

Discrimination of binocular color mixtures in dichromacy: evaluation of the Maxwell–Cornsweet conjecture

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We tested the Maxwell–Cornsweet conjecture that differential spectral filtering of the two eyes can increase the dimensionality of a dichromat's color vision. Sex-linked dichromats wore filters that differentially passed long- and middle-wavelength regions of the spectrum to each eye. Monocularly, temporal modulation thresholds (1.5 Hz) for color mixtures from the Rayleigh region of the spectrum were accounted for by a single, univariant mechanism. Binocularly, univariance was rejected because, as in monocular viewing by trichromats, in no color direction could silent substitution of the color mixtures be obtained. Despite the filter-aided increase in dimension, estimated wavelength discrimination was quite poor in this spectral region, suggesting a limit to the effectiveness of this technique.

Key words: color discrimination, dichromacy, binocular summation.

1. INTRODUCTION

Theories of color vision lead naturally to speculation about ways to cure or to ameliorate color-vision deficiencies. Thus Dalton's hypothesis¹ that his own defective color vision (sex linked and congenital in nature) was due to a discoloration of his ocular media would predict that one could be cured of such a condition by viewing the world through a *single* color-compensating filter. That this was not true was demonstrated by Seebeck,² who studied the manner in which color filters altered the perceptions of color-defective individuals and by the postmortem examination of Dalton's eye.³

Our current understanding of color vision as being initiated by absorption in visual photopigments broadly overlapping in the spectrum and of the most common color-vision defects as arising in part from alteration of the absorption spectrum or from loss of one of these photopigments would not ordinarily suggest a filter-based approach to treating discrimination losses in color-vision defects (but see Ref. 4). Under conditions of photopigment (or neural) loss, for example, no filter could restore the missing sensitivity function.

Whereas no benefit could be gained from viewing the world through a single filter, one might obtain additional information about the spectral content of light by looking through two filters. Maxwell⁵ first proposed this idea by noting that red and green lights that appeared identical to one of his observers could be distinguished by their differential brightness when alternately viewed through red and green filters. He noted of this case:

By furnishing Mr X. with a red and a green glass, which he could distinguish only by their shape, I enabled him to make judgements in previously doubtful cases of colour with perfect certainty. I have since had

a pair of spectacles constructed with one eye-glass red and the other green. These Mr X. intends to use for a length of time, and he hopes to acquire the habit of discriminating red from green tints by their different effects on his two eyes. Though he can never acquire our sensation of red, he may then discern for himself what things are red, and the mental process may become so familiar to him as to act unconsciously like a new sense.

Rood⁶ mentions Maxwell's suggestion in his textbook on color, but the idea seems to have lain dormant until Cornsweet⁷ elaborated it in physiological terms. His idea was that a filter in conjunction with the photopigments of one eye would effectively constitute an additional set of independent spectral sensitivities with which to sample the chromatic environment, thus doubling (or at least increasing) the dimension of color discrimination.

We illustrate this idea in Fig. 1. The top panel shows the peak-normalized short-wavelength-sensitive- (S-) and middle-wavelength-sensitive- (M-) cone spectral sensitivities of a protanopic observer based on the Smith–Pokorny fundamentals.⁸ Because of the steep falloff in sensitivity of the photopigments at long wavelengths, the discrimination of such observers in the fovea is effectively monochromatic for wavelengths greater than approximately 540 nm. The middle panel of Fig. 1 shows the transmission curves of two filters that differentially attenuate light in this region of the spectrum. The bottom panel shows the product of each transmission curve with the M-cone spectral sensitivity, giving the effective spectral sensitivity of each eye plus filter. With the filters in place, two different spectral sensitivities mediate discrimination in this spectral region, where formerly there was only one. Because it is not necessary, as shown here, that the filters completely block the part of the spectrum

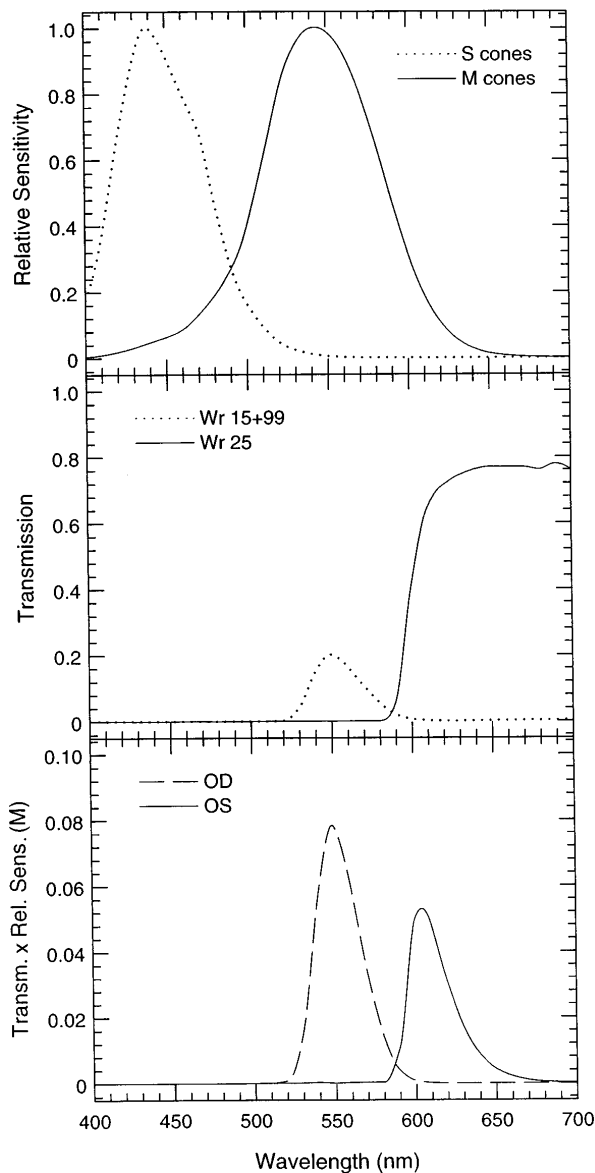


Fig. 1. Top: relative sensitivity of the Smith-Pokorny S and M cones plotted (dotted and solid curves, respectively) as a function of wavelength in nanometers. Middle: measured transmission of a Wratten (Wr) 25 filter (solid curve) worn over the left eye (OS) and a combination of Wratten 15 and Wratten 99 filters (dotted curve) worn over the right eye (OD) plotted as a function of wavelength. Bottom: relative spectral sensitivity of OD (dashed curve) and OS (solid curve) for a protanope when the filters used for the middle panel are placed over each eye.

in which the S cones are active, the possibility exists that with a different choice of filter the dichromat could have, between the two eyes, either three or four different cone sensitivities. In honor of the two individuals who first proposed this strategy, we refer to the potential increase in dimension of discrimination by differential filtering of the two eyes as the Maxwell-Cornsweet conjecture. Such an arrangement need not improve discrimination, however, because if the signals from the two eyes simply summate centrally no increase in dimensionality will result.

