

Hue signals from short- and middle-wavelength-sensitive cones

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Hue sensations resulting from the selective stimulation of short-wavelength-sensitive (S) and middle-wavelength-sensitive (M) cones were deduced from measurements of spectral unique green and unique blue under conditions of high or low S-cone sensitivity relative to M- and long-wavelength-sensitive-cone sensitivity. Selective reduction of S-cone stimulation shifted unique blue toward shorter wavelengths and unique green toward longer wavelengths, implying losses of perceived yellowness and short-wavelength redness relative to perceived blueness. The results imply that, under achromatic adaptation conditions, M-cone stimulation yields a sensation of predominately bluish cyan and S-cone stimulation yields a sensation of predominately reddish magenta. S-cone stimulation also appears to be indirectly responsible for yellowish sensations at long wavelengths and, by cancellation of the M-cone blueness signal, for greenish sensations at middle wavelengths.

A central goal of color vision research is to understand how responses from the cone photoreceptors are transformed to produce hue sensations. Current models of trichromatic color vision postulate that the visual system transforms univariate (i.e., color-blind) responses from three cone types into color sensations consisting of an achromatic dimension and two chromatic dimensions. In the chromatic dimensions the four perceptually fundamental hues (red, yellow, green, and blue) are organized into two mutually exclusive opponent pairs (red-green and yellow-blue). As illustrated in Fig. 1A, short-wavelength-sensitive (S) cones typically are modeled as contributing to blueness and redness, middle-wavelength-sensitive (M) cones to greenness and yellowness, and long-wavelength-sensitive (L) cones to redness and yellowness.¹ Thus this model predicts that exclusive stimulation of S, M, or L cones would produce reddish-blue, yellowish-green, or yellowish-red sensations, respectively.²

M cones are more sensitive than L cones in the short-wavelength half of the visible spectrum. Therefore when S-cone signals are selectively removed, the conventional model predicts that short-wavelength stimuli will appear yellowish-green with no trace of redness or blueness. Also, as S-cone sensitivity is reduced, the conventional model predicts that unique green and unique blue will both shift toward shorter wavelengths.^{3,4}

Contrary to the predictions of the conventional model, the results of previous studies suggest that blueness sensations at short wavelengths are poorly correlated with S-cone sensitivity. Subjects who are reported to have acquired unilateral tritanopia (selective loss of S-cone function) describe long-wavelength lights as predominately red and short-wavelength lights as predominately blue; yellow and green sensations are either weak or absent.⁵ Although these observations must be interpreted cautiously, for the color deficiency is produced by acquired disease and neither the normality of the fellow eye nor the normality of the L- and M-cone pathways in the affected eye can be guaranteed, normal subjects report similar hue sensations for small stimuli presented at the center of the fovea⁶ or in the peripheral retina,⁷

where S cones are relatively scarce. Also contrary to the predictions of the conventional model, at low adapting intensities⁸ (where S cones are relatively insensitive) yellow and green sensations are reduced, and unique green moves to longer wavelengths.^{8,9}

In this Communication I compare the wavelengths of spectral unique green and unique blue under conditions in which S-cone sensitivity is either high or low relative to L- and M-cone sensitivities. Relative S-cone sensitivity was manipulated by changing the stimulus size, duration, intensity, and retinal eccentricity; that is, low S-cone sensitivity is associated with small size, brief duration, and foveal location,¹⁰ and with high intensities because of the limited response range¹¹ of S cones. Also, under conditions of low relative S-cone sensitivity, S-cone signals theoretically could be eliminated entirely by keeping the stimulus intensity below the S-cone threshold. Possible rod contributions to blueness¹² were minimized with a photopic, perceptually achromatic background field.¹³ Because the background continuously stimulated all three cone types, here I use sensitivity to refer to the differential sensitivity to an incremental test stimulus.

Under stimulus conditions that selectively reduce the sensitivity of S cones, spectral unique blue shifts to shorter wavelengths as expected, but spectral unique green shifts to longer wavelengths. This result disagrees with the conventional model but agrees with other types of evidence regarding tritanopic color perception. Two modifications to the conventional color-transformation model, shown in Fig. 1B, can account for the data.

