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THE RED AND GREEN CONE VISUAL PIGMENTS OF DEUTERANOMALOUS TRICHROMACY

BY M. ALPERN AND J. MOELLER*
From the Vision Research Laboratory, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

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SUMMARY

1. Three 'simple' deuteranomalous trichromats match with abnormally low 'red' tristimulus values throughout the spectrum and abnormally high 'green' tristimulus values in the long wave end of the spectrum which become normal (and then low) in the yellow-green. The spectrum locus of this transition differs from one anomalous to the other. Differences in the matches of two of these cannot be due to differences in eye media transmissivities alone. Therefore these two deuteranomalous have different cone visual pigments.

2. The analytical anomaloscope was used in the confrontation of one deuteranomalous with six deuteranopes in turn. In each confrontation the deuteranope set the anomaloscope in his mode and adjusted the intensity of the monochromatic light for a match. Deuteranomalous matches were rejected by four of these six deuteranopes.

3. They were accepted by two of the six. These two rejected each other's matches in a way not attributable to differences in eye media transmissivity.

4. Three different psychophysical techniques were used to measure the action spectra of the long wave cones of these two deuteranopes. All three methods reveal small but systematic differences in $\lambda_{\max}$ and shape of the curve for the one deuteranope compared with that of the other.

5. In the red–green spectral range, these spectra are accurately described by different linear combinations of the color matching functions of the same deuteranomalous whose matches the two deuteranopes accept. Linear combinations of those of a second deuteranomalous, with at least one different kind of cone, fit less well.

6. The wave-length discrimination curve of the former deuteranomalous was measured with a new method. The curves of two normals were also obtained for comparison. Wave-length discrimination predictions from

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* Present address: Department of Psychology, New York University, New York City, New York.

the Stiles (1946) line element theory were compared to the anomalous curve. The deuteranopic action spectra were used in the line element to compute this deuteranomalous' discrimination. There is reasonable first order correspondence between prediction and observation, but the prediction is sensitive to small changes in the derivatives of the logarithms of the action spectra.

7. Line element prediction of the deuteranomalous step-by-step luminous efficiency curve is insensitive to such uncertainties. The agreement with expectation from the above assumptions and the measured step-by-step deuteranomalous luminous efficiency curve in the red–green part of the spectrum is therefore good.

8. It is concluded that the erythrolabe in one deuteranope's long wave cones has the action spectrum of this deuteranomalous' long wave cones and the erythrolabe in the other deuteranope's long wave sensitive cones has that of this deuteranomalous' medium wave cones. This leads to a general hypothesis about the nature of all forms of red–green colour vision defects transmitted recessively on the X chromosome.

INTRODUCTION

Two previous papers in this series studied foveal vision in deuteranopic dichromacy. Every one of fifteen deuteranopes lacked one foveal photolabile pigment (Alpern & Wake, 1977) and subtle individual differences were found in erythrolabe (the remaining red-green cone pigment) even in addition to any differences imposed by variability in eye media losses (Alpern & Pugh, 1977). If, as is commonly believed, deuteranopia is a reduced form of trichromatic vision then similar individual differences must appear in the long wave cone visual pigment of trichromats. Alpern & Pugh (1977) found that four of five deuteranopes rejected the colour matches of one normal trichromat presumably because the erythrolabe in his long wave sensitive cones had spectral characteristics similar to those of the erythrolabe in only one of the five dichromats. It was expected that the colour matches of other normals would agree with those of other deuteranopes and recent experiments, still unpublished, show this to be true. Do similar individual differences occur among abnormal trichromats?

This paper concerns deuteranomalous trichromacy, the most common of all abnormalities of colour vision, first discovered in that most uncommon of families, the Gascoyne-Cecils (Rayleigh, 1881) .In the usual view (Alpern & Torii, 1968*b*; Mitchell & Rushton, 1971*b*; Rushton, Powell & White, 1973*b*; Piantanida & Sperling, 1973; Rushton, 1975) deuteranomalous have two 'normal' cone pigments (a single erythrolabe and a single cyanolabe) and a single 'abnormal' pigment (Piantanida & Sperling's 'deutanolabe'). From this perspective individual differences in deuteranomalous colour matches are completely explained by differences in eye media transmissivity (Pokorny, Smith & Katz, 1973).

The colour matches of deuteranomalous have been measured by Koenig & Dieterici (1892), von Kries (1899), Abney & Watson (1913) and, with the trichromator of W. D. Wright (1927), by Pitt (1935) and especially by Nelson (1938). In the first part of this paper three simple deuteranomalous are similarly studied, but in a way (Alpern, Bastian, Pugh & Gras, 1976) that allows a statistical statement as to the probability that individual differences in matching are due to differences in absorption properties of the underlying cone visual pigments rather than to differences in eye media transmissivity. The rest of this paper describes the identification (Part II) and validation (Part III) of the spectral properties of the long and medium wave sensitive cones in deuteranomalous trichromacy.

PART I. DEUTERANOMALOUS COLOUR MATCHING FUNCTIONS

METHODS

The apparatus is the trichromator previously described (Alpern, Bastian, Pugh & Gras, 1976; Alpern & Pugh, 1977). A disk-annulus matching field is supplied by three primaries (444·5, 550, and 650 nm) made 'monochromatic' by narrow band (10 nm half band width Baird Atomic) interference filters, two of them in light beams illuminating the annulus (3° outer diameter) the third, in one supplying the central disk (1° diameter). Monochromatic light (2 nm half band width) from a Bausch & Lomb grating double monochromator also fills the disk whose outer edge is contiguous with the inner border of the annulus. The wave-length of the desaturating primary must, of course, be changed during a full traverse of the spectrum; this is achieved by exchanging the interference filters in the beam illuminating the disk and that in one of the beams illuminating the annulus at certain wave-lengths. The ensemble is seen in Maxwellian view through a 1 mm square artificial pupil and a lens correcting for the chromatic aberration of the normal eye (Bedford & Wyszecki, 1957). A single 150 W xenon light source provides all four light beams. Radiometry utilized a calibrated silicon photodiode; filter and wedge calibrations were facilitated by a Beckman Acta II Spectrophotometer. To obviate distortions due to regional differences in receptor distribution and/or ocular pigmentation with the disk-annulus color matching field, the observer matched fixating one disk-annulus border (say at 3 o'clock) but only identified it as such after its confirmation with a change of fixation to the disk-annulus border directly opposite (i.e. at 9 o'clock).

The apparatus, useful, for a variety of experiments, lacks many features of the more elegant zero dispersion instruments of Wright (1927) and of Stiles (1955*a*). In particular, Stiles' (1955*b*) procedure of isomeric matching at the reference wave-length with three lights in each half of the colorimetric field is not possible. This is especially unfortunate because we use filter primaries which have much wider band widths than the test monochromator. The resulting imprecision of the 'isomeric' matches is manifest by an occasional deviation from unity of the colour matching functions at the wave-length of the primaries. No effort has been made to normalize such discrepancies where they occur.

The amounts of three primaries required to match monochromatic lights of known quantum content and wave-length were determined. The wave-length of the latter was varied at 10 nm intervals throughout the spectrum (from 650 to 400 nm) and a spectral traverse was completed in each experimental session (which lasted about 3 h). The process was repeated at least five times for each subject, the results averaged.

Subjects

Experiments have been carried out on three congenital deuteranomalous, one acquired deuteranomalous and four normal subjects. For the present purposes the colour matching functions of the congenital deuteranomalous are of interest; the results on normals and the acquired anomalous subject are described elsewhere (Alpern *et al.* 1976).