This idea was exploited commercially with the introduction of the X-chrom lens,⁹ a red contact lens designed to

be worn monocularly and prescribed to ameliorate discrimination losses suffered by color-deficient individuals. Validation of the efficacy of this approach, however, has been contentious.¹⁰ Although the X-chrom lens does allow some color-defective individuals to identify pseudoisochromatic figures, no improvement in performance on color ordering or identification tests has been found.¹¹ Although these results accord with Maxwell's sentiment that the color-defective observer will not acquire new sensations from this arrangement, little research has been done to quantify what actual improvement (if any) occurs. In the present study we sought to measure directly the effects of differential color filtering of the two eyes on the dimensionality of discrimination in dichromatic observers. As we were interested mainly in the effects of binocular filtering on chromatic discrimination and less in the question of what is the best filter for ameliorating dichromatic vision, we restricted stimuli to the Rayleigh region of the spectrum, where sex-linked dichromats are normally monochromatic, thus simplifying the analyses.

2. METHODS

A. Apparatus and Calibration

All the stimuli were generated on an Electrohome color display controlled by three 12-bit digital-to-analog converters (Data Translation) from a PC-XT computer running at 8 MHz. The screen was masked except for a disk-shaped region in the center, which subtended 1 deg at the viewing distance of 2 m. A piece of black masking tape subtending approximately 6 min of visual angle was placed in the center of the field to aid fixation and binocular fusion.

Calibrations of the display were performed with a spectroradiometer and a luminance meter (EG&G) and were checked periodically with a hand-held luminance meter (Minolta CS-100). The CIE chromaticity coordinates of the guns were B (0.161, 0.072); G (0.255, 0.610); R (0.606, 0.356). The luminance-voltage relation, calibrated for each gun individually, was linearized by means of software lookup tables.

The spectral transmission curves of Wratten filter combinations used in this study were calibrated with a spectroradiometer *in situ*.

B. Subjects

Two protanopes (the authors, ages 21 and 40) served as the principal subjects. In addition, data were collected from one deuteranopic observer (age 41) and two trichromatic observers (one normal and one deutan, ages 23 and 30, respectively). The protanopes' dichromacy had been extensively verified previously in several laboratories. The diagnoses of the deutans were determined by anomaloscopy. The trichromacy of the deuteranomalous and the normal observers was verified in their discrimination data, collected over the course of the experiment. The acuity of each subject was at least 20/20, corrected if necessary. All the subjects gave informed consent before participating in the study.

C. Stimulus and Procedures

Dichromatic observers viewed the display through goggles that differentially passed long- and middle-wavelength

regions to each eye. In the monocular conditions an opaque patch was placed over one eye of the goggles. Trichromatic observers viewed the display monocularly without filters. At the start of an experimental session observers dark adapted for 5 min; this period was followed by 5 min of light adaptation to the unmodulated test stimulus.

In the first two experiments the R and the G guns of the display were modulated sinusoidally either in phase or in counterphase at a temporal frequency of 1.5 Hz about a fixed value ($x = 0.32$, $y = 0.32$, $Y = 100$ cd/m²). The luminance of the B gun was held constant. Using a button box that allowed the amplitude to be increased or decreased by steps of 0.1 log unit, observers adjusted the amplitude of the modulation to a level at which they could just detect the temporal variation of the stimulus. They did this for each of 12 (or 10, for the normal trichromat) R/G luminance ratios. The ratios were presented in random order, with each one being repeated five times in a single session. Observers participated in several preliminary sessions, which served to familiarize them with the task and to stabilize their threshold criteria.

3. RESULTS

A. Experiment 1

In pilot studies we found that, if the unmodulated stimulus presented binocularly did not appear to be approximately of the same color and same brightness to the two eyes, the observers had great difficulty fusing the images. With the filter configuration illustrated in Fig. 1, the unmodulated images of each eye appeared yellowish and approximately of the same brightness to the protanopic observers in this study.

Figure 2 shows the mean threshold settings and standard deviations of the luminance amplitudes of the R and the G components of the sine-wave-modulated stimulus plotted against each other for monocular viewing by each eye (left-hand and middle panels) and for binocular viewing (right-hand panels) from two protanopes. The stimulus was modulated symmetrically about the mean level, so that the peak and the trough of the threshold amplitude are plotted as symmetric points about the origin. In this representation in-phase modulations of the two guns are plotted in quadrants I and III, and counterphase modulations appear in quadrants II and IV.

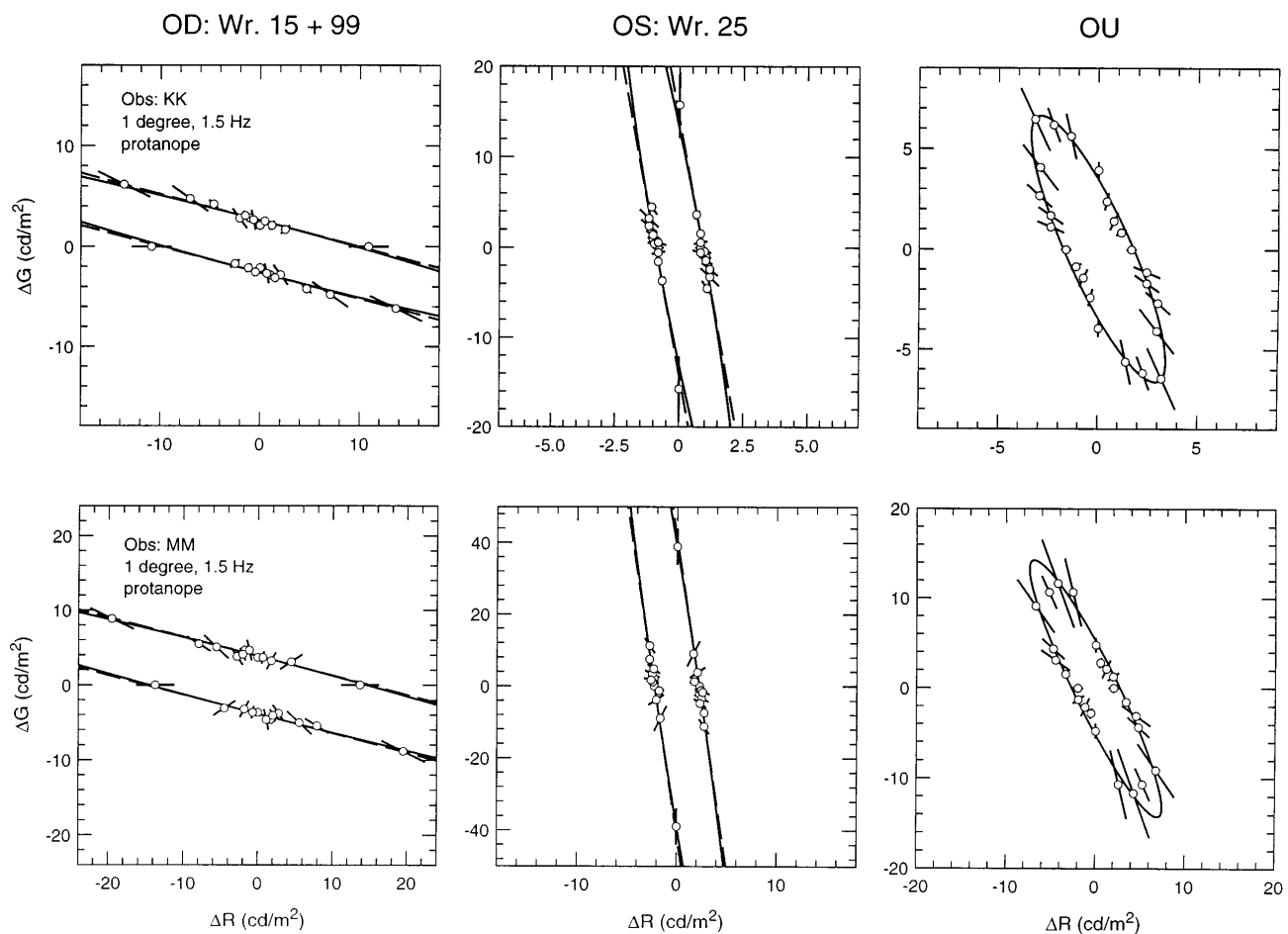


Fig. 2. Color-mixture thresholds for two protanopes plotted as circles in terms of the luminance amplitudes in candelas per square meter of the R and the G display primaries. Error bars, ± 1 standard deviation. The left-hand and the middle panels show thresholds obtained under monocular conditions with each of the color filters from Fig. 1 in place. The right-hand panels show the color-mixture thresholds obtained with binocular (OU) viewing. The solid curves and the dashed lines fitted to the data are described in the text. Note the differences in scaling of the axes between observers and conditions. Obs, observer.

