptor filtering of the 664 nm primary. In this case, a photopic colorimetric

metric match can be used. The CIE 10° Standard Observer for colorimetry has a unique match for the mixture of 459 and 561 nm matched to the mixture of 516 and 664 nm:

$$b_1 459 \text{ nm} + b_2 561 \text{ nm} \equiv b_3 516 \text{ nm} + b_4 664 \text{ nm}, \quad (4)$$

where b_1, b_2, b_3, b_4 are the tristimulus values calculated from CIE 10° color-matching functions.

For an individual observer, the values of the 459, 516, and 561 nm primaries are first corrected for the individual prereceptoral filtering differences measured by the scotopic matches, then they are fixed at the matching value $b_1, b_2,$ and b_3 . If the observer can make a color match by adjusting the radiance of the 664 nm only, the observer has receptor spectral sensitivities that can be approximated by linear transforms of the Standard Observer data for the spectral distributions of the four colorimeter primaries. The difference of the 664 nm setting between the individual observer and the Standard Observer corrects for the individual prereceptoral variations for 664 nm primary.

Procedure

1. *Scotopic luminance matches:* First, isomeric matches were made between the center and surround for each of the four primary pairs. For the scotopic matches, the 561 nm primary was the reference light. Center primaries 459 and 516 nm were matched to surround 561 nm. Then surround primaries 459 and 516 nm were matched to center 561 nm. The ratio of the individual observer's match to the Standard Observer's match was computed and used to correct for prereceptoral filter variation.
2. *Photopic colorimetric matches:* The next step was to attempt a photopic colorimetric match by adjusting the radiance of the 664 nm primary with the 459, 516, and 561 nm primaries fixed at the expected matching values calculated from the Standard Observer and the individual scotopic matches. If a satisfactory color match was achieved, the difference in 664 nm primary between the individual setting and the calculation was computed and used to correct for prereceptoral filtering variation. Ten color matches were made with 664 nm in the center and in the surround, respectively.
3. To transform into cone-based chromaticity from the CIE 10° color matching, we used the Smith–Pokorny transformation⁵ applied to the 1964 10° CMFs¹:

$$\begin{bmatrix} \bar{l}_{10}(\lambda) \\ \bar{m}_{10}(\lambda) \\ \bar{s}_{10}(\lambda) \end{bmatrix} = \begin{bmatrix} +0.15516 & +0.54308 & -0.03287 \\ -0.15516 & +0.45692 & +0.03287 \\ 0.00000 & 0.00000 & +1.00000 \end{bmatrix} \times \begin{bmatrix} \bar{x}_{10}(\lambda) \\ \bar{y}_{10}(\lambda) \\ \bar{z}_{10}(\lambda) \end{bmatrix}. \quad (5)$$

Results

The scotopic luminance matches of the two observers differed, but both observers could make satisfactory color

TABLE I. The ratio a_s/a_0 for two observers. This ratio represents the difference in prereceptoral filtering between the Standard Observer and the individual observer.

Observer	459 nm	516 nm	561 nm	664 nm
HS	0.885	0.963	1	0.825
HH	1.15	0.885	1	1.04

matches by adjustment of the radiance of the 664 nm primary with the other three primaries fixed at the values calculated from the Standard Observer data and the individual scotopic matches. (By satisfactory, we mean that at the color match the observer could not identify the direction of color difference between the center and the surround fields.) Thus, the observers differed in their prereceptoral filtering (Table I), but had receptor spectral sensitivities that could be approximated by linear transforms of CIE 10° Standard Observer data.

EXPERIMENT 2

The temporal contrast sensitivity functions for the S, M, and L cones and the rods were measured using the silent substitution method.^{6,7} Silent substitution is a technique of heterochromatic modulation where the effective quantal absorption by the silenced photoreceptor is kept constant for the modulated heterochromatic lights. With the 4-primary colorimetric system, it is possible to silence up to three photoreceptors with different spectral sensitivities. The maximum contrasts that could be obtained from the colorimeter for the S, M, and L cones and the rods in silent substitution were about 0.85, 0.20, 0.20, and 0.35.

