

Tyndall's paradox of hue discrimination

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We confirm a remarkable but forgotten property of human color vision that was described over 50 years ago by Tyndall [J. Opt. Soc. Am. 23, 12 (1933)]: if wavelength discrimination is measured in the region of 455 nm, the sensitivity of the eye improves when a large fraction of the monochromatic light in each half of the matching field is replaced by white light that is common to the two halves. We demonstrate that a similar facilitation also occurs when the shortwave monochromatic components are held constant in luminance and a long-wave desaturant of increasing luminance is added to the shortwave discriminanda. We relate these phenomena to the properties of postreceptoral visual channels.

INTRODUCTION

In 1933, Tyndall reported some measurements on color vision that he had made in 1926 at the National Bureau of Standards. His paper¹ has occasionally been cited for its control data on the discrimination of the wavelengths of monochromatic lights, but his main results, extraordinary though they are, did not fit the theoretical frameworks then available, and they have gone almost unremarked for over 50 years.² What Tyndall investigated was the way in which wavelength discrimination varied as purity was reduced, as, in other words, a portion of the monochromatic light was replaced by white light. Over much of the spectrum he found that colorimetric purity could be reduced to 50% without an impairment of wavelength discrimination.³ This result is remarkable in itself, but for blue lights near 455 nm, the discrimination actually improved when purity was reduced to 20%. We refer to the latter finding as Tyndall's paradox.

Figure 1 illustrates the stimuli used by Tyndall. For the condition of 100% purity (represented on the left-hand side of the figure), the observer viewed a 2-deg bipartite field that was monochromatic in both its halves. One half of the field was fixed in wavelength (λ), and for the conditions that are of interest here, its troland value was 40. The observer adjusted the wavelength of the other half of the field until the two halves exhibited a just-noticeable difference of hue that could not be eliminated by adjusting the luminance of the variable half-field. For lower purities, Tyndall removed some fraction of the monochromatic light from both sides of the field and replaced it with white light that was common to the two sides (Fig. 1, right-hand side). The total retinal illuminance was held at 40 Td. To obtain a wavelength threshold, the subject adjusted the monochromatic component of one half of the field, as before.

Our perception of hue depends on the relative quantum catches in the different classes of retinal photoreceptor.⁴ In

order to detect a difference in the hues of two fields, the subject must be able to detect differences between two sets of quantum catches. Yet, in Tyndall's experiment, as monochromatic light is replaced by white light that is common to the two fields, the differences in quantum catches must become smaller, both absolutely and relatively: absolutely because part of the blue light has been removed, and relatively because white light has been substituted for blue light.

Tyndall's result is indeed a paradox; it must tell us something essential about human color vision. It certainly reveals an inadequacy of most classical line-element models of color discrimination,⁵ insofar as such models require discrimination to deteriorate as the two sets of quantum catches become more similar. We therefore set out to replicate Tyndall's finding. We confirm the paradox and, in attempting to explain it, are led to examine some related phenomena.

Tyndall used only one subject, himself, and relied on his subjective judgment of when the fields were just noticeably different. So his paradox might have arisen artifactually if his criterion changed as purity changed, for the appearance of the fields would be different at high and low purities. We thus sought a less-subjective index of the observer's ability to discriminate, a performance measure in the terminology of modern psychophysics. The method of average error^{6,7} recommended itself for our purpose: our observers adjusted a variable half-field until it matched a standard half-field in hue and luminosity, and the dependent measure was the standard deviation (SD) of a set of wavelength matches.

METHODS

Apparatus and Stimuli

Stimuli were presented by means of a three-channel Maxwellian-view optical system, which was under computer con-

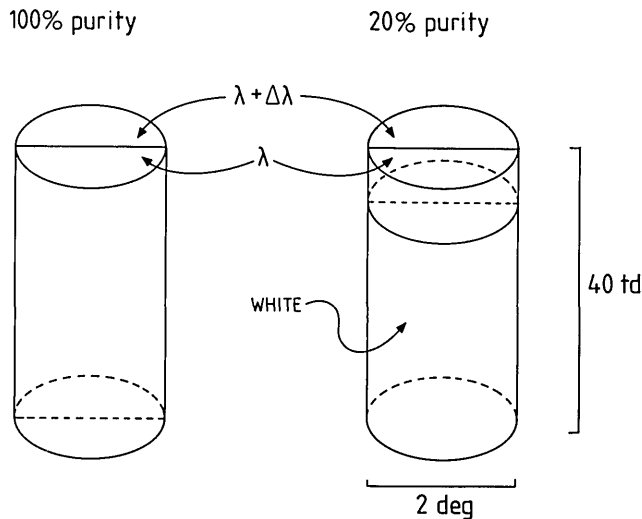


Fig. 1. The stimulus conditions used by Tyndall. The observer is required to discriminate between two halves of a horizontally divided stimulus field that subtends 2 deg of visual angle. The upper half-field is adjustable in wavelength. In the case of 100% purity (left-hand side of figure), both half-fields are monochromatic. To secure purities of less than 100%, some fraction of the monochromatic light is replaced by white light that is common to the two halves of the field (right-hand side of figure). The total retinal illuminance remains at 40 Td throughout.

trol. The light source for all three channels was a 12-V 50-W tungsten halogen lamp. Two channels provided monochromatic light for the upper and lower halves of a 2-deg field. These channels contained matched monochromators with integral stepping motors (Bentham Instruments, model M300E), which permitted the wavelength to be varied in steps of 0.05 nm. The boundary between the two half-fields was provided by the beveled edge of a thin mirror, with one beam being transmitted over the mirror and one being reflected at its front surface. The lower half-field was fixed in wavelength and luminance during a given experiment. The luminance of the upper field could be adjusted in steps of $\sim 0.01 \log_{10}$ unit by means of a neutral-density wedge. The bandwidths of the two half-fields were 1.8 nm. A Wratten filter, appropriate to the test wavelength and common to the two half-fields, was always present, in order to block any stray light. The third channel permitted a congruent desaturating field to be added to the field formed by the first two channels. In the first experiment two 80A Wratten filters filtered the tungsten light of the third channel to give a desaturant with chromaticity coordinates of approximately $x = 0.25, y = 0.25$. In subsequent experiments, a Jobin-Yvon monochromator (model H10, with 1-mm entrance and exit slits) was introduced into the third channel to give narrow-band desaturants. A blocking filter appropriate to the desaturant wavelength was always present.

