The Luminosity Curve of the Deuteranomalous Fovea

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ABSTRACT Analogous to protans, the two types of deutan color-defectives—the dichromats (deuteranopes) and the anomalous trichromats (deuteranomalous)—do not differ in spectral sensitivity in the red-green range at threshold (either in the dark or against bright colored backgrounds). However, luminosity curves obtained by heterochromatic brightness matching show the latter to be slightly more sensitive in the blue-green, and slightly less so in the red, than the former. Experiment proves that these differences are due (at least in part) to contributions of cones containing the deuteranomalous anomalous pigment which are missing from the deuteranope's eye. The absorption spectrum of the anomalous pigment can be inferred with assumptions (analogous to those already made with protanomalous trichromats) about how the different cone mechanisms pool their responses to yield luminosity. Two alternatives thus revealed are (a) the normal red pigment in dilute solution or (b) a spectrum very similar to that of the normal red pigment but shifted slightly toward the short wave end of the spectrum. Since the spectrum inferred by (a) has the same \( \lambda_{\text{max}} \) as the normal red pigment, (a) predicts that deuteranomalous observers will require a negative red primary when matching monochromatic lights of wavelengths near the \( \lambda_{\text{max}} \). This is not observed.

In the previous paper (Alpern and Torii, 1968), it was found that though protanopes and protanomalous subjects could not be separated by their spectral sensitivity curves measured at threshold, there were small but significant differences in their respective step-by-step luminosity curves measured by brightness matching. In the present paper, the problem is examined in deuteranomalous trichromats. 4.9% of the male and 0.38% of the female population have this anomaly of color vision, defined by the need for a larger than normal amount of green in a red-green mixture matched to yellow. This almost certainly means that at least one of the three deuteranomalous cone pigments is different from the comparable normal pigment(s).
One explanation for the protanomalous mystery (red cone) pigment, suggested by the luminosity measurements, was a dilute concentration of the normal red pigment, erythrolabe, assuming that in the normal red cones the erythrolabe is in dense solution. The analogous hypothesis for deuteranomalous trichromats—dilute concentration of normal green pigment (chlorolabe) in the green-sensitive cones—is clearly wrong: it leads to protanomalous, not deuteranomalous, anomaloscope matches.

The suggestion (Walls and Mathews, 1952) that deuteranomalous green cones contain some mixture of normal chlorolabe and normal erythrolabe (assumed dilute) can be dismissed in a similar way; it leads to perfectly normal anomaloscope matches.

METHODS

The methods used are those already described (Alpern and Torii, 1968). Heterochromatic brightness matches step-by-step through the spectrum were achieved for a 0.5° centrally fixed test target of wavelengths 400 nm–700 nm in 10 nm steps. The test was matched in intensity to a standard monochromatic 1° surround annulus which produced a retinal illuminance of about 2.0 trolands. The wavelength of this standard was changed six times in a single spectral traverse in order to keep hue differences small. The measurement proceeded from the blue to the red end of the spectrum and then back to the blue, the entire experimental session lasting about 45 min. Measurements were also made under the influence of chromatic adaptation in the manner described by Walraven et al. (1966). Spectral brightness matches were completed within 1.5 sec after 4.5 sec exposure to the adapting field whose retinal illuminance was 2(10)° trolands. This field, 5.5° in diameter, was either green (500 nm) or red (650 nm). Finally, brightness matches were made, as in the previous paper, within 15 sec immediately after 4.5 sec exposure to 4.2 log10 trolands of green (527 nm) or red (605 nm) adapting field. The measurements of the differential (against green or red monochromatic backgrounds) and absolute thresholds for foveal testing were similar to procedures followed on protanomalous trichromats already described.

RESULTS

The results of these experiments in some ways are analogous to those already described for protanomalous subjects.

1. Thresholds

At thresholds the spectral sensitivity curve of the deuteranomalous fovea cannot be distinguished from that of the deuteranope (Fig. 1 A). The curves in this figure are obtained at the absolute threshold; identical results (in the red-green range) were also obtained when thresholds were measured against either bright green or red backgrounds. This confirms completely the observation of Rushton (1965 a) and of Wald (1966).
2. **Brightness Matches**

As in protanomalous subjects, the heterochromatic brightness match, step-by-step luminosity curve in deuteranomalous observers shows a very subtle but consistent difference from that of the corresponding dichromat (Fig. 1B).

**Figure 1 A.** Logarithm of the absolute threshold spectral sensitivity curve. Mean of results from four deuteranopes (open circles, broken line) and four deuteranomalous observers (solid line). B. Means of the brightness-matching results from the same subjects.