The principle subject *W.*, a 45 yr old experimental psychologist, had considerable experience in visual psychophysical experiments, although none in color matching. The other two, both young adult males, were inexperienced but quickly learned a systematic technique for colour matching. All had normal acuity and made anomaloscope matches within narrow limits, crisply in the deuteranomalous range. The precision of the matches of the experienced subject was not obviously better than that of the two naive observers, any one of them being equivalent to normal subjects. In this respect they are similar to the five deuteranomalous originally described by Rayleigh (1881) rather than the 'extreme' deuteranomalous subsequently discovered. The latter typically will match over a wide range of settings of the red and green anomaloscope primaries including those of a normal.

RESULTS

The tristimulus values (log ordinate scale) are plotted as a function of wave-length (linear scale) in Fig. 1. The points enclosed by vertical lines show the means ± 1 S.E. of mean of the measured colour matching functions of deuteranomalous *H.* (left panel), *W.* (middle panel) and *M.* (right panel). The triangles give results obtained with the 'red' (650 nm), the squares those for the 'green' (550 nm), and the circles those for the 'blue' (444·5 nm) primary. Filled symbols represent measurements with the primary desaturating the monochromatic test, open symbols those obtained with primaries in the annular matching field.

Alpern *et al.* (1976) showed that normal colour matching functions measured on this apparatus were reasonably described by the mean results (2° field) of the pilot study of Stiles & Burch (1955) on ten subjects (ages 20–53, mean age 31), converted from an equal energy to an equal quantum spectrum and transformed to the present reference primaries. These are the lines in Fig. 1. (The 'red' and 'blue' tristimulus values are shown as continuous lines, the 'green' as an interrupted line.)

The results in Fig. 1 are in general agreement with those of Nelson's (1938) Group I (*A*, *D* and *F*) in that the 'red' tristimulus value is abnormally

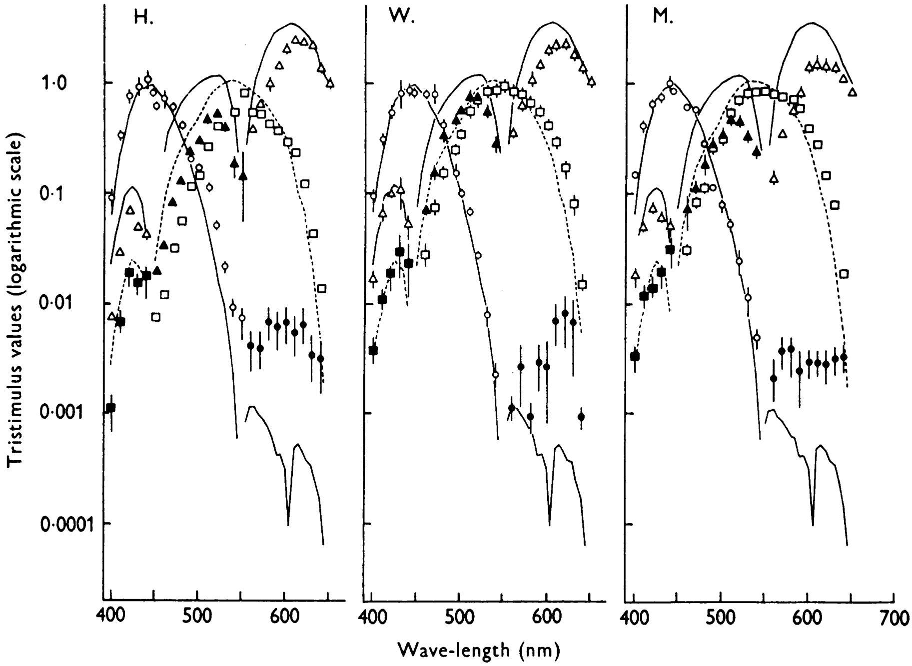

Fig. 1. Spectral colour matching functions of three 'simple' congenital deuteranomalous subjects *H.*, *W.* and *M.* Ordinate gives the tristimulus value on a logarithmic scale: triangles for the 'red' (650 nm), squares for the 'green' (550 nm) and the circles for the 'blue' (444·5 nm) primary. The solid symbols designate values obtained with the relevant primary as a desaturant; absolute values are plotted in such cases; open symbols were obtained with the two primaries in the mixture field. The error bars enclose the mean ± 1 S.E. of the mean of five experimental repetitions. The lines are the average colour matching functions obtained with a 2° field by Stiles & Burch (1955) quantized and transformed to the relevant set of reference primaries. (Continuous line representing both the 'red' and the 'blue' tristimulus values, the interrupted line representing the 'green' tristimulus value.)

low everywhere in the spectrum while the 'green' is abnormally high at the red end of the spectrum, becomes normal (and then abnormally low) at a region in the yellow-green which differs from one anomalous to another. This last observation, i.e. individual differences in colour matching of different anomalous, is also seen in Nelson's measurements. Are they due solely to differences in eye media transmission?

The eye media transmissivity at any given test wave-length can be eliminated by forming the *ratio* of two different tristimulus values at that wave-length, e.g. by calculating ('red' tristimulus value)/('green' tristimulus value) at each wave-length. Therefore observers with the same visual pigment absorptions who differ only in eye media transmissivity must show the same shaped curve, when such a *tristimulus ratio* is plotted as a function of wave-length. Thus the hypothesis that two observers differ only in media transmissivity can be rejected by showing that the ratio of their respective tristimulus ratios is non-constant as a function of wave-length (von Kries, 1899).

Each set of results have been compared in this way with one another and with those obtained from a representative normal subject in Fig. 2. The ordinates of these graphs are the differences in the $\log_{10}$ of the ratio of the ('red'/'green') tristimulus values of two observers plotted as a function of wave-length. In the left column each deuteranomalous is compared with the normal whose results are given in Fig. 3 of Alpern *et al.* 1976. In the right hand column each deuteranomalous is compared with one of the other two. Each graph contains a dotted line showing the best fitting estimate of a horizontal line through the data points. At every wave-length the open circles give the mean differences in the log ratios ± 1 S.E. of mean difference (limited by the extremes of the vertical lines).

The problem of specifying with some statistical confidence that the results in Fig. 2 differ significantly from the interrupted line is treated as in Alpern *et al.* 1976.

Let $\hat{k}$ be the estimate of the ordinate of the best horizontal line, Δ the observed ordinate (difference in mean log ratios) at any wave-length, and σ_Δ the estimated standard error of Δ at a given wave-length. We choose $\hat{k}$ so as to minimize the weighted error sum,

$$S(k) = \sum_{400}^{650} \frac{(k-\Delta)^2}{\sigma_\Delta^{\,2}}.$$

The minimum value is denoted S. If the null hypothesis (wave-length independence) were true, then the distribution of S (evaluated from twenty-three wave-lengths would be approximately χ^2 with 22 degrees of freedom. In each graph the value of the S statistic and the probability that a χ^2 variable with 22 degrees of freedom would exceed the S value are also shown.

The results in the left column verify that the matches of each of the three deuteranomalous are abnormal in a way not attributable to abnormal prereceptor distortions. This finding confirms von Kries' (1899) observation (made only in the red–green spectral range, and on only a single deuteranomalous) throughout the visible spectrum and provides a statistical basis for the assertion that congenital deuteranomalous colour matches are abnormal because at least one of their cone visual pigments is abnormal.