Procedures

Before each trial, the computer displaced the wavelength and the radiance of the variable half-field by amounts that were random in size and direction. The observer adjusted this field until it matched the lower half-field in hue and brightness: left-right movement of a joystick altered the wavelength, forward-backward movement altered radiance, and a push button was available for the observer to signal when a satisfactory match had been secured. The depen-

dent measure was the SD of 25 such matches. The upper and lower half-fields were briefly occluded between trials, while the wavelength and radiance of the variable field were being offset; the desaturant field was not occluded, in order to avoid transient tritanopia.⁸ During an individual setting, viewing was continuous, without constraint of fixation.

Within one experimental run, settings were obtained for a single value of purity. Different purities were tested in random order. To combine data from separate repetitions of the same condition, the root mean square (rms) was calculated from the individual SD's; i.e., the variances of the two runs were averaged. Radiances of monochromatic lights were measured by means of a United Detector Technology PIN 10 photodiode, which had been spectrally and absolutely calibrated by the National Physical Laboratory. The white field used in the first experiment was equated by flicker photometry to a monochromatic yellow field that had been measured radiometrically. The wavelength scales of the monochromators were calibrated with a helium-neon laser.

Observers

The observers were the authors, who are male and have normal color vision. The precision of their matches was found to improve in the course of preliminary experiments, and they underwent extensive practice before obtaining the results reported here.

RESULTS AND DISCUSSION

Tyndall's Paradox

Figure 2 shows the result of a direct attempt to reproduce Tyndall's result by using the method of average error. The standard half-field had a wavelength (λ) of 455 nm and a luminance of 40 Td, as in Tyndall's experiments. Tyndall himself gave results for a number of desaturant fields of different color temperatures. Our own desaturant was a bluish white, chosen to simulate the chromaticity of the desaturant ($x = 0.25, y = 0.25$) for which Tyndall found the maximal facilitation. His results for this desaturant are replotted in the uppermost panel of the figure. The results for our observers (lower two panels) are concordant with those of Tyndall. In neither case does wavelength discrimination deteriorate monotonically as purity is reduced; instead, it is optimal between 10 and 20% purity.

The reader may wonder what the targets look like. At 100% purity, they are a glaring blue and vary little in appearance as the wavelength is changed. At 20% purity they are of delicate pastel shades, and the variable half-field changes quickly from reddish to greenish as the joystick is moved in the direction of longer wavelengths.

In this and subsequent experiments we stored the observer's setting of luminance for each individual match. The SD's of these matches always proved to be positively and strongly correlated with the SD's of the wavelength matches.⁹

The Shortwave Pessimism

As a preliminary to suggesting an explanation of Tyndall's paradox, we note the proximity of (a) the one wavelength (455 nm) at which Tyndall found the paradox and (b) the wavelength at which the wavelength-discrimination thresh-

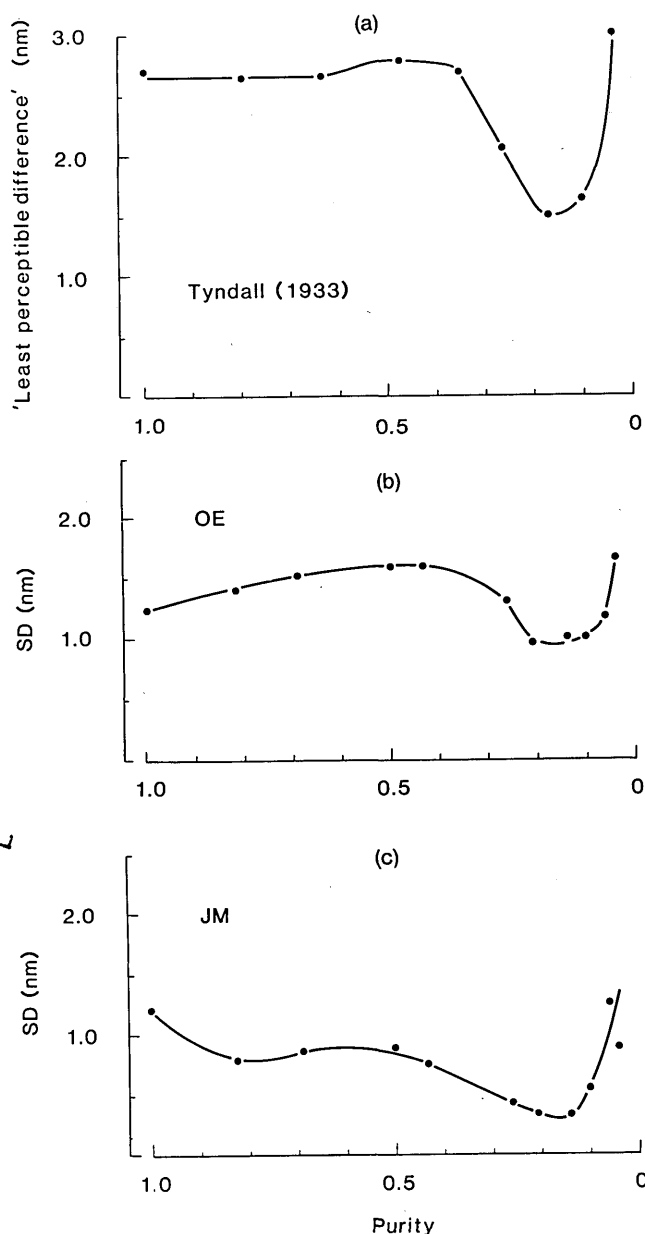


Fig. 2 (a) Results for the single observer of Ref. 1, showing the wavelength threshold at 455 nm as a function of colorimetric purity. (Colorimetric purity is the luminance of the monochromatic component expressed as a percentage of the total luminance of the mixture.) Tyndall used a number of desaturating fields of different color temperatures; the data replotted here are for the desaturant that gave the maximum facilitation, a bluish white with chromaticity coordinates of approximately $x = 0.25, y = 0.25$. (b) and (c) Precision (SD) of wavelength matches at 455 nm as a function of purity for observers OE (b) and JM (c). Each data point represents the rms value for two independent sets of 25 matches. The desaturating field had chromaticity coordinates of approximately $x = 0.25, y = 0.25$.

old typically exhibits a local maximum, the short-wave pessimum.^{6,10,11} Using lights of 100% purity and a standard luminance of 50 Td, we measured for our own observers the precision of wavelength matches in the range 445–500 nm. In order to locate the pessimum more precisely than was done in previous studies, we sampled values of λ at 5-nm intervals. The different values of λ were tested in different standard orders in two independent runs. The results (Fig.