Equating the deuteranomalous curve to that of the deuteranope at the $\lambda_{\text{max}}$, the former is somewhat less sensitive in the red and somewhat more sensitive in the blue-green (with an uncertain overlap for wavelengths less than 450 nm). These differences between the deuteranomalous curve and that of the deuteranope are less obvious even than the small differences found between protanomalous subjects and protanopes. It is only by averaging the curves of a number of different experimental repetitions (on the same subject and/or on a representative sample of subjects) that one is convinced that these small differences represent two different population samples and not chance vari-
ability within a single population sample. The results in Fig. 2 show the mean ±SEM of the log luminosity on 7 deuteranopes and 11 deuteranomalous trichromats. Clearly the differences in both the red and blue-green, although small, are statistically significant.

3. Relation to Normal Luminosity Curve

It is usually stated (for example, Judd, 1943) that the deuteranomalous luminosity curve is well within normal limits. This interpretation is based on the familiar wide variability in luminosity among color-normal observers. This variability among normal observers has recently been interpreted, not as varying along a continuum, but being clustered into three subgroups depending upon the ratio of chlorolabe to erythrolabe (ratio of red cones to green cones?) in the fovea (Lee, 1966). Viewed in this way, the deuteranomalous luminosity curve (by brightness matching) is different from that of the majority (about 70%) of the color-normals whose luminosity curve agrees quite well with C.I.E. standard luminosity curve (except for a mild increased sensitivity at the extreme blue end of the spectrum). This is shown in Fig. 3 A. The filled circles represent the mean ± SEM of 10 experimental repetitions on one of us (M.A.) whose log luminosity curve agrees with the C.I.E. curve (solid line). The open circles illustrate a single repetition of the experiment on
a deuteranomalous observer. Clearly, the two curves in this figure are quite different, the deuteranomalous curve showing much reduced sensitivity to the blue-green part of the spectrum compared with the C.I.E. curve. However, there is a much better agreement between the results on deuteranomalous trichromats and those obtained on some 25% of the normal color vision popu-

Figure 3. Logarithm of the brightness match luminosity of a deuteranomalous trichromat (open circles, broken line) compared with results on two color-normal subjects—M.A., whose curve agrees with C.I.E. photopic luminosity curve (smooth solid line) in (A), and S.T., whose luminosity curve is deuteranopic (B).

lation who, by these methods, have a deuteranopic curve. This is shown in Fig. 3 B in which the open circles represent the same measurements on the deuteranomalous subject shown by the open circles in Fig. 3 A and the filled circles represent the measurements on one of us (S. T.) whose anomaloscope matches and the results of all other standard tests indicate normal color vision. Rushton and Baker (1964) have examined a population of such color-normal subjects by retinal densitometry and found a relatively reduced
amount of chlorolabe in their foveas compared with subjects with a normal luminosity curve.

It is possible to show an experimental distinction in brightness match

![Graph of luminosity curves showing brightness matches within 1.5 sec following 4.5 sec of intense chromatic adaptation. Top figure for deuteranomalous subject whose results are shown in Fig. 3. Upper set of curves, chromatic adaptation 3.3 log_{10} trolands; lower set of curves, 4.2 log_{10} trolands at 500 nm and 4.6 log_{10} trolands at 650 nm adaptation. Middle curves on color-normal S.T., who under the usual conditions has a deuteranopic luminosity curve (Fig. 3 B) 3.6 log_{10} trolands. Lower set of curves on a deuteranope 3.3 log_{10} trolands.]

luminosity between normal observers with a deuteranopic curve and deuteranomalous observers, even though in experiments such as those which gave the results in Fig. 3 B they behave so similarly. In Fig. 4 results from single experimental runs after strong red (filled circles) or green (open circles) adaptation are compared on a deuteranope, a deuteranomalous trichromat and a normal observer (S. T.) whose luminosity curve is deuteranopic. For the normal observer the luminosity curve after strong red adaptation is obviously
different from that after strong green adaptation. Two different pigments must contribute to his luminosity curve in the red-green part of the spectrum. For the deuteranope, the curve obtained after red adaptation runs hand in hand with the curve obtained after green adaptation—a fully anticipated result since the deuteranope has only a single photosensitive cone pigment, erythrolabe, in this part of the spectrum (Rushton, 1965 b, Wald, 1966). The

deuteranomalous subject gives results much closer to those obtained on the deuteranope compared with those obtained on the normal observer. At first glance it appears as though the deuteranomalous luminosity curve, like that of the deuteranope, reveals only a single pigment in the red-green range. Closer examination shows this not to be the case.