Unique hues were measured with a constant-stimulus technique. On the basis of informal preliminary observations, three to five wavelengths, 5-nm apart, were preselected to cover a range that included the estimated wavelength of the unique, or equilibrium, hue.³ Increment thresholds for all stimuli were then measured by an adjustment method. The subject controlled the stimulus presentation switch in order to maximize fixation accuracy. For the hue judgments, the stimulus intensities were set to the desired

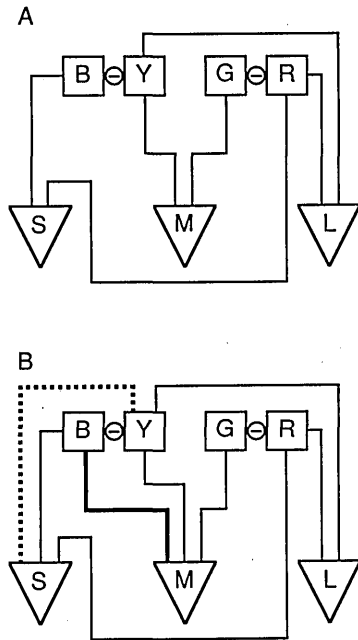


Fig. 1. A, Conventional wiring-diagram model of transformations from cone responses to hue sensations. Triangular boxes indicate L-, M-, and S-cone types. Centers of red (R), yellow (Y), green (G), and blue (B) color sensations are indicated by square boxes linked by opponent operators, which are shown as circled minuses. These operators do not necessarily represent linear subtraction but merely mutual exclusivity between opponent hues. Connecting lines indicate contributions from cone types to hue centers. Transformations for achromatic sensations are not included. B, Modified color-transformation model, incorporating an M-cone contribution to blueness (heavy solid line) and a special indirect S-cone contribution to yellowness (heavy dotted line).

amount above threshold by removing a fixed neutral-density filter and then were presented in pseudorandom order until each wavelength had been presented at least five times. After each flash, the subject reported which of the nonequilibrium hues was visible. No equilibrium hue responses were permitted; that is, yellow and blue were the only permitted responses for unique green measurements, and red and green were the only permitted responses for unique blue measurements. The equilibrium point was taken to be the wavelength (interpolated if necessary) that elicited an equal number of each type of response.

Unique green and unique blue wavelengths were measured foveally for stimulus sizes and durations that were designed to produce a range of relative S-cone sensitivities. Figure 2A shows data for a single subject with normal color vision. Qualitatively similar results were obtained from three additional normal subjects.¹⁴ Large long-duration stimuli (2° diameter, 1-sec duration), which produce the highest S-cone sensitivity, yielded unique green and unique blue wavelengths of approximately 500 and 480 nm, respectively. Reducing the stimulus diameter to 10' raised the unique green wavelength to 545 nm and lowered the unique blue wavelength to approximately 430 nm. Reducing the duration of the 10' stimulus to 50 msec (circular symbols, Fig. 2A) further lowered unique blue to 415 nm and appeared to lower unique green to approximately 530 nm. This unique green result, however, is probably an artifact related to a general loss of chromatic sensitivity. The stim-

uli appeared desaturated in the 520–570-nm wavelength region, and no green could be seen at or above the measured yellow–blue equilibrium wavelength. In fact, this point could be described better as the lower boundary of a broad neutral zone, or achromatic region, that was called yellow only because it was the only permissible response other than blue. The short-wavelength red–green equilibrium point also was almost achromatic but was clearly bounded by red below and green above, even though the green was a minor component of a predominately bluish cyan. This cyan hue appeared roughly equivalent to that of a large long-duration stimulus of 485 nm. It was virtually constant between 415 and 530 nm, although saturation was obviously greater toward the middle of the range.