3) show the shortwave pessimum clearly. Near 495 nm the SD of the settings is as low as 0.2 nm, but both observers exhibit poor discrimination at 460 nm.

A Provisional Theory

To explain Tyndall's paradox, we consider several of the possible ratios of cone signals on which hue discrimination could be based, and we consider what is happening to these ratios in the region of the shortwave pessimum. We denote by $N_S, N_M,$ and N_L the rates of quantum catch in the short-wave, middle-wave, and long-wave cones, respectively, and we discuss separately the ratio N_M/N_L on the one hand and the ratios N_S/N_M and N_S/N_L on the other.

1. The Shortwave Maximum in the Ratio N_M/N_L .

It is unlikely that the ratio N_M/N_L can support good hue discrimination near 460 nm. It is well established that tritanopes (who lack the shortwave cones and are obliged to depend only on N_M/N_L) show an exaggeration of the shortwave pessimum of wavelength discrimination,¹² and a similar result is found for normal observers under tritan conditions of viewing¹³⁻¹⁵ (see Fig. 4). The reason why N_M/N_L yields poor discrimination near 460 nm is that N_M/N_L passes through a maximum in this spectral region and the rate of change of the ratio with wavelength slows down in passing the maximum. This can be seen from Fig. 5(a), which shows a modern set of König cone fundamentals, those derived by Estévez using the Stiles-Burch color-matching functions.¹⁶ Figure 5(b) shows the logarithms of

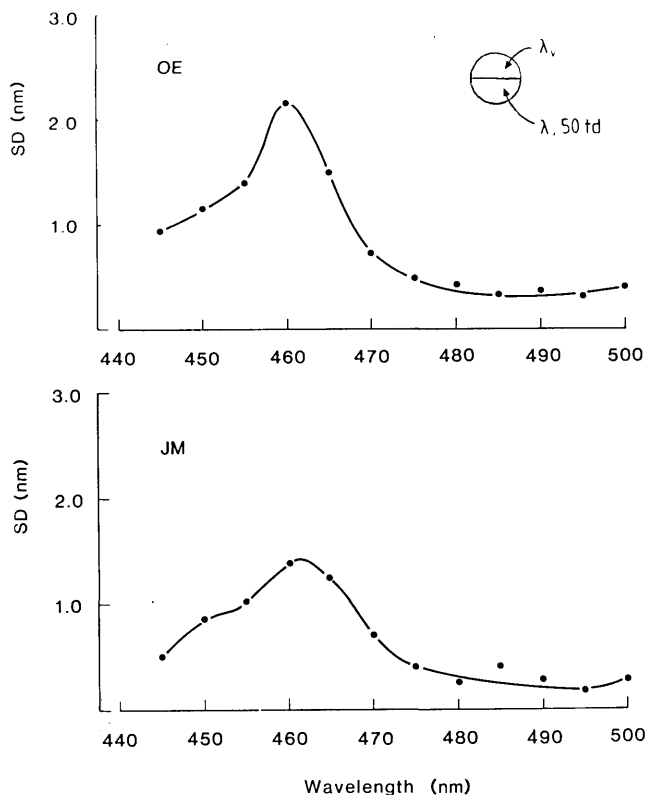


Fig. 3. The precision (SD) of settings of the variable wavelength (λ_0) when matching standard wavelengths (λ) in the range 445–500 nm. Each data point represents the rms value for two independent sets of 25 matches. Note the well-defined peak in the function at 460 nm, the shortwave pessimum.

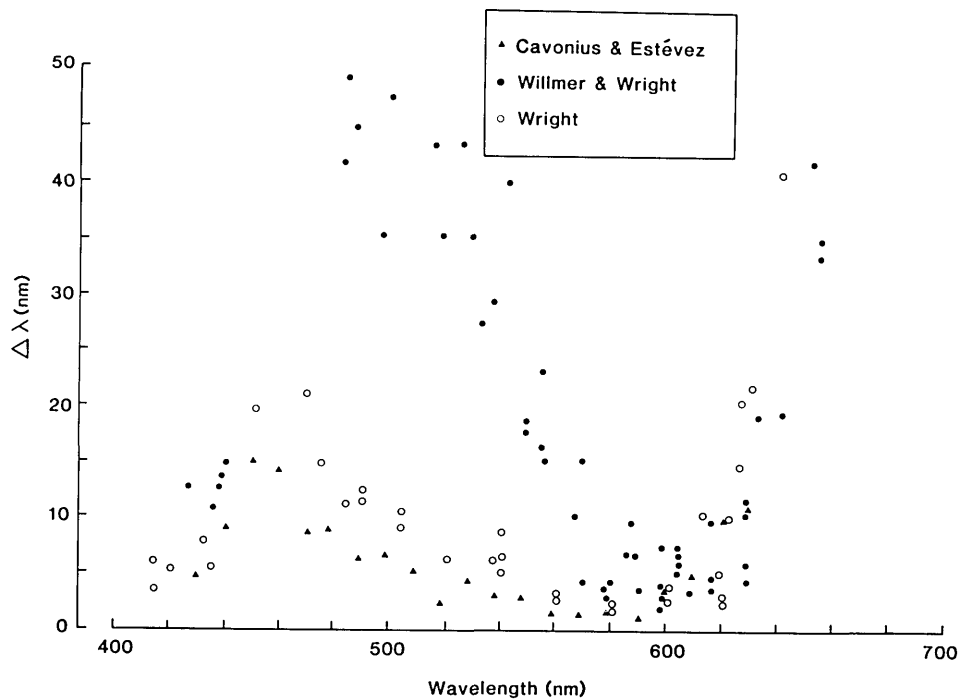


Fig. 4. Wavelength discrimination by tritanopes (O) and by normal observers when viewing under tritan conditions (●, ▲).

the ratios N_M/N_L and N_S/N_M . The former ratio has its maximum near 460 nm. This result is not peculiar to the present set of fundamental sensitivities: the fundamentals of Vos and Walraven and of Smith and Pokorny also place the maximum value of N_M/N_L at 460 nm.¹⁷ Independent evidence is provided by direct electrophysiological recordings from photoreceptors: in Fig. 5(b) we reproduce the plot made by Nunn *et al.*¹⁸ of the log ratio of the sensitivities of middle- and long-wave cones from macaque retinas. Again, the ratio has a maximum at 460 nm.