The thresholds of observer KK were on average a factor of 2 lower than those of MM. This sensitivity difference is most likely due to the greater practice that the senior author has had with the task.^{12,13} These sensitivity differences do not affect the principal conclusions of this paper, as they rely mainly on the qualitative rather than the quantitative characteristics of the data.

Under monocular conditions the data appear to fall along pairs of parallel lines. The main effects of a filter over an eye were to shift the orientation of these parallel lines and to change the threshold for each gun modulated alone in a fashion consistent with the transmission characteristics of the filter worn. In each of these cases the color direction that corresponded to the long axis of the parallel lines was initially included in the set of stimuli tested, but a threshold could not be obtained because the observer could detect no modulation all the way to the limit of the color gamut of the display. As a threshold could not be estimated in these directions, they are not included in the analyses presented below. With binocular viewing the data deviate from a pair of parallel lines. A modulation threshold was easily set in each color direction tested.

An ellipse was fitted to each data set individually by estimation of the linear parameters a , b , and c in the equation

$$a\Delta R_i^2 + 2c\Delta R_i\Delta G_i + b\Delta G_i^2 = 1, \quad (1)$$

which best fit the data, by means of the singular-value decomposition algorithm¹⁴; here ΔR_i and ΔG_i represent the mean luminance amplitude of each gun at threshold in the i th direction tested.¹⁵ The best-fit ellipses are shown as solid curves in each figure. The dashed curves in the left-hand and the middle panels represent the best-fitting pair of parallel lines to each data set. We derived these by first using the singular-value decomposition on the matrix of the quadratic form associated with Eq. (1) to obtain

$$\begin{bmatrix} a & c \\ c & b \end{bmatrix} = U^T D U,$$

where a , b , c come from the fits of Eq. (1) to the data; U is an orthogonal matrix (with the superscript T indicating its transpose); and D is a diagonal matrix. Then the smaller diagonal element of D was set to zero to give a new matrix D_0 . The best-fit parallel lines were then determined by the points $\mathbf{x} = (\Delta R, \Delta G)$ satisfying the equation

$$(\mathbf{x}^T U^T D_0 U \mathbf{x})^{1/2} = 1. \quad (2)$$

The goodness of fit for each equation was evaluated by computation of the statistic

$$\chi^2 = \sum_{i=1}^N \left(\frac{r_{i,\text{obs}} - r_{i,\text{fit}}}{\text{sd}_i} \right)^2, \quad (3)$$

where $r_{i,\text{fit}}$ is the vector distance to the fitted equation in the i th color direction, $r_{i,\text{obs}}$ is the threshold amplitude in the i th color direction, and sd_i is the standard deviation of the observer's settings in this direction. If the measurement errors are normally distributed, the statis-

tic given above is a χ^2 variable with $N - M$ degrees of freedom,¹⁶ where M is the number of free parameters for each equation ($M = 3$ for the ellipse; $M = 2$ for the parallel lines). The χ^2 values for each of the fits shown in Fig. 2 are given in the top section of Table 1 for each equation.¹⁷ Parallel lines are rejected for each of the binocular conditions. In contrast, the ellipse provides little benefit over the parallel lines in fitting the monocular data.

Figure 3 shows the modulation thresholds collected monocularly without filters from a normal and a deuteranomalous trichromat. Both data sets are best characterized by a closed contour (χ^2 values are given in the middle section of Table 1), but the orientations of the best-fitting ellipses are quite distinct from each other, with the long axis of the normal traversing quadrants I and III and that of the anomalous observer being more similar to that shown in the binocular condition by the dichromats.

In a two-dimensional mixture space we can differentiate one-dimensional from two-dimensional discrimination.¹⁸ If vision is mediated by a single, linear mechanism, the discrimination thresholds should lie on a pair of parallel lines whose slope determines the ratio of the primaries that, when exchanged, produces a silent substitution. The monocular panels of Fig. 2 fit this expectation very well. If the two eyes exhibited linear summation when stimulated together, we would expect the binocular mixture thresholds also to lie on parallel contours with slope intermediate to the monocular conditions. However, in the binocular condition, the thresholds lie on a closed contour, as do the monocular thresholds from the trichromats who are known to have two visual channels operating under the conditions of this experiment. For these data there is no direction that would permit silent substitution. Thus the binocular thresholds reject a model in which the two eyes' outputs summate linearly and also the hypothesis that discrimination is mediated by a single linear mechanism. Therefore we conclude that differential color filtering of the two eyes allows dichromats to increase the dimension of their color-discrimination space.

Table 1. Summary of χ^2 Statistics from Fits to Discrimination Data

Observer	Condition	Linear Model	Elliptical Model
Figure 2			
KK	OD	5.965	5.808
	OS	1.659	1.623
	OU	1386.95 ^a	3.807
MM	OD	2.585	2.404
	OS	1.719	1.515
	OU	39117.8 ^a	10.390
Figure 3			
RM	OD	217.18 ^a	1.520
RC	OD	4088.47 ^a	1.515
Figure 5			
KK	OU	719.42 ^a	5.229
MM	OU	21499.3 ^a	2.409
RS	OU	1432.82 ^a	2.462

^aStatistically significant at $P < 0.001$. Degrees of freedom are 10 for the linear model and 9 for the elliptical model for all the observers except RM, for whom the degrees of freedom are 8 and 7, respectively.