On the right in Fig. 2 the colour matches of each anomalous are similarly compared with those of the other two deuteranomalous. Although the matches of *W.* do not significantly differ from those of deuteranomalous

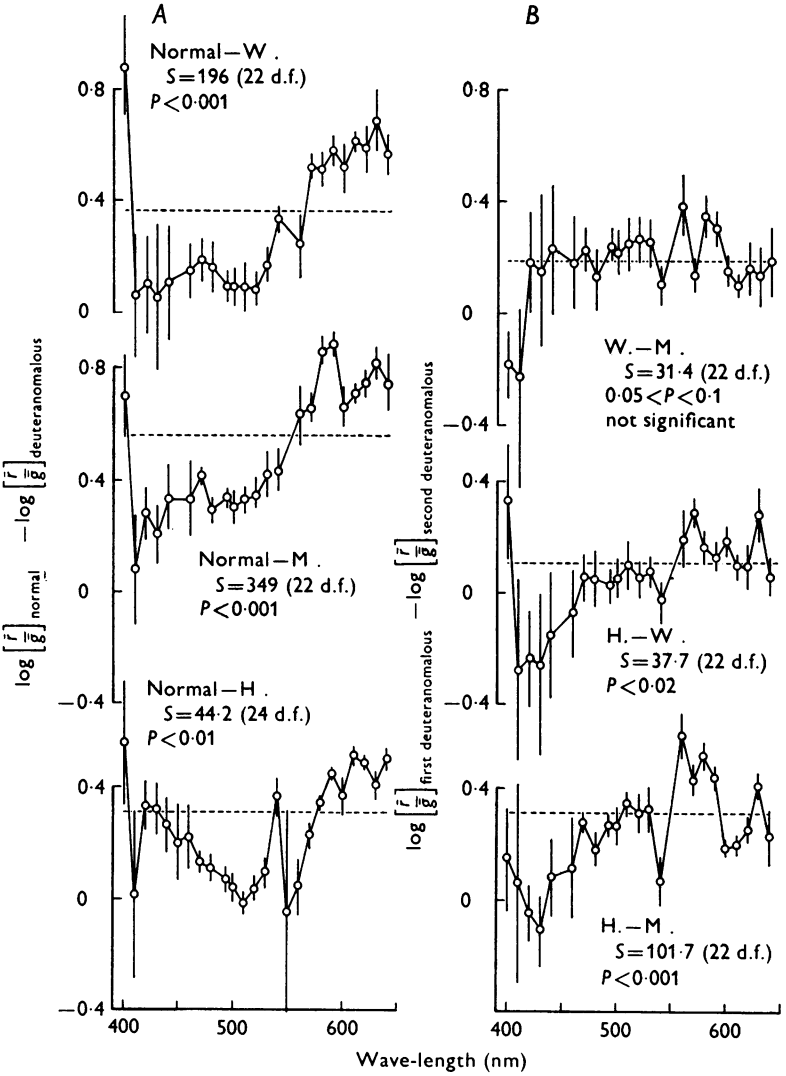

Fig. 2. Comparison of the 'red' and 'green' colour matching functions of three deuteranomalous and one normal. Each graph shows on the ordinate the differences in the logarithms of the ratio of the 'red' to the 'green' tristimulus values for two subjects. In the left-hand column the colour matches of the three deuteranomalous from Fig. 1 are each compared with those of the normal subject of Alpern *et al.* (1976) (cf. their Fig. 3). In the right hand column each deuteranomalous is compared with every other. The dotted lines show the most likely estimate of the wave-length independent constant $\hat{k}$ which best approximates overall differences. Note that all three of the deuteranomalous significantly differ from the normal in a wave-length dependent way, as do two of the three deuteranomalous from one another.

M. when analysed in this way (top right hand comparison in Fig. 2) the other two comparisons in the figure show that the matches of *W.* and *H.* differ from each other as do those of *H.* and *M.* The conclusion is clear and inescapable, the cone visual pigments which underlie the colour vision of every deuteranomalous are by no means identical to those of every other. The view (Alpern & Torii, 1968*b*; Pokorny *et al.* 1973; Rushton *et al.* 1973*b*; Piantanida & Sperling, 1973; Rushton, 1975) that the matches of all deuteranomalous are based on 'normal' cyanolabe, 'normal' erythrolabe and 'abnormal' deutanolabe is therefore rejected. Rather, different deuteranomalous have different cone visual pigments whose action spectra are distinctly, however subtly, different.

Hence specifying the spectral characteristics of the cone visual pigments in deuteranomalous subjects is most likely to be achieved with one subject at a time. Even so, establishing that this has been done is not easy. In the rest of this paper both of these things are attempted for a single deuteranomalous, the principle subject *W.* The identification was made possible by a fortuitous discovery when he confronted six different deuteranopes in turn in the analytical anomaloscope (Mitchell & Rushton, 1971*b*). Those experiments are described in the next section (Part II) along with further measurements of his two cone action spectra in the red-green regions of the spectrum. In the final section (Part III) we try to make this identification persuasive.

PART II. IDENTIFICATION OF THE DEUTERANOMALOUS LONG AND MEDIUM WAVE-LENGTH SENSITIVE CONE ACTION SPECTRA

(*a*) *Analytical anomaloscope.* One deuteranomalous trichromat (*W.*) confronted six deuteranopes in this instrument. The details of the apparatus have already been described (Alpern & Pugh, 1977). The two primaries were orthogonally polarized and their respective intensities at maximum transmission equated for equal effect on the long wave sensitive cones of each deuteranope in his turn. The rotatable analyser in the common beam varied the proportion of the primaries, allowing the deuteranomalous to match the monochromatic light at the intensity previously set by the deuteranope. If rotating the analyser sufficed for the trichromat's match, he set it and the deuteranope verified the match once more before proceeding to the next wave-length where the process was repeated. On the other hand, if the trichromat could not accept the dichromat's match by rotating the analyser alone, he was permitted to readjust the intensity of the monochromatic light as well. The deuteranope then re-evaluated this new match. Almost always, he rejected these deuteranomalous adjustments resetting the monochromatic wedge (within the measurement precision) to its previous position. On occasion, however, the deuteranope found a slightly disparate deuteranomalous setting as good as, or a better match than, his own prior adjustment. These instances were allowed as acceptable agreement between the trichromat's and the dichromat's matches; they are plotted in Fig. 3 as the tip of the arrows (the tail being the original dichromat settings). This procedure was carried out at 10 nm intervals in the part of the spectrum between the red (671 nm) and green (550 nm) primaries.

(*b*) *Action spectra of long wave sensitive foveal cone in deuteranopia.* Since deuteranopes have only two foveal cone pigments rather than three (Rushton, 1965; Mitchell & Rushton, 1971*a*; Alpern & Wake, 1977) the problem of establishing the action spectrum of their long wave sensitive cones is less difficult than is the case for trichromats. However, avoiding contributions of the short wave sensitive cones is still a problem and only one of the three methods unequivocally excluded them. That is the method of Maxwell, employed in the previous paper (Alpern & Pugh, 1977); the spectrum so obtained is valid only for $\lambda \geqslant \lambda_c$ (about 520 nm in the present cases). The two other methods obviate the effects of the short wave sensitive cones in different ways, the step-by-step heterochromatic brightness match luminosity curve because short wave sensitive cones are thought to make little contribution to luminosity (Stiles, 1946), the threshold method by using a 'blue' background to suppress the short wave sensitive cones. None of these methods rigorously defines the action spectrum of the long wave sensitive cones in the short wave regions of the spectrum and we are fully confident of having identified this spectrum in the two dichromats of concern only for $\lambda \geqslant 520$ nm.

(i) *Step-by-step luminosity curve.* The procedure of Alpern & Torii (1968*a*) was carried out on the apparatus described by Alpern *et al.* (1976); (see Alpern & Pugh, 1977, Fig. 1). The 1° test field was changed at 10 nm intervals from 400 to 700 nm and vice versa in separate sessions. This light was made monochromatic by a grating double monochromator with 2 nm half band width. Beginning at the 'violet' end of the spectrum the 3° annular surround was set at the maximum intensity wedge position and a 400 nm (10 nm half band width Baird Atomic) interference filter placed in the beam. The test was adjusted for a match which was usually about 16 td. The centre was changed to 410 nm and the match repeated; next a match was completed at 420 nm. After this a 420 nm interference filter replaced the 400 nm filter in the surround and its wedge adjusted for an isochromatic match to the central disk left at its last setting. The wave-length of the test disk was then reset at 430 nm and the spectral traverse continued in the same way. During the course of the run, the interference filter providing the dominant wave-length of the annular surround was changed twelve times at intervals of 20–30 nm. With each filter change the intensity of the surround was readjusted to match the centre, the intensity of the latter being fixed by the immediately preceding heterochromatic match. The transition was always made when the wave-length of the centre reached that of the peak transmission of the interference filter next to be used as standard.