2. Saturation of the Signals Representing N_S/N_M and N_S/N_L

It is probable, then, that our discrimination of monochromatic lights near 460 nm depends on the shortwave receptors, that is, on the ratio N_S/N_M or N_S/N_L or, say, the ratio of N_S to some combination of N_M and N_L . However, the discrimination offered by these ratios apparently remains poor so long as the discriminanda are monochromatic. In this case the explanation cannot lie in the rate of change of the ratios with wavelength, since all plausible sets of cone fundamental sensitivities show that N_S/N_M and N_S/N_L change quickly in the region of 460 nm.^{4,16,17} (See Fig. 5, in which the ratio of shortwave to middle-wave cone sensitivities is plotted in the lower panel.) Rather, we may turn to the evidence that postreceptoral chromatic signals are subject to a two-sided compressive nonlinearity.^{14,19} In other words, the neurons that extract the ratios of cone signals are thought to be most sensitive in the middle of their operating range and to become less sensitive to perturbations of their input as they are driven to one or another extreme of their range.^{20,21} Monochromatic lights of 460 nm will produce high values of N_S/N_M and of N_S/N_L , and we suggest that chromatic signals that represent these ratios will be close to their saturating values.

3. Tyndall's Paradox as Recovery from Saturation

We are now in a position to explain Tyndall's paradox. When, in Tyndall's experiment, white light is substituted for a portion of the monochromatic light, the ratios N_S/N_M and N_S/N_L will be reduced. Those postreceptoral neurons that extract these ratios will be brought to a more-sensitive part of their operating range, and the observer's hue discrimination will improve.

The König-Dieterici Anomaly

However, the results presented so far do not show unambiguously that it is the ratio signals that saturate at some postreceptoral site. It could be the shortwave cone signals themselves that saturate, as in the model of wavelength discrimination described by Vos and Walraven.²² Recall one feature of Tyndall's experiment: when the white light is added, the monochromatic components of the field are attenuated, and thus the absolute level of excitation of the shortwave receptors is reduced. A second anomaly occurs in the region of the shortwave pessimum: around 460 nm, and nowhere else in the spectrum, wavelength discrimination can be improved by reducing the luminance in the range 100–1 Td. We shall call this effect the König-Dieterici anomaly, since a crossing over of the curves for low and high intensities can be seen near 450 nm in the wavelength-discrimination data of König and Dieterici.^{6,23} Figure 6 shows detailed measurements of the König-Dieterici anomaly for observer JM. On the basis of our own measurements of the position of the shortwave pessimum (Fig. 3) and estimates of the wavelength at which the rate of change of N_M/N_L is minimal (Fig. 5), we adopted 460 nm as the value of λ in this experiment. No desaturant was present. In the region of 100 Td (Fig. 6) the SD of wavelength matches was over 2 nm (and the subject noted that the hue changed in the same way whether the joystick was moved to the left or to the right), whereas between 1 and

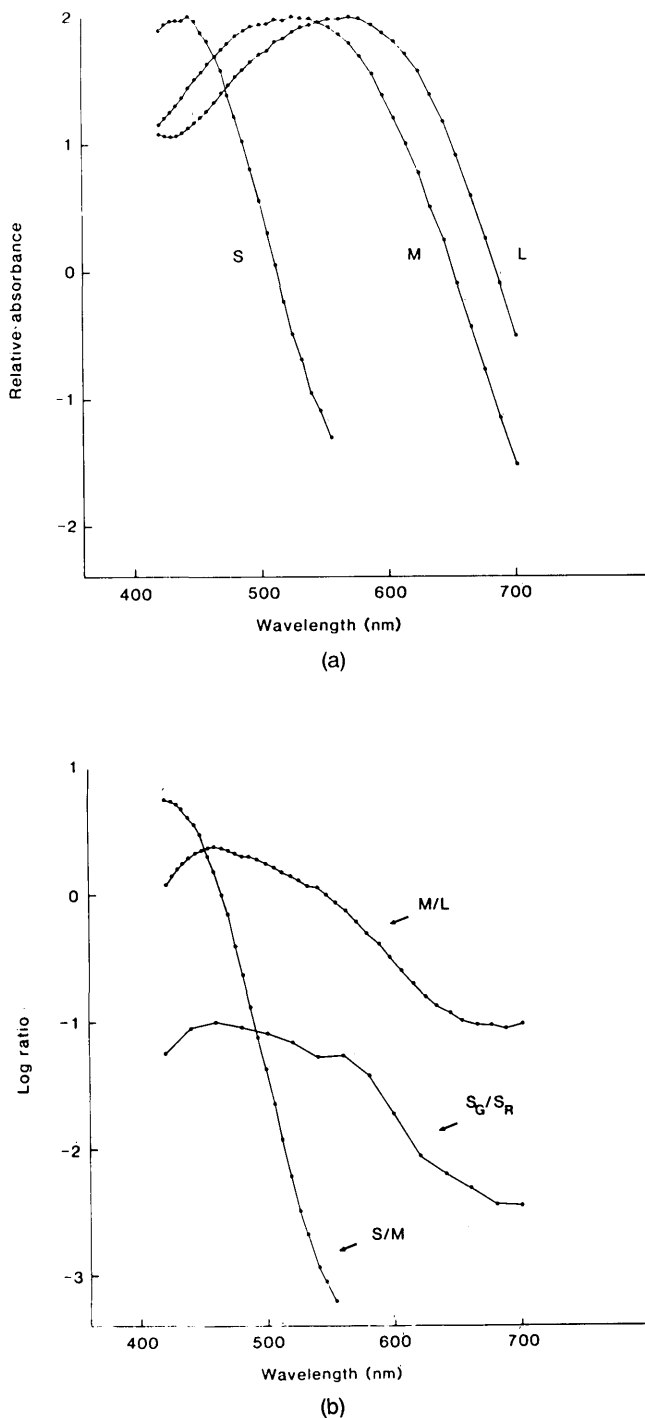


Fig. 5. (a) Spectral sensitivities of the shortwave (S), middle-wave (M), and long-wave (L) cones. These König fundamentals are those derived by Estévez from the Stiles-Burch 2-deg color-matching data.¹⁶ (b) Plots of the log ratio of middle-wave to long-wave cone sensitivity (M/L), the log ratio of shortwave to middle-wave sensitivity (S/M), and the log ratio of middle-wave to long-wave cone sensitivity as obtained by electrophysiological recording from individual cones of *Macaca fascicularis* by Nunn *et al.*¹⁸ (S_G/S_R). In order to permit direct comparison with the electrophysiological results, which were obtained by transverse illumination of receptors, the sensitivities of the König fundamentals are given as absorbances for a pigment solution of low concentration. There is only a small shift in the position of the maximum of M/L when allowance is made for self-screening of the pigment *in vivo*, and prereceptor absorption cannot change the position of the maximum.

