

## Blue-sensitive cones do not contribute to luminance

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By using violet backgrounds we selectively altered blue-cone sensitivity but found no change in flicker photometric sensitivity. This indicates that blue cones do not contribute to luminance as defined by flicker photometry.

There is no compelling evidence in the literature for or against a blue-cone contribution to luminance as measured by flicker photometry. There is a general consensus that any blue-cone contribution is small relative to that of the red and green cones, but there are conflicting opinions as to just how small. Vos and Walraven<sup>1</sup> assumed that luminance represents a summation of outputs of all three cone types. With this assumption they deduced that  $B$  crosses  $G$  at about 425 nm where  $B$  and  $G$  represent the spectral sensitivities of the blue-sensitive and green-sensitive cones, respectively, normalized to represent relative luminance contributions. Walraven<sup>2</sup> revised his estimates so that  $B$  and  $G$  crossed near 435 nm. On the other hand, Smith and Pokorny<sup>3</sup> worked with the assumption that blue cones do not contribute to luminance, and noted that lowering the test frequencies and luminances for heterochromatic flicker photometry did not seem to alter sensitivities as might have been expected if, in fact, blue cones did contribute to luminance.

Wagner and Boynton<sup>4</sup> have shown that MDB and flicker photometry seem to be nearly equivalent measures of luminance. Tansley and Boynton<sup>5</sup> have shown that blue-cone activity does not influence border perception, implying blue cones do not contribute to luminance as measured by MDB. This suggests that the blue cones do not contribute to luminance as defined operationally by flicker photometry. But a small blue-cone contribution cannot be ruled out.

One of the problems in deciding whether or not blue cones do contribute to luminance is that there are large interobserver differences in sensitivity at short wavelengths, where the blue

cones would be expected to contribute, chiefly because of great individual differences in preretinal absorption at these wavelengths (cf. Wright<sup>6</sup>). Calibration errors, greatest usually at short wavelengths, may disguise small blue-cone contributions as well. This makes it quite difficult to deduce the relative blue-cone contribution to luminance accurately with a curve fitting approach.

An alternative approach is either to disadvantage or enhance the blue-cone contribution selectively and look for changes in flicker photometric sensitivity within a given observer. For instance, adding a violet background to the photometric field will desensitize the blue cones relative to the other two types with the consequence that any blue-cone contribution to luminance will be correspondingly reduced.

The experimental procedure for measuring flicker photometric sensitivity is to alternate two lights in counterphase and allow the observer to vary the radiance of one of them so as to minimize subjective flicker. Usually the frequency of alternation is chosen to be high enough to eliminate completely any perception of color changes. Observers can, however, minimize flicker even at low frequencies where the change of color is perceived along with any luminance flicker.<sup>7</sup> Equality of luminance is operationally defined by the radiance required for the variable light to cancel or minimize the flicker of the standard light, and measurement of that radiance for a series of monochromatic lights across the spectrum defines the flicker photometric luminosity curve.

In order to distinguish changes in the blue-cone contribution to luminance from changes in the red- and green-cone

contribution (for the added violet background might differentially depress the sensitivities of the red versus green cones), we employed a pair of tritanopic confusion wavelengths as our standard and test. If the blue cones do not contribute to luminance there should be no modulation of either red or green cone excitation when the radiance of the test is set so as to produce a flicker photometric null with the standard. This result should apply for any frequency of flicker, because the quantum catch for each of those two cone types, but not the blue cones, is then the same for both standard and test. Adding a nonbleaching background will not disturb the equality and thus the null setting will not be disturbed. Any change in the null setting must be due to a blue-cone contribution.

We chose 439 and 492 nm as the standard and test, respectively, for observer AE, who has normal color vision, and 439 and 510 nm, respectively, for observer DM, who is deuteranomalous.<sup>8</sup> The standard and test were modulated in sinusoidal counterphase. They formed a 1.5° circular field which the observer fixated centrally. The observer adjusted the radiance of the test so as to eliminate or minimize subjective flicker. The peak luminance of the 439-nm standard was 10 td. The 492 and 510 nm stimuli each had a half bandwidth of 7 nm and the 439-nm stimulus had a half bandwidth of about 10 nm. They were supplied by a Maxwellian view system with effective pupil dimensions considerably smaller than the natural pupil. The circular violet background was of wavelength 420 nm. It was centered on the test field and extended beyond it to a diameter of 7°.

Since the blue cones may be poor at following rapid flicker,<sup>9</sup> we used frequencies of 10 Hz and less in order to maximize any blue cone effects. By using several frequencies, 2 Hz, 5 Hz, and 10 Hz, we had a second means of varying blue cone contribution to luminance since the lower frequencies would be expected to favor the blue cones more than higher frequencies.