At the beginning, and whenever the surround filter was replaced, the matches were 'isochromatic'; they could be precisely made. All other matches were inexact; subjects had to '...disregard differences in hue and match for equal brightness'. Since wave-length differences were never large, even normals found this manageable. Deuteranopes had no difficulty in making very repeatable settings. When a run from 400 to 700 nm had been completed the experiment was interrupted to allow the subject to rest. The spectrum was then traversed in a similar fashion in the opposite direction beginning with a 700 nm filter in the surround; the intensity of this surround was adjusted for a match to the last setting of the central disk in the spectral traverse completed immediately prior to the interval. The entire procedure was repeated on a second day.

(ii) *Increment thresholds* for deuteranope 23 were measured on a blue (Wratten 47B) background set at 1·7 log td, a blue-green (Wratten 47) background 4·6 log td, and a purple (Wratten 35) background set at 3·75 log td. His measurements on the different backgrounds did not differ significantly and the mean results were calculated after normalizing each curve for minimum scatter. Deuteranope 38 made all settings only on the blue background.

The experiment began with the test at the 'violet' end of the spectrum. The subject adapted for about 5 min to the background, or until the threshold settings reached a steady level. A pair of cross hairs placed at the far point of the subject's eye in the background field served as fixation target as he looked into the Maxwellian view system through the 1 mm^2 artificial pupil. He adjusted the intensity of the mono chromatic light so that the 1° in diameter circular test (λ = 400 nm) was just visible as it was pulsed for 50 msec, once each second. The result was recorded, the wave-length of the test changed to 410 nm and the measurement repeated. In this way the spectrum was traversed in 10 nm intervals until a threshold at the 'red' end (700 nm) was determined. After a rest interval the process was repeated, beginning this time at 700 nm and progressing in 10 nm intervals to 400 nm. The entire procedure was then repeated still a third time beginning again at the 'violet' and progressing to the 'red'. After this third spectral traverse those test wave-lengths were identified which for one reason (for example a progressively larger or smaller setting on each of the three runs) or another (log threshold values different in the three runs by an amount greater than 0·2) justified further testing. Additional measurements were then made at these wave-length until such discrepancies were resolved (which occurred with as few as three, or as many as ten, determinations).

The entire experiment was repeated, for deuteranope 38 nm on a separate day in which the traverse began at the 'red', and progressed to the 'violet', end of the spectrum. The mean of the logarithm of the intensity settings from the separate runs was determined after normalizing for minimum scatter.

(iii) *Maxwell's matches*. This method is described in Alpern & Pugh (1977) and the results presented in Fig. 3 of that paper.

RESULTS

(*a*) *Analytical anomaloscope*. One surprising, and quite fortuitous, outcome of the anomaloscope experiment was that deuteranomalous trichromat *W*. accepted the matches of two dichromats with different long wave sensitive foveal action spectra, while rejecting the matches of four other deuteranopes. This is illustrated in Fig. 3, which shows six different graphs. The ordinate of each is the logarithm of the intensity of the central monochromatic light at the match. Open circles connected by the continuous line show the dichromat's settings, dots (and dotted lines) the matches of deuteranomalous *W*. In each graph the maximum intensity of the anomaloscope primaries were set for the 'isolept' (Rushton *et al.* 1973*a*) of the deuteranope whose position in the distribution of settings of the anomaloscope found by Alpern & Wake (1977) is given by a number (1 is the least, 38 the most, 'protanoid') in a population of thirty-eight deuteranopes. Open circles in that graph are the settings of that deuteranope. Fig. 3 shows that *W*. rejected the matches of deuteranopes 12, 1, 8 and 27 while accepting those of both deuteranope 38 and deuteranope 23.

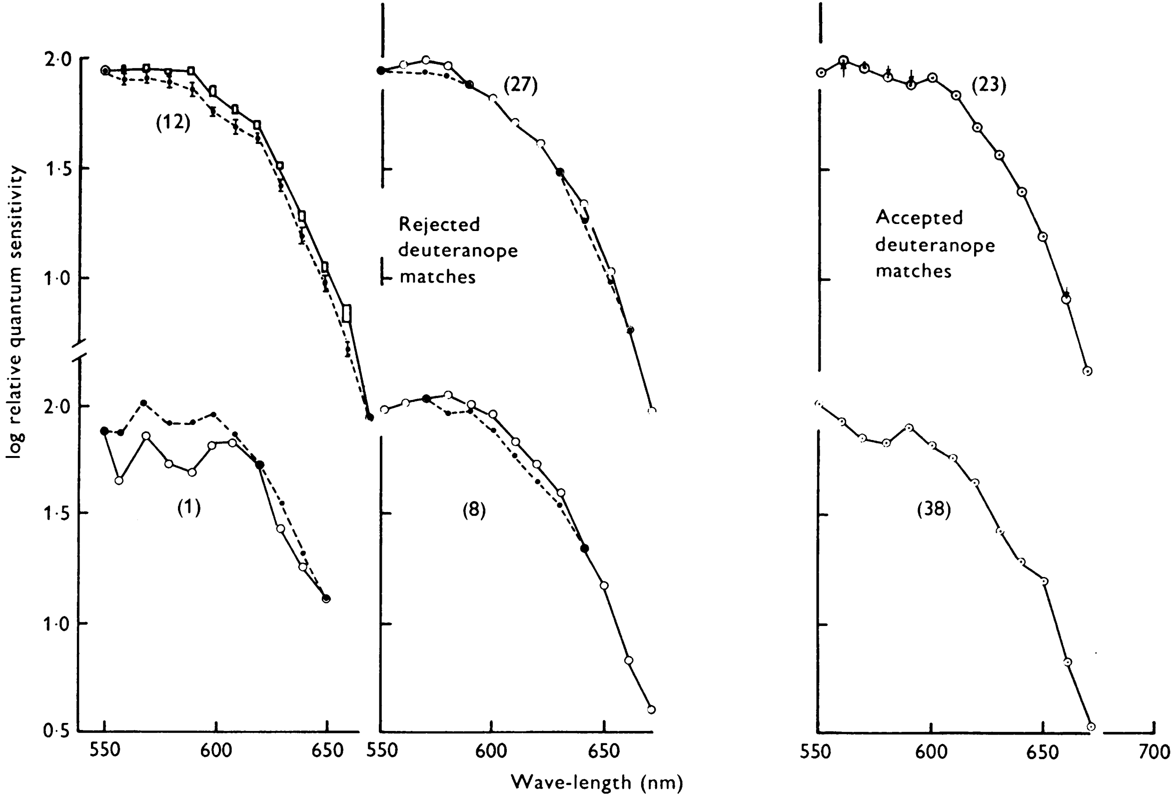

Fig. 3. Results of the 'confrontations' of deuteranomalous subject *W*., with six different deuteranopes in the analytical anomaloscope of Mitchell & Rushton (1971*a*, *b*). Data in each panel were obtained by setting the anomaloscope in the mode of a different deuteranope (identified by the number in the distribution of deuteranopes of Alpern & Wake, 1977). The number specifies the deuteranope's rank in the distribution of relative sensitivities at 645 and 535 nm of the long wave cone system of the thirty-eight deuteranopes of that study (1 specifies the deuteranope furthest in the distribution from, 38 the one closest to, the protanopes). The open symbols connected by a continuous line show the deuteranope settings, the dots (and interrupted line) the deuteranomalous matches.