10 Td the SD had a value of only 0.5 nm. Thus, if we repeat Tyndall's experiment but simply block off the white beam, we still get an improvement. It could be that a 40-Td blue field is sufficient to saturate the signals of the shortwave receptors themselves and that it is a receptor site, not a postreceptor one, that is being restored to a more sensitive part of its operating range when purity is reduced.²⁴

Adding Desaturants to a Shortwave Field of Fixed Radiance

To establish whether facilitation can genuinely arise at a postreceptor, chromatically opponent site, we must hold fixed the quantum catch of the shortwave cones while altering the quantum catches of the middle- and long-wave cones. We therefore repeated the experiment shown in Fig. 2 but held the luminance of the monochromatic standard field at 40 Td while adding a desaturant field of varying luminance. The desaturant was a monochromatic field of 560 nm, instead of the white field used earlier. The use of a monochromatic desaturant simplifies the interpretation of this experiment: even at its highest luminance, the 560-nm field would be likely to have only a negligible effect on the shortwave cones themselves^{4,17} (see Fig. 5). The value of λ was 460 nm, for the reasons given in the preceding subsection.

Figure 7 shows the results of this experiment. For both observers, the SD of the shortwave hue matches can be halved by the addition of yellowish-green light to the two sides of the field. For observer OE, the optimum discrimination occurs when the luminance of the 560-nm field lies between 2.0 and 2.8 log Td; for JM the optimum occurs at values between 2.6 and 2.8 log Td. In this experiment, the excitation of the shortwave receptors is held constant (or, at least, it is not reduced) as the yellow-green field is made more intense. Thus it is impossible to explain the facilitation by supposing that it depends on the release from saturation of the shortwave signal itself (and, *a fortiori*, the facilitation cannot be explained by the release from saturation of a rod signal). In summary, our hypothesis is that hue discrimination can be impaired when postreceptor neurons are operating in extreme regions of their response range and that performance can be restored by returning such units to a more-favorable operating region.

It is parsimonious to suppose that the phenomenon shown in Fig. 7 is essentially the same as combinative euchromatopsia,^{21,25} an effect discovered within the Stilesian tradition of increment-threshold measurements but usually explained in terms of the properties of chromatic differencing channels.^{20,21,25} Combinative euchromatopsia is observed when increment thresholds for colored targets are measured on bright, colored fields. If, for example, the threshold is measured for a 2-deg violet (423-nm) target on a blue (473-nm) field of $10^{9.7}$ quanta $\text{sec}^{-1} \text{deg}^{-2}$, and if a complementary yellow field is then combined with the first field, then the increment threshold will fall as the radiance of the yellow field increases. Combinative euchromatopsia is a phenomenon that occurs at high field radiances, but (for some subjects, at least) it can be observed when the quantal flux of a 473-nm field is as low as $10^{8.75}$ quanta $\text{sec}^{-1} \text{deg}^{-2}$ (Ref. 21, Fig. 3), or about 54 Td. In its effect on the shortwave cones, a 473-nm field of 54 Td would be equivalent to a 460-nm field of approximately 80 Td.¹⁶ This quantitative compari-

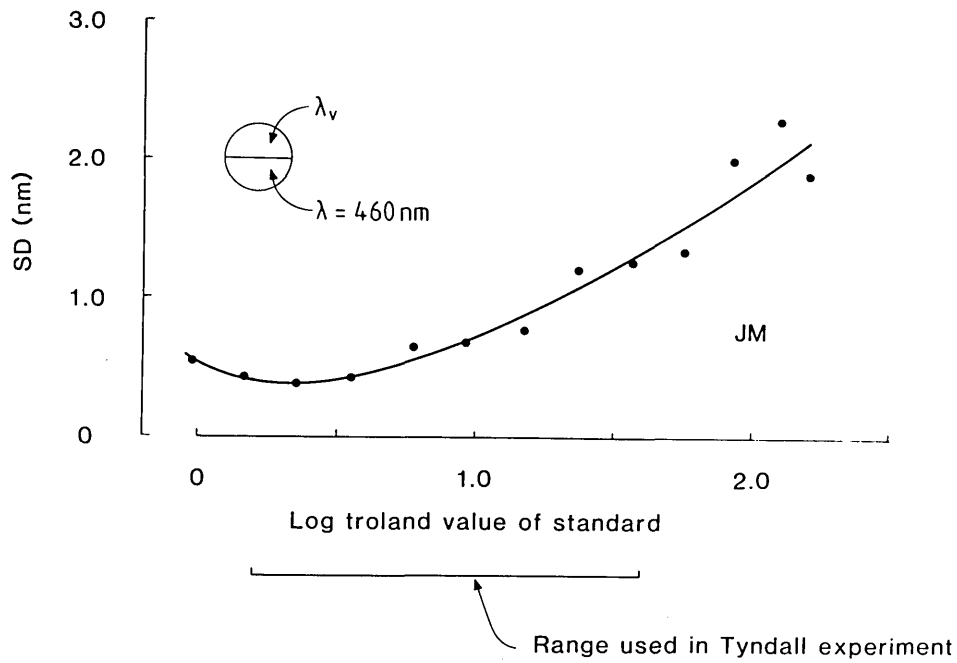


Fig. 6. The König-Dieterici anomaly. The figure shows the precision (SD) of wavelength matches for monochromatic standard lights of 460 nm plotted as a function of their luminance (observer JM). Each data point represents the rms value for three independent sets of 25 matches. No desaturating field was used in this experiment. The secondary abscissa indicates the range of troland values used for the standard field in our first experiment [Figs. 2(b) and 2(c)].

