

VARIATION IN THE ACTION SPECTRUM OF ERYTHROLABE AMONG DEUTERANOPEs

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SUMMARY

1. Eight deuteranopes matched a mixture of a monochromatic light on the long wave side of the neutral point and a violet (450 nm) primary to a fixed white as well as a monochromatic light on the short wave side of the neutral point mixed with a red (650 nm) primary, to the same white. For $\lambda > 530$ nm, the former set of matches defined the action spectrum of the long wave sensitive foveal cones, and for $\lambda < 480$ nm, the latter that of the short wave sensitive cones.

2. Individual differences in the former matches were approximately correlated with the respective ratio of the sensitivities of the wave-length of the anomaloscope primaries, in a way that individual differences of the latter were not.

3. Assuming that eye media differences alone account for the differences in long wave sensitive foveal action spectra, the spectral reflectivity of the foveal fundus was predicted for these deuteranopes. The prediction is inconsistent with measurement.

4. Thirteen deuteranopes matched monochromatic spectral lights with a green (535 nm) and a blue (460 nm) primary. The results were analysed by von Kries' method in which differences in matching due to differences in eye media absorption are obviated. The matches of five differed significantly from one another when so analysed. It was concluded that at least one of the two action spectra of the foveal cones of every one of these five differed from that of all of the others.

5. The canon that deuteranopes accept normal colour matches was evaluated by confronting a single normal with five deuteranopes in the analytical anomaloscope of Baker & Rushton, set in the mode of each of the five in turn. Obvious differences existed between this normal's matches and those of four of five deuteranopes.

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6. Explanations for differences in the spectrum of erythrolabe in different deuteranopes are evaluated. The possibilities that all have the identical visual pigment but (a) in cones with different optical funnelling properties or (b) in different optical densities are considered. Preliminary results are not in agreement with the expectations of either of these ideas.

7. It is suggested that the visual pigment in the foveal long wave sensitive cones of different deuteranopes (and of different normals) may have different extinction spectra. The idea is consistent with micro-spectrophotometric measurements of rhodopsin in individual rods from different frogs (Bowmaker, Loew & Liebman, 1975).

INTRODUCTION

In the preceding paper (Alpern & Wake, 1977) the ratios of sensitivities at the wave-lengths of the primaries of the Nagel anomaloscope of thirty-eight deuteranopes was shown to vary over a range of about 0.25 log unit. This variability, much too large to be accounted for by imprecise matching, leads to the suggestion that different deuteranopes can have distinct long wave cone action spectra.

Before serious consideration is given to this hypothesis, however, two others must be excluded. The first is that while some deuteranopes have but a single red-green cone visual pigment (erythrolabe alone) others have two (erythrolabe and chlorolabe). This possibility was examined in the previous paper; it was found by foveal retinal densitometry that each one of fifteen deuteranopes had only a single measurable photolabile foveal pigment in the red-green part of the spectrum while all normal trichromats had significant concentrations of two.

The second is the possibility that all deuteranopes have the same red-green photolabile foveal pigment and that individual differences are due to differences in absorption of a prereceptor (photostable) pigment (Pokorny, Smith & Katz, 1973). That suggestion is evaluated in this paper.

In the first part, the action spectra of the two kinds of foveal cones of eight deuteranopes are defined by minimum saturation spectral colour matches. The method, due to James Clerk Maxwell (1860), was employed by him to study the colour vision of his wife and himself, both trichromats. His explicit intention was to use the procedure to study dichromats and in the postscript to his paper he gives results on 'Mr James Simpson formerly a student of Natural Philosophy in my class...', a protanope. There is no evidence that he ever made measurements of this kind on deuteranopes. Surprisingly, in the 117 years since, neither has anyone else.

PART I. DICHROMATIC MAXWELL MATCHES

Maxwell added three selected spectral primaries and adjusted their intensities to match a fixed white. One primary was then replaced by a monochromatic light whose wave-length was changed in the experiment as the independent variable, traversing the spectrum. At every wave-length the intensities of two primaries and the spectral light were set to match the white. The primaries used with a spectral 'red' were, of course, different from those used with a spectral 'green' or 'blue', but since the amount of each primary needed to match the white (when all three were mixed together) was known, the spectral colour matching functions were readily calculated (on the basis of Grassmann's third law).

The dichromatic case is simpler. Only two primaries are needed to match the white; alternatively, at the wave-length of the dichromatic neutral point, the intensity of the monochromatic light alone can be adjusted for a match. At every other wave-length it is necessary to mix only a single primary with the spectral light for the match.

METHODS

The apparatus was the tristimulus colorimeter previously described (Alpern, Bastian, Pugh & Gras, 1976) (Fig. 1). Different experiments used the same apparatus, so its design was more complicated than necessary for some. The source of light S, a 150 W xenon arc, provided four beams, only three of which were now required (beam 2 was occluded). Beam 4 is rendered monochromatic by a Bausch & Lomb grating double monochromator GM (f:10) with a 2 nm spectral band pass. It is mixed (at the mixing cube $MC_{3,4}$) with a monochromatic primary either violet, 450 nm (to study long wave-lengths) or red, 650 nm (to study the short wave-lengths) obtained by attenuating the light beam in channel 3 with one or the other Baird-Atomic narrow band (10 nm half width) interference filters at F_3 . The combined beam was seen in Maxwellian view formed by the lens ML_1 . It produced images of the aperture stops in the plane AP, a 1 mm² square artificial pupil mounted between the eye and an afocal lens (AL) correcting for the chromatic aberration of the average human eye (Bedford & Wyszecki, 1957). PC, a photometric cube was at the focal plane of ML_1 . The mixed beam was seen in the centre of a disk-annulus test, the disk being 1° in diameter and the annulus extending beyond it an equal amount. The annulus was filled with light from channel 1 reflected at the photometric cube, PC. It had the spectral distribution of the xenon arc (colour temperature about 5200° K) unattenuated by any spectral filters but reduced by a series of neutral Inconel filters to an intensity which varied from one experiment to another in the range 2.6–3.2 log photopic td.

The observer adjusted the wedges in channels 3 (W_3) and 4 (W_4) to match the disk to the white annulus. To obviate regional retinal asymmetries, he made the match while fixating a border between the disk and the annulus (say at 3 o'clock) but identified it as such only after satisfying himself that it held upon shift of fixation to the opposite border (i.e. 9 o'clock). At least two matches were made at each wave-length and the entire spectrum studied (at 10 nm intervals for $\lambda > 600$ nm, and generally at 5 nm intervals for $\lambda < 600$ nm), usually in a single session.

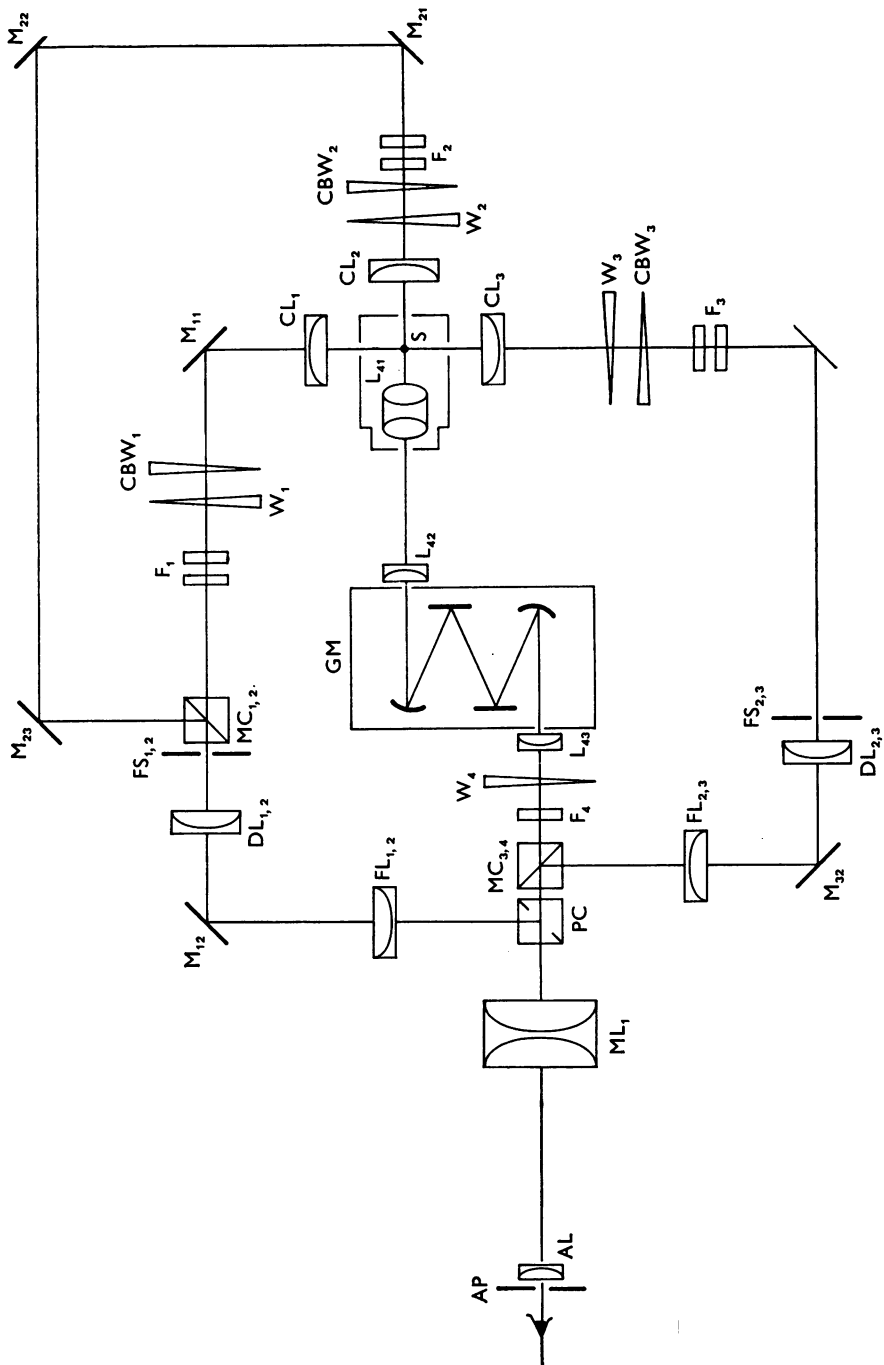


Fig. 1. The line drawing of the apparatus used in these experiments as viewed from above. For details see text.

Sometimes, however, one session was devoted exclusively to the spectrum on only one side of the neutral point.

Measurements were made on eight deuteranopes one of whom (subject 5) completed only a single experiment. The others repeated it at least once, one repeated it twice and a third, three times.

RESULTS

The results of a single spectral traverse are illustrated in Fig. 2. The log of the intensities [quanta (steradian.sec)⁻¹] of monochromatic light (circles) and that of the primary (squares) with which it was mixed to match the white are plotted on the ordinates as a function of the wave-length. The error bars in the figure show the range of the measurements. Though occasional matches were not, most settings proved remarkably reliable; a spot check of unrepeatable matches confirmed the reliability of the average.