The last fact, namely that a deuteranomalous trichromat accepts the analytical anomaloscope matches of two deuteranopes with different long wave sensitive cone action spectra can be interpreted in one of three ways: (i) *W.* has the long wave sensitive cones of only one of the two deuteranopes but his poor hue discrimination does not allow the distinction in this instrument; (ii) abnormally imprecise deuteranopic matches conceal identical action spectra of the long wave sensitive cones of deuteranopes 23 and 38; (iii) trichromat *W.* has the long wave sensitive cones of deuteranope 38 in common with one of his three sets of foveal cones and that of deuteranope 23 in common with a second set of his foveal cones.

Possibility (i) is quite out of the question. *W.*'s hue discrimination is extremely good. Measurements (see Fig. 6) show that in precisely the spectral region of concern, his sensitivity to changes in wave-length (of the order of 1 nm) is *better* than normal. *W.* clearly rejected the anomaloscope settings of one deuteranope 27 whose matches placed him between the two deuteranopes with acceptable matches.

It is also possible to exclude possibility (ii). In Fig. 6 of Alpern & Pugh (1977) the maximum saturation colour matching functions of deuteranope 23 differed significantly from those of deuteranope 38 even after effects due to eye media differences were obviated. Furthermore, the action spectrum of deuteranope 23's long wave sensitive cones, however operationally defined, is systematically and regularly different from that of deuteranope 38 (see Fig. 4) always in the same way and always to an extent greater than the precision of the measurements.

Fig. 4. Action spectra of the long wave foveal cone pigment of deuteranope 23 (filled circles) and of deuteranope 38 (open circles). Top comparison shows results from Maxwell matches measured by Alpern & Pugh (1977). The ordinate scale of the entire figure is appropriate for these open circles. The comparison marked 'Stiles' is for measurements of spectral increment threshold on a blue background. The curve labelled 'Brightness match' compares the heterochromatic step-by-step luminous efficiency curves of the two deuteranopes. The bottom comparison is the weighted geometrical mean of the above three sets of measurements. For reasons discussed in the text uncertainties remain for $\lambda \leqslant 520$ nm. For all other wave-lengths this is the best estimate of the action spectra of the long and medium wave-length sensitive cones in deuteranomalous *W.* The lower most solid line shows a linear combination of *W.*'s colour matching functions which best describes deuteranope 23's long wave action spectrum for $520 < \lambda < 650$ nm. The dashed line shows a linear combination of *W.*'s colour matching functions which best describes deuteranope 38's long wave cone action spectrum for $520 < \lambda < 650$ nm. The dotted line is the best fit of the filled circles from deuteranomalous *H.*'s colour matching functions. It is a noticeably poorer fit than the continuous line. Analogous fitting of the open circles from *H.*'s matches are not shown but the result is similar when compared to the dashed line.

We conclude that deuteranomalous *W.* has the visual pigment of deuteranope 23's long wave sensitive cones in his own long wave sensitive cones and that of deuteranope 38's long wave sensitive cones in his medium wave sensitive cones.

(*b*) *Action spectra of the long wave sensitive cones of deuteranope 23 and 38.* The results from the various ways of measuring the action spectra

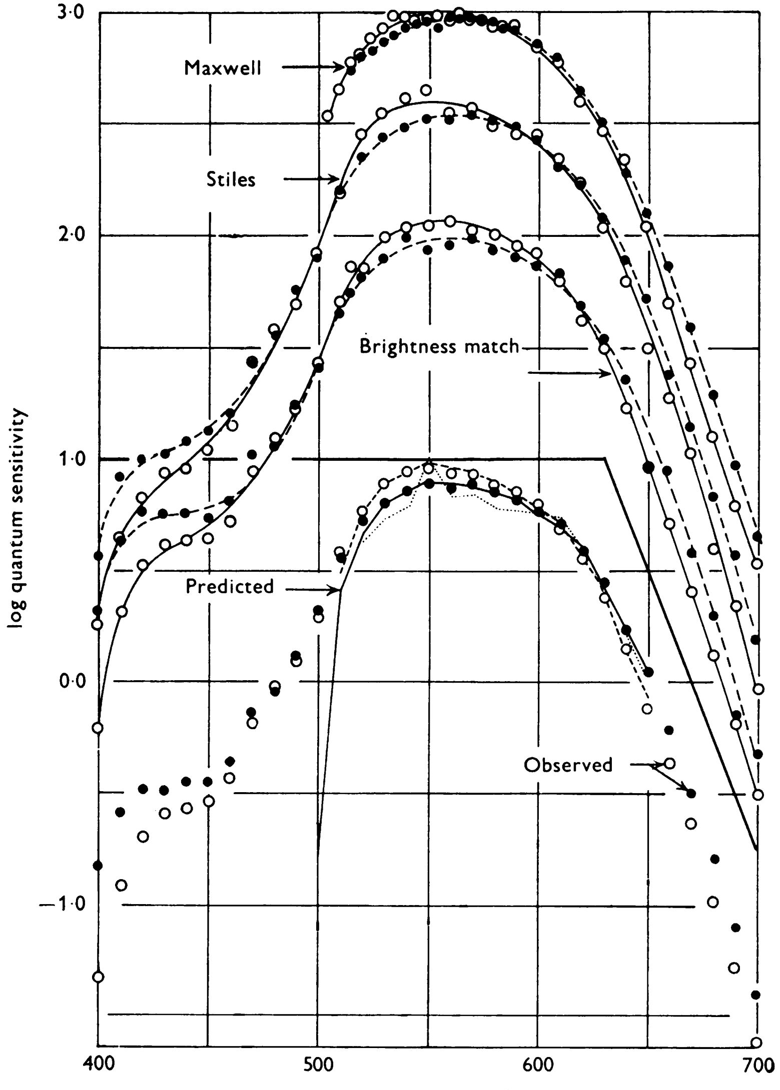

Fig. 4. For legend see opposite.

of the long wave sensitive cones of the two deuteranopes who accept *W.*'s colour matches are summarized in Fig. 4 (open circles for deuteranope 38, filled circles for deuteranope 23). In each set the two curves have been arbitrarily shifted so that they agree in the yellow or orange spectral region. The top curves show the comparison by 'Maxwell matches' and the log ordinate scale of the entire Figure is appropriate for the open circles of this set. The comparison labelled 'Stiles' shows the increment threshold measurements and the comparison labelled 'Brightness match' shows the small step heterochromatic luminous efficiency curves.

The different methods yield slightly different spectra, due in part, perhaps, to the contribution of the short wave sensitive cones to the results and in part to day-to-day variability. But each of the three comparisons in Fig. 4 demonstrates that the action spectrum of the long wave sensitive cones of deuteranope 38 peaks at lower wave-length ($\lambda \sim 555$ nm) than that of deuteranope 23 ($\lambda \sim 560$ nm) and the major differences between the two spectra are duplicated in all three comparisons. This fact justified pooling the various estimates and comparing the means of the results of the individual experiments. This has been done in the bottom comparison in Fig. 4. Although the differences are not large they are quite systematic.

We infer that the filled and open circles at the bottom of Fig. 4 are the respective action spectra of *W.*'s long and medium wave-length sensitive cones (at least for $\lambda \geqslant 520$ nm). In the final section of this paper we try to make this inference strong.

PART III. VALIDATION OF THE LONG AND MEDIUM WAVE SENSITIVE CONE ACTION SPECTRA

Having concluded that *W.*'s long wave sensitive cones have the action spectrum of the long wave cones of deuteranope 23 and *W.*'s medium wave sensitive cones the action spectrum of the long wave cones of deuteranope 38, it seemed important to examine the validity of this deduction.

Unfortunately a full evaluation is handicapped by two uncertainties: (i) the forms of the respective spectra for $\lambda \leqslant 520$ nm and (ii) the action spectrum of the short wave sensitive cones which underlie *W.*'s colour matches. With these reservations in mind, an attempt has been made to test this interpretation of *W.*'s trichromacy.