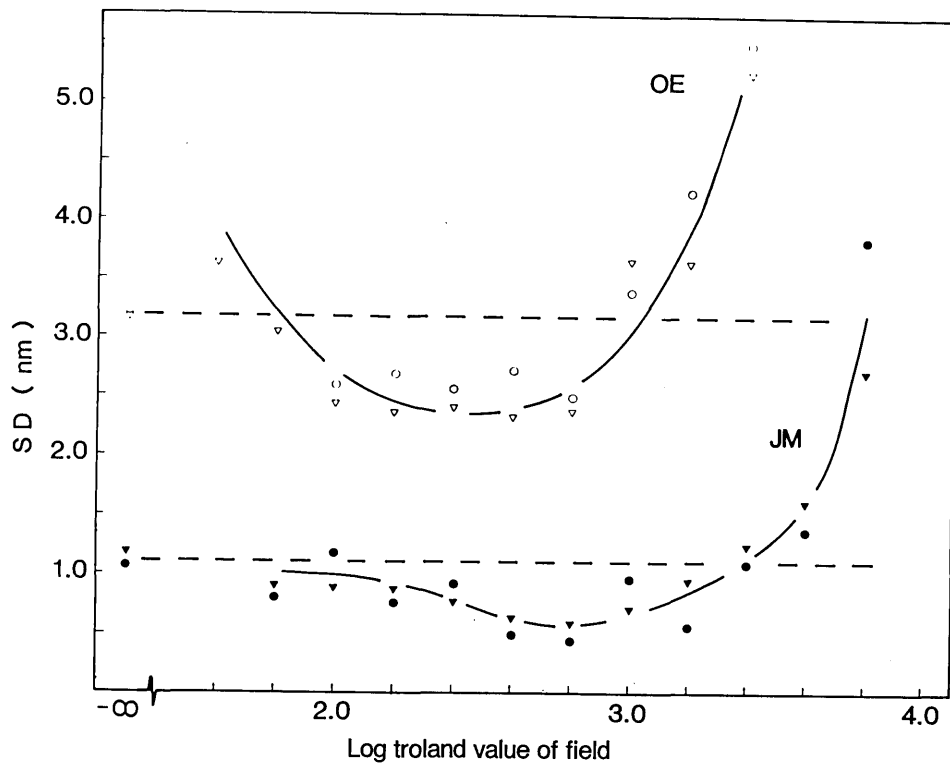


Fig. 7. The precision (SD) of wavelength matches at 460 nm as a function of the log troland value of a 560-nm desaturating field. We used a monochromatic desaturating field in this experiment because the 560-nm light will affect only negligibly the quantum catch of the shortwave cones, and thus the experiment is conceptually simpler. The 460-nm standard field was fixed at 40 Td. Data are shown for two independent runs for each of the observers, OE (open symbols) and JM (solid symbols). The results for OE have been displaced vertically by 2 nm. The horizontal dashed lines indicate the precision of matches when no desaturant was used.

son suggests, if combinative euchromatopsia is indeed the same as the phenomenon shown in Fig. 7, that our present stimulus luminances lie at the bottom margin of the range within which a facilitation of shortwave discrimination can be expected. The results shown in Fig. 6 point to a similar conclusion. However, the increment-threshold task, which was originally used to demonstrate combinative euchromatopsia, is operationally an intensity-discrimination task, and it is always possible that the subject uses a nonopponent mode of detection at low field radiances.²⁶ The present approach, by obliging the subject explicitly to depend on color-differencing channels, may offer the more-direct way to examine the range and the properties of combinative euchromatopsia.

The phenomenon shown in Fig. 7 is possibly also related to an informal observation made by Stiles during the National Physical Laboratory's investigation of color matching.²⁷ His subjects experienced particular difficulty in matching stimuli that lay in the range 420–460 nm: "... the range on the green (or blue) primary wedge over which 'acceptable' matches can be made by adjustments of the blue (or green) and red primaries only, is unexpectedly large." Stiles noted that the error could be reduced by adding the green primary (526 nm) to both sides of the matching field, so that the matches of test colors below 460 nm were made in a less-saturated field. "Sufficient green primary was added to keep the resultant field chromaticity on the line in the chromaticity diagram joining the points of the spectrum locus corresponding to 21 500 cm⁻¹ and 15 420 cm⁻¹ [465 nm and 649 nm]."²⁸

Spectral Sensitivity of the Long-Wave Signal

We have postulated that a shortwave signal is opposed at a postreceptor site by a signal originating in another class of receptor. We refer to the latter signal as the opponent signal. Figure 8 shows the results of a preliminary attempt to identify the source of the opponent signal. The standard half-field was held fixed at 40 Td throughout and had a wavelength of 460 nm. Desaturant fields of varying radiance were added to the discriminanda, and in different experimental sessions the wavelength of the desaturant was varied. The desaturants ranged from 500 to 640 nm and were tested in random order.

In Fig. 8(a) the SD of wavelength matches is plotted as a function of the absolute quantal flux of the desaturant field. For each set of data the leftmost point represents the SD of matches when no desaturant is present. For desaturants in the range 560–600 nm a clear minimum is seen in the functions, extending the range of the results shown in Fig. 7. At shorter wavelengths the minimum is slightly less clear, and in this region it is possible that the desaturating light significantly adds to the quantum catch of the shortwave receptors. In the case of 640 nm we may not have had sufficient light to establish the minimum.

If the opponent signal originated in a single class of receptor, if those receptors obeyed the principle of univariance,²⁹ and if the desaturant light had no direct effect on the shortwave receptors, then each of the sets of data in Fig. 8(a) should be described by a function of the same fixed form. As the wavelength of the desaturant field was varied, the function should simply be displaced laterally without distortion. The lateral displacement would arise solely and di-