Figure 2B shows a comparison of unique hues for 10'-diameter, 1-sec-duration stimuli at eccentricities of 0 and 1°. Although S cones are sparse at the center of the foveola, they are near their greatest concentration at 1° eccentricity.¹⁵ On the other hand, the area of spatial summation increases with eccentricity for S cones as it does for L and M cones,¹⁶ making the effective size of the target even smaller at 1° than at 0°. If stimulus size were the critical factor, the eccentric green and unique blue wavelengths therefore would resemble results for a foveal target even smaller than 10'. Instead, the eccentric results resemble those for a larger foveal target, indicating that the extreme values for the 10' foveal target are related to low S-cone stimulation rather than to small stimulus size *per se*. It is also worth noting that a rod contribution to blueness at the 1° eccentricity should not affect the unique blue wavelength and should shift unique green to a longer wavelength than the foveal setting, opposite in direction to the observed shift.

If foveal tritanopia is caused by a scarcity or relative insensitivity of foveal S cones rather than their complete absence, it might be less pronounced at stimulus intensities well above the S-cone threshold. This prediction was tested by measuring foveal unique green and unique blue wavelengths with the 10'-diameter, 1-sec target at four intensities of approximately 0.5, 1.0, 1.5, and 2.0 log units above threshold. Figure 2C shows the result. The unique green wavelength becomes progressively shorter, and the perception of green grows dramatically with increasing intensity, which is in agreement with the prediction. The unique blue wavelength, however, reaches a maximum approximately 1 log unit above threshold and then becomes shorter again. This reversal is consistent with findings that the dynamic range of the S-cone response is limited to between 1 and 2 log units.¹¹ As intensity increases, the S-cone response reaches its maximum while the M- and L-cone responses continue to grow, resulting in an increasingly tritanopic overall response. No reversal occurs for unique green, nor is one expected; S cones are so insensitive in this wavelength range that they begin to function only at high-luminance contrasts.

It is interesting to compare the unique hue shifts in Fig. 2C with the well-known Bezold–Brücke hue shift,¹⁷ which is the effect of increasing intensity on the hues of spectral stimuli. The stimuli for Bezold–Brücke experiments typically are presented on a dark background rather than on a photopic white background, as in the present study. As stimulus intensity increases, yellow and blue hues spread over larger portions of the spectrum. This effect traditionally has been explained by postulating a steeper gain function for the

yellow-blue than for the red-green opponent mechanism.¹⁸ The present findings, however, suggest the possibility that blue and yellow are dominant at high intensities because S cones are saturated at short wavelengths¹⁹ but are functioning optimally at long wavelengths.

At short wavelengths, the small brief condition and the large long-duration condition shown in Fig. 2A appear to differ mainly in relative S-cone sensitivity. Since the short-wavelength red-green equilibrium hue for the small brief target appeared to be nearly achromatic, I attempted to observe the hue generated by S cones directly by presenting a large long-duration target of the same wavelength, i.e., 415 nm. The result of this exercise was startling; the target appeared *pink* rather than violet. In other words, it was mainly red mixed with only a small amount of blue. A

quantitative color-naming study, reported elsewhere,²⁰ showed that when only S cones are stimulated under the same adaptation conditions, the relative amount of redness can reach 90%, i.e., redder than a comparable 660-nm increment.

The present results shed new light on color perception under conditions of weak or absent S-cone stimulation. Compared with normal trichromatic vision, tritanopic vision can be characterized as a single color-opponent system in which the short-wavelength half of the spectrum is seen as varying saturations of a predominately bluish cyan and the long wavelength half is seen as varying saturations of a nearly pure red tinged with only a trace of yellow. No red is seen at short wavelengths, and no yellow-green is seen at middle wavelengths. Two neutral zones are present, one near 400

