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SPECTRAL SENSITIVITY OF LONG-WAVELENGTH-SENSITIVE PHOTORECEPTORS IN DICHROMATS DETERMINED BY ELIMINATION OF BORDER PERCEPTS[1]

BRIAN W. TANSLEY[2] and ROBERT J. GLUSHKO
Psychology Department, University of California, San Diego, La Jolla, CA, U.S.A.

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Abstract—Whatever the spectral distribution of the two components of a split field, the border separating them can be made to disappear completely for protanopes and deuteranopes. The relative energies required for border disappearance can be used to specify the spectral sensitivity of the remaining cone type. The results imply a loss of spatial vision for these dichromats under conditions where normal subjects can easily make discriminations.

INTRODUCTION

Tansley and Boynton (1976) recently demonstrated that the two long-wavelength-sensitive cone types (R and G cones) of the trichromatic eye were the sole contributors to the perception of borders formed by lights of equal luminance. Tansley and Boynton's results suggest that the B cones do not contribute to border perception, which turn implies that the elimination of the percept of the border between lights of different spectral energy distribution equates such stimuli for the quantal catch of R and G cones.

Only a particular set of lights at the minimally distinct border setting (MDB) will fail to support a contour between them. For the trichromatic observer such lights all plot along a tritanopic confusion line in chromaticity space. Any observable color or brightness difference between the lights of such a set can only be due to the differential activity of the B cones.

Consider the protanope and deuteranope, each of whom functionally lacks one of the long-wavelength-sensitive cone types, but who possesses B cones. For these two types of dichromat, it would seem from the above argument that each has only one cone type remaining that contributes to the perception of borders. Equating the quantal catch for the contributing cone type should then eliminate the perceived contour in a bipartite field configuration.

Assuming that protanopia and deuteranopia are reduced forms of normal color vision, the no-border condition can be expressed in the following way:

Bipartite Field
(left) (right)

$$\text{Trichromat:}\quad \text{when} \int_{400}^{700} g_\lambda N_\lambda^{\mathrm{L}}\,\mathrm{d}\lambda = \int g_\lambda N_\lambda^{\mathrm{R}}\,\mathrm{d}\lambda$$

$$\text{and} \quad \int r_\lambda N_\lambda^{\mathrm{L}}\,\mathrm{d}\lambda = \int r_\lambda N_\lambda^{\mathrm{R}}\,\mathrm{d}\lambda;\ (1)$$

$$\text{Protanope:}\quad \text{when} \int g_\lambda N_\lambda^{\mathrm{L}}\,\mathrm{d}\lambda = \int g_\lambda N_\lambda^{\mathrm{R}}\,\mathrm{d}\lambda;\ (2)$$

$$\text{Deuteranope:}\quad \text{when} \int r_\lambda N_\lambda^{\mathrm{L}}\,\mathrm{d}\lambda = \int r_\lambda N_\lambda^{\mathrm{R}}\,\mathrm{d}\lambda.\ (3)$$

In these equations, r_λ and g_λ are the spectral response functions of the R and G cones, respectively, and N_λ^{L} and N_λ^{R} are the relative spectral radiance values for the light from the left and right hemifields, respectively.

If the above reasoning is correct, the following predictions can be made:

1. For any two lights presented in a bipartite field configuration, a protanope or a deuteranope should be able to find a radiance of one light relative to the other such that the percept of a border formed between the two hemifields can be made to disappear.
2. The spectral sensitivity of the G cone in the protanope and the R cone in the deuteranope can be determined by the elimination of border contour such that equations (2) and (3) are satisfied, respectively, for each type of dichromat.

The purpose of this paper is to report two experiments which test these predictions.

SELECTION OF DICHROMATS

(i) *Initial screening*

Our selection of protanopes and deuteranopes for these experiments required a large battery of tests. We set rather stringent diagnostic criteria for this study and approximately 75% of the color-weak observers tested failed to meet our standards. From responses to an advertisement in the campus newspaper, and from in-class appeals, we tested a large number of individuals who suspected that they were "colorblind". Each observer was initially screened with the use of the Ishihara and Dvorine Pseudoisochromatic plates, the Farnsworth-Munsell 100-hue test, the H and D Color-Rule and the Nagel Anamaloscope (Rayleigh equation). The reflectance-type color screening tests were illuminated with a Macbeth Daylight lamp. From the results obtained from these

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[2] Current address: Psychology Department, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada.

tests a small group of "potential protanopes and deuteranopes" were chosen. They were further tested, and remained in the study if the following criteria were met:

(a) They failed all of the Pseudoisochromatic plates relating to red–green defects in both the Dvorine and the Ishihara;

(b) They gave error scores of greater than 200 on the F–M 100-hue test in non-random fashion;

(c) They met the criterion for red–green dichromacy on the H and D Color-Rule as established by Biersdorf (1977);

(d) With suitable adjustments of the luminance of the yellow standard of the anomaloscope, they could find a color and brightness match between *any* ratio of the red and green primaries in the Rayleigh equation and the yellow standard.