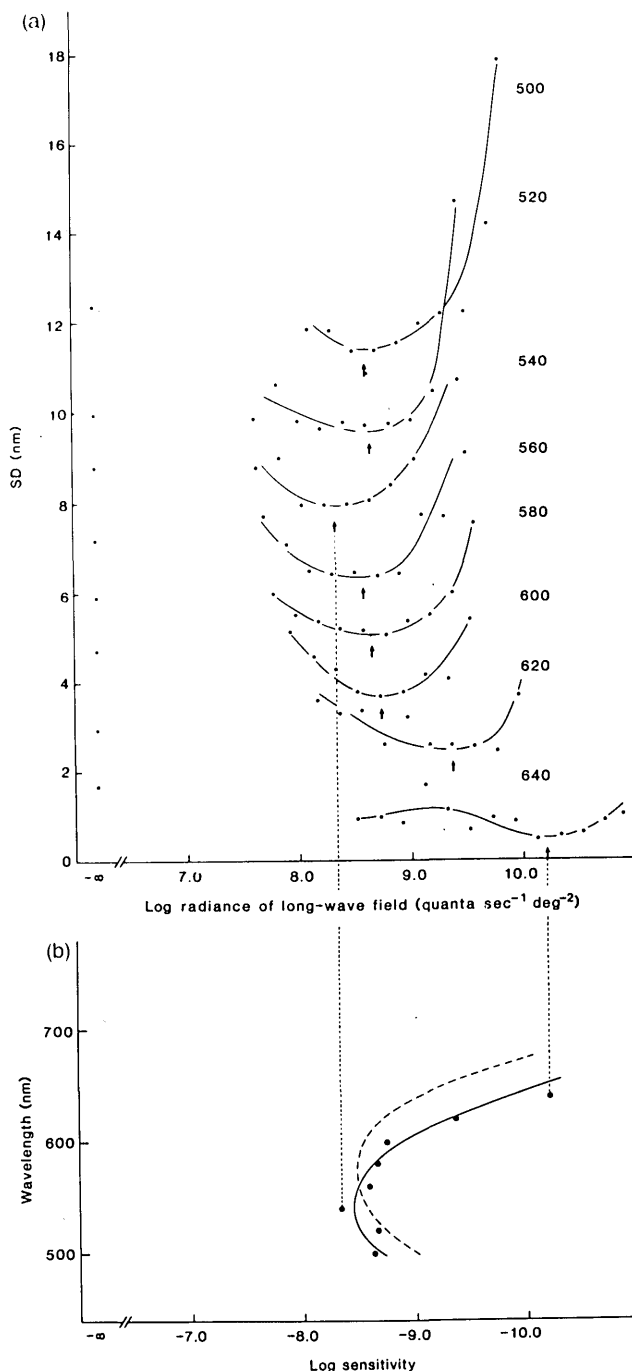


Fig. 8. (a) The precision (SD) of wavelength matches at 460 nm as a function of the log₁₀ radiance of long-wave desaturating fields. The parameter is the wavelength of the long-wave field. The lowermost set of data points is correctly placed; the other sets are displaced vertically in increments of 1.5 nm. The field wavelength is shown against each set of data. The leftmost data point in each case indicates the precision of matches when no desaturant field is present. The vertical arrows represent the approximate field radiances at which the matches are most precise. (b) The reciprocal of the log desaturant radiance needed to secure maximum precision (horizontal axis) plotted as a function of the wavelength of the desaturant field (vertical axis). This plot represents the spectral sensitivity of a hypothetical opponent signal (see the text). The solid curve represents the (corneal) spectral sensitivity of the middle-wave fundamental of Estévez,¹⁶ and the dashed curve represents the long-wave fundamental. The vertical dashed lines indicate, for two field wavelengths, how the plots in (b) are derived from the plots in (a).

rectly from the changing probability that a given photon would be absorbed from the desaturant field.

It is not clear that the data sets shown in Fig. 8(a) can, in fact, be described by a single template. Nevertheless, we tentatively indicate by a vertical arrow the approximate minimum of each function, and we show in Fig. 8(b) the spectral sensitivity that would then be derived for the opponent signal.³⁰ The solid curve in Fig. 8(b) represents the (corneal) sensitivity of the *M* fundamental of Estévez, whereas the dashed curve represents the *L* fundamental. Our data are preliminary, but they appear sufficient to rule out one possibility, the possibility that the opponent signal arises exclusively in the long-wave cones. More-precise experiments would be needed to establish whether the opponent signal arises exclusively in the middle-wave cones or whether it represents some combination of the middle- and long-wave signals.

CONCLUSION

We confirm Tyndall's original finding that wavelength discrimination around 460 nm can be improved by substitution of white for part of the monochromatic blue light. However, Tyndall's paradox is less straightforward to explain than is the phenomenon shown in Figs. 7 and 8: in the former case the quantum catches of both the shortwave and the middle-wave receptors are altered concurrently, whereas in the paradigm of Figs. 7 and 8 the shortwave signal is held approximately constant. It remains possible that Tyndall's paradoxical improvement in hue discrimination is due to a release from saturation at both a receptor site and a post-receptor site. In our modified paradigm (Figs. 7 and 8), however, the improvement could be due only to a release from saturation at a postreceptor site. Our results show that wavelength discrimination cannot be limited only by the rate of change of quantum catches in different classes of cone.

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9. For example, in the case of the experiments for which results are shown in Fig. 2, the SD of the luminance settings for observer OE (calculated as for the wavelength settings) was 0.022 log unit when no desaturant was present and 0.016 log unit at 14% purity; for observer JM the corresponding values were 0.031 and 0.015 log unit.
10. O. Steindler, "Die Farbenempfindlichkeit des normalen und farbenblinden Auges," *Sitzungsber. Akad. Wiss. Wien Math. Naturwiss. Kl. Abt. 2A* **115**, 39–62 (1906); W. D. Wright and F. H. G. Pitt, "Hue-discrimination in normal colour-vision," *Proc. Phys. Soc. London* **46**, 459–473 (1935).
11. To indicate a peak or maximum in the wavelength-discrimination curve, we adopt the useful term *pessimum*, which was introduced in this context by R. A. Weale, "Hue discrimination in paracentral parts of the human retina measured at different luminance levels," *J. Physiol. (London)* **113**, 115–122 (1951). The term avoids the ambiguity that may be aroused in the reader's mind by reference to a maximum in the wavelength-discrimination curve.
12. F. P. Fischer, M. A. Bouman, and J. Ten Doesschate, "A case of tritanopia," *Doc. Ophthalmol.* **5**, 55–87 (1952); W. D. Wright, "The characteristics of tritanopia," *J. Opt. Soc. Am.* **43**, 509 (1952).
13. E. N. Willmer and W. D. Wright, "Colour sensitivity of the fovea centralis," *Nature* **156**, 119–121 (1945). These authors write, "In the neighbourhood of 0.46 μ there is an effective discontinuity in the [wavelength-discrimination] curve, since the change of hue with wavelength falls to zero at this point."
14. C. R. Cavonius and O. Estévez, " π -mechanisms and cone fundamentals," in *Visual Psychophysics and Physiology*, J. C. Armington, J. Krauskopf, and B. R. Wooten, eds. (Academic, New York, 1978), pp. 221–231.
15. P. Kaiser and R. M. Boynton, "Role of the blue mechanism in wavelength discrimination," *Vision Res.* **25**, 523–529 (1985).
16. G. Wyszecki and W. S. Stiles, *Color Science* (Wiley, New York, 1982).
17. J. J. Vos and P. L. Walraven, "On the derivation of the foveal receptor primaries," *Vision Res.* **11**, 799–818 (1971); V. C. Smith and J. Pokorny, "Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm," *Vision Res.* **15**, 161–171 (1975). Ultimately, the colorimetric evidence that N_M/N_L is maximal at 460 nm is provided by the fact that a tritanope, or a normal observer under tritan conditions, can match all wavelengths between 420 and 650 nm with a positive mixture of 460-nm and 650-nm primaries. See the references cited in Notes 12 and 13 and H. G. Sperling, "Case of congenital tritanopia with implications for a trichromatic model of color reception," *J. Opt. Soc. Am.* **50**, 156–163 (1960); M. Alpern, K. Kitahara, and D. H. Krantz, "Classical tritanopia," *J. Physiol. (London)* **335**, 655–681 (1983); L. C. Thomson and W. D. Wright, "The colour sensitivity of the retina within the central fovea of man," *J. Physiol. (London)* **105**, 316–331 (1947); K. H. Ruddock and G. J. Burton, "The organisation of human colour vision at the central fovea," *Vision Res.* **12**, 1763–1769 (1972). It is this property of tritan color-matching functions that constrains the ratio of *M*