The violet backgrounds ranged in luminance from near threshold, about 0.1 td, to 30 td. The brightest background induced a state of functional tritanopia so that no color difference could be seen between the test and standard alternating at 2 Hz. With this background the alternation was detected, if at all, only by attending to the slight misregistration and spatial nonuniformity of the test fields. With no background at all, as well as with the dimmer backgrounds, peripheral rods were sensitive enough to detect light scattered within the eye from the flickering fields. For these conditions observations were preceded by a white Ganzfeld bleaching exposure. Observations commenced 4 min after the bleaching exposure by which time the blue cones had regained their full sensitivity.<sup>10</sup> The observations continued until intrusion of the peripheral rods became apparent to the observer. Against the dimmer backgrounds the color differences between the alternating fields gave rise to "chromatic flicker" at 2 Hz and 5 Hz. Even so one observer found that this blue-green alternation did not affect his ability to make reliable flicker nulls. The other found this a problem at 2 Hz. At 10 Hz no chromatic flicker was ever seen. Each observer made four settings during each condition for which he felt he could make clearly defined settings.

If the blue cones were contributing in an additive fashion

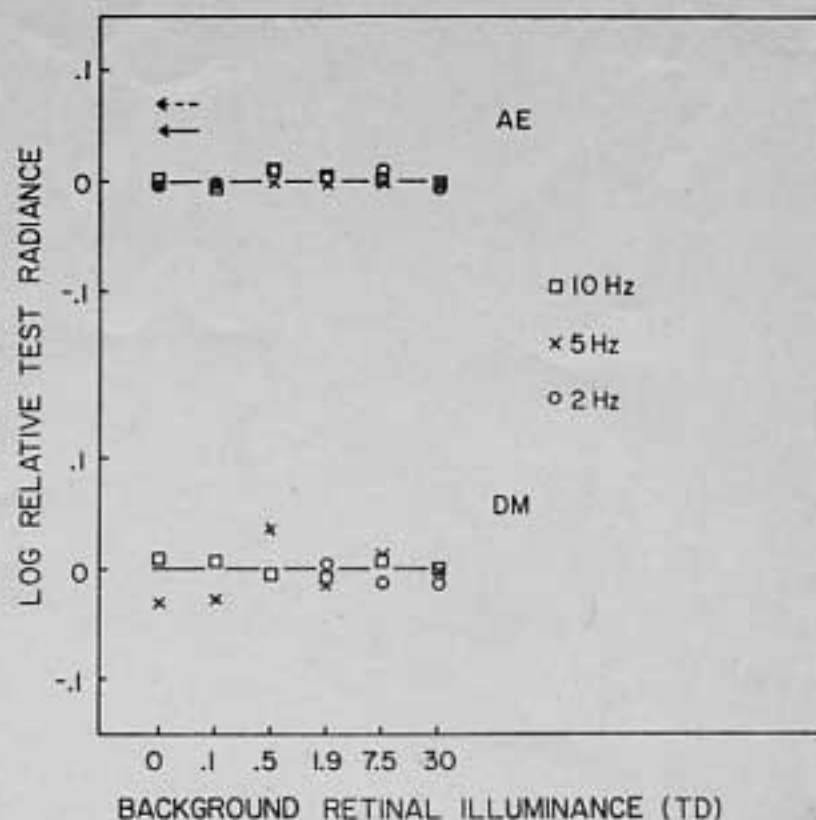


FIG. 1. Deviation of log test radiance from baseline as a function of background retinal illuminance where baseline is defined as the average test radiance for 10-Hz flicker. The heavy arrow indicates the expected difference in log test sensitivity between the 0 td and 30 td background conditions if blue and green cones contribute equally to luminance, as measured with 2 Hz flicker, at about 425 nm (Ref. 1); the dashed arrow indicates the difference if blue and green cones contribute equally at about 436 nm (Ref. 2).

to luminance, then the radiances of the midspectral test required to produce a null in flicker would decrease with increasing background luminance and with increasing frequency, since the 439-nm standard would lose the extra effectiveness derived from its greater blue-cone contribution. The actual radiances required were independent of both background luminance and frequency, indicating a lack of any measurable blue-cone contribution to luminance. The data are graphed in Fig. 1. The data for observer AE lie on a horizontal line and are superimposable across frequencies. The largest deviation from baseline is about 0.011 log unit. The greatest standard error of the mean is 0.007 log unit, with an average of less than 0.004 log unit. For observer DM the data are less exact but still show no systematic deviations that would indicate a blue-cone contribution. The largest deviation from baseline for DM is about 0.035 log unit, but deviations at 10 Hz, where the settings were subjectively least ambiguous, do not exceed 0.01 log unit. The greatest standard error of the mean is 0.01 log unit, with the average about 0.006 log unit. Any blue cone contribution, positive or negative, would have to be reflected by a shift of less than about 0.01 log unit for AE or about 0.02 log unit for DM; and contributions as small as this at 2 Hz imply still tinier contributions at the higher frequencies usually employed in flicker photometry. Theoretical proposals that include even a small blue cone contribution<sup>1,2</sup> make incorrect predictions for Fig. 1. For example, if the blue and green cones contributed equally to luminance (as measured with 2-Hz flicker) at about 425 nm,<sup>1</sup> the settings would have changed by about 0.05 log unit with changing background luminance. If the crosspoint were near 435 nm as suggested by Walraven<sup>2</sup> then there would have been a shift from baseline of about 0.07 log unit.<sup>11</sup> A third (normal)



observer was tested at frequencies of 5, 10, and 15 Hz. Settings fell within 0.01 log unit of baseline with the exception of the 5-Hz dark-adapted condition, where there was a shift of less than 0.04 log unit in the direction consistent with a slight negative blue-cone contribution.