Stimuli

The center field was sinusoidally modulated at frequencies between 2–20 Hz. The surround was either fixed at the time-average center illuminance and chromaticity or was dark. The time-average illuminance of the center was fixed at one of the following levels: 50, 5, 0.5, 0.05 photopic td, corresponding to 24.13, 2.413, 0.241, 0.024 scotopic td. The time-average chromaticity of the center was $x = 0.33, y = 0.33$.

Procedure

Two protocols were used: (1) the method of adjustment, (2) a staircase with 3-alternative temporal forced choice. For the adjustment protocol, the center modulation was continuously present. For the staircase protocol, the center was modulated as a 2 s Gabor with sine phase (sinusoid with Gaussian envelope). The observer first dark adapted for 30 min, then light adapted to the time-average illuminance for 3 min, and then ran either an adjustment or a staircase session. For the adjustment protocol, frequencies were randomized from trial to trial; five settings were obtained for

each frequency in one session. The threshold means and standard deviations were calculated from the ten settings from two sessions. For the staircase protocol, the temporal contrast sensitivity at each frequency was estimated using a temporal 3-alternative forced choice staircase with 2 “yes,” 1 “no,” and 10 reversals. Each session included five interleaved staircases for five frequencies. Each staircase was terminated after 10 reversals at the smallest step size (0.05 log unit). The threshold for one staircase session was the average of the last six reversals. The mean threshold at each frequency was an average of two staircase sessions. The temporal contrast sensitivity function was fitted with a sum of two exponential functions.

Results

There were no appreciable differences between data obtained by the adjustment and staircase protocols. The data for the adjustment protocol are shown in Figs. 2–6.

Figures 2 and 3 show temporal contrast sensitivity functions of the S, M, and L cones with the equiluminant surround for subjects HS and HH, respectively. Figure 4 shows temporal contrast sensitivity functions for the S, M, and L cones with the dark surround for subject HS. For S, M, and L cones, the temporal contrast sensitivity increased with luminance level. Consistent with literature data,⁸ the flicker sensitivity was slightly higher with the equiluminant surround.

Figures 5 and 6 show the rod temporal contrast sensitivity functions measured with equiluminant and dark surrounds for the two subjects. For the rods, the temporal contrast sensitivities increased between 0.05 td (0.024 scotopic td) and 5 td (2.413 scotopic td), then decreased at 50 td (24.13 scotopic td). Contrast sensitivity at 50 td was higher with the dark surround than with the equiluminant surround. Perhaps, for the dark surround condition, the detection was of stray light at the dark borders of the test field.

DISCUSSION

The silent substitution method allows modulation of one photoreceptor type, while keeping the other photoreceptors at steady excitation levels. This technique does not imply that the temporal contrast sensitivity functions can be attributed solely to the properties of the modulated photoreceptor type, as Kelly and van Norren⁹ pointed out. L and M cones provide inputs to both magnocellular and parvocellular pathways. Modulation of either L or M cone will affect both pathways. The temporal contrast sensitivity may be limited by higher-order neural elements sensitive to the achromatic and the chromatic components of the modulation. Smith *et al.*⁷ evaluated the extent to which temporal contrast sensitivity functions obtained with silent substitution revealed different contributions of magnocellular and parvocellular pathway activity. Their data indicated that, for both L and M cone temporal contrast sensitivity functions, the chromatic pathway contributed at low frequencies and the achromatic pathway contributed at higher frequencies.