(*a*) *Colour matching.* A linear combination of a given set of colour matching functions must always exist which defines the action spectrum of each visual pigment which underlies those matches. Any putative pigment spectrum must pass this test. How accurately can the long wave spectra of deuteranopes 38 and 23 be described by combinations of *W.*'s colour matches? To answer this we computed the linear combinations of his matches (Fig. 1) which best fit the two spectra in Fig. 4 for $\lambda \geqslant 520$ nm, i.e. those wave-lengths for which the uncertainties just enumerated are unlikely to make important differences. The results are shown by the solid (for deuteranope 23) and dashed (for deuteranope 38) lines in the lower set of comparisons in Fig. 4. The predicted spectra provide a fairly accurate description of the filled and open circles which – as noted – represent the best guesses of the action spectra of the long wave cones of deuteranope 23 and 38 respectively.

Although the fit is inexact, for $\lambda \geqslant 520$ nm the discrepancies are no larger than those found between individual measurements. It is concluded that in this part of the spectrum, each of these curves is reasonably described by a linear combination of *W.*'s colour matching functions. It is conceivable that an equally satisfactory fit could be achieved by linear combinations of the colour matching functions of other trichromats. Though we cannot exclude this possibility, the best linear combinations of the colour matching functions of the one deuteranomalous studied whose matches differ significantly from those of *W.* (for reasons unrelated to eye media differences) are noticeably poorer fits to the spectra in Fig. 4 than are the best combinations of *W.*'s matches. This is shown in the bottom of Fig. 4 by the interrupted line, the linear combination of deuteranomalous *H.*'s colour matching functions which best describe the filled circles $520 \geqslant \lambda \leqslant 650$. Though the two predictions are about equally good for $\lambda \geqslant 620$ nm, *H.*'s matches are unquestionably poorer predictors elsewhere in the spectrum. Hence the continuous line (i.e. *W.*'s colour matches) accounts for all but 0·558 % of the variance in the filled circles, *H.*'s matches (interrupted line) leave about 12·5 % of the variance unaccounted for. A similar result is obtained when the two sets of matches are used to predict the open circles at the bottom of Fig. 4. (This comparison is not shown in the Figure for clarity of display.)

Thus the putative long and medium wave sensitive spectra of *W.*'s fovea are much better described as linear combinations of his colour matching functions than by those of a second deuteranomalous who differs from *W.* in that at least one of the sets of cones which underlie their matches differ.

Evidently *W.*'s metameric matching is consistent with the identification of the filled circles in the bottom of Fig. 4 with his long wave sensitive cones and the open circles with his medium wave sensitive cones. How adequately can other aspects of *W.*'s vision be so described?

Unfortunately the assumptions which underlie the physiology of the phenomena which come to mind are not as compelling as is the case in matching. Hence, disagreements between data and expectation may shed more light on the invalidity of theoretical assumptions than on the inappropriateness of the action spectra to *W.*'s long and middle wave-length sensitive cones. However, Stiles (1946) line element predicts normal wave-length discrimination given reasonable estimates of what are now generally agreed to be the action spectra of the visual pigments in 'normal' human cones and so we have used it – with incomplete success, as it turned out – to predict *W.*'s wave-length discrimination.

(*b*) *Wave-length discrimination.* How small a difference in wave-length can be detected between two lights of the same brightness? The usual experimental answer requires subjects simultaneously to vary both the wave-length and the luminance of one light while estimating a threshold difference in wave-length between it and a standard (cf. Corbett, 1936). This procedure compounds the difficulty of maintaining a criterion everywhere in the spectrum and we have modified it so that the subject adjusts only the intensity of one of two nearly identical monochromatic lights. After equating brightness, he must judge whether its wave-length is greater, or less, than that of the fixed light.

METHODS

It was supposed that one of a large series of monochromatic interference filters could be used as standards in the beam illuminating the surround of the colorimeter, the subject setting the intensity of the light emerging from the monochromator. This proved unsatisfactory because of band width differences (10 nm *vs.* 2 nm) between the pair of lights. Therefore the apparatus (Fig. 1 of Alpern & Pugh, 1977) was redesigned to allow monochromatic lights of identical band widths in centre and surround. The modifications (cf. Fig. 5*A*) facilitated the transition to other apparatus arrangements rather than utilized the most economical optical systems for the task. In the current form of the apparatus (as in the previous one) light emerging from the grating double monochromator (GM_1) with two (1200 grooves/mm) gratings in tandem has a spectral band width of 2 nm at every wave-length. It fills the centre of the disk-annulus target which is seen in Maxwellian view by the observer looking through the artificial pupil and achromatizing lens. Unlike the previous apparatus, the annulus light comes from an identical monochromator (GM_2). It is collimated by lens $L_{2,3}$. The collimated beam is brought to a focus in the plane of field lens $FL_{1,2}$ which forms an image of the homogeneously illuminated lens, $DL_{1,2}$ in the plane of the photometer cube PC. Suitable baffles, not shown in the Figure, are required to screen stray light.

Procedure

Each wave-length was evaluated in separate sessions in the spectral range 460–650 nm. The standard λ in the annulus was light from S_2, and remained constant in any given determination. The experimenter first fixed the wave-length control of the monochromator GM_2 and used filters to set the annulus intensity at 10 td (the brightest level with which we could study an appreciable range of the spectrum with this apparatus). He then picked a wave-length obviously different

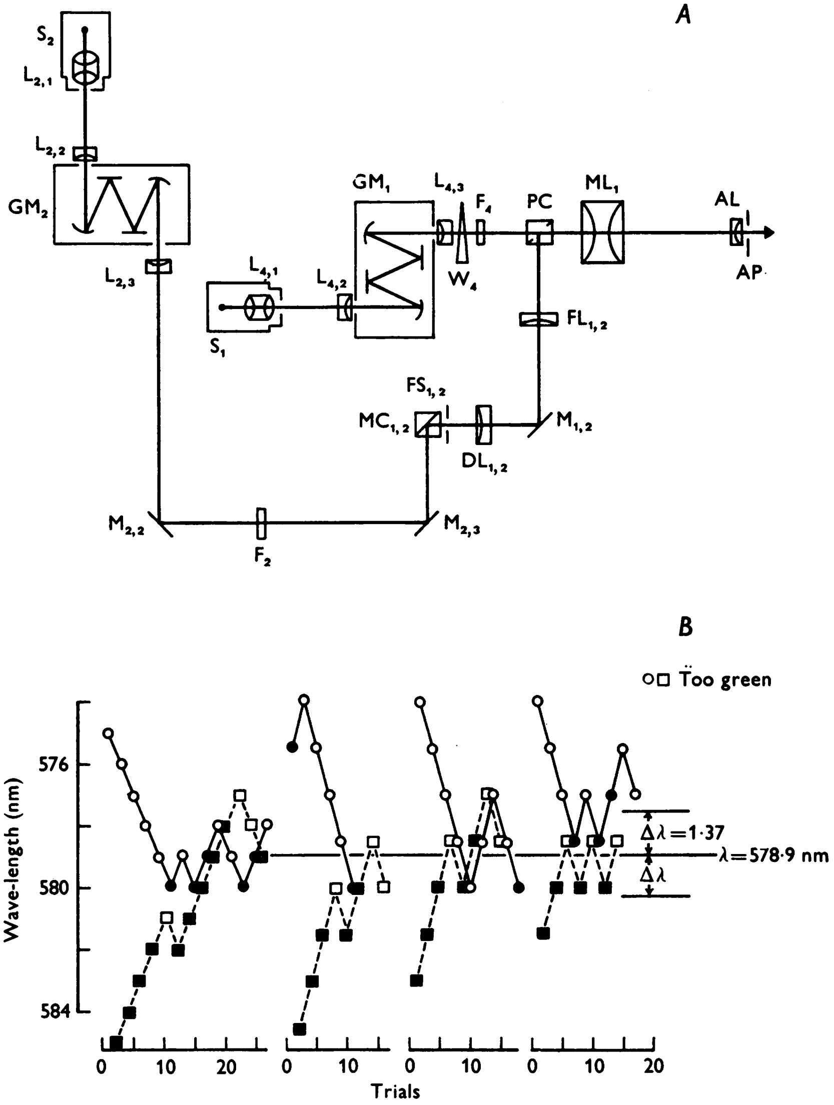

Fig. 5. *A*, (above) modifications of the apparatus shown in Fig. 1 of Alpern & Pugh (1977) made to test wave-length discrimination. The additions include $L_{2,3}$, GM_2, $L_{2,2}$, $L_{2,1}$ and S_2 mounted as a unit on triangular saddles which fit on to the optical rails of the apparatus. Baffles to exclude stray light are not shown. Those symbols in common with Fig. 1 of Alpern & Pugh (1977) indicated identical apparatus components in the two arrangements of this equipment. *B*, (below) a representative measurements of wave-length discrimination for deuteranomalous *W.* at 580 nm. The interleaved double staircases are done in two stages. A preliminary set of trials (in this case) of twenty-seven judgments and a measurement set with six subsets each continuing for four responses after the initial reversal. Open symbols depict the response 'too green', filled symbols, 'too orange'. Squares show results for staircases beginning on the long wave side, circles those beginning on the short wave side.