Might a significant blue-cone contribution be present under conditions different from the ones investigated here? We consider it unlikely. The 439-nm standard was roughly 25 times more effective in quanta absorbed/deg<sup>2</sup>/s for the blue cones than the 492-nm test thus giving an effective blue cone modulation of more than 90%. Use of an even shorter wavelength standard could have provided only slightly greater blue-cone excitation at a given photopic luminance. Use of a long wavelength background, however, could favor the blue cones appreciably more by selectively desensitizing the red and green cones. With this in mind we repeated the basic experiment on AE with a 60 td 563 nm background always present and found still no evidence of any blue-cone contribution.

The results, therefore, show beyond reasonable doubt that the blue cones make no significant contribution to luminance.

## ACKNOWLEDGMENT

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- <sup>1</sup>J. J. Vos and P. L. Walraven, "On the derivation of the foveal receptor primaries," *Vision Res.* 11, 799-818 (1971).
- <sup>2</sup>P. L. Walraven, "A closer look at the tritanopic convergence point," *Vision Res.* 14, 1339-1343 (1974).
- <sup>3</sup>V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," *Vision Res.* 15, 161-171 (1975).
- <sup>4</sup>G. Wagner and R. M. Boynton, "A comparison of four methods of heterochromatic photometry," *J. Opt. Soc. Am.* 62, 1508-1515 (1972).
- <sup>5</sup>B. W. Tansley and R. M. Boynton, "Chromatic border perception: the role of red- and green-sensitive cones," *Vision Res.* 18, 683-697 (1978).
- <sup>6</sup>W. D. Wright, "The characteristics of tritanopia," *J. Opt. Soc. Am.* 42, 509-521 (1952).

<sup>7</sup>M. Ikeda and H. Shimozono, "Luminous efficiency functions determined by successive brightness matching," *J. Opt. Soc. Am.* 68, 1767-1771 (1978).

<sup>8</sup>These wavelengths were selected for each observer as producing the same ratio of red to green cone excitation on the basis of their similar appearance when viewed side by side in a bipartite field upon a 30 td 420 nm background which desensitized the blue cones. When AE searched for a wavelength to match 439 nm under these conditions, the range of matches included 492 nm. 439 nm and 492 nm also agree well with Walraven's summary of tritanopic metamers (Ref. 2) as well as being concordant with Smith and Pokorny's estimates of  $M$  and  $L$ . For the anomalous observer, 510 nm was near the center of the matching range. We determined that a 30 td 420 nm background has at most a small effect on the relative red versus green cone contributions to luminance, so the choice of wavelengths is not very critical: an error of up to 10 nm in the chosen test for the normal observers would produce only negligible deviations in the data. The latitude for the deuteranomalous observer is even greater.

<sup>9</sup>G. S. Brindley, J. J. DuCroz, and W. A. H. Rushton, "The flicker fusion frequency of the blue sensitive mechanism of colour vision," *J. Physiol. (London)* 183, 497-500 (1966). D. H. Kelly, "Spatio-temporal frequency characteristics of color-vision mechanisms," *J. Opt. Soc. Am.* 64, 983-990 (1974). The amply documented inability to detect rapid modulation of blue-cone excitation could be due either to limitations of the receptors themselves or of the pathways through which they must transmit their signals. This distinction is not an essential one here, however, since in either case increasing the flicker frequency should reduce the effectiveness of blue-cone output.

<sup>10</sup>This was ascertained by recording thresholds as a function of time after the bleaching exposure, for a 420-nm test spot upon a 220 td 574 nm background.

<sup>11</sup>In making these predictions we assumed that flicker is minimized when

$$k_R R_{439} + k_G G_{439} + k_B B_{439} = c(k_R R_\lambda + k_G G_\lambda + k_B B_\lambda)$$

where  $k_R$ ,  $k_G$ , and  $k_B$  reflect red, green, or blue cone sensitivity in the presence of some background and  $c$  reflects the radiance the observer must set to minimize flicker.  $k_R$  is about equal to  $k_G$ .  $R_\lambda$ ,  $G_\lambda$ , and  $B_\lambda$  are taken from either Vos and Walraven<sup>1</sup> or Walraven.<sup>2</sup> We estimated the depression in red and green cone sensitivities by determining thresholds for detecting 2-Hz flicker of a 492-nm test upon the 420-nm background. We found a total depression, at the highest background luminance, of about 0.4 log unit, to about 40% of the dark adapted sensitivity. To estimate the depression in sensitivity of the blue cones we noted the effects of the various backgrounds on the visibility of 2-Hz chromatic flicker produced by an alternation of standard and equiluminous test. The intensities required for detecting chromatic changes at 2-Hz varied by a factor of at least 8 for AE and at least 10 for DM as a function of background intensity. Thus the background did fulfill its intended function of selectivity depressing blue cone sensitivity.