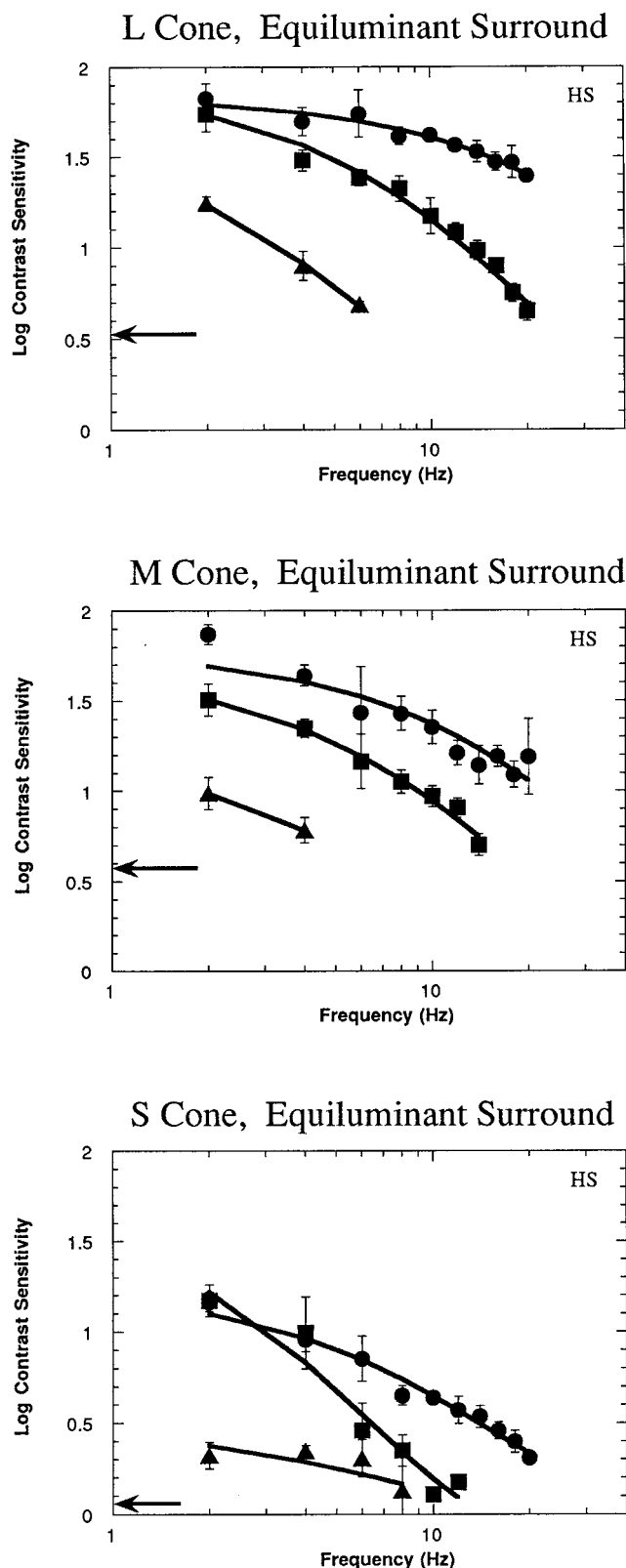


FIG. 2. Temporal contrast sensitivity functions of the S, M, and L cones with equiluminant surround for subject HS. Data are shown for three light levels: (circle) 50 td, (square) 5 td, (triangle) 0.5 td. Solid lines represent fits of sums of two exponential functions. Error bars show standard deviations. The arrows show the maximum available contrasts.