There was a surprising (wave-length independent) constancy in the settings of the primary with which the monochromatic lights were mixed except in the region near the neutral point (λ_0). In Fig. 2 on the short wave side of the neutral point there is some wave-length (λ_c') (near 490 nm) such that for every $\lambda \leq \lambda_c'$ the range of the average of the settings of the 650 nm primary is considerably smaller than 0.1 log₁₀ unit, i.e. less than the range of the most imprecise setting at a fixed wave-length. Similarly, on the long wave side of the neutral point there is some wave-length λ_c (near 520 nm) such that for $\lambda \geq \lambda_c$ the average setting of the 450 nm primary at any wave-length falls well within 0.1 log unit range of the others. Repeated measurements on this and other deuteranopes confirmed the observation that for $\lambda \geq \lambda_c$ the intensity of the 450 nm primary, and for $\lambda \leq \lambda_c'$ the intensity of the 650 nm primary, needed for the match remained relatively constant. The results in Fig. 2 are characteristic, although the exact wave-lengths of λ_c and λ_c' varied from subject to subject and often in the same subject from one spectral traverse to the next. This finding has led to two simplifications; the first is experimental, a relatively trivial modification of the procedure. The second is analytical and by no means trivial; its description will be taken up in the analysis part of this section.

The experimental change was a subtle difference in the way matching was completed. With experience it was possible to make a reasonable guess as to those regions in the spectrum in which the primary setting would remain unchanged with further change in wave-length. When these regions were reached the primary was set at the estimated intensity and the subject instructed to try to complete the match by varying the intensity of the monochromatic light alone (i.e. by adjusting only wedge W_4). If the match could be completed the wave-length was set to the next position moving away from the neutral point and the experiment continued with no further change of the intensity of the primary. If it could not,

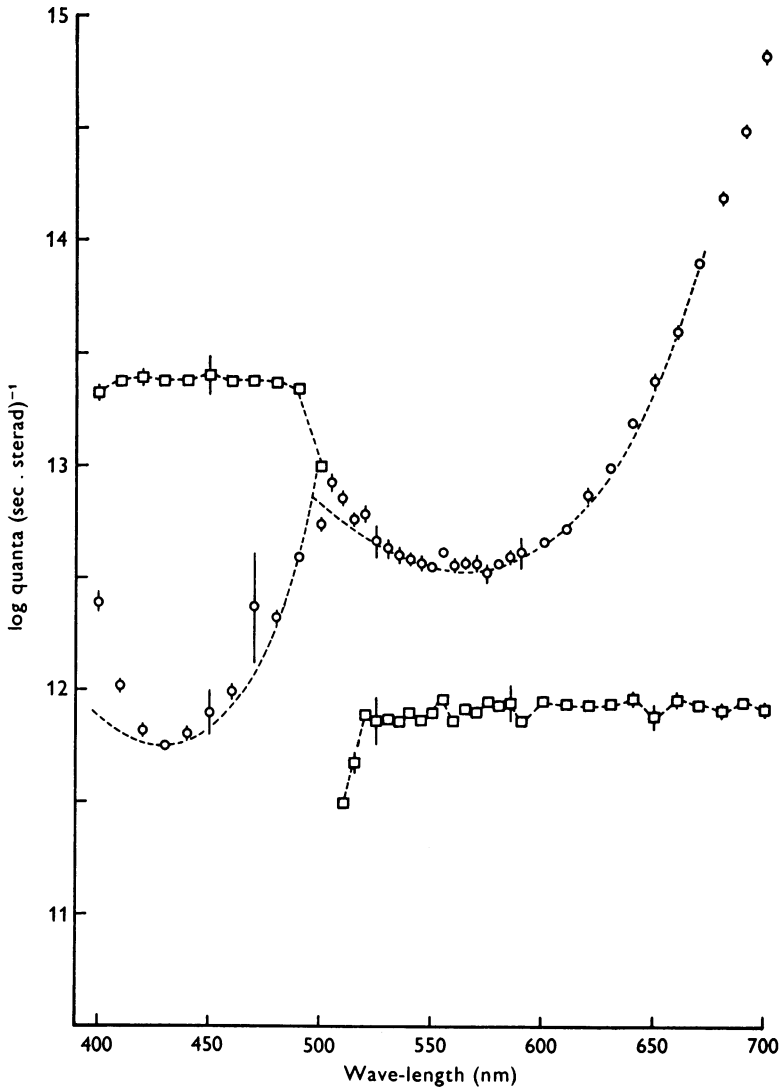


Fig. 2. Dichromatic Maxwell matches of the spectrum obtained in a single experimental session. The squares give the mean and the range of the intensity setting of the mixture primary; the circles give the mean and range of the monochromatic light intensity settings. At least two matches were completed at every wave-length. In this experiment the neutral point was 505 nm. Deuteranope 23.

both wedges were simultaneously adjusted in the usual way, but the procedure repeated in this same manner when the wave-length was changed to the next position more remote from λ_c . For each dichromat it was always possible eventually to find ranges of wave-lengths ($\lambda \leq \lambda_c'$, $\lambda \geq \lambda_c$) where matches were made with the fixed setting of the primary.

In Fig. 3 the average settings of the intensity of the monochromatic beam of all eight deuteranopes has been brought together in a single Figure. For the sake of clarity only the intensity of the spectral light (and not that of the primary with which it was mixed) is shown. However, the filled circles are values obtained whenever the primary was different from (it was always less than) the fixed intensity used for the matches represented by the open circles. The latter symbols give the results in the ranges $\lambda \leq \lambda_c'$, $\lambda \geq \lambda_c$. The settings of the various subjects are arbitrarily shifted vertically with respect to those of the others, and for any given deuteranope the amount of shift of the matches on the long wave side of the neutral point is independent of that on the short wave side. The vertical order on the two sides of the neutral point is, however, the same. That order is defined by the position in the distribution of anomaloscope matches of the previous paper (Fig. 2 of Alpern & Wake, 1977). In Fig. 3 the numbers just to the right of the long wave action spectrum designate that position for each deuteranope (38 being the subject closest to, 1 being the furthest from, the protanope distribution).

The position of a given deuteranope in the distribution of anomaloscope settings appears uncorrelated with the action spectrum of the short wave-length matches but closely related to that of his matches in the red and green spectral regions. To facilitate the comparison in Fig. 3 two smooth template curves have been drawn by eye to show best the trends of the results for deuteranope 38 (one for those on the long wave, the other on the short wave, side of the neutral point). These template curves were then displaced vertically to fit all of the other matches in the low frequency part of their respective spectral regions.

A casual glance at this Figure suffices to show that while the long wave template predicts a systematically higher sensitivity in the unnormalized spectral regions than experiment reveals, and that this becomes progressively more pronounced as the deuteranope under consideration is less and less 'protanoid', no such trend is evident in the prediction provided by the short wave-length template (the sole exception being, perhaps, deuteranope 1). Before attempting to interpret this result it is necessary to discuss the significance of these matches.

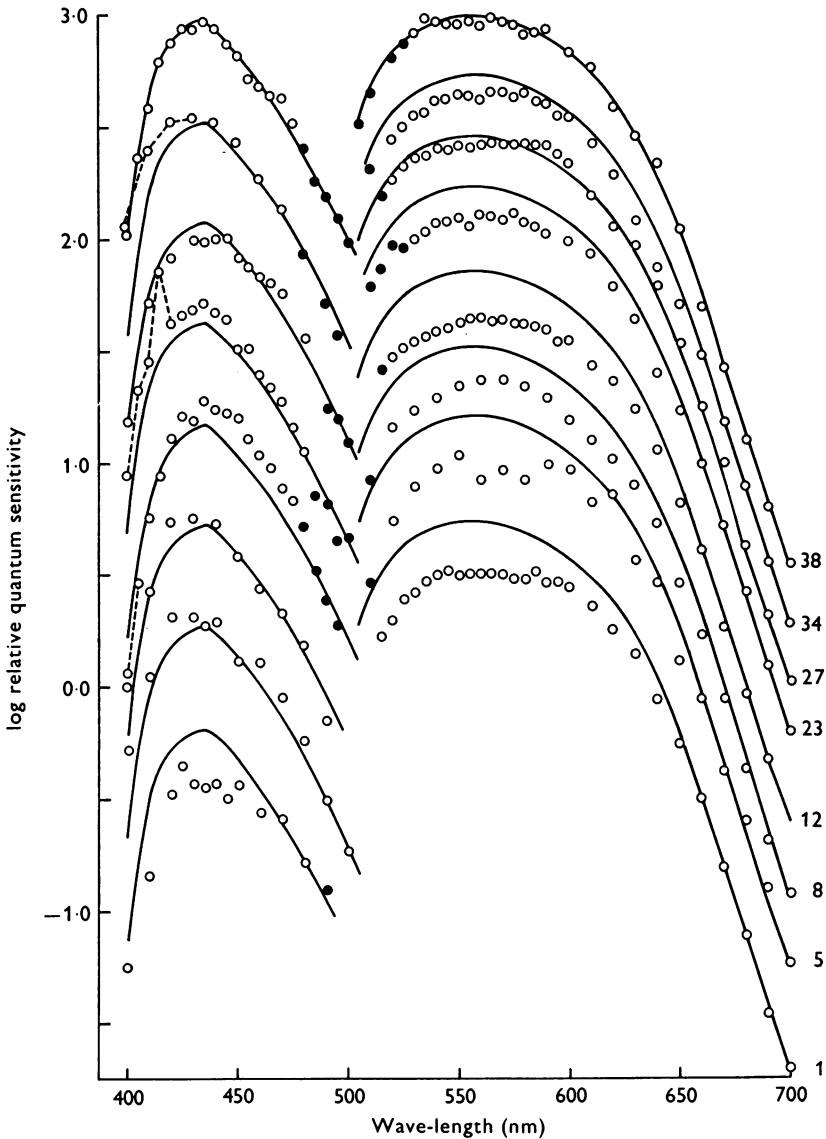


Fig. 3. Mean settings of the monochromatic intensities required for the Maxwell match by each of eight deuteranopes. The numbers to the right identify the position of the deuteranope in the distribution of thirty-eight deuteranopic sensitivities at the wave-length of the anomaloscope primaries (1 being furthest from, 38 closest to, the protanopes). For each deuteranope two sets of results are given, one for the intensity settings on the long wave side, the other for those on the short wave side, of the neutral point. The relative height is arbitrary but the order of each member of the pair on the two sides of the neutral point is the same. The two smooth curves are drawn to show the trends of deuteranope 38 matches. These were then used as templates and vertically displaced to fit the matches at the respective long wave extremities of each member of the pair for every other deuteranope's matches in turn. For each deuteranope the open circles are matches made with a fixed intensity of the mixture primary, the solid circles indicate matches made when the intensity of the mixture primary was appreciably smaller than this constant value.