(ii) *Selection of protanopic and deuteranopic observers*

Subsequent to this initial screening, each of the smaller group of these observers was recalled and tested further. All of the tests reported in this section were performed monocularly (right eye only).

First, each observer was retested with the Pseudoisochromatic plates and the 100-hue test, under the illumination from a Macbeth Daylight lamp. Spectral neutral point determinations were carried out, as was suggested by Bailey and Massoff (1974), by having the observers find a spectral color that matched illuminant "C". In general, there were two reasonably discrete neutral point distributions, although the subsequently diagnosed deuteranopes appear to have a larger range of values than the protanopes. Each observer saw no color difference when asked to compare a series of spectral lights ranging from 525 to 640 nm against a 640 nm standard. In addition, the suspected protanopes were shown a 640 nm spectral light and asked to adjust the radiance of this stimulus until it could not be seen. This radiance was much higher than the settings made by normals, deuteranopes and one protanomalous observer previously screened out.

From the smaller group of observers tested in the manner above, six protanopes and four deuteranopes were chosen. In addition to meeting the criteria of Section (i), then, observers showed no wavelength discriminations above 530 nm, failed all of the monocularly presented Pseudoisochromatic plates, and gave characteristic responses in neutral point determinations.

EXPERIMENT 1

This experiment was designed to test the first hypothesis stated in the introduction: protanopes and deuteranopes should be able to eliminate the contour separating any two lights by the suitable adjustment of the radiance of one of them.

Method

Apparatus. The apparatus used in this experiment was a two-channel colorimeter, fully described elsewhere (Tansley, 1976). The distinctive feature of this device is the precise spatial configuration of the bipartite field that the observer views. This field is made with the use of a beam-splitter cube that has been coated with an evaporated metal layer over one-half of the area of the surface of the hypotenuse of one of its prisms. The juxtaposition of the hemifields is such that when metameric lights of equal luminance are presented, no border is visible in the field and a single luminous circular field of uniform color and brightness is seen. Each channel has the capability of providing a mixture of broad-band filtered light plus a given monochromatic light to one of the hemifields. To correct for the axial chromatic aberration of the human eye, an achromatizing lens was positioned directly in front of the observer's eye. A small adjustment of the lens in a plane perpendicular to the optic axis of the apparatus was used to improve the alignment of heterochromatic light mixtures for a given observer. For stability, a dental bite bar mounted on an adjustable three-position stage was used. The diameter of the bipartite field of this apparatus subtended a visual angle of 1° 30′.

Procedure. Each of three protanopes and two deuteranopes was presented with a pair of lights, one to a hemifield, to the right eye. The 15 possible pairwise presentations of six stimuli whose chromaticities are shown in Fig. 1 were presented in randomized fashion. For each presentation, one of the two lights was set at a fixed retinal illuminance of 30 td while the luminance of the other could be adjusted by the observer. For a given pair, the subject's task was to adjust the luminance of one hemifield relative to the other while observing the border between the juxtaposed fields, and to note if there was any setting where the border disappeared or "melted away". Each observer was shown an isomeric pair of lights of unequal luminance and then shown the same pair at equal luminance to demonstrate that it was possible to produce an invisible border in the apparatus.

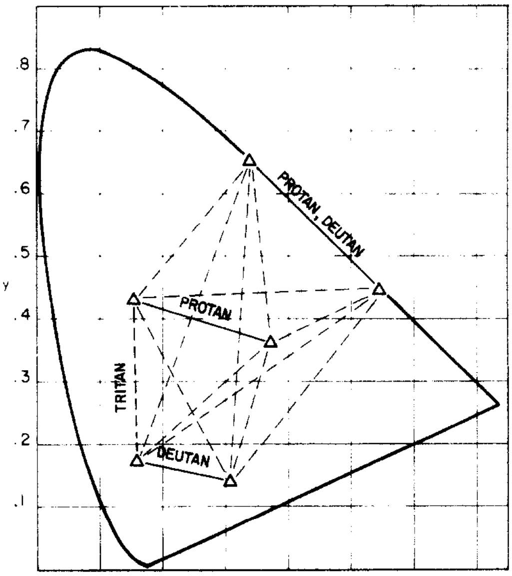

Fig. 1. Schematic representation of the chromaticities of each of the spectral and non-spectral lights used in experiment 1, plotted in the 1931 CIE (x,y) chromaticity space. As can be seen by reference to the labels, one pair will be seen as identical by both classes of dichromat while each class will see one other identical pair. All other pairwise comparisons of these chromaticities (connected by dotted lines) will be discriminably different with respect to color. Nevertheless, all of the observers in this study could eliminate the border between all 15 pairs.