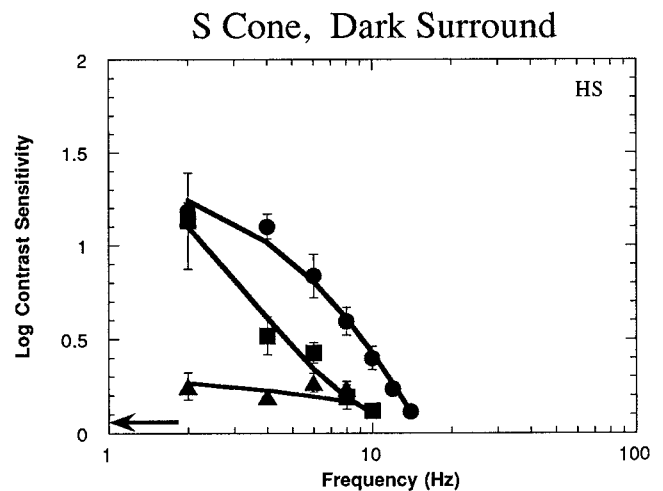
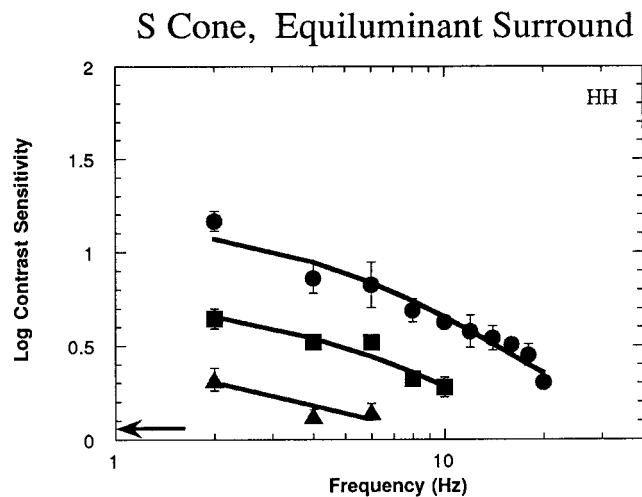
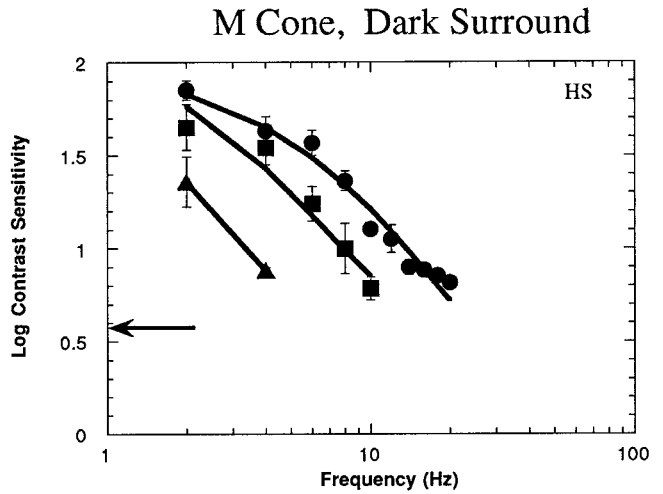
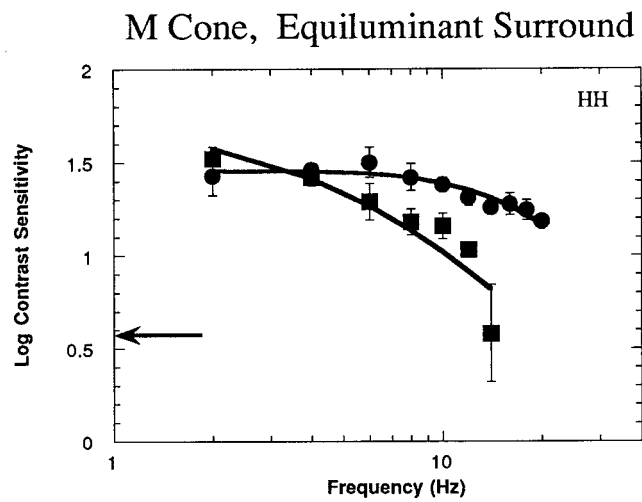
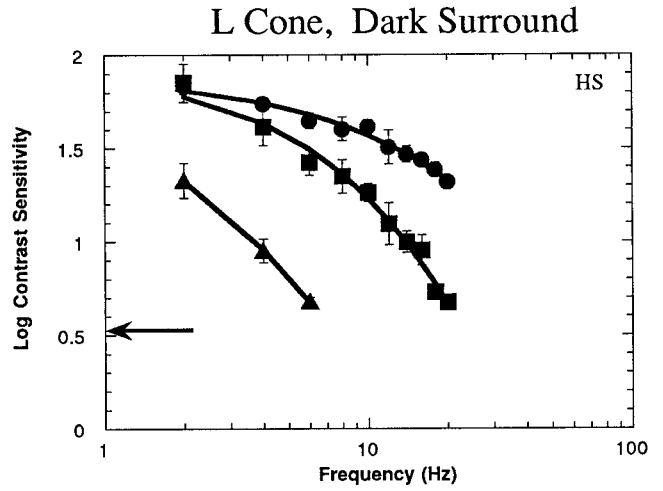
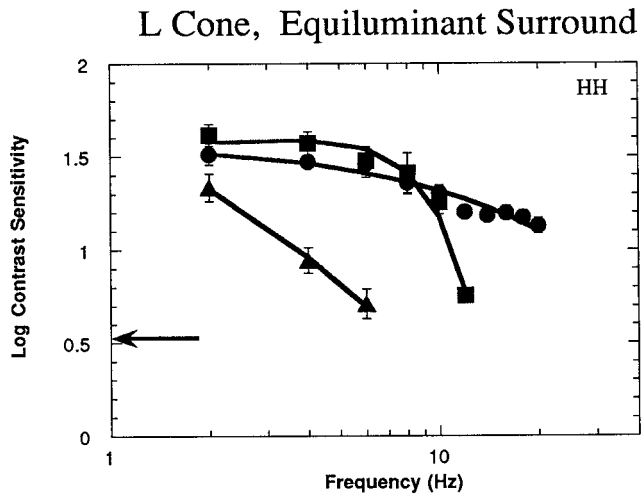