from this standard for the central disk and the subject, after adjusting W_4, decided on a term to describe the residual hue difference (for example, 'too orange'). This was then repeated, the differences being in the opposite sense. A double staircase, two alternative, forced choice psychophysical procedure (Cornsweet, 1962) now began. (See for example, the representative run at 580 nm, initial step size 1 nm, in Fig. 5*B* starting on the left). On the first trial the experimenter set the central wave-length to 575 nm; the subject (*W*.) set W_4 to minimize the colour difference and then reported the centre 'too green' (left open circle). On the next trial the second staircase was started, the experimenter setting the central wave-length at 585 nm and the subject responded 'too orange' (leftmost filled square). On the third trial the wave-length of the central disk was set in accordance with the previous response of the first staircase at 576 nm and on the fourth according to the previous response on the second staircase at 584 nm. In each case the subject set W_4 to minimize differences and then estimated whether the central disk was 'too orange' or 'too green'. A response was required for every trial and the category 'both the same' not allowed. At the 10th and 11th trials the responses in the two staircases reversed; therefore the directions of the traverses reversed. The procedure continued until at least four reversals had occurred in each staircase (i.e. in the illustrated case, on the 27th trial of the preliminary run). This information was used to decide if the arbitrarily selected step size was equal to the standard deviation of the assumed normal distribution of the estimates and whether or not the point of subjective equality was in agreement with the nominal wave-length in the annular surround. In the illustrated example neither was exactly so. The step size (1 nm) was too small and the point of subjective equality closer to 579 than to 580 nm. The latter discrepancy was so small that no change in the region of wave-length selected was required but the step size was increased to 1·5 nm. The actual measurement then began, proceeding in the way just described. The run was divided into six subsets each consisting of a single staircase lasting at least four judgements after the first reversal in the subset. Two subsets were interleaved in the double staircase, each member of the pair beginning on opposite sides of the spectrum. Though in Fig. 5 alternate staircases were evaluated on alternate trials, in practice two or even three successive trials were occasionally made on the same staircase (the procedure just outlined was suggested by Professor Daniel Weintraub of the Department of Psychology of this University who used it studying visual illusions (Weintraub & Krantz, 1971; Weintraub, Tong & Smith, 1973). Formulas for calculating the point of subjective equality and the standard deviation of its assumed normal distribution curve are to be found in Weintraub *et al.* (1973). For a detailed discussion of the mathematical assumptions see Dixon (1965). The illustrated example yields 578·9 nm ± 1·37 (mean ± 1 S.D.). Since the step size (1·5 nm) was fairly close to the standard deviation of the distribution, 1·37 was regarded as a satisfactory determination of $\Delta\lambda$ at 578·9 nm. Whenever the measured standard deviation of the assumed normal distribution agreed within a factor of 1·4 with the step size, the run was considered satisfactory. If outside these limits, the experiment was repeated using the step size of the measured standard deviation. If the new result fell within the criterion only it was utilized but occasionally the new distribution would be off in the opposite sense; in that event the two sets were averaged. (*W*. became unavailable for further testing with four wave-lengths (ratios 1·95, 1·87, 1·67 and 1·5 respectively) still to be repeated. The results of measurements made in these cases are plotted as open circles in Fig. 6 right.) Small differences between the point of subjective equality and wave-length of the surround were sometimes found (as in the illustrated case) but these were never large or systematic.

The psychometric functions in these experiments are defined over the wave-length axis. The index of discriminability of λ from $\bar{\lambda}$ is the expected frequency with which the variable wave-length λ is perceived as longer (or shorter) in wave-length than $\bar{\lambda}$. We determined the psychometric functions for spectral lights of equal brightness, and from them calculated the $\Delta\lambda$s, assuming that across the spectrum equal values of the discrimination index correspond to equal differences in perceived hue. In computing these $\Delta\lambda$s each psychometric function was assumed to be the ogive of a normal distribution. The mean of the normal distribution underlying each psychometric function was assumed to be known precisely while the variance was the unknown to be estimated.

The maximum likelihood estimate of the variance at each $\bar{\lambda}$ was obtained from the results of six staircases. The normality assumption was inspected by rescaling all the obtained psychometric functions by the corresponding inverse of the square root of the estimated variance. According to this assumption the rescaled psychometric functions will all have the same shape, an ogive of unit variance. When functions for a given subject were shifted for coincidence at the 50 % ordinate, the rescaled curves were found to coincide with each other and to a remarkable extent with the expected ogive. This agreement was reassuring validation of the reasonableness of the assumption that, independent of wave-length, the psychometric functions all had the shape of the normal ogive.

W.'s results are shown by the circles to the right in Fig. 6. This Figure depicts (on the logarithmic ordinate scale) the just perceptible change in wave-length (as measured by the standard deviation of the assumed normal distribution) as a function of wave-length (linear scale). *W.*'s surprisingly low thresholds were quite unexpected from previous measurements of this kind on deuteranomalous (Nelson, 1938) and on normals as well. To emphasize this a brief review of previous measurements on normal subjects has also been summarized in Fig. 6 (on the left).

This (representative, rather than exhaustive) survey includes results from the five subjects of Wright & Pitt (1934), the mean curve of Steindler (1906), measurements of Jones (1917), of Laurens and of Hamilton (1923) and the two observers of Bedford & Wyszecki (1958). The mean ± 1 S.E. of mean of these eleven sets of measurements each given equal weight are displayed as open circles enclosed in vertical brackets to the left in the figure. These thresholds are generally higher than those we found on *W.*, a result which could be due, at least in part, to methodological differences. Therefore the experiment was repeated on the two authors each of whom has normal trichromatic vision. The thresholds so obtained are plotted as diamonds and triangles on the left in Fig. 6. Evidently forced choice staircases yield considerably lower thresholds than those obtained by earlier methods whether measured on anomalous, or on normal, trichromats. (The exception to be found in the literature is Lord Rayleigh, 1910, who estimated on the basis of measurement and calculation that his own normal eye could readily distinguish between the lines of the sodium doublet (i.e. 0·6 nm). The triangles and diamonds in Fig. 6 fully confirm his estimation.)