4. Deuteranomalous Luminosity after Red and Green Adaptation

The luminosity curve of the deuteranomalous observer after red adaptation shows slightly less sensitivity in the red part of the spectrum than after green adaptation. The results in Fig. 4 show only very small differences which might be due only to chance. It is necessary to establish that these small discrepancies are significant if we wish to infer that the deuteranomalous luminosity curve is synthesized by two cone pigments in the red-green range. Fig. 5 illustrates the brightness matches (log10 luminosity) made by five deutera-
nomalous trichromats within 15 sec after 45 sec exposure to 4.2 log10 trolands of red (solid line) or green (open rectangles) adapting fields. The vertical limits of the bars and rectangles represent the limits of the mean ±1 sem so that wherever the bars and rectangles do not overlap the probability that a difference as large as that obtained could have occurred by chance where no differences in the two samples exist is less than 0.05 (Student’s t test). The two curves are arbitrarily shifted to agree in the middle of the spectrum so that significant differences appear at the ends of the curves. The differences in deuteranomalous log luminosity after red and green adaptation are small but statistically significant. We conclude that the deuteranomalous luminosity curve—like the normal—is synthesized by more than one cone visual pigment in the red-green part of the spectrum.

**DISCUSSION**

Retinal densitometry shows that the red cones in the deuteranope have the same action spectrum of bleaching as that of the normal red cones (in both cases due to the absorption spectrum of erythrolabe) (Baker and Rushton, 1965). Deuteranopes have normal red cones and normal blue cones. They lack completely the green-sensitive pigment, chlorolabe, found in the green cones of normal observers, protanomalous trichromats, and protanopes (Rushton, 1965 b).

Analogous to the assumption of the previous paper on the protanomalous subjects, assume that the differences between the deuteranomalous and deuteranopic luminosity curves (Fig. 2) are due solely to the contribution of the anomalous (green) pigment to deuteranomalous luminosity. To infer the absorption spectra of the anomalous pigment as before, two alternative modifications of the Helmholtz line element, namely that of Schroedinger (1920) and of Stiles (1946), were used. The relevant equations are given by equations 1–3 in the previous paper.

For the high-intensity curve from the Stiles (1946) line element, this assumption leads to the inference of the deuteranomalous green cone pigment $M_\lambda'$ by

$$\frac{1}{\gamma} \log M_\lambda' = \log D_\lambda - \left[ \left( \frac{1}{\rho} \right)^2 + \left( \frac{1}{\beta} \right)^2 \right] \log X_\lambda + k'. \quad (1B)$$

The low-intensity Stiles line element yields in the same way,

$$\frac{1}{k_\lambda} \left( \frac{\varepsilon}{\gamma} \right)^2 (M_\lambda')^2 = D_\lambda - \left[ \left( \frac{\alpha}{\rho} \right)^2 + \left( \frac{\epsilon}{\beta} \right)^2 \right] \frac{X_\lambda^2}{k_\lambda}. \quad (2B)$$

The Schroedinger line element (linear adding of cone response for brightness) gives analogously

$$\delta M_\lambda' = [D_\lambda - (\alpha + \epsilon)X_\lambda]. \quad (3B)$$
In these equations $D_x$ represents the normalized deuteranomalous, $X_x$ the normalized deuteranopic, luminosity curve, respectively. The remaining symbols are defined in the previous paper.

The results shown in Fig. 6 are calculated with these equations from the mean results illustrated in Fig. 2. The solid circles show the deuteranopic luminosity curve which, except for small deviations in the extreme blue end of the spectrum—due to the small but uncertain contribution of the blue cones to deuteranopic luminosity—can be assumed to represent the absorption spectrum of the normal red pigment, erythrolabe. The squares in this figure show the spectral sensitivity of the anomalous cones inferred from the Schrödinger line element, assuming that only the normal red cones determine deuteranomalous luminosity at the extreme red end of the spectrum ($\lambda \geq 670$ nm).\(^1\) The open circles and the x’s represent the spectral sensitivity of the

\(^1\) This assumption is valid within the precision of the measurements, provided $(\alpha + \epsilon) \gg \delta$, a quite
anomalous pigment inferred from the Stiles (1946) modification of the Helmholz line element. The open circles represent the results predicted by the upper asymptote of the Stiles relationship, the x's those predicted by the lower (where the two coincide, only the open circles are plotted).