Analysis

The first step in the experimental procedure is the establishment of a match between the fixed white and a monochromatic light at the observer's neutral point λ_0 . When the match is made, the quantum catch in each class of foveal cones is identical on the two sides of the colorimetric field.

Let

$\beta_l(\lambda')$ = Napierian density of the visual pigment in the long wave sensitive cones;

$\beta_s(\lambda')$ = Napierian density of the visual pigment in the short wave sensitive cones;

$\epsilon(\lambda') = 1 - \exp[-\beta_l(\lambda')]$, the absorption spectrum of the long wave-length cones;

$\kappa(\lambda') = 1 - \exp[-\beta_s(\lambda')]$, the absorption spectrum of the short wave-length cones;

$E(\lambda')$ = spectral distribution of the white light in quanta $\text{sec}^{-1} \text{cm}^{-2}$ of retina at the cornea nm^{-1} of wave-length;

$\tau(\lambda')$ = transmittance of prereceptor ocular media at wave-length λ' ;

I_0 = intensity (quanta $\text{sec}^{-1} \text{cm}^{-2}$ of retina, at the cornea) of the monochromatic light at the neutral point match;

$I_1(\lambda)$, $I_2(\lambda)$ = intensities of the long (650 nm) and short (450 nm) wave-length primaries, respectively;

τ_0 , τ_1 , τ_2 = transmittances of ocular media at the monochromatic wave-lengths.

The theoretical equations for the neutral point match are

$$\left. \begin{aligned} \int_0^{\infty} E(\lambda') \tau(\lambda') \epsilon(\lambda') d\lambda' &= I_0 \tau_0 \epsilon(\lambda_0), \\ \int_0^{\infty} E(\lambda') \tau(\lambda') \kappa(\lambda') d\lambda' &= I_0 \tau_0 \kappa(\lambda_0). \end{aligned} \right\} \quad (1)$$

Once this match was completed, a dichromatic match was made between the white light of fixed intensity and monochromatic light of intensity $I(\lambda)$ at every wave-length in the spectrum. For those wave-lengths longer than the neutral point the short wave (450 nm) primary was mixed with the monochromatic light and its intensity $I_2(\lambda)$ measured. The theoretical equation for the long wave-length pigment is

$$I_0 \tau_0 \epsilon(\lambda_0) = I(\lambda) \tau(\lambda) \epsilon(\lambda) + I_2(\lambda) \tau_2 \epsilon(450). \quad (2)$$

The results in Figs. 2 and 3 show that for some wave-length $\lambda_c > \lambda_0$ $I_2(\lambda)$ is a constant. When this is the case,

$$I(\lambda) = C / \tau(\lambda) \epsilon(\lambda), \quad (3)$$

in which C is also a constant. Evidently under these conditions $I(\lambda)$ defines the action spectrum (at the cornea) of the visual pigment with the absorption spectrum $\epsilon(\lambda)$.

The results in Figs. 2 and 3 also show that there is a wave-length $\lambda_c' < \lambda_0$ such that for wave-lengths $\lambda \leq \lambda_c'$ the intensity $I_1(\lambda)$ of the 650 nm primary remains constant. Reasoning analogous to that which led to eqn. (3), applied to matches made for $\lambda \leq \lambda_c'$, allows one to define the action spectrum (at the cornea) of the short wave absorbing cone visual pigment for $\lambda \leq \lambda_c'$. It is possible to extend the spectral range for which the latter spectrum is defined to include all wave-lengths $\lambda < \lambda_0$ by the further quite realistic assumption that $I_0 \tau_0 \kappa(\lambda_0) \gg I_1(\lambda) \tau_1 \kappa(650)$, i.e. that the relative absorption by the short wave-length sensitive pigment of the 650 nm primary is negligibly small (a more detailed theoretical treatment of this experiment is given in the Appendix).

DISCUSSION

This analysis leads to the conclusion that (with the exception of the filled circles to the long wave side of the neutral point), the points plotted in Fig. 3 represent the action spectra (at the cornea) of the two cone visual pigments which underlie the foveal dichromacy of these eight deuteranopes. According to eqn. (3) individual differences in either the long or short wave spectra of Fig. 3 can only be due to differences in prereceptor absorbances or to differences in cone absorbances or to both.

There are two reasons (neither, by itself, compelling) for believing that differences in the anomaloscope matches of these deuteranopes are not due only to differences in ocular media pigmentation, but to differences in absorbances of the long wave sensitive cone visual pigments. (i) In the anomaloscope range, i.e. $\lambda \geq 535$ nm, eye media are more or less neutral (Wyszecki & Stiles, 1967) for healthy subjects less than 30 yr old as these subjects are. The common substances which colour the light before it becomes absorbed in foveal cones are the lenticular and macular pigments. Macular pigment has zero absorption for wave-lengths greater than 520 nm. The lens absorbs some light of all wave-lengths, but Said & Weale's (1959) measurements of lens absorption for subjects of the age for which the results in Fig. 3 are relevant are virtually constant in the red-green spectral range (though this is by no means the case for older subjects). (ii) In Fig. 3 the deviations from the template curves occur systematically in a way related to anomaloscope settings for the long wave cone mechanism alone rather than throughout the spectrum as expected from differences in ocular media transmissivity.

However the chance that variability of the action spectrum of the long wave cones of the different deuteranopes in Fig. 3 are due to rather special (and quite unfamiliar) prereceptor filters is not rigorously excluded

by these considerations. Therefore the attempt has been made to detect such filters objectively by measuring the spectral reflexion coefficient of the fovea of these subjects after all visual pigments have been bleached.

PART II. SPECTRAL REFLECTANCE OF THE DEUTERANOPE

Fovea

The Florida retinal densitometer (Hood & Rushton, 1971; Alpern, Maaseidvaag & Ohba, 1971) was used to obtain the spectral reflectance of the fovea. The fraction of incident monochromatic light reflected back through the pupil after traversing the eye media, reflexion from the fully bleached macular fundus and retraversing the eye was divided by that resulting from similar passage through an artificial eye with a magnesium oxide fundus. Given the spectral reflectance of one deuteranopic eye, that expected from a second can be calculated on the assumption that the only difference between them is a prereceptor filter defined by differences in the action spectra of their respective long wave cones. How accurately does this calculation predict spectral fundus reflectance in deuteranopia?

METHODS

The basic principle of the method, including the derivation of the relevant equations has been given by Brindley & Willmer (1952). The methods differ only in that the radiometric null of the densitometer measuring light is used instead of Brindley & Willmer's photometric match. A circular patch of the fovea 2° in diameter illuminated by a monochromatic measuring light is further reduced in area by a concentric field stop in front of the photomultiplier tube. The measurements are made during a prolonged full bleach of the retina by a tungsten 'white' light 10° in diameter, concentric with the measuring light. This bleaching light produced about $6.2 \log_{10}$ photopic td of retinal illumination. A light this bright will bleach nearly all of the erythrolabe and chlorolabe of the normal fovea in 10 sec and about the same amount of erythrolabe in deuteranopes. Measurements began after about 2 min by which time the equilibrium bleaching level at this intensity had long been achieved (with about 2% unbleached). At least five measurements were made as rapidly as possible, one after the other, at each of eight wave bands in the spectrum (isolated by interference filters in the densitometer measuring beam) in a single experimental session. Such sessions were repeated at least twice for each subject and in some, as many as fourteen times.

Fig. 4 depicts on the ordinate the foveal spectral reflectance (logarithmic scale) as a function of wave-length (linear scale). Only six of the fourteen sets of results are plotted. (This is as many as can be shown without rendering the Figure hopelessly cluttered.) The illustrated examples are typical in every respect of all and are from deuteranopes whose Maxwell's matches were also measured. Two sets of scales are shown in Fig. 4.

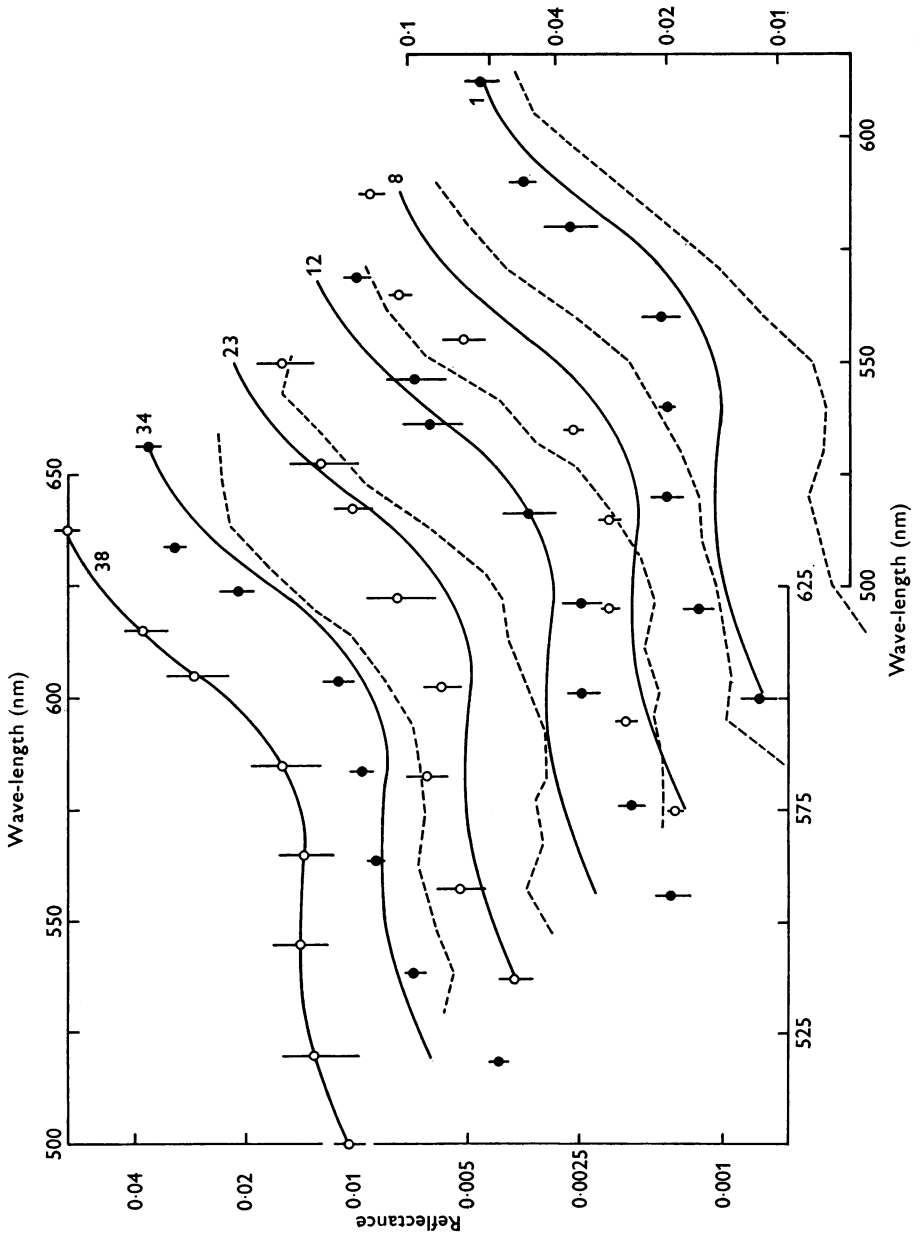


Fig. 4. For legend see opposite.