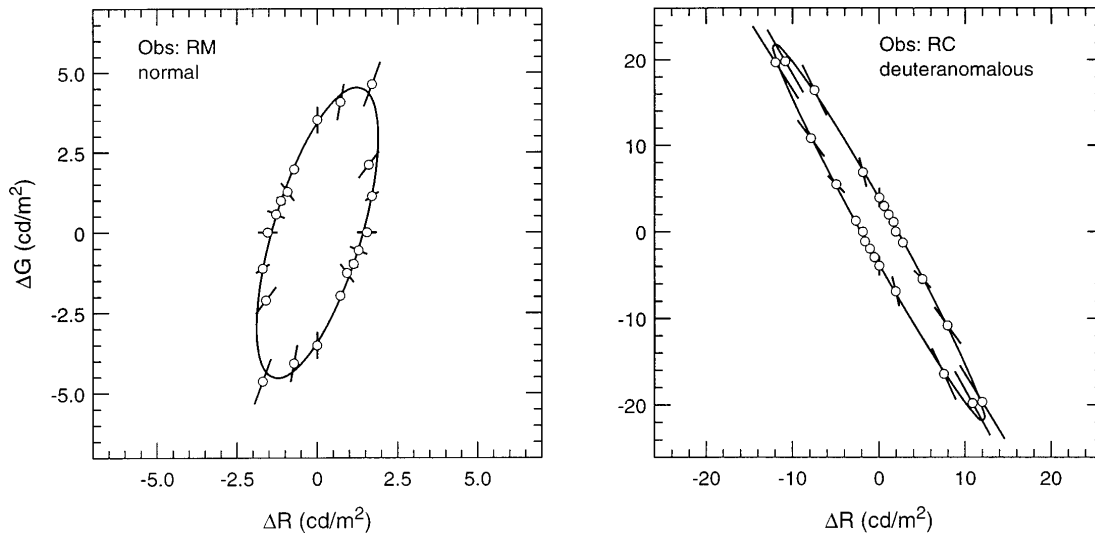


Fig. 3. Color-mixture thresholds for normal (left) and deuteranomalous (right) trichromatic observers, monocularly and unfiltered, plotted as in Fig. 2.

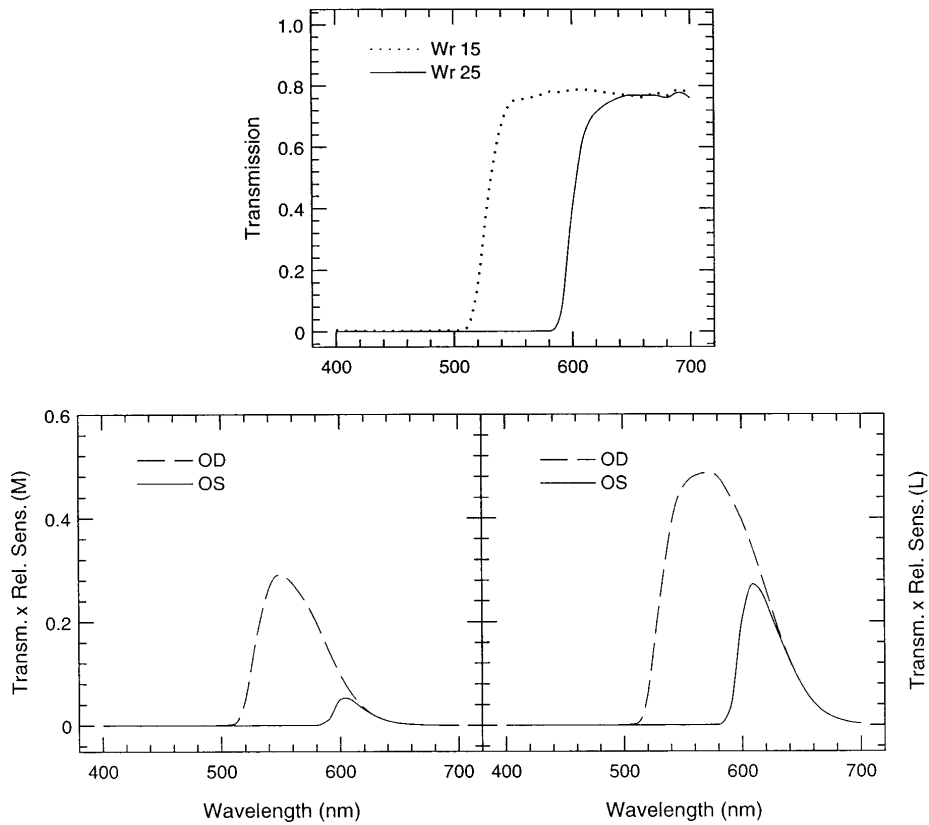


Fig. 4. Top: transmission curves of Wratten 15 (dotted) and Wratten 25 (solid) filters worn over OD and OS, respectively, in second experiment. Bottom: spectral sensitivities of OS (solid) and OD (dashed) of a protanope (left-hand panel) and of a deuteranope (right-hand panel) when the filters above are placed over each eye. L, long-wavelength sensitive.

B. Experiment 2

The effective spectral sensitivities for the dichromats in experiment 1 overlapped minimally, thus yielding a system with little basis on which to distinguish spectrally differing lights. Greater spectral overlap of the sensitivity functions, however, would tend to reduce the effective contrast between lights of different spectral composition.

Would the increased dimensionality of the discrimination be maintained with greater spectral overlap of the two eyes' sensitivities?

To evaluate the effect of greater overlap on sensitivity and to assess spectral discrimination in the subsequent test, the filters were changed to those shown in the top panel of Fig. 4. The eye-filter sensitivities are shown in

the bottom two panels for a protanope (left) and a deuteranope (right). In the actual experiments neutral-density (ND) filters were placed before the right eye of each observer to equate the brightness and the appearance of the monocular views (protan, 0.9 ND; deutan, 0.3 ND).

In Fig. 5, thresholds for binocular viewing with this filter combination are shown as circles for two protanopes and one deuteranope. The solid curves represent the best-fitting ellipses as described above. The χ^2 values for these fits are given in the bottom section of Table 1. It is evident that, even with the greater overlap in sensitivity of the two eyes, the data are still better described by a closed contour rather than by a pair of parallel lines. In addition, the sizes of the ellipses for the protanopes are similar to those shown in Fig. 2, so the greater spectral overlap does not necessarily entail a loss of sensitivity.

C. Experiment 3

Up to this point, we have demonstrated that differential filtering of the two eyes increases the dimension of the discrimination space for color mixtures. How is this increase in dimension reflected in wavelength discrimination? To investigate this question, we first consider the equivalence between wavelength and modulation direction in the stimulus space used to plot the data above. Given the spectral sensitivities of the OS (Lt) and the OD (Rt) eye-filter combinations shown in Fig. 4, $S_{Lt}(\lambda)$ and $S_{Rt}(\lambda)$, respectively, and the spectral energy distributions of the two modulated display primaries, $R(\lambda)$ and $G(\lambda)$, we can compute the relative amounts of each primary that would be necessary to make a metameric match with an arbitrary monochromatic light at a fixed luminance. In other words, we can determine a set of color-matching functions in the colorimetric system of the display primaries. Assuming that such matches occur when two fields produce the same excitation for each eye-filter sensitivity function, we obtain the color-matching functions by solving the following two linear equations for the constants a_λ and b_λ at each test wavelength λ :

$$a_\lambda \frac{\int R(\lambda)S_{Lt}(\lambda)d\lambda}{V_R} + b_\lambda \frac{\int G(\lambda)S_{Lt}(\lambda)d\lambda}{V_G} = \frac{S_{Lt}(\lambda)}{V(\lambda)},$$

$$a_\lambda \frac{\int R(\lambda)S_{Rt}(\lambda)d\lambda}{V_R} + b_\lambda \frac{\int G(\lambda)S_{Rt}(\lambda)d\lambda}{V_G} = \frac{S_{Rt}(\lambda)}{V(\lambda)}, \quad (4)$$

where $V(\lambda)$ is the normal photopic luminosity function as defined by the CIE for the 1931 Standard Observer,¹⁹ used here to express the results on the same basis as the figures above, and $V_X = \int X(\lambda)V(\lambda)d\lambda$. All the integrals were approximated by summation over the range 400–700 nm at 10-nm intervals.