As can be seen by reference to Fig. 1, some of the pairs of lights were complete matches for protanopes, while some other pairs could not be discriminated by deuteranopes. For either the protanope or the deuteranope, only two pairs would be color matches, one along the spectral locus and the other as shown in Fig. 1.

Results

The results of this experiment were as follows: each of the three protanopes and two deuteranopes could find a setting of the luminance of one hemifield relative to the other that eliminated the perception of a border between the hemifields. This could be done for every pair of stimuli presented, whether or not a color difference was perceived. These results support the first prediction stated in the introduction and provide further support of the notion that the B cones, whose level of activation differs for the two components of most pairs, do not contribute to the perception of borders.

EXPERIMENT 2

A second experiment was designed to test the hypothesis that the spectral sensitivity of the long-wavelength-sensitive cone type could be determined by the elimination of contour as a criterion. Wagner and Boynton (1972) have shown that the spectral luminous efficiency function obtained with the use of the MDB criterion is very nearly equivalent to that obtained by heterochromatic flicker photometry. Because of the more sluggish temporal response characteristics of the B cones (Boynton & Baron, 1975; Brindley, du Croz & Rushton, 1966; Kelly, 1974) one might expect the trichromatic luminous efficiency function obtained either way to be relatively unaffected by B cone responses. As a check on the comparability of flicker and MDB settings for equating lights of different color for the hypothesized achromatic activity of the visual system which they elicit, one of us (BWT) determined his spectral luminous efficiency function using both methods in the same apparatus. In order to achieve the levels of light required to maintain a constant adaptation level of 30 td throughout the experiment, a two-channel Maxwellian-view optical stimulator was used. For the main part of the experiment, where hypothesis 2 is tested, three protanopes and two deuteranopes were used. In effect, this experiment adds a fifth subject to the four already studied by Wagner and Boynton (1972).

Method

Apparatus. Figure 2 shows a schematic representation of the apparatus used in this study. In channel 1, white light from S_1 was filtered appropriately to provide a standard of constant retinal illuminance (30 td) whose color temperature was close to that of illuminant "C" ($x = 0.30$, $y = 0.31$). Calculation of the chromaticity of this light was carried out by the method of vector colorimetry (Guild, 1925). Channel 2 has the output from a Bausch and Lomb Hi-Intensity Grating Monochromator (GM) whose half-peak bandwidth was about 10 nm. The output from this channel could be continuously adjusted over a range of 2 log units with the use of a Kodak Inconel circular neutral density wedge (W), and discrete neutral density filters could be placed in filter holders in either channel (FH). The position of the circular neutral density wedge was determined by referring to the output of a digital voltmeter connected to a power supply and a variable resistor geared to the wedge shaft. Each channel could be presented in the opposing spatial or temporal configuration by manipulating the position of two apertures (A_1, A_2). These could be either full circular (for temporal alternation) or semi-circular (for spatial juxtaposition), and the alignment of one with respect to the other was accomplished through the use of a micropositioner (MP_1) to which the aperture holder of channel 2 was attached. Temporal alternation