(Those on the left refer to measurements on deuteranope 38, i.e. the most 'protanoid', those on the right to deuteranope 1, i.e. the least 'protanoid'.) The continuous curve is an 'eye fit' to the measurements on deuteranope 38. Results for the other five have each been shifted both horizontally and vertically for clarity of the display. The amount of the shift can be identified from the solid smooth curve, i.e. the curve for deuteranope 38, shifted the same amount as the experimental points.

The hypothesis to be excluded is that individual differences in the long wave cone action spectra in Fig. 3 are due to individual differences in prereceptor absorbances in the ocular media of each deuteranope. According to this hypothesis the deviations of the long wave spectra from the curve in Fig. 3 yield a quantitative estimate of deuteranopic foveal reflectance (Fig. 4) given that of deuteranope 38, assuming all other factors in the determinations of fundus reflectivity constant. The dashed lines drawn with the data from the five other deuteranopes illustrate these predictions. A result consistent with the hypothesis would be that the dashed lines describe the measured reflectivity. In none of the five deuteranopes is this reasonable. (The shifted continuous curve, in fact, provided a much better prediction of the measurements in each case.) This is consistent with the hypothesis that the variability in the long wave spectra of Fig. 3 is due to different long wave cone visual pigments in the foveas of different deuteranopes. Of course, the idea that all deuteranopes in Fig. 4 have the same foveal fundus reflectivity and the same ocular media transmissivity is unlikely to be exactly true, as will be evident to anyone with ophthalmoscopic experience. Deviations of the actual measurements in Fig. 4 from the shifted continuous curve are consistent with what may be expected from different normal young Caucasians of nearly identical ages. However, this inference is drawn from a quantitative study of only a few more than a dozen normal subjects, and is not very strong. The alternative *ad hoc* hypothesis, that some

Fig. 4. Foveal spectral reflectance coefficient of six deuteranopes after a full bleach. The top and left hand set of co-ordinates are correct for the results from deuteranope 38 and the smooth curve is an 'eye fit' to his results. The other results have all been shifted horizontally and vertically for the sake of clarity. The amount of shifting can be gleaned from the continuous curve which has been displaced as a template equally with the experimental points. The bottom and left hand set of co-ordinates are appropriate for deuteranope 1. The ordinate scales are logarithmic, the abscissa scales linear. The dashed line predicts the spectral reflexion expected if the differences between the long wave action spectra given in Fig. 3 for a given deuteranope and that one for deuteranope 38 are due to prereceptor ocular media differences alone. The fit in each case is sufficiently poor to reject that possibility.

other factors dominate the foveal reflectivity in Fig. 4 in a way that obscures the abnormal photostable colour filters responsible for the difference in Fig. 3 is perhaps still tenable, if not very plausible.

To exclude the possibility that all differences in deuteranopic settings of the anomaloscope can be explained by such an *ad hoc* hypothesis, we have sought still another way in which individual differences in deuteranopes' colour vision occur which cannot be explained by differences in prereceptor distortions. The results are described in the next section.

PART III. MAXIMUM SATURATION COLOUR MATCHES

The matches of a mixture of primaries and monochromatic lights to a fixed white in Maxwell's method are sensitive to the influence of pre-retinal absorption in a way that can be obviated if pure spectral lights are matched (von Kries, 1899). Two observers matched a mixture of two primaries (one 'red' the other 'green') to monochromatic lights in the red-green part of the spectrum. Dividing the intensity of the red primary by that of the green for each subject, von Kries compared the two subjects' matches by taking a ratio of the divided quantity obtained from one to the divided quantity obtained from the other. If the matches of the two differed only because of preretinal pigmentation, this ratio should be wave-length independent. Comparing the matches of one deuteranomalous and one normal von Kries found that this was not so; nor was it true when he compared those of a protanomalous to a normal. He concluded (appropriately) that the two anomalous trichromats were altered forms of normal trichromacy.

METHODS

Maximum saturation dichromatic colour matches were obtained on each of thirteen deuteranopes in the range ($465 \text{ nm} < \lambda < 530 \text{ nm}$) outside of which deuteranopes are monochromatic. The two primaries selected were 460 and 535 nm. The monochromatic light was held at approximately the same quantum flux in any given run in a 1.4 log unit intensity range (12.0 to $10.6 \log_{10}$ quanta (sterad. sec⁻¹ at 500 nm) although the level varied arbitrarily from run to run and from one subject to another. This range is sufficiently bright to facilitate reasonable matches and dim enough that metameric matches of trichromats (Wright, 1936) and of dichromats (Miller, 1972) remain luminance independent (as they do not at levels sufficiently high that bleaching is measurable).

We used beams 1, 2 and 4 of the apparatus in Fig. 1, channel 3 was occluded. The two primaries were provided by Baird-Atomic 'narrow band' interference filters (10 nm half band width) of dominant wave-lengths 460 nm (in channel 1) and 535 nm (in channel 2). The usual experiment began at the violet end of the spectrum. The subject established matches at 5 nm intervals, up to 530 nm, after which the measurements were repeated traversing the spectrum in the opposite

way. The same process was repeated in at least five separate sessions. Occasionally three (instead of only two) runs through the spectrum were completed in a single experimental session. In analysis each spectral traverse was given equal weight.

Analysis

Suppose the bistimulus colour matching functions \bar{g} , \bar{b} and \bar{g}' , \bar{b}' of two dichromats differ (although the action spectra of the pairs of cones which underlie the matches are identical) because the transmissivities of the ocular media $\tau(\lambda)$, $\tau'(\lambda)$ of the two subjects differ.

For each kind of cone (with action spectra $\epsilon(\lambda)$, $\kappa(\lambda)$) it is assumed that the quantum catch on the two sides of the colorimetric field will be identical at the match point.

$$I_1\tau_1\epsilon_1 + I_2\tau_2\epsilon_2 = I(\lambda)\tau(\lambda)\epsilon(\lambda)$$

with a similar equation for $\kappa(\lambda)$.

I_1 , I_2 and $I(\lambda)$ are the required intensity settings of the reference primaries and of the monochromatic light at the match. Since $\bar{g} = I_1/I(\lambda)$ and $\bar{b} = I_2/I(\lambda)$

$$\begin{pmatrix} \epsilon_1 & \epsilon_2 \\ \kappa_1 & \kappa_2 \end{pmatrix} \begin{pmatrix} \bar{g}\tau_1/\tau(\lambda) \\ \bar{b}\tau_2/\tau(\lambda) \end{pmatrix} = \begin{pmatrix} \epsilon(\lambda) \\ \kappa(\lambda) \end{pmatrix}. \quad (4)$$

Given two dichromats with different colour matching functions and identical cone visual pigments, the log ratios of their respective colour matching functions will differ by a constant which is wave-length independent, since

$$\log(\bar{g}/\bar{b}) + \log(\tau_1\tau_2'/\tau_2\tau_1') = \log(\bar{g}'/\bar{b}'). \quad (5)$$

RESULTS

The colour matching functions in the five panels in Fig. 5 each represent results from a different deuteranope (identified in the same numerical code used in Figs. 3 and 4). In each graph, the logs of the means ± 1 s.e. of mean of the bistimulus values \bar{g} (rectangle) and \bar{b} (vertical) are plotted as a function of wave-length. The smooth curves drawn through the data represent trends and have no theoretical significance. The results in Fig. 5 are typical of those obtained on all thirteen deuteranopes. However, these five are distinctive in the sense that the colour matches of each differ significantly from those of the other four in a way that cannot be explained by differences in transmissivity of the ocular media.

To demonstrate this, it is necessary to find (i) the maximum likelihood estimate \hat{k} of the constant closest to the over-all differences in the logs of the ratios of the colour matching functions of any given pair of deuteranopes and (ii) the probability that the measured differences between the two log ratios could deviate from \hat{k} purely by chance.

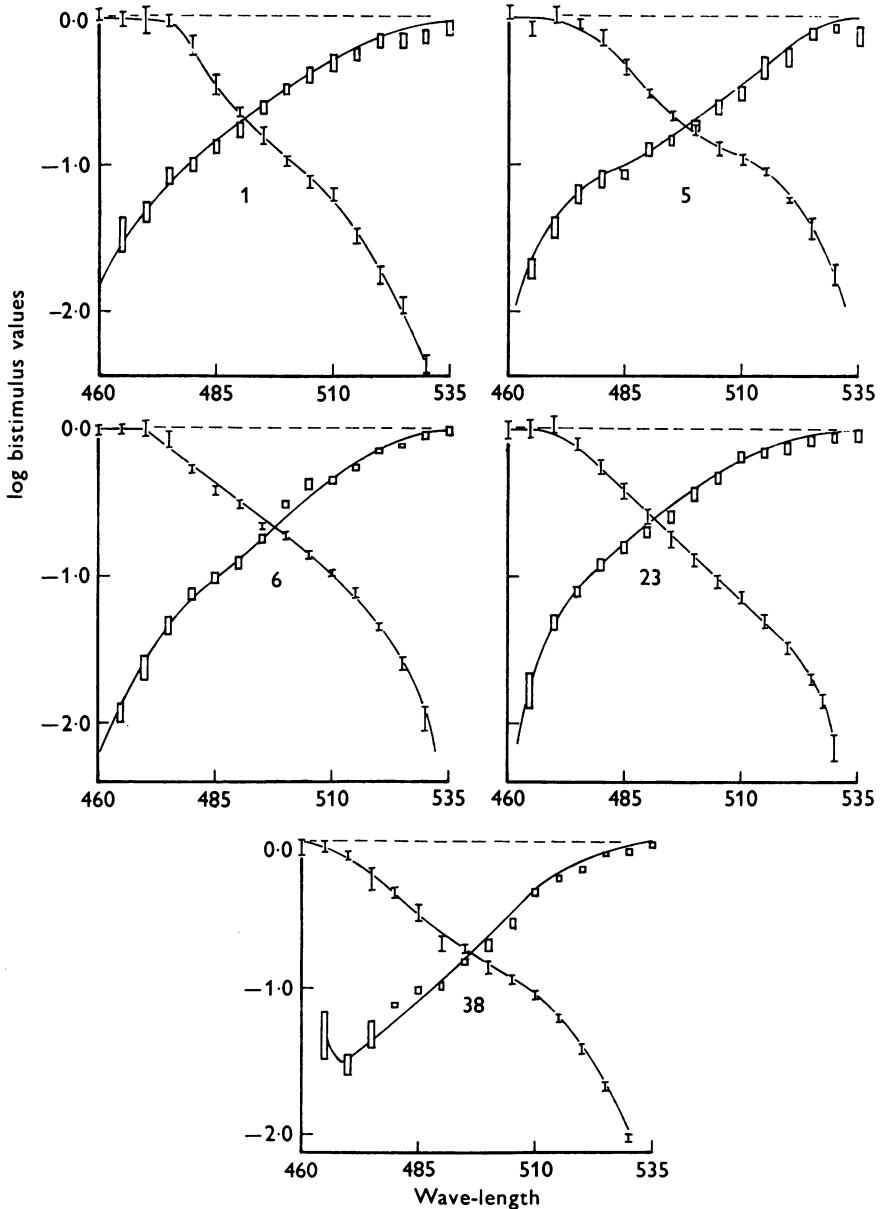


Fig. 5. Maximum saturation spectral colour matching functions of five deuteranopes (identified as in Figs. 3 and 4). The abscissae show the wave-lengths of the matched spectral lights on a linear scale. The ordinates show the ratio of the intensity of the primary to that of the spectral light at the match on a logarithmic scale. The open rectangles give the settings of the 535 nm primary [$\log \bar{g}(\lambda)$], the continuous line the settings of the 460 nm primary [$\log \bar{b}(\lambda)$]. The limits on the lines and rectangles enclose the means ± 1 s.e. of the means. The curves are smooth estimates illustrative of the trends and have no theoretical significance.