The ratio b_λ/a_λ , based on the luminances of the R and the G primaries at each wavelength, defines an equivalence between modulation of the R and the G primaries in a given direction in the color-mixture space and addition of the corresponding (or metameric) wavelength. The mapping between wavelength and modulation direction determined by Eqs. (4) for a protanopic observer is illustrated by the labeled spokes in Fig. 6. The pie sector defines the gamut of all in-phase modulations of the two eyes. The outside or boundary spokes mark the directions of silent substitution for each eye and thus isolation of the other. Note that, with the filters used, only the wavelength range of 520–610 nm provides a basis for discrimination, as outside these limits all the wavelengths tend to map into one of two directions. The dashed contour shows schematically the type of discrimination ellipse estimated for this observer from experiment 2. In the next set of measurements we exploited the equivalence between modulation direction and wavelength to estimate the wavelength discrimination permitted by differential filtering of the two eyes.

The observer was presented with a pair of lights flickering in square-wave counterphase at 1.5 Hz. One of these lights was fixed at a magnitude 5 times the modulation threshold in a given direction, as indicated by the + in Fig. 7. The second light was chosen to be a fixed angular difference θ from the first with respect to the uniform mixture used as the origin in the threshold modulation

OD: Wr. 15; OS: Wr. 25

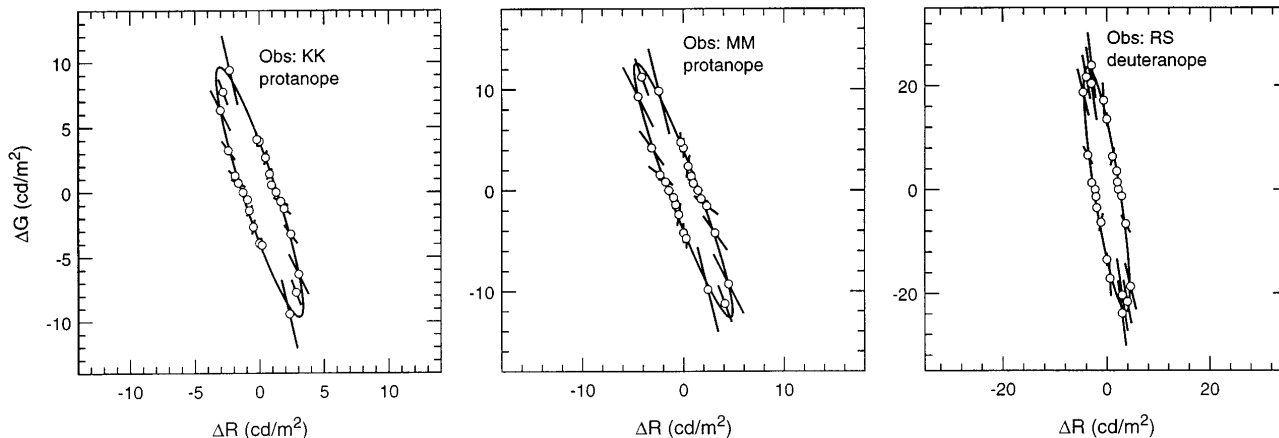


Fig. 5. Color-mixture thresholds for two protanopes and one deuteranope with binocular viewing when the filters used for Fig. 4 are worn over each eye.

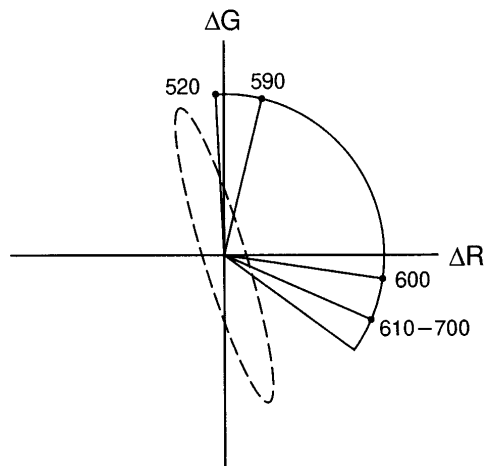


Fig. 6. Mapping of equivalent metameric wavelength to color-mixture directions for a protanope wearing a Wratten 15 filter over one eye and a Wratten 25 filter over the other. The pie sector indicates the gamut of directions that correspond to in-phase mixtures with respect to the two eyes. The ellipse shows schematically the type of discrimination ellipse presented in Fig. 5 and shows the part of the discrimination contour equivalent to the incremental addition of spectral lights.

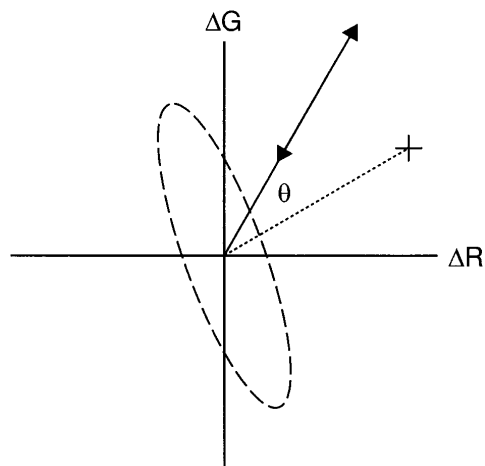


Fig. 7. Schematic representation of the color mixtures used in experiment 3. The + indicates a fixed light at a modulation value 5 times greater than the color-mixture threshold, defined by the ellipse, in the direction shown by the dotted line. The variable light was adjusted along the solid ray with fixed angular difference θ from the fixed light with respect to the mean mixture used as origin in experiments 1 and 2.

measurements, but its magnitude was variable, as indicated by the arrows shown along the solid line. The observer adjusted the variable light along the given ray until the appearance of the flicker was minimized. The minimum flicker point was recorded, and the observer also noted whether the flicker could be eliminated. In a given session, one fixed light and ten variable lights (five to each side of the fixed light) were presented. The variable lights were presented in random order, with the entire set being repeated five times.

Figure 8 shows the data collected from two protanopes for each of three fixed lights, in the mixture directions corresponding to wavelengths of 640, 595, and 580 nm (left to right, respectively). The ellipse in each figure corresponds to the best-fitting threshold contour from Fig. 5

for each observer. The dashed curve represents the same ellipse with each point scaled by a factor of 5. The +'s indicate the fixed light. They do not lie exactly on the scaled contour because the setting was based on each observer's own mean threshold rather than on that predicted by the curve. The filled symbols indicate the mean setting along directions for which flicker could be eliminated on more than 50% of the trials. The open symbols similarly indicate mean settings for which flicker could be eliminated on less than 50% of the presentations. The transition between the two groups of symbols was estimated by linear interpolation and served to assign an angular-discrimination limen to both sides of the fixed light. These limits were mapped to equivalent wavelength by use of the equivalence demonstrated in Fig. 6, and the difference in wavelength between the limits on both sides was computed.

The wavelength discrimination data are plotted in Fig. 9 with the convention adopted in Ref. 20. The circles are plotted at the equivalent fixed wavelength on the abscissa and at the half-width of the wavelength interval within which flicker could be eliminated on greater than 50% of the presentations on the ordinate. The bars indicate the wavelength end points of the discrimination interval. Qualitatively, both observers showed similar behavior. The ends of the spectrum were discriminable from the middle. As plotted, discrimination in the center of the spectrum showed a tendency to be worse than that at the extremes. This difference may be an artifact of the truncation of the spectrum, however, because the angular-discrimination contours for at least one side of each discrimination interval extended into extraspectral regions. Observer MM failed to discriminate mixtures equivalent to both ends of the spectrum from a light equivalent to 595 nm. We suspect that the large discrimination interval at this particular point may reflect fatigue or habituation factors because his data were collected over a short period of time and were obtained last.