- and L König fundamentals to be maximal at 460 nm. Independent psychophysical evidence for the position of the maximum of N_M/N_L is given by O. Estévez and C. R. Cavonius, "Human color perception and Stiles' π mechanisms," *Vision Res.* **17**, 417–422 (1977). Those authors used a modified form of Stiles' field-sensitivity method. Their use of auxiliary fields probably allowed them to isolate π_4 and π_5 at short wavelengths more securely than did Stiles himself.
18. B. J. Nunn, J. L. Schnapf, and D. A. Baylor, "The action spectra of rods and red- and green-sensitive cones of the monkey *Macaca fascicularis*," in *Central and Peripheral Mechanisms of Colour Vision*, D. Ottoson and S. Zeki, eds. (Macmillan, London, 1985).
 19. Y. Le Grand, "Les seuils différentiels de couleurs dans la théorie de Young," *Rev. Opt.* **28**, 261–278 (1949); L. F. C. Friele, "Analysis of the Brown and Brown–MacAdam colour discrimination data," *Farbe* **10**, 193–224 (1961); R. M. Boynton and N. Kambe, "Chromatic difference steps of moderate size measured along theoretically critical axes," *Color Res. Appl.* **5**, 13–23 (1980). The line-element of Friele explicitly includes compressive terms that depend on the relative signals of different classes of cone. These references give particularly good evidence that a compressive nonlinearity characterizes the channel that extracts the ratio N_M/N_L , and if this is so, this evidence offers a second reason why wavelength discrimination is unlikely to depend on this ratio at 460 nm, for this is the wavelength that would maximally polarize the putative channel. For discriminations along a tritan axis, the analyses of Le Grand and of Boynton and Kambe do not show any analog of Tyndall's paradox; in part this may be because the analyzed experiments did not include stimuli on the spectrum locus.
 20. E. N. Pugh, Jr., and J. D. Mollon, "A theory of the Π_1 and Π_3 color mechanisms of Stiles," *Vision Res.* **19**, 293–312 (1979).
 21. P. G. Polden and J. D. Mollon, "Reversed effect of adapting stimuli on visual sensitivity," *Proc. R. Soc. London Ser. B* **210**, 235–272 (1980).
 22. J. J. Vos and P. L. Walraven, "An analytical description of the line element in the zone-fluctuation model of colour vision. I. Basic concepts," *Vision Res.* **12**, 1327–1343 (1972).
 23. The anomaly was rediscovered by K. J. McCree, "Small-field tritanopia and the effects of voluntary fixation," *Opt. Acta* **7**, 317–323 (1960).
 24. An alternative, although less likely, possibility is that rods assist discrimination when the troland value of the blue field is reduced. A 40-Td field of 460 nm has a scotopic troland value of 941 Td and so would saturate the rods.
 25. J. D. Mollon and P. G. Polden, "Further anomalies of the blue mechanism," *Invest. Ophthalmol. Vis. Sci. Suppl.* **16**, 140 (1977); C. E. Sternheim, C. F. Stromeyer III, and L. Spillmann, "Increment thresholds: sensitization produced by hue differences," in *Visual Psychophysics and Physiology*, J. C. Armington, J. Krauskopf, and B. R. Wooten, eds. (Academic, New York, 1978), pp. 209–220.
 26. J. D. Mollon, "Color vision," *Annu. Rev. Psychol.* **33**, 41–85 (1982).
 27. W. S. Stiles, "Interim report to the Commission Internationale de l'Éclairage, Zurich, 1955, on the National Physical Laboratory's investigation of colour-matching," *Opt. Acta* **2**, 168–176 (1956).
 28. W. S. Stiles and J. M. Burch, "N.P.L. colour-matching investigation: final report (1958)," *Opt. Acta* **6**, 1–26 (1959).
 29. The principle was named by K. I. Naka and W. A. H. Rushton, "An attempt to analyse colour reception by electrophysiology," *J. Physiol. (London)* **185**, 556–586 (1966). They state it thus: "For each pigment system, every quantum that is effectively absorbed makes an equal contribution towards vision." The concept is explicit, but unnamed, in earlier publications, e.g., W. S. Stiles, "The physical interpretation of the spectral sensitivity curve of the eye," in *Transactions of an Optical Convention of the Worshipful Company of Spectacle Makers* (Spectacle Makers' Company, London, 1948), p. 98. Direct evidence that isolated primate cones obey univariance is given by D. A. Baylor, B. J. Nunn, and J. L. Schnapf, "Spectral sensitivity of cones of the monkey *Macaca fascicularis*," *J. Physiol. (London)* **390**, 145–160 (1987).
 30. The derivation attempted in Fig. 8 is closely analogous to the derivation by Polden and Mollon of an action spectrum for combinative euchromatopsia (Ref. 21, experiment 4). Those authors concluded that the hypothesized opponent signal did not originate in a single class of receptors.