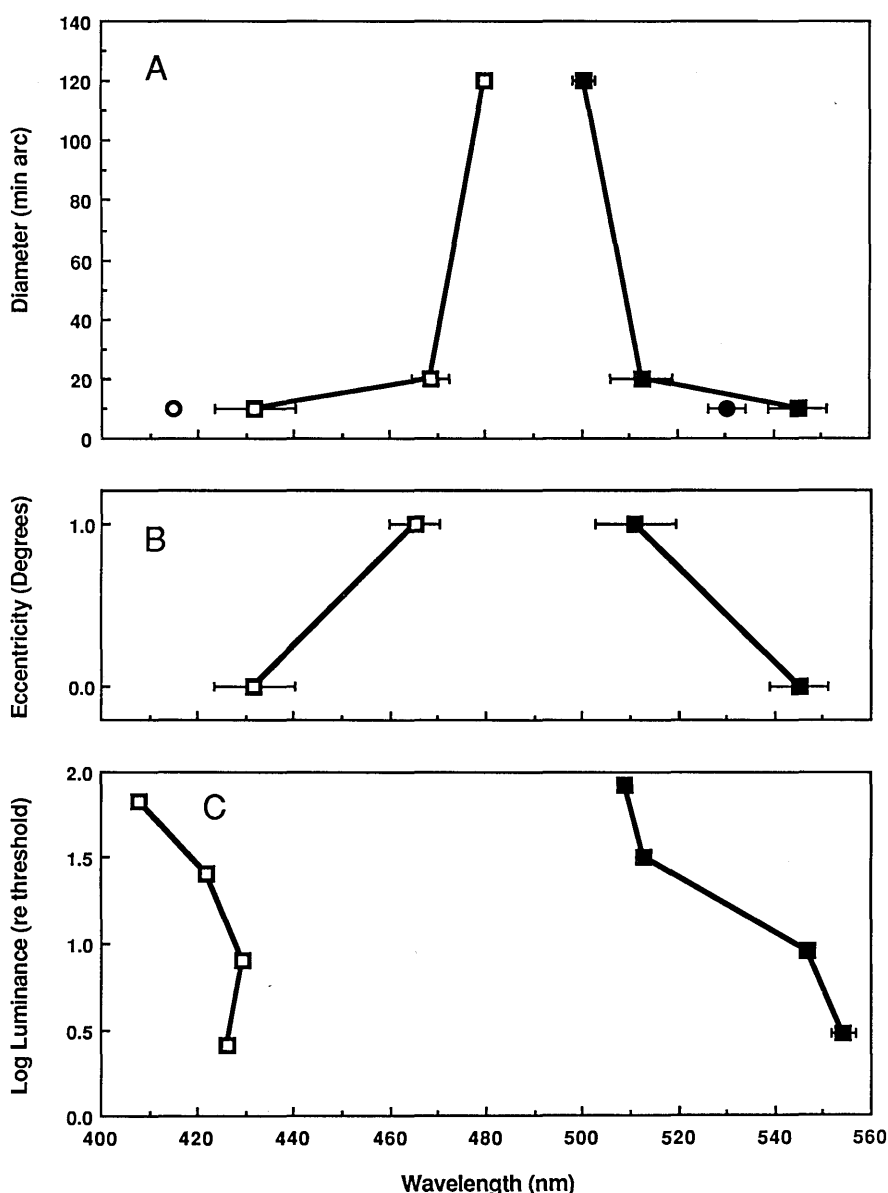


Fig. 2. Unique blue (open symbols) and unique green (filled symbols) wavelengths for one normal subject. Each data symbol indicates the mean of three to seven measurements. Error bars indicate standard deviations greater than 2 nm. A, Foveal measurements for 1-sec-duration stimuli as a function of diameter (squares) and 50-msec-duration stimuli at 10' diameter (circles). B, Measurements for 10'-diameter, 1-sec-duration stimuli at 0 and 1° eccentricity. Foveal data are copied from A. C, Measurements for foveal, 10'-diameter, 1-sec-duration stimuli as a function of luminance above threshold.

nm and the other near 570 nm. These findings lead directly to several surprising conclusions (from the standpoint of the conventional color vision model in Fig. 1A) about the roles of the M and S cones in color appearance. First, the M cones must mediate a major part of the blueness signal, probably even the dominant part for wavelengths greater than ~460 nm. Second, the S cones must be responsible for generating, or at least greatly amplifying, yellow sensations. The mechanism for this remains to be established, but the presence of yellow at wavelengths well beyond the range of S-cone sensitivity suggests an indirect mechanism, perhaps related to spatial and/or temporal chromatic contrast. Electrophysiological evidence that retinal ganglion cells receiving S-cone input are strongly inhibited by spatial or temporal transitions from white to yellow stimulus chromaticities, regardless of the polarity or magnitude of luminance contrast, also supports a spatiotemporal contrast mechanism.²¹ Third, the S cones must play a key role in the expression of green sensations. This cannot be a direct role, given the evidence that S cones mediate short-wavelength redness.²² The most straightforward interpretation is that yellowness cancels the blue component of the M-cone signal, thus revealing the green component. Fourth, S cones must be responsible for canceling the green component of the M-cone signal at short wavelengths, thus dictating the unique blue wavelength. This is similar to the conventional interpretation except that most of the blueness signal, at least at wavelengths above 460 nm, is probably produced by M cones rather than by S cones.