4. DISCUSSION

The increase in dimensionality demonstrated by dichromatic observers in these experiments cannot be attributed to S cones. Dichromats can discriminate lights on the basis of wavelength differences in the Rayleigh region when the stimulus is sufficiently intense to drive S cones.²¹ Our luminance levels were orders of magnitude below such levels, and, in addition, our wavelength-discrimination curves are inconsistent with those obtained when S cones contribute.

Rods can also enhance discrimination in this spectral region at mesopic levels when the field size is enlarged.²² We used a centrally viewed 1-deg stimulus to limit rod participation. Each monocular field was reported to appear yellow by the dichromatic observers when viewed with the filters. Thus cones must have been participating in the discriminations. The monocular data are univariant, however. Therefore only one cone class or a stable combination of rod and cone signals exhibiting univariant behavior could be contributing to each eye's data. The former hypothesis is more parsimonious and is consistent with the slopes of the monocular-detection contours shown in Fig. 2. Our stimulus also should have

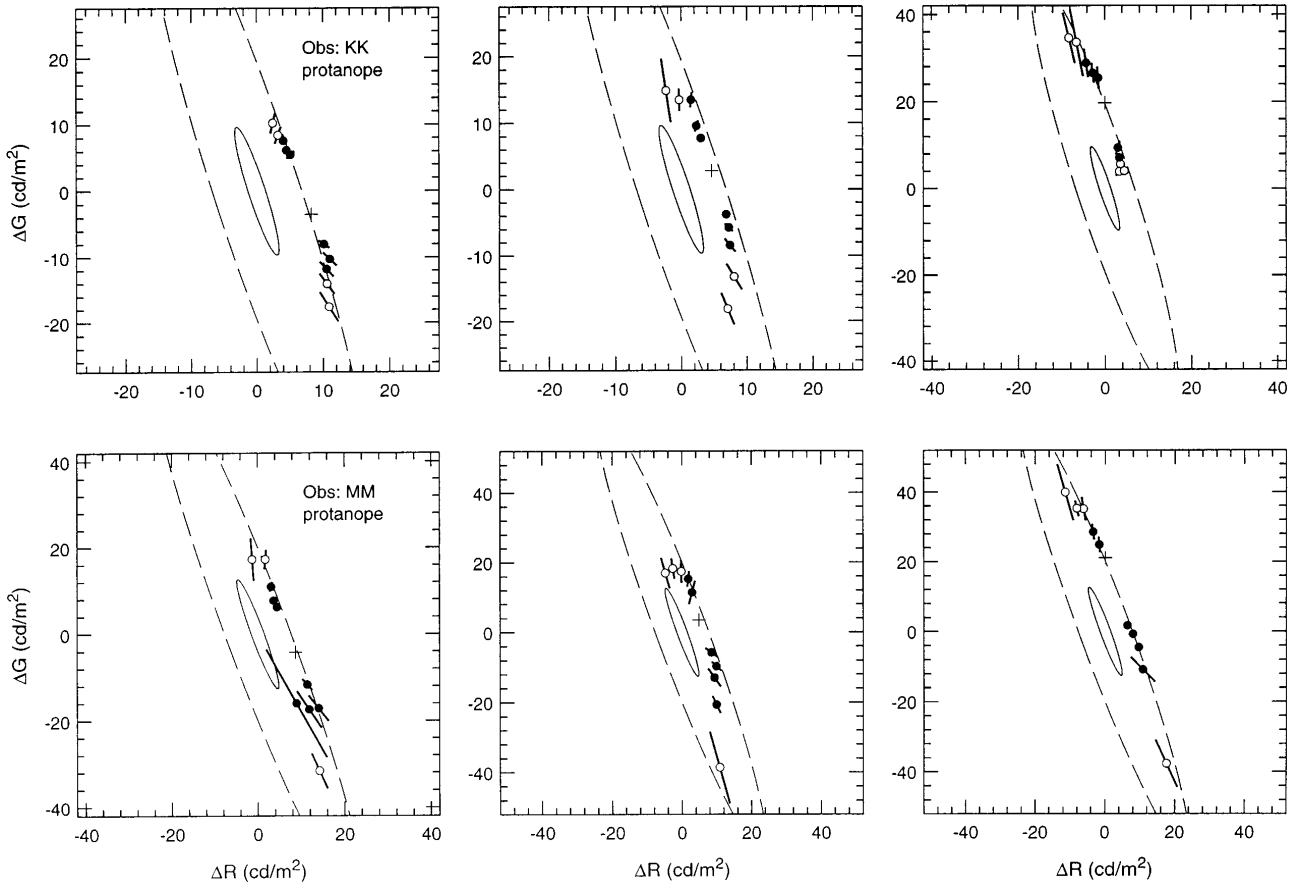


Fig. 8. Minimum flicker for different angular separations in color-mixture space. The results from two protanopes are plotted in the upper and the lower panels, respectively. The + in each panel indicates the fixed light. The circles indicate the color mixtures that yielded a minimal percept of flicker when adjustments were restricted along the ray through the disk and the origin. The filled circles indicate the conditions on which flicker could be eliminated on more than 50% of the trials. The open circles indicate the reverse. The solid ellipse is the best-fitting threshold contour for each observer from Fig. 5. The dashed curve is the threshold ellipse scaled by a factor of 5.

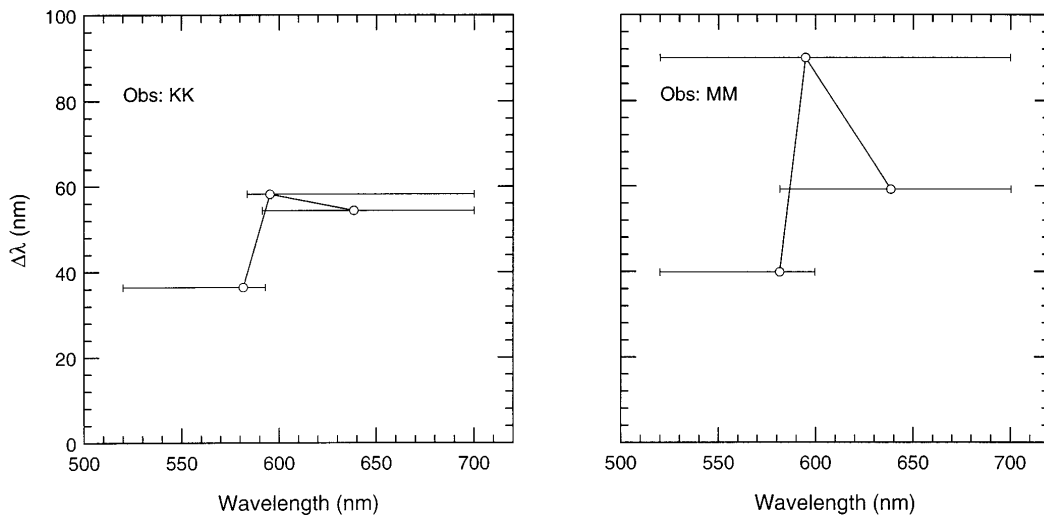


Fig. 9. Wavelength-discrimination functions calculated from the angular-discrimination data of Fig. 8 for two protanopes.

limited the possible participation of anomalous cones, as these have been demonstrated in dichromatic observers only for large fields at high radiances.²³ Previous data obtained with the same apparatus revealed no significant alteration in spectral sensitivity for field sizes of as much as 4 deg in diameter.¹²

Because dichromats operate monochromatically with one class of cones over the region of observation of these experiments, the monocular signals at a physiological level can be viewed simply as varying in brightness. In this sense our experiments merely repeat previous observations on binocular summation of increments and decre-

ments of luminance.²⁴ The aspect that distinguishes our study is the exploitation of interocular lightness differences for encoding wavelength differences. Taylor²⁵ previously reported substantial improvement in wavelength discrimination of a deuteranomalous observer who wore an X-chrom lens monocularly. Because this observer was a trichromat, his results provide no insight as to what should occur in dichromacy.