Assuming normal distribution of the differences and homogeneity of variance independent of wave-length, this is a straightforward application of the F test to the mean of the differences in the log ratios. However, the results show a fair amount of inhomogeneity of variance as a function of wave-length. To obviate this difficulty, the following procedure (suggested by J. Moeller of this laboratory) was employed (Alpern *et al.* 1976). If Δ is the difference in the means of the log ratios for a pair of observers at a given wave-length and σ_{Δ} is the estimated standard error of this difference, we examine the statistic:

$$S(k) = \frac{\sum_{465}^{530} (k - \Delta)^2}{\sigma_{\Delta}^2}$$

for a value $k = \hat{k}$, such that the sum $S(k)$ will be a minimum. Call that minimum value S .

Since each experiment has been repeated at least 10 times at fourteen different wave-lengths, the distribution S when eqn. (5) is true, becomes approximately the χ^2 distribution with 13 degrees of freedom. Therefore the hypothesis that eqn. (5) is true can be evaluated by comparing S with the critical upper percentile of the χ^2 distribution.

The bistimulus colour matching functions for the deuteranopes of Fig. 5 are compared with each other in this way in Fig. 6. Plotted are a matrix of graphs, the abscissas of which are the wave-lengths matched, while the ordinates are the differences in log ratios \bar{b}/\bar{g} of two deuteranopes, designated A and B . Every column of graphs holds A fixed and allows B to vary; each row holds B fixed while A varies. Two other items of information are provided on every graph. One is the interrupted line which gives the maximum likelihood estimate \hat{k} ; the other is the computed value of S . Since with 13 degrees of freedom the 95th percentile of the χ^2 distribution is 22, it is evident from the comparisons in Fig. 6 that the colour matches of every deuteranope in Fig. 5 differ significantly from every other in a way that cannot be attributed to differences in preretinal absorbances.

The conclusion is clear. Since the differences in colour matches are not caused by differences in preretinal absorbance, they must be due to individual differences in the action spectra of at least one of the two foveal cone pigments which underlie these dichromatic matches.

By itself, this analysis does not indicate in which of the two pairs of cone action spectra underlying the matches the individual differences in spectra occur (if, indeed, they occur in only one of the two). Hence, a series of tenuous, but perhaps still tenable, *ad hoc* hypotheses can be assembled which together are consistent with the idea that action spectra at the retinal level of all the long wave cone visual pigments of the deuteranopes in this study are identical. The last of these would be that individual differences (at the retinal level) of the short-wave foveal cones are responsible for all individual differences in colour matching. Granting

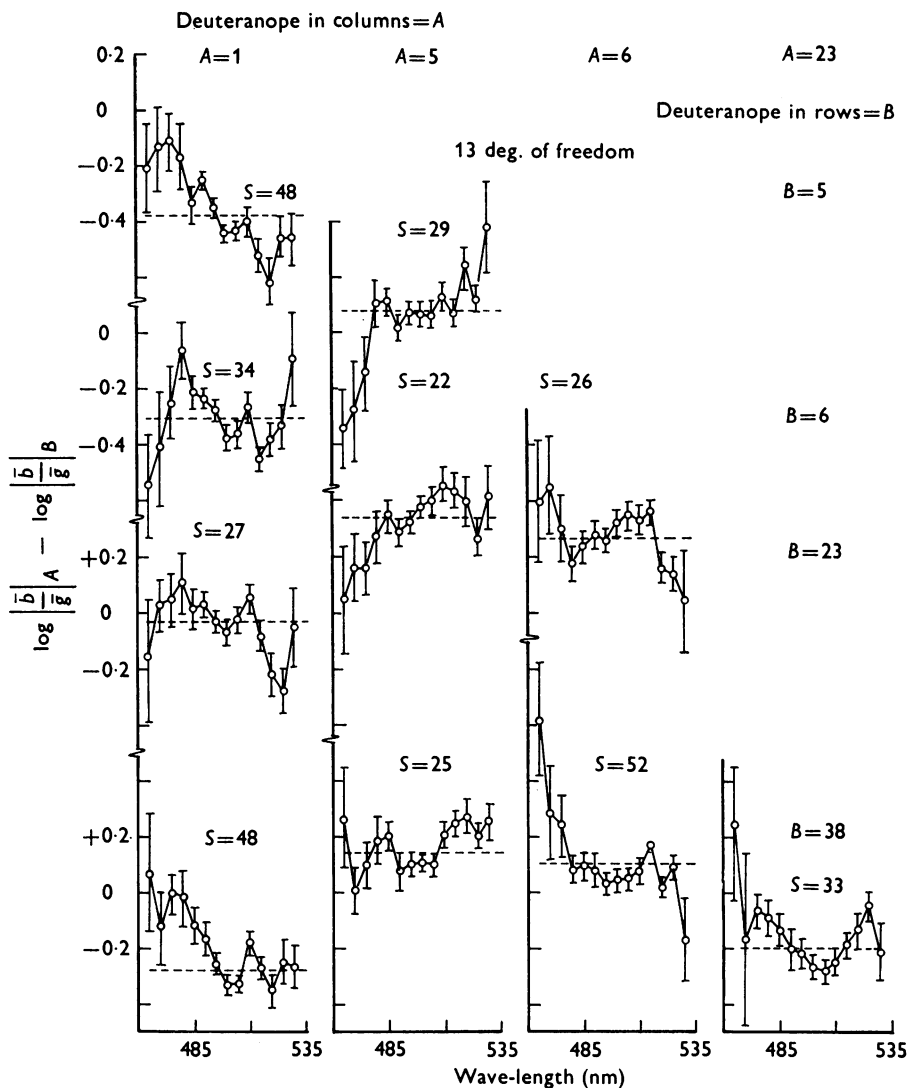


Fig. 6. The differences in the logs of the ratio of the blue to the green colour matching functions of each deuteranope and every other shown in Fig. 5. The plotted points are the logs of the mean differences ± 1 s.e. of the mean. A graph compares two deuteranopes A and B . It contains a horizontal dotted line, the estimate \hat{k} of the wave-length independent constant best describing the differences as well as the statistic S (with 13 degrees of freedom the 95th percentile of the χ^2 distribution is 22). In every column of this Fig. A remains fixed, while in any row B remains the same. Each set of matches in Fig. 5 are significantly different from every other in a way not explained by ocular media differences.

this unlikely possibility shifts the variability from erythrolabe bearing, to cyanolabe bearing cones but does not weaken the inference that individual deuteranopes have quite different cone visual pigments. Moreover it is much less in accord than its alternative, with the results in Fig. 3 which emphasize that differences in the long (not the short) wave sensitive cones correlate with the differences in the anomaloscope matches of deuteranopes.

PART IV. WHICH DEUTERANOPE HAS NORMAL ERYTHROLABE?

An established dogma of colour theory is that '...except for the effects of ocular-media pigmentation dichromats accept normal colour matches' (Judd, 1949). But how can several deuteranopes, each of whom rejects the other's matches in a way not due to ocular-media pigmentation, accept in turn those of the same normal? In the previous section of this paper it was shown that deuteranopes do reject each other's matches in a way not to be attributed to photostable pigment differences. It is therefore essential to inquire into the extent to which the established view happens to be true.

For such a widely accepted canon, the evidence for it is rather sparse. It seems to have been tested only by von Kries (1897), by Pitt (1935), and by Mitchell & Rushton (1971), although a closely related retinal densitometric experiment of Baker & Rushton (1965), not sensitive enough to test the subtle distinctions we find among different deuteranopes, led to a similar conclusion.

According to Pitt:

One of the most fundamental facts to be used to establish this connection (between the dichromatic and trichromatic systems) is that the colour match of a normal trichromat is also a colour match for a dichromat. This was tested in the present research and was found to be rigidly true with but few exceptions at the violet end of the spectrum. These exceptions are readily explained by the variation of the amount of yellow pigment covering the fovea centralis of the eye... (Pitt, 1935, p. 36).

One infers that Pitt, like von Kries, made a normal trichromatic match and inquired whether or not dichromats agreed with it.

A more exact comparison of the red-green colour matches of dichromats and trichromats is afforded by the analytical anomaloscope of Baker & Rushton (1963) employed by Mitchell & Rushton (1971). In their instrument the red (a broad band of tungsten light extending from 620 nm to

the end of the spectrum) and green ($\lambda = 550$ nm) primaries were orthogonally polarized and their proportion varied by the adjustment of the analyser rotating in the common beam. The full intensities of these primaries were set in what Mitchell & Rushton called the 'deuteranope's mode' (i.e. equated for equal visual effect on the long wave mechanism of the average of nine deuteranopes). Once this equation was established, normals matched a mixture of the two primaries to monochromatic lights by setting two controls: (1) the rotating analyser which varied the proportion of the two primaries in the mixture and (2) the intensity of monochromatic light required for the match. The former setting was unique for the trichromat and depended on a cone pigment which the dichromat lacked; but the latter depended only on the pigment the normal and the dichromat allegedly share. The average adjustments of the monochromatic intensities at the dominant wave-lengths of the two primaries and at three intermediate wave-lengths made by seven normal subjects were compared with the average matches of nine deuteranopes. Mitchell & Rushton found an approximate agreement; they concluded that the same cone pigment (erythrolabe) is common to deuteranopes and normals.

This experiment has been repeated in a re-evaluation of the canon that deuteranopes accept normal matches in the red-green spectral range where the effects of ocular pigmentation are negligible. The matches of normal trichromats in this part of the spectrum are dichromatic (as red-green dichromats are monochromatic). For the present purpose, we cannot follow Mitchell & Rushton in averaging across subjects and in testing only the primaries and three intermediate wave-lengths. One normal subject was individually compared with each of five different deuteranopes, the anomaloscope being set, in turn, in each deuteranope's mode, i.e. at his 'isolept' (Rushton, Powell & White, 1973). In three cases, this was done by a 'confrontation', with the normal and the deuteranope alternately making ten successive settings of the intensity of the monochromatic light during the same experimental run.