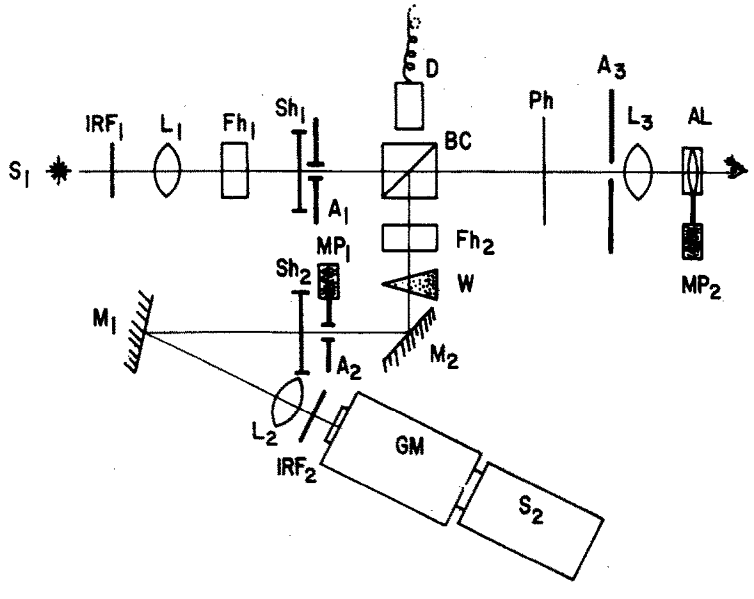

Fig. 2. Schematic layout of the Maxwellian-view optical stimulator used for studies reported in experiment 2. S = tungsten ribbon filament source; IRF = infrared-absorbers filter; L = lens; FH = filter holder; A = aperture (circular and semi-circular); SH = shutter; BC = beam-splitter cube; PH = pinhole aperture; M = first-surface mirror; MP = micropositioner; GM = grating monochromator; W = Kodak Inconel neutral density wedge; AL = achromatizing lens. The observer could adjust the semi-circular aperture (A_1) and the achromatizing lens to achieve precise alignment of the bipartite fields in the minimally-distinct border studies.

of the two channels was achieved with the use of two Uniblitz solenoid-operated shutters (Sh_1, Sh_2) driven by the appropriate electronics and triggered by an A.D. Data Systems digital timer. The diameter of the bipartite field subtended 1.2 degrees of visual angle. A dental bite bar mounted on a translation stage was used to provide the necessary stability for the observer, and the axial chromatic aberration of the eye was corrected with the use of an achromatizing lens fashioned on the formula of Bedford and Wyszecki (Wyszecki & Stiles, 1967).

Calibration of the rise and fall times of the two shutters was carried out with the use of a silicon photodiode circuit and Tektronix oscilloscope, and were within the manufacturer's specifications (minimum effective exposure of 1.5 msec). At the temporal alternation rates used there was no visible flicker when lights which were identical in spectral energy distribution and luminance were alternated. The radiant output of channel 2 was determined with the use of an EG&G Radiometer, whose detector head was positioned at D in Fig. 2. Spectral calibration of the monochromator was carried out by placing a series of discrete Fabry–Perot-type interference filters in the filter holder of channel 2 and adjusting the wavelength scale of the monochromator until the maximum radiometer reading was given to the same wavelength on the monochromator as that of a given interference filter. This was carried out for ten different filters, and the maximum error calculated after calibration was of the order of 2 nm from 400–680 nm. For lights below 480 nm a second order blocking filter was always used, both in calibration and in the experiments. The spectral sensitivity of the radiometer was checked in the following way. A Gamma Scientific luminance standard (whose spectral energy distribution had been recently measured for us at the manufacturer's facility) was placed directly in front of the radiometer head. Each of a set of ten interference filters, whose peak transmittances and bandwidths were known, was placed between the radiometer head and the luminance standard, and an average of 5 radiometer readings was determined at each wavelength. The relative radiance of each of the ten positions in the spectrum was then determined from the supplied calibration using the luminance standard, and each of these values was divided by the corresponding averaged reading. The resulting values were compared with the "characteristic" spectral sensitivity curve supplied with the radiometer. Where the values were discrepant, a correction factor was used in the subsequent measurements. Although more than these ten wavelengths were used in the studies reported here, they were representative of the spectral range, and the spectral sensitivity curve of the radiometer contained no sharp discontinuities.

Calibration of the retinal illuminance was carried out by the method described by Westheimer (1966). The maximum retinal illuminance obtainable at 400 nm was very nearly 30 td. All wavelengths longer than this could be presented at higher levels.

Part 1: Comparison of spectral luminous efficiency functions obtained by the heterochromatic flicker and minimally distinct border method.

Procedure (Flicker method). In this section of the experiment, observer BWT (who has normal visual acuity and normal trichromatic vision) was presented with the standard white light from channel 1 alternating with a given monochromatic light from channel 2. For each pair presented in this way, the observer's task was to adjust the radiance of the light from channel 2 until the perception of flicker was minimized. This was carried out for each of 29 monochromatic lights paired with the white from channel 1—a range of 410 to 690 nm in 10 nm steps. Five settings were made for each pair and the average of these values was calculated. This mean value was then used in the calibration procedure.