Although in our study differential filtering of the two eyes yielded a two-dimensional discrimination contour, the actual improvement that we observed was quite modest when compared with normal discrimination in this spectral region (as in Fig. 3). The color-mixture discrimination contours more closely resemble those shown by the anomalous trichromat that we tested. It should not be assumed, however, that differential filtering transforms a dichromat into an anomalous trichromat. The anomalous observer, for example, described the suprathreshold appearance of counterphase modulation of the R and the G primaries as alternating reddish and greenish, respectively. The filtered dichromats described this stimulus as lustrous or shiny and gave no indication that they could distinguish between the appearance of those color modulations that trichromats referred to as "reddish" and "greenish." Because there is no reason to believe that observers can distinguish between the appearance of a left-eye dark-right-eye bright and a left-eye bright-right-eye dark stimulus,²⁶ the dichromats' behavior was consistent with the view that they could distinguish on the basis of appearance between lights that a trichromatic observer would call under our stimulus configuration red and yellow or green and yellow but not between those that would be called red and green. In other words, they seem to lack information about the sign of the chromatic modulation. In this sense the discrimination behavior demonstrated may have features in common with certain forms of achromatopsia arising from cortical damage.²⁷

We did not obtain a wavelength-discrimination curve from a trichromatic observer. Some insight into what might be expected from a normal observer can be gained, however, by the following computation. First note that, in viewing Fig. 8, one can approximate the region within which flicker is eliminated by simply translating the threshold contour so that it is centered at the coordinates of the fixed light. When this is done to a first order the borders of the ellipse define the boundary between the filled and the open symbols. By sliding the threshold ellipse to the locus of each fixed light, one might then estimate the wavelength-discrimination functions shown in Fig. 9. Such an operation requires the assumption that color-mixture space is homogeneous with respect to discrimination. Whereas this assumption is certainly false for large displacements, it is likely to hold approximately under the relatively local translations used here. For example, with a Weber fraction of 0.02 for luminance modulation, the luminance amplitude threshold would be expected to increase by only 10% on a background 5 times above the threshold. Returning to the threshold modulations of the normal observer, shown in Fig. 3, we slid the fitted ellipse around a similar contour 5 times above threshold and estimated the angular separations of just-discriminable lights. Positions around the contour and the angular separations were mapped to a wavelength

axis as described above, but instead with the normal M- and L-cone fundamentals.

The wavelength-discrimination curve so obtained is plotted in Fig. 10 and is distinctly different from the ones shown in Fig. 9. More intervals are discriminable across the spectrum, and there is a minimum at 570 nm at which the discrimination limen is nearly 2 nm. For clarity the bars for the interior four wavelengths are not shown, though these would be nearly the size of the symbols themselves. Above 570 nm, discrimination deteriorates rapidly, with lights being indiscriminable within the region 600–700 nm. Such a decline in discrimination is consistent with the data of Calkins *et al.*²⁸ who demonstrated that normal observers under somewhat different conditions cannot discriminate lights in this spectral region within 0.7 log unit of threshold. They argued that such a discrimination failure was limited by a postreceptoral cone-antagonistic site mediating red-green discrimination. The minimum in the function recalls the type of sensitivity optimum that Le Grand²⁹ first demonstrated in his analysis of MacAdam's ellipses and is also probably due to such opponent processing. We suppose that it is just such a site that dichromats do not possess, notwithstanding the artificial imposition of two sensitivity functions in this spectral region. Indeed, line elements in which receptor signals are combined independently predict the poorest sensitivity approximately where sensitivity is optimal for an opponent interaction.³⁰

Better wavelength discrimination might have been obtained from a different set of filters. Those that we used are cutoff filters; the spectral regions over which both filters are flat or over which only one is transmissive would still yield monochromatic discrimination. Note, for example, in Fig. 6 how the metameric wavelengths from 520 to 580 nm at one end and from 610 to 700 nm at the other end of the spectrum tend to map into single directions. A better filter might be one that distorts a dichromat's missing long-wavelength photopigment to the one that (s)he is

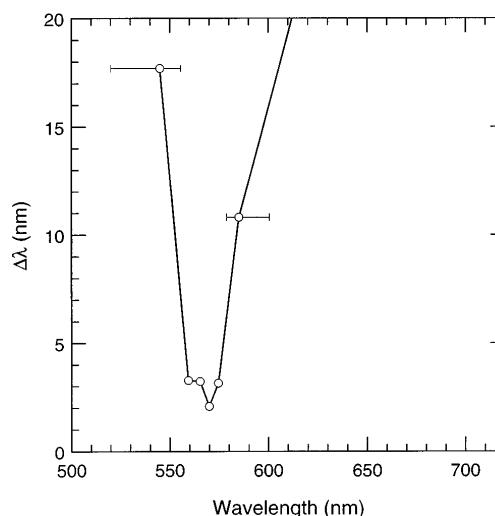


Fig. 10. Wavelength-discrimination function calculated for a normal trichromat based on the threshold modulation contour of Fig. 3 and assuming the equivalence between color-modulation direction and wavelength given by the Smith-Pokorny M and L fundamentals.

missing. Such a filter's transmission curve would have to be proportional to the ratio of the normal M- and L-cone sensitivities (L/M for protan, M/L for deutan). Our limited attempts to fabricate such filters from multiple layers of color-correcting filters have so far resulted in too great of a luminance attenuation. Given the discussion of the previous paragraph, however, it would be surprising to find qualitatively different results with filters that yielded better approximations to normal cone spectral sensitivities.

Recently the idea has been advanced that viewing the world through multiple color filters is like viewing it over changes of illuminant,³¹ which has been shown within certain limits to provide sufficient information to specify surface colors.^{31,32} It is interesting to consider that, by using differential color filters over the two eyes, we have produced multiple views or lightness maps of the world—one for each eye. Despite the fact that our stimulus situation is more limited spatially than would be required for color constancy, the poverty of color-discrimination under our conditions highlights the critical role of postreceptoral processing in extracting chromatic information from such lightness maps.

In summary, we have shown the Maxwell–Cornsweet conjecture to be correct in that differential spectral filtering of the two eyes of a dichromat *does* yield higher-dimension discrimination contours. In other words, by use of such filters, lights that had formerly formed silent-substitution pairs no longer did so, and, within the region of color space studied here, no such pairs were shown to exist. In this strictly formal sense the filters enhanced dichromatic color vision. The type of discrimination so afforded, however, is rather limited, being no better than that which would be predicted on the basis of probability summation between monocular-brightness signals. It differs both qualitatively and quantitatively from that of a normal observer in this spectral region. It would be quite surprising if the minimal additional discrimination between spectral distributions resulting from wearing such filters yielded an advantage in any practical situation.