The above deductions can be incorporated into a modified color-transformation model, shown in Fig. 1B. Only two additional connections are necessary to account for the changes in color vision that accompany the loss of S-cone stimulation: first, the addition of an M-cone contribution to the blueness signal (heavy solid line, Fig. 1B) and second, an indirect S-cone contribution to the yellowness signal (shown as a heavy dotted line in Fig. 1B and tentatively operationalized as an inhibitory successive contrast response to white-yellow chromatic transitions). Given that the S cones have long been known as "blue" cones and often have been assumed to be concerned primarily with signaling blueness, it is ironic to find that they are actually more essential for signaling greenness, yellowness, and (short-wavelength) redness than for signaling blueness.

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REFERENCES AND NOTES

1. Representative examples of this model can be found in L. M. Hurvich, *Color Vision* (Sinauer, New York, 1982), pp. 128-135, and R. M. Boynton, *Human Color Vision* (Holt, Rinehart and Winston, New York, 1979), pp. 211-215. A notable exception is the model of C. R. Ingling, Jr., and B. H.-P. Tsou ["Orthogonal combination of the three visual channels," *Vision Res.* 17, 1075-1082 (1977)], in which M cones also contribute to the blueness signal.
2. The univariance of single cone types implies only that the responses to any two wavelengths can be made identical with suitable adjustments of intensity. It does *not* imply a lack of perceived color when only one cone type is stimulated. For example, it is easy to demonstrate with long-wavelength foveal stimuli in the dark-adapted eye that exclusive L-cone stimulation produces a predominately reddish hue sensation.
3. The unique hues are defined as lights that produce perceptually pure sensations containing only one of the four fundamental hues of red, yellow, green, or blue. Along with the achromatic colors (white, gray, and black), they compose the set of equilibrium hues for which the response of at least one of the color-opponent systems is zero. Thus unique red and unique green are yellow-blue equilibria and unique yellow and unique blue are red-green equilibria.
4. This paper is concerned with manipulating relative cone contributions to color perception, which is *not* necessarily the same as manipulating relative responses of the cones themselves. Perception does not occur at the photoreceptors but only after many intervening stages of neural processing that may substantially alter the space-, time-, and intensity-dependent properties of the visual signal. Thus the term cone sensitivity is used here to mean the sensitivity of the entire visual system to stimuli that produce responses in one or more of the L-, M-, and S-cone classes.
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10. The phenomena of small field tritanopia [G. S. Brindley, "The summation areas of human colour-receptive mechanisms at increment threshold," *J. Physiol. (London)*, 124, 400-408 (1954)] and foveal tritanopia [D. R. Williams, D. I. A. MacLeod, and M. Hayhoe, "Foveal tritanopia," *Vision Res.* 21, 1341-1356 (1981)] are well-known consequences of the relative scarcity of S cones in comparison with L and M cones, especially in the central foveola. Brief stimulus duration takes advantage of the supposed slow temporal response of S cones [D. O. Weitzman and J. A. S. Kinney, "Appearance of color for small, brief, spectral stimuli in the central fovea," *J. Opt. Soc. Am.* 57, 665-670 (1967)]. Some recent evidence [A. Stockman and D. I. A. MacLeod, "Visible beats from invisible flickering lights: evidence that blue-sensitive cones respond to rapid flicker," *Invest. Ophthalmol. Vis. Sci. Suppl.* 27, 71 (1986); A. Stockman, D. I. A. MacLeod, and D. D. DePriest, "An inverted S-cone input to the luminance channel: evidence for two processes in S-cone flick-