Two temporal frequencies were used: 33 Hz and 40 Hz. Only 7 points in the spectrum were chosen for the 40 Hz condition because of the limited time that the shutters could maintain such a high rate of alteration before failing to maintain calibrated exposure characteristics.

MDB method. The same observer carried out determinations of the spectral luminous efficiency function employing the MBD technique. For this part of the experiment, a continuously visible bipartite field was presented. The right hemifield contained the fixed white 30 td standard from Channel 1, while the left hemifield contained each of the 29 spectral lights in turn from channel 2.

For a given spectral light, the observer's task was to find the MDB point relative to the white standard. Five settings were made for each of the 29 pairs and the average of each set was used in the calibration procedure.

Results

Figure 3 shows the luminous efficiency functions obtained for observer BWT using the heterochromatic flicker and MDB methods. Plotted with these data is the modified luminous efficiency function, V_λ of Judd (Wyszecki & Stiles, 1967), and the flicker curve of Wagner and Boynton (1972) (which did not differ significantly from their MDB curve) for the average of four subjects. Although there is good agreement with Judd's function above about 490 nm, there is a discrepancy below this wavelength. The data of observer BWT suggest a greater sensitivity to lights of shorter wavelength. This is true for both the heterochromatic flicker and MDB determinations. It can be seen that the data obtained by both methods of heterochromatic photometry do not differ significantly from one another. This suggests that the short-wavelength-sensitive cones, or B cones, do not contribute to either function. Table 1 presents these data.

Part 2: The spectral sensitivity of the long-wavelength sensitive cone types found in the protanope and deuteranope determined by the MDB method.

Procedure. Three protanopes and two deuteranopes viewed the vipartite field with the use of a dental bite bar

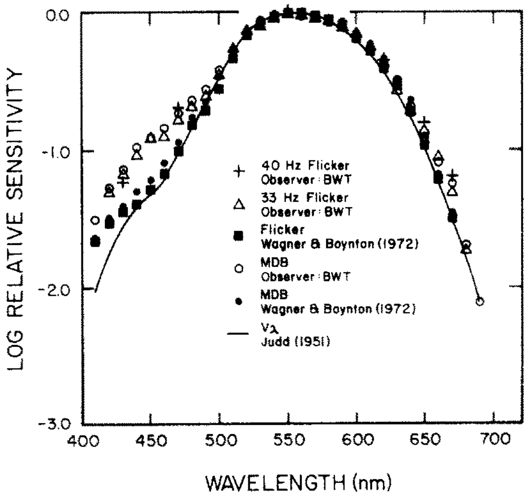

Fig. 3. Luminous efficiency functions for observer BWT (normal trichromat) obtained by two methods of photometry: heterochromatic flicker and the minimally distinct border criterion. Plotted with these results is Judd's (1951) modified visibility function, taken from Wyszecki and Stiles (1967), and data from the average of 4 observers (using the MDB method and heterochromatic flicker photometry) form Wagner and Boynton (1972).

Table 1. The relative spectral luminous efficiency function for observer BWT (trichromat) using two photometric methods

	Log relative sensitivity			
400	MDB	33 Hz	40 Hz	Judd (1951)
10	−1.50	—	—	−2.03
20	−1.27	−1.30	—	−1.76
30	−1.14	−1.17	−1.23	−1.56
40	−0.98	−1.03	—	−1.42
50	−0.91	−0.92	—	−1.33
60	−0.84	−0.90	—	−1.22
70	−0.73	−0.78	−0.695	−1.04
80	−0.64	−0.68	—	−0.86
90	−0.56	−0.60	—	−0.68
500	−0.42	−0.45	—	−0.49
10	−0.28	−0.25	—	−0.30
20	−0.16	−0.13	—	−0.149
30	−0.06	−0.09	—	−0.064
40	−0.03	−0.04	—	−0.02
50	0	0	0	−0.002
60	−0.025	−0.02	—	−0.002
70	−0.03	−0.035	—	−0.021
80	−0.07	−0.06	—	−0.06
90	−0.11	−0.105	—	−0.121
600	−0.16	−0.15	—	−0.200
10	−0.26	−0.25	—	−0.30
20	−0.375	−0.38	−0.35	−0.42
30	−0.49	−0.56	—	−0.577
40	−0.68	−0.71	—	−0.757
50	−0.91	−0.86	−0.80	−0.97
60	−1.09	−1.05	—	−1.215
70	−1.24	−1.31	−1.19	−1.495
80	−1.69	−1.73	—	−1.77
90	−2.11	—	—	−2.086
700	—	—	—	—

Included in this table are the values for Judd's modified luminous efficiency function (taken from Wyszecki and Stiles, 1967).