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REFERENCES AND NOTES

1. J. Dalton, "Extraordinary facts relating to the vision of colours," *Mem. Manchester Lit. Philos. Soc.* **5**, 28–45 (1798).
2. A. Seebeck, "Ueber den bei manchen Personen verkommen Mangel an Farbensinn," *Ann. Phys. Chem.* **118**, 177–233 (1837).
3. Reported in E. Boring, *Sensation and Perception in the History of Experimental Psychology* (Irvington, New York, 1942), Chap. 5, p. 184.
4. S. P. Richer, A. J. Adams, and A. C. Little, "Toward the design of an optimal filter for enhancement of dichromatic monocular chromatic discrimination," *Am. J. Optom. Physiol. Opt.* **62**, 105–110 (1985).
5. J. C. Maxwell, "Experiments on colour, as perceived by the eye, with remarks on colour-blindness," *Trans. R. Soc. Edinburgh* **21**, 275–298, reprinted in *Scientific Papers*, W. D. Niven, ed. (Dover, New York, 1855).
6. O. N. Rood, *Modern Chromatics* (Appleton, New York, 1879), Chap. 8, p. 98.
7. T. N. Cornsweat, *Visual Perception* (Academic, New York, 1970), Chap. 8, pp. 194–198.
8. V. C. Smith and J. Pokorny, "Spectral sensitivity of color-blind observers and the cone pigments," *Vision Res.* **12**, 2059–2071 (1972).
9. H. I. Zeltzer, "Method of improving color discrimination," U.S. Patent 3,701,590 (October 31, 1972).
10. K. W. Welsh, H. I. Zeltzer, and I. Siegal, "Letters," *Surv. Ophthalmol.* **26**, 229–230 (1982).
11. K. W. Welsh, J. A. Vaughn, and P. G. Rasmussen, "Aero-medical implications of the X-chrom lens for improving color vision deficiencies," *Aviat. Space Environ. Med.* **50**, 249–255 (1979).
12. K. Knoblauch, "Large-field and small-field discrimination of long-wavelength mixtures by protanopes," *Perception* **19**, 36 (1990).
13. K. Knoblauch, "Dual bases in dichromatic color space," *Colour Vision Deficiencies XII*, B. Drum, ed. (Kluwer, Dordrecht, The Netherlands, 1995), pp. 165–176.
14. W. H. Press, B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling, *Numerical Recipes in Pascal* (Cambridge U. Press, Cambridge, UK, 1989), Chap. 2, pp. 61–74.
15. The n data pairs are transformed into an $(n \times 3)$ matrix whose columns are the values ΔR_i^2 , ΔG_i^2 , and $2\Delta R_i \Delta G_i$, respectively. The system of equations to be solved is formed by multiplication of this matrix times the (3×1) column vector (a, b, c) , which is set equal to a $(n \times 1)$ column vector of 1's. The algorithm determines the least-squares solution.
16. Ref. 14, Chap. 14, p. 551.
17. A more conservative approach would be to use the standard errors of the mean of each observation in place of the standard deviations in Eq. (3). Because each point is based on five observations, each χ^2 value would be increased by a factor of 5. This manipulation would result in two tests from the data shown in this figure (and none for tests performed on data from succeeding figures), changing their outcomes: the test of the linear model for KK in the OD condition and the test of the elliptical model for MM in the binocular condition would be rejected. Perhaps a more informative comparison of the fits is provided by the difference in χ^2 values for the two models. This statistic is also distributed as a χ^2 variable, but with only 1 degree of freedom. Regardless of the error term used, in none of the monocular conditions does this statistic attain significance, thus indicating that the added parameter of the elliptical model yielded no significant benefit to the fit. Additionally, in both binocular conditions the linear model provided a significantly poorer fit to the data.
18. E.-J. Chichilnisky, D. Heeger, and B. A. Wandell, "Functional segregation of color and motion perception examined in motion nulling," *Vision Res.* **33**, 2113–2125 (1993); A. B. Poirson and B. A. Wandell, "The ellipsoidal representation of spectral sensitivity," *Vision Res.* **30**, 647–652 (1990).
19. G. Wyszecki and W. S. Stiles, *Color Science* (Wiley, New York, 1982), Chap. 4, p. 256.

20. M. Alpern, K. Kitahara, and D. H. Krantz, "Classical tritanopia," *J. Physiol. (London)* **335**, 655–681 (1983).
21. M. J. McMahon and D. I. A. MacLeod, "Color blind color vision at high light levels: red/green discrimination using the blue-sensitive cones," *Invest. Ophthalmol. Vis. Sci. Suppl.* **35**, 1572 (1994).
22. V. C. Smith and J. Pokorny, "Large-field trichromacy in protanopes and deuteranopes," *J. Opt. Soc. Am.* **67**, 213–220 (1977); A. L. Nagy, "Large-field substitution Rayleigh matches of dichromats," *J. Opt. Soc. Am.* **70**, 778–783 (1980).
23. M. E. Breton and W. B. Cowan, "Deuteranomalous color matching in the deuteranopic eye," *J. Opt. Soc. Am.* **71**, 1220–1223 (1981); A. L. Nagy, "Homogeneity of large-field color matches in congenital red–green color deficient," *J. Opt. Soc. Am.* **72**, 571–577 (1982).
24. P. A. Anderson and J. A. Movshon, "Binocular combination of contrast signals," *Vision Res.* **29**, 1115–1132 (1989); C. R. Cavonius, "Binocular interactions in flicker," *Q. J. Exp. Psych.* **31**, 273–280 (1979); C. R. Cavonius, O. Estévez, and L. H. van der Tweel, "Counterphase dichoptic flicker is seen as its own second harmonic," *Ophthalmic Physiol. Opt.* **12**, 153–156 (1992); T. E. Cohn and D. J. Lasley, "Binocular vision: two possible central interactions between signals from two eyes," *Science* **192**, 561–563 (1976).
25. S. P. Taylor, "The X-chrom lens—A case study," *Ophthalmic Physiol. Opt.* **2**, 165–170 (1982).
26. T. E. Cohn, H. Leong, and D. J. Lasley, "Binocular luminance detection: availability of more than one central interaction," *Vision Res.* **21**, 1017–1023 (1981).
27. J. D. Victor, K. Maiese, R. Shapley, J. Sidtis, and M. S. Gazzaniga, "Acquired central dyschromatopsia: analysis of a case with preservation of color discrimination," *Clin. Vision Sci.* **4**, 183–196 (1989).
28. D. Calkins, J. Thornton, and E. N. Pugh, Jr., "Monochromatism determined at a long-wavelength/middle-wavelength cone-antagonistic locus," *Vision Res.* **32**, 2349–2367 (1992).
29. Y. Le Grand, "Les seuils différentiels de couleurs dans la théorie de Young," *Rev. Opt.* **28**, 261–278 (1949).
30. Ref. 19, Chap. 8, p. 689.
31. M. D'Zmura, "Color constancy: surface color from changing illumination," *J. Opt. Soc. Am. A* **9**, 490–493 (1992).
32. L. T. Maloney and B. Wandell, "Color constancy: a method for recovering surface spectral reflectance," *J. Opt. Soc. Am. A* **3**, 29–33 (1986).