FIG. 3. Temporal contrast sensitivity functions of the S, M, and L cones with equiluminant surround for subject HH. The format is the same as for Fig. 2.

FIG. 4. Temporal contrast sensitivity functions of the S, M, and L cones with dark surround for subject HS. The format is the same as for Fig. 2.

The S cone is known to provide vigorous input to the chromatic pathway, but negligible or no input to the achromatic pathway¹⁰; the temporal contrast sensitivity of the S

cone is more likely to represent the property of the S cone and its pathway.

Measurements of scotopic temporal contrast sensitivity

functions in normal observers with neutral chromatic adaptation have been typically restricted to light levels below 1 scotopic td.^{11,12} The technique presented here allows measurements at levels high into the low photopic region without using a long wavelength adapting field. The rod temporal contrast sensitivity functions showed maximal sensitivity at intermediate light levels. This pattern is consistent with rod monochromat data^{13,14} in exhibiting rising contrast sensitivity with increasing retinal illuminance from scotopic to mesopic light levels, and decreasing contrast sensitivity with further increases in retinal illuminance into the photopic range. The effect was more pronounced when an equiluminant surround was present. Perhaps, in the dark

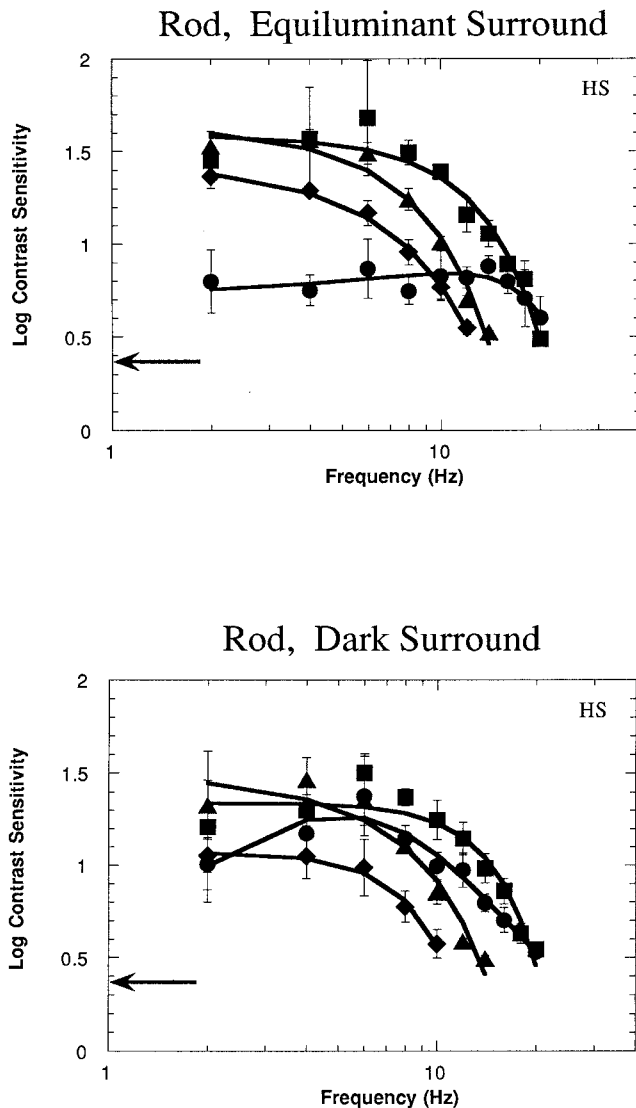


FIG. 5. Temporal contrast sensitivity functions of the rods for subject HS: (upper panel) data obtained with an equiluminant surround; (lower panel) data obtained with a dark surround. Data are shown for four light levels: (circle) 50 td, (square) 5 td, (triangle) 0.5 td, (diamond) 0.05 td. Solid lines represent fits of sums of two Gaussian functions. Error bars show standard deviations. The arrows show the maximum available contrasts.

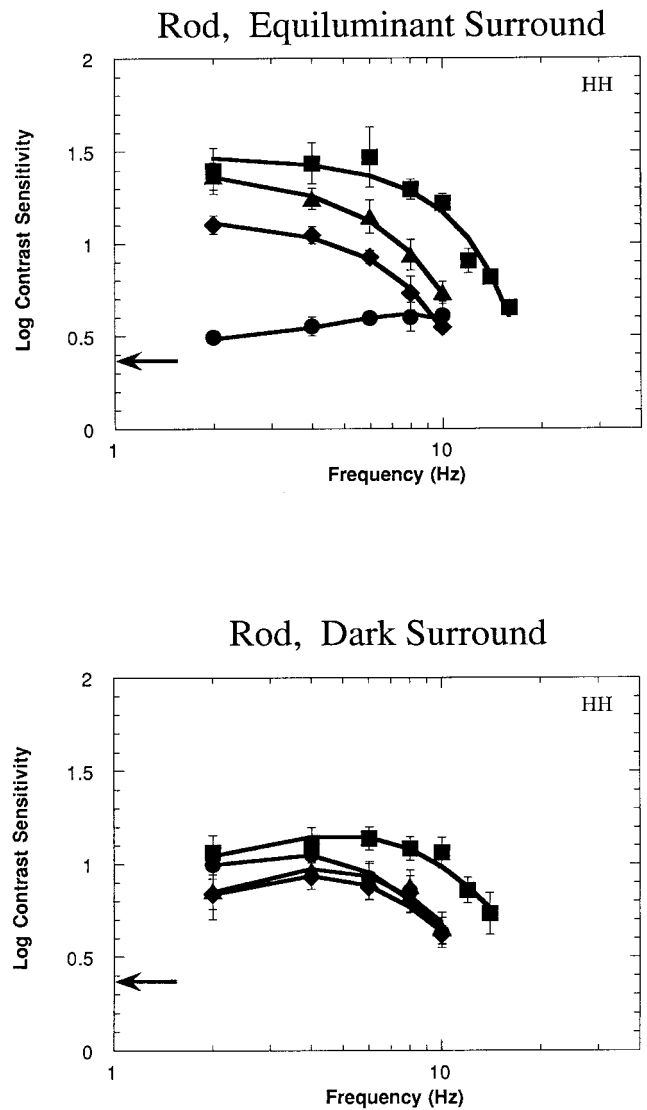


FIG. 6. Temporal contrast sensitivity functions of the rods for subject HH. The format is the same as for Fig. 5.

surround condition, flicker was detected outside of the stimulus area due to spread light.

The 4-primary colorimetric technique offers unique advantages over other procedures designed to favor rod vision. For example, it does not require a high degree of head stabilization compared with methods that use an eccentric pupil entry position to take advantage of the difference in Stiles-Crawford functions between the rods and the cones.¹⁵ The technique allows control of stimulus chromaticity in contrast to the limited chromaticity of procedures that use long wavelength adapting fields to produce a rod sensitivity advantage.¹⁶

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