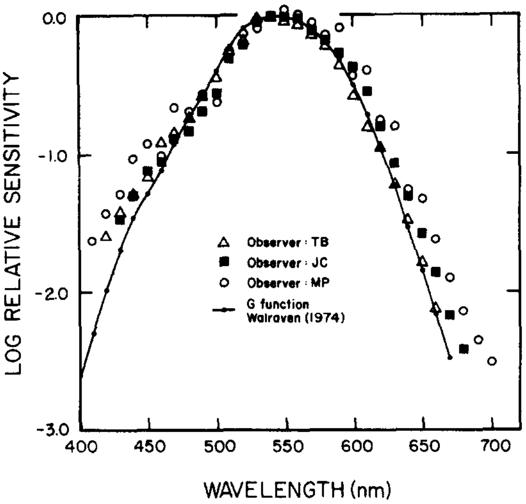

Fig. 4. The spectral sensitivity of the long-wavelength-sensitive cones of three protanopes determined by the elimination of the border in a bipartite field. Plotted with these data is Walraven's (1974) G function.

and spatially adjustable achromatizing lens. The dichromats were not required to find a *minimum* border but rather a setting for which *no* border was visible. A given pair of hemifields could be carefully aligned by changing the position of the semicircular aperture of channel 2 which defined the left bipartite field. Because these observers had some initial difficulties with the task, the position of the achromatizing lens was fixed by having each observer view the right white standard hemified by itself and allowing him to adjust the position of the lens until a sharp straight-edge was seen. Alignment of the left (spectral) hemified was done for each new monochromatic stimulus presented. The observer could tell that the alignment was incorrect if a bright or dark band appeared at the junction of the two hemifields. The observers were kept uninformed as to the spectral nature of the stimuli while performing the experiment. All observers had normal or corrected-to-normal visual acuity, and wore their own prescription spectacles if of the latter class. Each observer made settings for all of the spectral lights paired with the standard in a single experimental session. Presentation of these pairs was randomized within each session. On average, an observer made two settings for each spectral light and the standard in a 2-hr session. The data from at least three such sessions were averaged to yield a mean setting for each of the 29 wavelengths. Radiometric measurements were taken for each wavelength at the average setting for each observer.

Results

Figure 4 shows the average spectral sensitivity functions calculated for each of the three protanopes from their settings in this experiment. Plotted with these data is the theoretical G function of Walraven (1974). Figure 5 shows the average spectral sensitivity functions for two deuteranopes along with Walraven's R function. Table 2 lists the mean values for each observer and the grand mean for each dichromatic type as a function of wavelength.

Three of the five dichromats show an elevated sensitivity, relative to Walraven's functions, in response to light from the short-wavelength region of the spectrum. This is in agreement with the data from the trichromatic observer of Part 1. In addition, some of the observers show an increased sensitivity to long-wavelength lights as well. Nonetheless, all of these observers could eliminate border percepts in the manner described above.

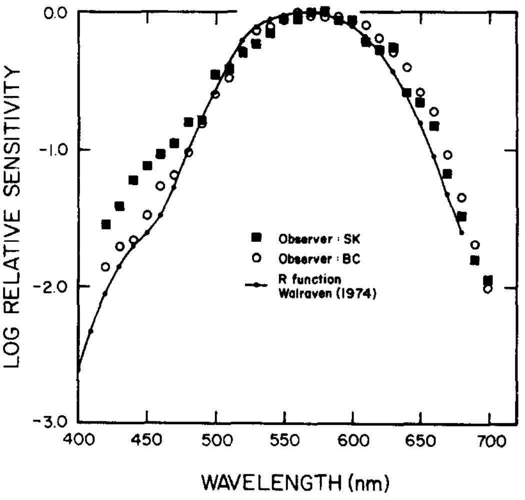

Fig. 5. The spectral sensitivity of the long-wavelength-sensitive cone of two deuteranopes determined by the elimination of the border in a bipartite field. Plotted with these is Walraven's (1974) R function.