Apparatus

Channels 1 and 2 were used for the red (671 nm) and green (550 nm) primaries respectively, channel 4 for the monochromatic light and channel 3 was occluded (Fig. 1). Orthogonal linear polarizing filters were mounted in channels 1 and 2 just before their mixture at the mixing cube $MC_{1,2}$. The orientation of the two polarizers was set to maximize the intensity taking into account the inherent polarization of the emergent beams. Immediately after the beams were mixed together they traversed the analyser, which by rotation varied the proportion of the two primaries in the mixture. The dichromat first adjusted the maximum intensity of each of the two primaries to match a fixed monochromatic standard, equating the two primaries in this way for the 'isolept' of his own long wave visual pigment.

The dichromat made ten settings of the channel 4 wedge for a match with a given monochromatic light. The normal subject then made ten settings using both the analyser and the wedge W_4 . The wave-length of the monochromatic beam was changed; the deuteranope placed himself in the apparatus and made ten settings at the new wave-length. After these settings were matched, the normal replaced him and made ten settings at this wave-length as before. The procedure continued in this way for all the monochromatic wave-lengths at 10 nm intervals between the two primaries (i.e. at 560, 570, . . . , 660 nm). These procedures were followed with a single normal trichromat (M.A.) 'confronting', in turn, each of four different deuteranopes. A fifth deuteranope who made only one or two (instead of ten) matches at each wave-length, was no longer available for testing when the normal 'confronted' the anomaloscope set in his mode.

Unfortunately a small amount of parasitic elliptical polarization caused by the reflexions at the mirror M_{12} and at the photometer cube PC introduced a slight deviation from the isolept as the analyser rotated. This effect was largest at 45° . In that position the light emerging in the mixture field was 0.0385 log units less intense than the 'isolept' intensity although the proportion of the two primaries in the mixture was unaffected. This obviated one elegant application of the analytical anomaloscope, i.e. the use of the deuteranope's settings of the monochromator wedge W_4 as a measure of the action spectrum of his foveal cones. However, in the present instance that spectrum has been derived in other ways and the anomaloscope used to decide whether the matches of a given deuteranope and a given normal agree. In this decision the normal and a deuteranope only rarely matched with analyser settings differing by more than $\frac{1}{3}$ the maximum deviation from the 'isolept', i.e. with a maximum deviation 0.013 log units (usually they were smaller than this). This discrepancy is well within the precision of individual matches, and is therefore reasonably considered negligible.

RESULTS

Not one of the five deuteranopes made identical settings of the monochromatic intensities as the single normal with which each was confronted. However, the matches of one of the five were so nearly those of the normal that no clear discrepancy could be identified. The results of 'confrontations' with those three of the five whose settings were closest to 'normal' are shown in Fig. 7. Plotted on the ordinate are the limits as defined by one standard deviation on either side of the mean of ten settings of the (logarithmic) intensities of the monochromatic lights by the deuteranopes (vertical rectangles) compared at each wave-length with these limits of the settings of the same normal subject (continuous vertical line). (The latter settings are, of course, different in the three parts of Fig. 7 because the primary settings of each deuteranope's isolept are different.)

The topmost comparison (*A*) is with a deuteranope whose settings systematically indicate a lower sensitivity at intermediate spectral wave-lengths than 'normal'; the bottom comparison (*C*) is with a deuteranope showing 'abnormally' high sensitivity. Only the middle comparison (*B*) shows reasonable agreement throughout the spectrum. Although even

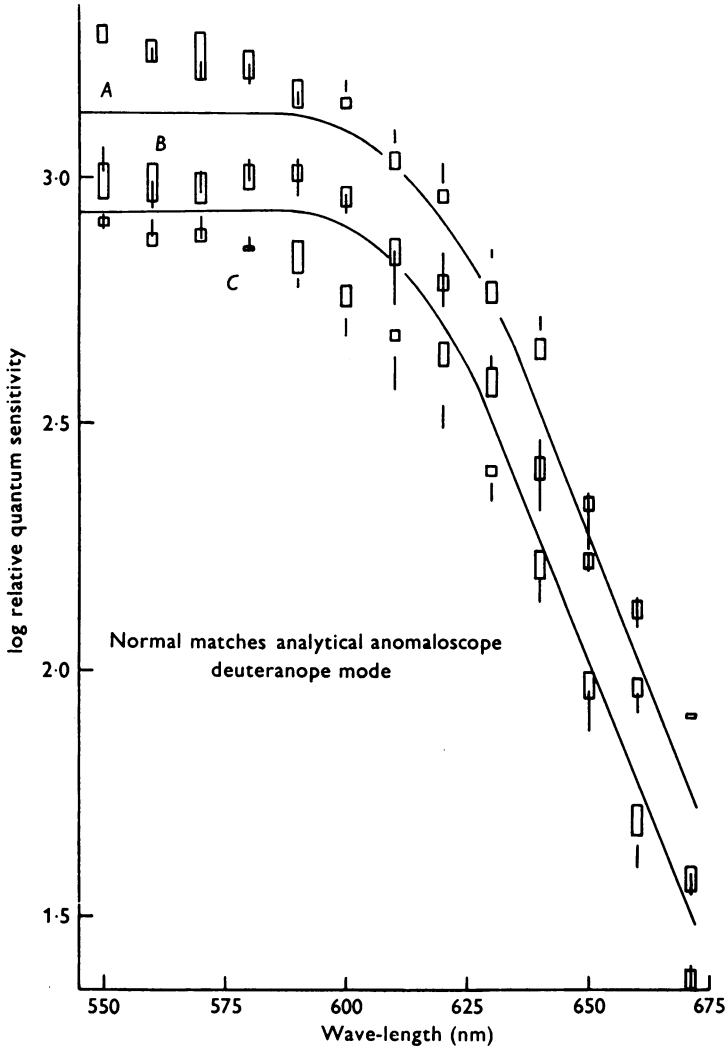


Fig. 7. Comparisons of the logarithms of the intensities of the monochromatic light set by one normal (columnar line) and three deuteranopes (open rectangles) in confrontations with the analytical anomaloscope. The instrument is set in each deuteranope's mode [i.e. with the intensities of the anomaloscope primaries with full transmission equated for the 'isolept' (Rushton, Powell & White, 1973) of his long wave foveal cones]. In *A* the anomaloscope primaries were equated for deuteranope 34 isolept; in *B* for deuteranope 10 isolept; in *C* for deuteranope 12 isolept. The limit enclosed by ends of the lines and the rectangles enclose the mean ± 1 s.d. of the ten settings of the monochromator intensity made in single experimental sessions. Two other deuteranopes similarly confronted with this normal mismatched to a greater extent than those illustrated in this Figure.

the slight differences shown in this confrontation are statistically significant ($\chi^2 = 45$, 10 d.f., $P < 0.001$) this is mainly due to the mismatch at $\lambda = 630$ nm. If this deviation is described to chance experimental error the results of these experiments suggest that one of the five deuteranopes for whom it was tested systematically matched in a way consistent with the dogma that a dichromat accepts normal matches; for none of the others was this true.

By themselves, such experiments cannot exclude the possibility that the 'abnormality' of the matches of the other four deuteranopes is due to differences in ocular-media pigmentation, although the regions of the spectrum tested were those in which individual differences in absorbance as a function of wave-length from these causes can, in young subjects, be presumed small. But taken together with the remaining results of this paper, this interpretation seems quite implausible. Deuteranopes differ significantly among themselves in their matches in a way not explained by media differences and systematic differences in action spectra appear in their long wave cones. The most reasonable interpretation is that one deuteranope accepts the matches of our 'typical' normal subject because the action spectrum of the long wave foveal cone visual pigment of each is the same and that the other four deuteranopes reject the 'typical' normal matches because the action spectrum of the latter's erythrolabe differs from that in their respective long wave foveal cones. In any event, it is clear that the 'rigid' truth observed by Pitt (1935) to the dogma that deuteranopes accept normal matches in the red-green spectral range is by no means a general rule. No doubt agreements of this kind are occasionally found with a fortuitous combination of individual normal and deuteranopic subjects.

DISCUSSION

In this paper it is shown that the action spectra of the long-wave sensitive cone visual pigments of a sample of different deuteranopes differ in ways not attributable only to individual differences in ocular media absorbances. The most unequivocal evidence for this is provided by the colour matching functions in Fig. 5, each set of which differs from the others because the visual pigments upon which the matches depend differ. This test does not allow a strong inference as to whether the variability is due to the long, or the short, wave foveal cone visual pigments. But other evidence leads to the inference that appreciable individual differences exist in the foveal erythrolabes of different deuteranopes: (i) the fact that in the anomaloscope range where these deuteranopes were distinguished, the ocular media are known to be neutral; (ii) the fact (Fig. 3) that the action spectra of the long, but not the

short, wave cones differ in a way anticipated by the anomaloscope settings; (iii) the fact (Fig. 4) that the measured fundal reflectances of these deuteranopes show no sign of differences capable of explaining the measured differences in the action spectra of their long wave cone pigment; (iv) the fact that there are individual differences in the difference spectra and kinetics of the long wave pigment directly measured with the densitometer (Alpern & Wake, 1977). To what are such differences to be attributed?

The densitometer results of Alpern & Wake (1977) suggest two possibilities. In Table 3 of that paper it is seen that there is wide variation among different deuteranopes in erythrolabe photosensitivity. Given pigments with identical absorption spectra, the action spectra of individual deuteranopes could vary because of receptor orientation differences and the wave-guide properties of long wave foveal cones.

This alternative would be difficult to deal with psychophysically if individual cone photoreceptors had very narrow acceptance angles as has been proposed (by Wright & Nelson, 1936; Makous, 1968; Safir, Hyams & Philpot, 1971). But Baylor & Fettiplace (1975) measuring the directional sensitivity of individual turtle cones, suggest that the directional sensitivity measured psychophysically is a direct reflexion of the directional selectivity of individual receptors (all of them in a given patch of retina having a relatively high degree of parallel alignment). The similarity of directional properties of single cones and the overall behaviour of the visual system with its convergent wiring provides some hope that a psychophysical study of the directional sensitivity of the long wave foveal cones of deuteranopes might exclude the hypothesis that individual differences in action spectra result from the visual pigment being contained in cones with variable orientation or different wave-guide properties.

The results on this point obtained so far are still too few to permit a categorical exclusion of this possibility. However, measurements on the brightness Stiles-Crawford effect of the long wave foveal cones of deuteranopes are not very encouraging to the view that the observed spectrum differences are due to wave-guide differences in cones with the same visual pigment.