Because of the uncertain contribution of the blue cone system, no importance can be given to the alternative anomalous spectra for wavelengths less than about 510 nm. However, Rushton's (1965 b) measurements on the deuteranope show that the blue cones make no measurable contribution to equal brightness luminosity for wavelengths \( \leq 516 \) nm, and the matter is unlikely to be otherwise in deuteranomalous subjects. Hence, for wavelengths longer than this lower limit, uncertainty about the spectrum of the blue pigment probably does not lead to serious errors in the inferences drawn about the nature of the red and green pigments in Fig. 6.

The smooth curve drawn through the squares in Fig. 6 is the same curve drawn through analogous points in the protanomalous curve (Fig. 7 of the preceding paper). It is the theoretical absorption spectrum of dilute erythrolabe based on the assumption that the deuteranope's luminosity curve represents the erythrolabe absorption with density at \( \lambda_{\text{max}} \) of 1.0. This curve, together with that of the normal (red) pigment, is consistent to the extent that it predicts the deuteranomalous anomaloscope setting in the correct direction. Furthermore, since the inference is that the anomalous pigment in both protanomalous and deuteranomalous subjects is the same, it is in agreement with the conclusions of Schouten (1937) based on matching and of de Vries (1948) based on flicker photometry and two-color thresholds.

Despite these agreements, there is one line of evidence which strongly suggests that the anomalous pigment in the green cones of deuteranomalous trichromats cannot be merely the erythrolabe of the normal red cones in dilute solution. This is the fact that the deuteranomalous red and green pigments would then both have the same \( \lambda_{\text{max}} \)! While predicted matches for test \( \lambda \)'s around 589 nm (i.e. the anomaloscope yellow) are straightforward, this is not the case for other parts of the spectrum. In particular, for color-matching of monochromatic lights near the \( \lambda_{\text{max}} \) of the pigments (i.e. 565 nm), the predicted matches have a negative red coefficient.

Deuteranomalous color-matching experiments have been carried out by von Kries (1924) and by Nelson (1938). Although neither gives positive evidence of a negative red mixture coefficient near the erythrolabe \( \lambda_{\text{max}} \), the work of each suggests the possibility of such a result in some subjects. von Kries describes the effect in this way:

"... if the experiment is made with a homogeneous light whose wavelength is decidedly less than 589 nm the settings become entirely uncertain and variable. Modern
reasonable hypothesis in view of the very small differences between deuteranomalous and deuteranopic luminosity, given the simple linear adding of luminosity in the Schroedinger line element."
ate amounts of red not only do not upset the match, but the red can be reduced to nothing. In other words, homogeneous light of 536 nm can be displayed alongside the yellow without the two fields ceasing to look... the same.”

One of Nelson’s observers also falls into this category. In these studies, it is not at all clear that the possibility of a negative red mixture coefficient near the $\lambda_{max}$ of erythrolabe has been unequivocally excluded. We have therefore studied the color-matching functions in the red-green range of eight deuteranomalous observers with an arrangement which made testing the requirement of a negative red coefficient quite easy. The following dominant wavelengths of the matching field were tested: 555, 563, 568, 579, 589, 605, 609, 625, and 638 nm. The wavelengths of the red and green primaries in this test were 527 and 650 nm. A blue (421 nm) primary was also available, but no subject required it. At each wavelength of the matching field the entire range of ratios of the red-green primaries in which matches were acceptable was measured. (The 2° bipartite field was foveally fixed.) Although some deuteranomalous subjects accepted a match made with a small amount of negative red near the $\lambda_{max}$ (565 nm) of erythrolabe, the midpoints of such matches were always positive (as was the largest proportion of the range). We were therefore completely unable to confirm the predicted color-matching functions of deuteranomalous observers, and this excludes (at least for these subjects) the possibility that the anomalous pigment in their green cones is only normal erythrolabe in dilute solution.

The possibility that the mystery pigment of the deuteranomalous green cones is some combination of a small amount of normal chlorolabe mixed with dilute erythrolabe cannot be excluded by this means. However, we know of no experimental evidence to support such an ad hoc hypothesis and see no obvious way of testing it.

A more likely possibility is that predicted by the Stiles modification of the Helmholtz line element; i.e., the open circles and/or the x’s in Fig. 6. It is evident that in $\lambda_{max}$, and in width, the spectrum of the anomalous pigment is very similar to the normal (red) pigment (solid circles, Fig. 6) shifted only slightly to the short wavelength side. This is essentially the conclusion already reached by Wald (1966) on quite different experimental grounds.

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