Table 2. The spectral sensitivity values of the long-wavelength sensitive cone photoreceptors of the dichromatic observers who participated in Experiment 2

	Log relative sensitivity						
	Protan	Deutan	TB(P)	JC(P)	MP(P)	SK(D)	BC(D)
400	—	—	—	—	—	—	—
10	—	—	—	—	−1.63	—	—
20	−1.51	−1.71	−1.59	—	−1.43	−1.55	−1.86
30	−1.39	−1.57	−1.41	−1.48	−1.29	−1.42	−1.71
40	−1.21	−1.45	−1.28	−1.31	−1.03	−1.23	−1.66
50	−1.07	−1.31	−1.16	−1.13	−0.92	−1.13	−1.48
60	−0.99	−1.27	−0.90	−1.06	−1.01	−1.04	−1.27
70	−0.79	−1.08	−0.83	−0.89	−0.66	−.096	−1.19
80	−0.75	−0.92	−0.73	−0.83	−0.69	−0.81	−1.02
90	−0.61	−0.80	−0.57	−0.69	−0.56	−0.79	−0.81
500	−0.54	−0.53	−0.43	−0.56	−0.62	−0.46	−0.60
10	−0.27	−0.46	−0.24	−0.31	−0.25	−0.42	−0.48
20	−0.17	−0.30	−0.17	−0.21	−0.13	−0.30	−0.29
30	−0.05	−0.19	0	−0.05	−0.09	−0.24	−0.14
40	0	−0.14	0	0	0	−0.16	−0.11
50	−0.003	−0.05	−0.03	−0.01	+0.05	−0.05	−0.06
60	−0.023	−0.03	−0.06	−0.02	+0.01	−0.06	0
70	−0.10	−0.01	−0.13	−0.11	−0.05	0	−0.03
80	−0.18	−0.02	−0.21	−0.18	−0.14	+0.01	−0.04
90	−0.24	−0.05	−0.35	−0.27	−0.09	−0.07	−0.03
600	−0.46	−0.07	−0.57	−0.37	−0.43	−0.06	−0.07
10	−0.58	−0.16	−0.79	−0.55	−0.39	−0.22	−0.10
20	−0.83	−0.24	−0.94	−0.80	−0.75	−0.28	−0.19
30	−1.03	−0.28	−1.21	−1.07	−0.80	−0.26	−0.29
40	−1.35	−0.50	−1.47	−1.31	−1.26	−0.59	−0.40
50	−1.56	−0.62	−1.78	−1.58	−1.33	−0.66	−0.58
60	−1.86	−0.78	−2.11	−1.86	−1.62	−0.83	−0.72
70	−2.04	−1.10	—	−2.17	−1.90	−1.17	−1.03
80	−2.28	−1.41	—	−2.42	−2.14	−1.48	−1.34
90	−2.35	−1.71	—	—	−2.35	−1.80	−1.68
700	−2.51	−1.96	—	—	−2.51	−1.94	−2.0

Included in this table are the average values of the protanopic and deuteranopic observers.

DISCUSSION

Taken together, the results of these experiments suggest that the B cones do not contribute to the perception of border contour in the visual systems of the protanope and deuteranope. This result is consistent with the findings of Tansley and Boynton (1976) for trichromatic observers, where it was demonstrated that pairs of lights that stimulate R and G cones in the same ratio at equal luminance do not form visible borders with one another.

If red–green dichromacies are simply reduced forms of trichromacy, this suggests that only one cone type contributes to the spatial vision of protanopes and deuteranopes. Borders and edges that are visible to the trichromat because of differential spatial excitation of the chromatic opponent mechanisms alone will not be visible to these two classes of dichromat. It would seem that red–green dichromats can suffer from a more serious loss of vision than previously may have been suspected, for not only is color perception truncated and less informative for these observers, but pattern vision under certain conditions is severely reduced as well.

The functional loss of one of the long-wavelength-sensitive cone types does not appear to result in a generalized loss of visual acuity. The results of these experiments, however, suggest that even if two lights appear as different colors to protanopes and deuteranopes, they will not be able to perform spatial vision tasks if the quantum catch for the one long-wavelength-sensitive cone type each uses for the perception of edges is not sufficiently different across the retina.

These findings suggest an accurate means of testing for color vision losses using heterochromatic patterns. For example, by presenting a heterochromatic pattern where the relative luminances of two chromatic stimuli were slowly alternated through a range that included equal stimulation of R cones and equal stimulation of G cones, one could ask a given individual to note the condition where no spatial pattern was seen. For protanopes this would be at a distinctly different setting from that of the deuteranopes. Normal trichromats would always be able to see a pattern and thus could be screened out immediately. Of course, the idea of using spatially contingent responses to heterochromatic stimuli for color vision testing is not new—the reflectance Pseudoisochromatic plates are based on the same general principle.