Five deuteranopes from the present sample have been included in a separate study of the wave-length determined variation in the directional properties of the three kinds of foveal cones of the two varieties of red-green dichromacy (M. Alpern & F. Zwas, in preparation). The details of the apparatus and procedure will be given in the paper describing that work which is mainly concerned with the physiology of the Stiles-Crawford effect of the second kind (Enoch & Stiles, 1961). Here we ask only, 'To what extent can the measured differences in action spectra of the long

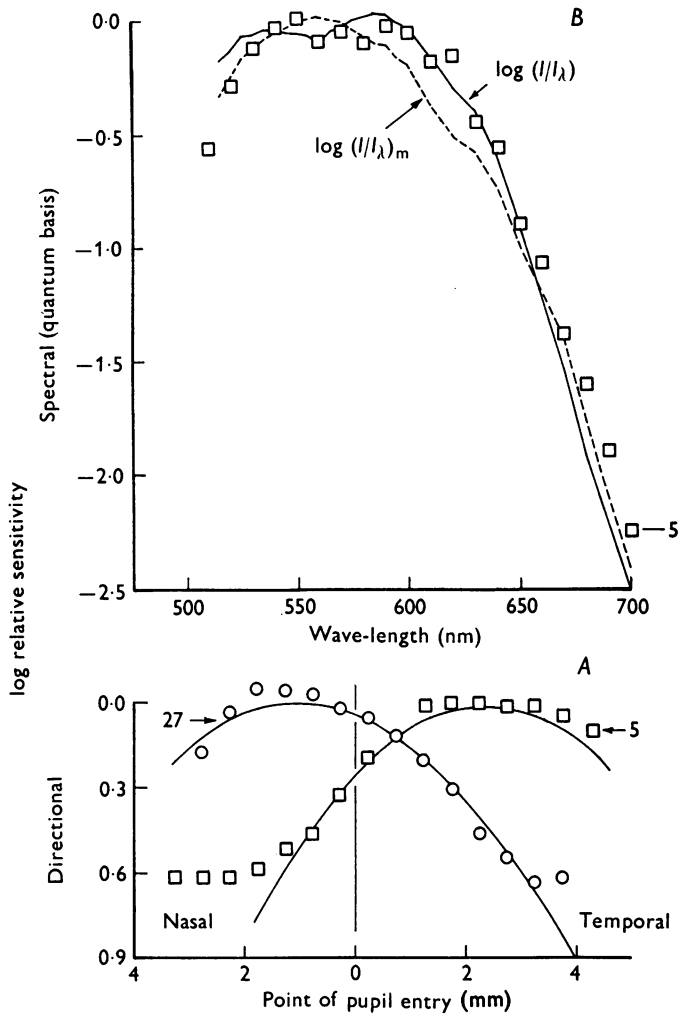


Fig. 8. *A*, directional sensitivity of long wave foveal cones of deuteranope 5 (squares) and 27 (circles) for threshold detection of 30 Hz flicker (100% modulated square-waves) of monochromatic light ($\lambda = 578$ nm). The continuous curve is a best fit parabola obtained by minimizing the squares of the deviations (but ignoring the four most nasal measurements on deuteranope 5). *B*, squares show the action spectrum of deuteranope 5 long wave sensitive cones as measured in Fig. 3. The continuous line shows the theoretical prediction assuming (a) the visual pigment in each set of long wave cones is identical, (b) differences are due solely to optical funnelling and (c) deuteranope 5's results in Fig. 3 were obtained at the optimal orientation but deuteranope 27's results were obtained with an entrance pupil 3.25 mm off the maximum orientation. The dashed line is the same prediction with the opposite assumption of (c), i.e. that the results in Fig. 3 for deuteranope 27 were obtained at optimum orientation and those for deuteranope 5 with an entrance pupil 3.25 mm off the maximum orientation. The wave-length variation of deuteranope 5 long wave cones was used for both calculations. If the wave-length variation in directional sensitivity of deuteranope 27's long wave sensitive cones are used instead, the resulting curves are different but the respective fits are no better.

wave foveal cones of two different deuteranopes be explained assuming both have the same visual pigment but in cones oriented in different directions in their respective foveas?' The most favourable combination for elucidating this possibility among the deuteranopes common to both studies is deuteranope of rank order 5 and deuteranope of rank order 27 whose long wave cone action spectra in Fig. 3 are clearly different.

That the directional properties of their cone vision are also different is shown in Fig. 8*A*. Plotted along the ordinate is the log of the reciprocal of the energy required to eliminate 30 Hz flicker as a function of point of pupil entry (squares for deuteranope 5, circles for deuteranope 27) for a test wave-length (578 nm) near the action spectra peaks. The smooth curve drawn through each set of results has the equation

$$\log_{10}(1/I_{\lambda}) = \log_{10}(1/I_{\lambda})_m - p_{\lambda}(r - r_m)^2, \quad (6)$$

which Stiles (1937) found to describe his measurements in a satisfactory way (our results fully substantiate his observation). The subscript m refers to the point of pupil entry at which the light is maximally sensitive, I is the minimum intensity of light required just to detect 30 Hz flicker and is both wave-length and directionally dependent, and r is the point of pupillary entry in millimetres. The constant p_{λ} is wave-length dependent but the constant r_m is not. The curves drawn through the data resulted from a computer search routine in which r_m and p_{λ} were selected to minimize the square deviations (excluding the four most nasal measurements on deuteranope 5).

Evidently the value of r_m for deuteranope 5 (1.75 mm temporal) differs from the value for deuteranope 27 (1.5 mm nasal). Having measured for deuteranope 5 the wave-length variation of p_{λ} (by repeating the procedures used to obtain the squares in Fig. 8*A* at least once at fifteen different wave-lengths in the visible spectrum) we used it and the action spectrum of deuteranope 27 long wave cones in Fig. 3 to predict the long wave cone action spectrum of deuteranope 5 with two alternative hypotheses. These are, assuming both spectra in Fig. 3 result from the same visual pigment in the same concentration, that (i) deuteranope 5's results in Fig. 3 were obtained at the peak (and therefore deuteranope's 27 result in Fig. 3 were obtained 3.25 mm off the peak) of the directional sensitivity curve and (ii) vice versa.

The results of this analysis are shown in Fig. 8*B*. The squares reproduce the action spectrum of the long wave foveal cones of deuteranope 5 from Fig. 3 and the interrupted and continuous lines are those predicted from the above calculation using hypothesis (i) and (ii) respectively. Neither curve is a satisfactory fit. Clearly the differences in the action spectra of the long wave foveal cones of these two deuteranopes is not easily

explained by the different orientations of foveal cones containing the same visual pigment. The same conclusion is reached though the predicted curves are slightly different if the wave-length variation $p(\lambda)$ of deuteranope 27 is used for the calculation.

The results just described are preliminary; no doubt a more elaborate *ad hoc* model of the wave-guide effects of different cones can reconcile the inconsistencies shown in Fig. 8. However, experiments so far do not encourage the view that all the documented differences in deuteranope long wave cone spectral sensitivity functions can be fully explained by a visual pigment with identical absorption properties contained in cones (at different orientations) with different wave-length dependent wave-guide properties.

Table 3 of the preceding paper hints at a second way of dealing with variability of the long wave cone spectra among deuteranopes with only a single erythrolabe extinction spectrum. Individual differences in the λ_{\max} estimate of density, $(T_o - T_D)/T_o$, shown in column 5 are roughly related to the anomaloscope settings in column 2. Since these measurements and other evidence (Miller, 1972; King-Smith, 1973*a, b*) suggest that the erythrolabe in the deuteranopes can be in high concentration, individual differences in density should result in different action spectra of individual long wave foveal cones due to self-screening. If, say, deuteranope 38 had dilute erythrolabe and deuteranope 1 had erythrolabe with an optical density of 0.5–0.6, the ratios of the sensitivities at the peak to that at 650 nm would differ by a factor of 0.2 log units in these two subjects, in reasonable agreement with what is found (cf. Fig. 3). The densitometric estimates show a slight difference in the expected direction for these two subjects, but the difference (0.05) is too small by one order of magnitude. For sixteen deuteranopes, the correlation coefficient between the anomaloscope value $V(645)/V(535)$ and the λ_{\max} 'density' measured with the densitometer was +0.306, not significantly different from zero ($P > 0.1$).

Unfortunately not much weight can be given to such estimates except in so far as a substantial value for $(T_o - T_D)/T_o$ was measured at the λ_{\max} in every deuteranope. This precludes the possibility that any of them has erythrolabe in so dilute a concentration that no significant self-screening occurs. Beyond this, inference is clouded by the fact that the densitometer estimations of density shown in Table 3 (Alpern & Wake, 1977) define values of $(1 - \sigma) [1 - \exp(2)(-2.3D)]$; where D is the optical density (common logarithmic units) in the cones at the λ_{\max} and σ is the fraction of densitometer measuring light which does not go through the cone visual pigment (King-Smith, 1973*a*; Alpern & Pugh, 1974). Since we do not know σ in any given deuteranope and there is no reason

to expect it to be exactly the same for all, it is impossible to infer from the results in column 5 of Table 3 whether or not all the measured differences in the action spectra of the long wave foveal cones are to be explained in this way. The matter deserves further analysis by techniques (King-Smith, 1973*b*) which obviate the above difficulty.

There are other ways of showing, however, that differences in the concentration of a single erythrolabe are unlikely to be responsible for all measured differences in the action spectra of long wave cones. In Fig. 9*A*, the quantized action spectra from Fig. 3 for the two most extreme subjects (i.e. ranks 1 and 38) are replotted as a function of wave number, the two curves normalized at their respective peaks. The results for deuteranope 38 (triangles) have then been horizontally shifted to the lower frequencies by 200 reciprocal centimetres in order to bring the two peaks into coincidence. If these two spectra were based on the same native pigment in different *in vivo* concentrations, it would be expected that at either side of the peak, the curve through the triangles would fall systematically below the curve through the small circles. No such trend is seen in Fig. 9*A* and the best generalization is that a single smooth curve describes both sets within the precision of the measurements and about equally well. This result is expected not if the same native pigment were in the respective deuteranope's long wave cones in different concentrations, but if these two sets of cones had two different visual pigments of the same concentrations with absorption spectra of the same general form but with λ_{\max} about 7 nm separated in the spectrum. A similar comparison of the remaining deuteranopes studied in the experiments of Part I lead to similar conclusions. The results of all eight long wave cone spectra from Fig. 3 plotted on a wave number abscissa, normalized and shifted horizontally for minimum scatter at the peak are shown in Fig. 9*B*, individual points representing the mean measurements at one spectral position for each deuteranope. There is remarkably small scatter when the data are plotted in this way and no clear evidence for conspicuous differences in *in vivo* concentrations.

In order to gain a quantitative idea of the differences in the action spectra a smooth template curve has been drawn through the data in Fig. 9*B*. This template was then shifted horizontally and vertically for best fitting of the plot of each set of long wave action spectra of Fig. 3 on an absolute wave number (i.e. frequency) abscissa scale. The values of the individual peak wave-lengths obtained by this procedure has been plotted in Fig. 9*C*. There is 7.4 nm difference between the extremes.