It is likely that borders produced by luminance steps appear as distinct to protanopes and deuteranopes as to trichromats. In any case, luminance contrast borders could be readily used to demonstrate the experimental task for the observer, for example, by showing how the percept of a border can be eliminated with the adjustment of a control. This makes possible the use of language about perceptual experience that is shared by trichromats and dichromats alike—something desirable when testing color vision but probably lacking when using most of the common color vision screening tests.

In this paper, spectral sensitivity curves of R and G cones have been deduced by (a) using dichromats who presumably lack one of them, and (b) following a procedure (MDB) that hopefully eliminates the contribution of the B cones. Although the use of MDB for this purpose is new, the philosophy of the method is not. In fact, the most salient experimental evidence that went into the derivation of the Walraven (1974) functions, and the similar curves of Pokorny, Smith and Katz (1973) is based on this idea but with flicker (rather than MDB) being used to eliminate input from B cones.

Some evidence exists to suggest that the "missing" photopigment in red–green dichromats may be present in small quantities, and that some of the subjects, at least, may hve some residual red–green discrimination (Scheibner & Boynton, 1968). It should be emphasized that such residual function probably would be much too weak to make a significant contribution under most conditions of experimental test, including those used to select the subjects, as well as the MDB procedure. The results presented here should not, therefore, be taken as evidence for or against the idea that some small amount of the "missing" pigment may remain. The fact that the spectral sensitivity curves determined by the elimination of border percepts are broader for some observers than those of Walraven suggests that there may be a contribution from either a cone photopigment of broader spectral sensitivity or a small population of the "missing" cone type. Pokorny, Smith and Starr (1976) have demonstrated that there are variations in the optical density of cones as a function of eccentricity from the foveal region, with the highest densities being found in the fovea. Cone photopigments whose densities are greater would be expected to have broader spectral sensitivity. As the spectral sensitivity functions of these observers were determined using a 1.2° field it may be that these broader functions reflect this density increase. This, of course, would not account for the inter-observer variability.

Most of the data presented in this paper tend toward higher sensitivity at shorter wavelengths than the data of Judd (1951) or of Wagner and Boynton (1972).

We do not attach much significance to this discrepancy, but it needs to be discussed. The following are some conceivable explanations.

(a) Shortwave sensitivity as evaluated by MDB may depend upon luminance level. Wagner and Boynton used the maximum radiance available to them, and as a result, their luminances varied from less than 10 td to more than 100 td in the region from 400 to 500 nm.

(b) B cones may contribute to the measured function. However, the results of this study for dichromats, and of the previous work by Tansley and Boynton (1976, 1978) for normal subjects argues strongly against this. Moreover, the agreement of BWT's high-frequency flicker data with his MDB results also constitutes strong negative evidence, as it is unlikely that B cones are able to follow these frequencies well enough to permit any significant contribution to spectral sensitivity.

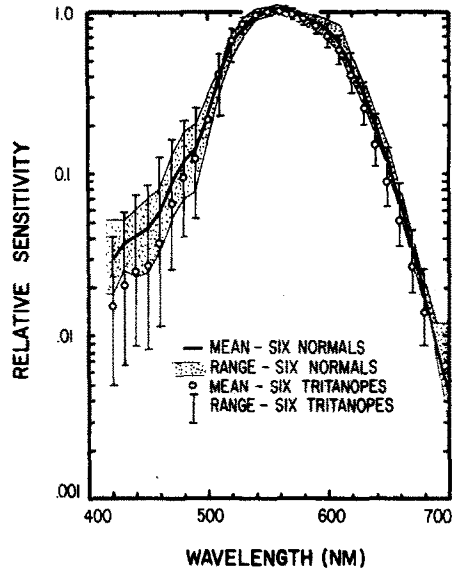

Fig. 6. Comparison of the relative spectral luminous efficiency functions of normal trichromats and tritanopes, from Sperling (1961). The shaded region represents the range of normal values for the trichromatic function.

(c) Ocular pigmentation varies significantly among subjects, becoming progressively greater with age. All of the subjects of the present experiment were under 25 years of age.

(d) Subjects vary in the relative numbers of R and G cones in their retinas (Baker & Rushton, 1964). This factor, plus ocular transmittance differences (and probably other factors), contribute to variability of the luminosity function. The range of such variation for normals and tritanopes as measured by Sperling (1961) is shown in Fig. 6.

(e) Accurate radiometry in the shortwave end of the visible spectrum is not easy. We relied upon the specification that were provided by the manufacturer of our radiometer. Calibration errors must make a contribution to the variability that is observed from one study to another; the extent of such errors is impossible to evaluate.

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