Finally then, instead of a single long wave cone visual pigment common to all deuteranopes and all normals, there remains the possibility of a family of such pigments, each member of which has slightly different

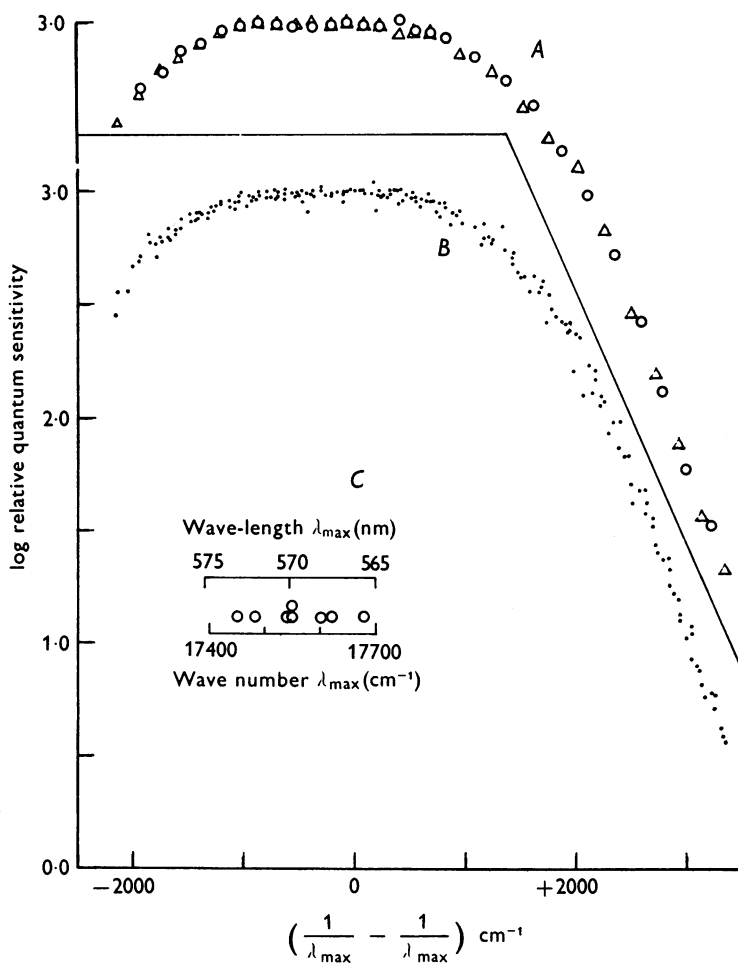


Fig. 9. *A* and *B*, relative quanta spectral sensitivity curves on the long wave side of the neutral points of the eight deuteranopes from Fig. 3 plotted as a function of relative wave number (i.e. $1/\lambda$) in reciprocal cm. *A* compares the results for deuteranope of rank 1 (circles) with those of deuteranope of rank 38 (triangles) after shifting the latter 200 reciprocal centimetres toward the lower frequencies. *B*, comparison of all eight deuteranopic long wave spectra from Fig. 3 after similar normalization and lateral shifting for minimum scatter. *C*, distribution of the λ_{\max} of the eight long wave action spectra of Fig. 3 obtained after plotting each curve on an absolute wave number abscissa scale, and then sliding a smooth curve (through the results in *B*) as a template vertically and horizontally for minimum deviation.

absorption characteristics. This idea does not now seem quite as extreme as it once might have, given the recent microspectrophotometric study of Bowmaker *et al.* (1975), who found that the λ_{\max} of rhodopsin in frog rods varied from animal to animal. Although their sample (fifty-four animals) was nearly 7 times larger than the population of deuteranopes in Fig. 3 the extremes of their distribution (8 nm) was almost exactly that shown in Fig. 9C. Their results can be attributed neither to differences in *in vivo* concentration of the same visual pigment nor to differences in wave-guide properties of individual rods. Although frog rods are by no means deuteranope long wave foveal cones, the factors which determine the absorption characteristics of their respective visual pigments are not likely to be very different. It is, therefore, reassuring to note the spectra of each seem to show rather prominent individual differences of about the same extent.

This sequence of papers began with a discussion of the concept of a deuteranopia as a reduction form of normal trichromacy. It has been shown that a sample of deuteranopes all have but a single foveal cone pigment in the red-green part of the spectrum although there are clear differences in the action spectrum of this pigment in that population. If each deuteranope is a reduced form of normal trichromacy, similar variability in the long wave sensitive cone visual pigment among trichromats can be expected to exist. This is not a popular idea to advance. Indeed much of current literature on colour (e.g. Thomson & Wright, 1953; Vos & Walraven, 1971; Rushton *et al.* 1973; Piantanida & Sperling, 1973; Smith & Pokorny, 1975, to mention only a few examples) is based on precisely the contrary view.

On the surface the concept of a single long wave sensitive pigment common to all normals is not only simpler to entertain but follows more directly in the historical context of the industrial requirements which gave rise to the 1931 C.I.E. standard observer. Hence the opposite conjecture risks the accusation that with it simple understanding is made complicated. But even a casual study (Alpern, 1976) of colour matching is sufficient to convince one how misleading the conventional view is. The ten subjects studied by Stiles (1955) with a 2° field did not match in agreement with the standard observer, and individual differences were large. Both of these were true even after the matches were normalized in a way that obviates differences in prereceptor filters. Unfortunately the study of individual differences of normal colour matching is not a popular enterprise. Therefore, there are no data available which allow a rigorous demonstration that each of the deuteranopes studied in this paper is a reduced form of the colour vision of some normal subject. Given our results in general, and such indications as there are (Stiles,

1955) regarding individual differences in the colour matches of normal subjects, that is certainly the simplest interpretation of available data.

More importantly, when consideration is given to foveal trichromacy in the larger sense this accusation appears to be quite inappropriate. Turning from normal, to anomalous, trichromacy, no student of the subject doubts how muddy the water already is when viewed in the conventional way. It is precisely here that the individual differences in the spectrum of erythrolabe among different deuteranopes introduce both simplicity and clarification. To show that this is the case is the purpose of the final paper in this series (Alpern & Moeller, 1977).

APPENDIX

The analysis of Maxwell matches of dichromats

There are two regions of the spectrum to be studied. Following the reasoning outlined in the derivation of eqn. (3), it is seen that for $\lambda < \lambda_0$,

$$I_0 \tau_0 \kappa(\lambda_0) = I(\lambda) \tau(\lambda) \kappa(\lambda) + I_1(\lambda) \tau_1 \kappa(650), \quad (\text{A } 1)$$

and
$$I_0 \tau_0 \epsilon(\lambda_0) = I(\lambda) \tau(\lambda) \epsilon(\lambda) + I_1(\lambda) \tau_1 \epsilon(650). \quad (\text{A } 2)$$

While for $\lambda > \lambda_0$

$$I_0 \tau_0 \kappa(\lambda_0) = I(\lambda) \tau(\lambda) \kappa(\lambda) + I_2(\lambda) \tau_2 \kappa(450), \quad (\text{A } 3)$$

$$I_0 \tau_0 \epsilon(\lambda_0) = I(\lambda) \tau(\lambda) \epsilon(\lambda) + I_2(\lambda) \tau_2 \epsilon(450). \quad (\text{A } 4)$$

The empirical results give wave-lengths $\lambda_c > \lambda_0$ and $\lambda_c' < \lambda_0$ such that

$$I_1(\lambda) = \bar{I}_1, \quad \text{for } \lambda \leq \lambda_c' \quad (\text{A } 5)$$

$$I_2(\lambda) = \bar{I}_2, \quad \text{for } \lambda \geq \lambda_c \quad (\text{A } 6)$$

where \bar{I}_1 and \bar{I}_2 are constants which do not depend on λ .

For $\lambda > \lambda_c$, according to (A 4) (which is also eqn. (2) in the main text)

$$\tau(\lambda) \epsilon(\lambda) = [I(\lambda)]^{-1} \cdot [I_0 \tau_0 \epsilon(\lambda_0) - \bar{I}_2 \tau_2 \epsilon(450)] \quad (\text{A } 7)$$

where $I_0 \tau_0 \epsilon(\lambda_0) > \bar{I}_2 \tau_2 \epsilon(450)$, since all transmission and absorption coefficients, and light intensities are positive definite numbers. For this same region of the spectrum, by eqns. (A 3) and (A 7),

either
$$\kappa(\lambda) = \text{const.} \epsilon(\lambda), \quad (\text{A } 8)$$

or
$$I(\lambda) \tau(\lambda) \kappa(\lambda) \leq I_0 \tau_0 \kappa(\lambda_0). \quad (\text{A } 9)$$

Eqn. (A 9) is more reasonable than (A 8) on the ground that $\kappa(\lambda)$ is almost surely decreasing monotonically with λ throughout this part of

the spectrum while $\epsilon(\lambda)$ peaks precisely there. Rejecting (A 8) on these grounds, implies that

$$I_0 \tau_0 \kappa(\lambda_0) = \bar{I}_2 \tau_2 \kappa(450). \quad (\text{A } 10)$$

Since $650 > \lambda_c$, and for all λ , $I_1(\lambda) \leq \bar{I}_1$, we may obtain for all $\lambda < \lambda_0$

$$\tau(\lambda) \kappa(\lambda) = [I(\lambda)]^{-1} \cdot I_0 \tau_0 \kappa(\lambda_0). \quad (\text{A } 11)$$

By combining (A 10) with (A 3) one finds, for $\lambda_0 < \lambda < \lambda_c$,

$$\tau(\lambda) \kappa(\lambda) = [I(\lambda)]^{-1} \cdot I_0 \tau_0 \kappa(\lambda_0) [1 - I_2(\lambda)/\bar{I}_2]. \quad (\text{A } 12)$$

This equation is impractical to use because of its sensitivity to the fraction $I_2(\lambda)/\bar{I}_2$, but in principle (A 11) and (A 12) allow $\kappa(\lambda)$ to be specified for all $\lambda < \lambda_c$.

For $\lambda < \lambda_c'$, eqns. (A 2) and (A 4) imply

$$\text{either} \quad \epsilon(\lambda) = \text{const.} \cdot \kappa(\lambda), \quad (\text{A } 13)$$

$$\text{or} \quad I(\lambda) \tau(\lambda) \epsilon(\lambda) \ll I(\lambda_0) (\tau_0) \epsilon(\lambda_0). \quad (\text{A } 14)$$

It is difficult to argue strongly for (A 14) over (A 13) in the context of the present experiments, though (A 14) is not so unreasonable as it might at first seem. For example, if $\epsilon(\lambda)$ had the action spectrum of Stiles's π_5 for $\lambda < \lambda_0$, then for the observer of Fig. 2 for $\lambda < 460$ nm, $I(\lambda) \tau(\lambda) \epsilon(\lambda)/I(\lambda_0) \tau_0 \epsilon(\lambda_0) < 0.023$. Such considerations suggest that eqn. (A 14) is quite reasonable for $\lambda < 450$ nm or so (to within an error of less than 1.5%). Use of $\lambda_2 = 430$ nm as a primary for $\lambda > \lambda_0$ would then allow direct deduction of the long wave-length pigment action spectrum for all wave-lengths $\lambda_c' < \lambda$ by equations exactly analogous to (A 11) and (A 12).

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