Deuteranomalous *W.*'s sensitivity in the yellow-green ($\lambda \cong 540$ nm) is poorer than it is at longer and shorter wave-lengths. His curve is roughly similar in shape to those of Nelson's (1938) five deuteranomalous: it has a minimum in the blue-green, a maximum in the yellow-green and a secondary minimum of intermediate sensitivity in the orange spectral region. *W.*'s maximum and his minima are generally shifted to shorter wave-lengths in comparison to the average for Nelson's subjects but with

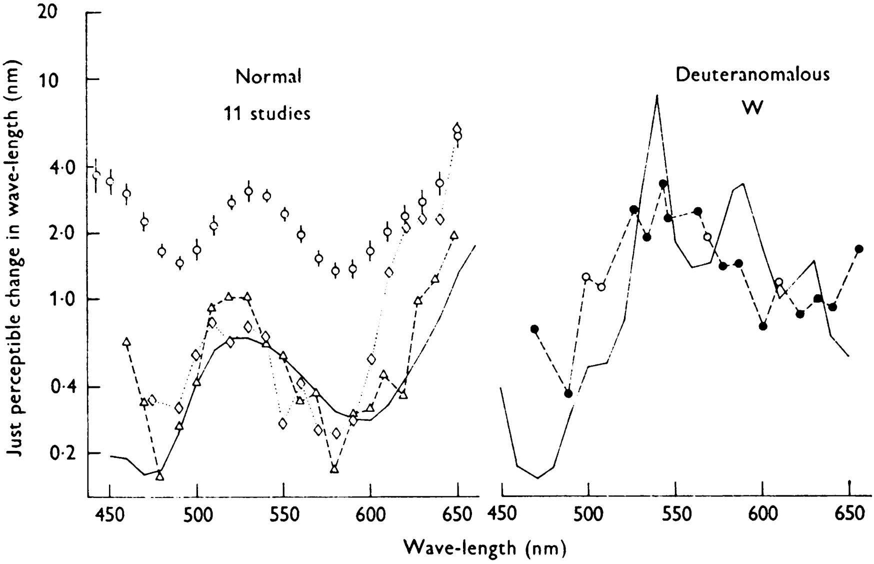

Fig. 6. Wave-length discrimination curves for three subjects in this study and for results found in the literature. Ordinate shows just perceptible changes in wave-length (logarithmic scale) plotted as a function of wave-length. The results in the left column are for normal subjects, those in the right, for deuteranomalous *W*. The left open circles show the mean results of eleven sets of measurements pooled from various literature sources. The triangles and diamonds give measurements on normal subjects J.M. and M.A. respectively. They are reasonably, but imperfectly, described by the continuous line drawn through them, a prediction made by the Stiles (1946) line element for the 10 td level of retinal illuminance with $R(\lambda)$, $G(\lambda)$ and $B(\lambda)$ from Stiles (1939) as modified by Stiles (1946). The circles on the right show the empirical wave-length discrimination results of deuteranomalous *W.*, the solid line is theoretical assuming the $R(\lambda)$ and $G(\lambda)$ curves from the bottom of Fig. 4, and the normalized $\bar{z}$ of the C.I.E. colour matching functions for $B(\lambda)$. Open circles on the right indicate data in which the ratio of standard deviation to step size was slightly larger than the arbitrary limit (1·4) but for which the subject was unavailable to repeat the measurements.

the exception of the maximum at 543 nm (Nelson's range is 560–600 nm) they are within the scatter of individual differences. *W.*'s thresholds, as already mentioned, are lower than those Nelson obtained. This (analogous to what is found with normal subjects) is perhaps attributable to the more refined psychophysical method and is almost certainly wave-length independent. Setting this to one side, the noteworthy characteristic of *W.*'s results compared to those of Nelson's subjects is his remarkable sensitivity at the red end of the spectrum. *W.* is *more sensitive* in this part of the spectrum than normal subjects in a way that not one of Nelson's deuteranomalous was. At least one of Pitt's (1935) deuteranomalous, however, behaved in a similar way.

Analysis

The line element ds of colour space (Stiles, 1946) allows one to calculate the difference of wave-length dλ of two just noticeably different monochromatic patches of light of equal brightness, given the spectral absorbances of the underlying cone visual pigments $R(\lambda)$, $G(\lambda)$ and $B(\lambda)$.

$$\left(\frac{\mathrm{d}s}{\mathrm{d}\lambda}\right)^2 = \left\{\left[(c_\mathrm{r}^2-1)\frac{\mathrm{d}\ln R(\lambda)}{\mathrm{d}\lambda}+c_\mathrm{g}^2\frac{\mathrm{d}\ln G(\lambda)}{\mathrm{d}\lambda}+c_\mathrm{b}^2\frac{\mathrm{d}\ln B(\lambda)}{\mathrm{d}\lambda}\right]^2\left[\frac{R}{\rho}\zeta(R)\right]^2\right.$$
$$+\left[c_\mathrm{r}^2\frac{\mathrm{d}\ln R(\lambda)}{\mathrm{d}\lambda}+(c_\mathrm{g}^2-1)\frac{\mathrm{d}\ln G(\lambda)}{\mathrm{d}\lambda}+c_\mathrm{b}^2\frac{\mathrm{d}\ln B(\lambda)}{\mathrm{d}\lambda}\right]^2\left[\frac{G}{\gamma}\zeta(G)\right]^2$$
$$\left.+\left[c_\mathrm{r}^2\frac{\mathrm{d}\ln R(\lambda)}{\mathrm{d}\lambda}+c_\mathrm{g}^2\frac{\mathrm{d}\ln G(\lambda)}{\mathrm{d}\lambda}+(c_\mathrm{b}^2-1)\frac{\mathrm{d}\ln B(\lambda)}{\mathrm{d}\lambda}\right]^2\left[\frac{B}{\beta}\zeta(B)\right]^2\right\}.$$

In this equation

$$c_\mathrm{r}^2 = \left[\frac{R}{\rho}\zeta(R)\right]^2\Big/\left\{\left[\frac{R}{\rho}\zeta(R)\right]^2+\left[\frac{G}{\gamma}\zeta(G)\right]^2+\left[\frac{B}{\beta}\zeta(B)\right]^2\right\},$$

and c_g^2 and c_b^2 are analogously defined; ρ, γ and β are constants (1·278, 1·646, 7·235 respectively) and $\zeta(R)$, $\zeta(G)$, and $\zeta(B)$ are the increment threshold curves (Stiles, 1939, 1946) for each of the three cone mechanisms.

This equation has been used to determine dλ as a function of λ for the two normal subjects and for deuteranomalous *W.* at 10 td with d$s = 8\,(10)^{-4}$ but no further *ad hoc* adjustments other than the values of the spectra $R(\lambda)$, $G(\lambda)$, $B(\lambda)$ under evaluation. For normals, the spectra employed by Stiles (1946) were assumed. For the deuteranomalous $R(\lambda)$ was the filled circles from the bottom of Fig. 4, $G(\lambda)$ the open circles from the same part of that Figure and $B(\lambda)$ was the normalized C.I.E. blue colour matching function $\bar{z}$.

The results from this analysis are plotted as continuous lines in Fig. 6. The line fits our normal data about as well as Stiles achieved (setting ds = 0·01) in fitting those of Wright & Pitt (1934). In either example the line element prediction indicates more sensitivity in the 'violet' than is measured. This trend is also seen, slightly exaggerated perhaps, in the prediction of *W.*'s judgements in this part of the spectrum. Since the fit in the 'violet' is very sensitive to the assumption about the short-wave action spectrum (of which nothing is known) we are not concerned with it here. Elsewhere in the spectrum the continuous line provides a very jagged approximation to *W.*'s wave-length discrimination. In the red-green part of the spectrum the contribution of the $B(\lambda)$ to discrimination is negligibly small and the line element equation simplifies to

$$\left(\frac{\mathrm{d}s}{\mathrm{d}\lambda}\right)^2 = \frac{\left[\frac{R}{\rho}\zeta(R)\right]^2\left[\frac{G}{\gamma}\zeta(G)\right]^2}{\left[\frac{R}{\rho}\zeta(R)\right]^2+\left[\frac{G}{\gamma}\zeta(G)\right]^2}\cdot\left\{\frac{\mathrm{d}\ln\left[G(\lambda)/R(\lambda)\right]}{\mathrm{d}\lambda}\right\}. \tag{1}$$

Because dλ depends upon

$$\frac{\mathrm{d}\ln\left[G(\lambda)/R(\lambda)\right]}{\mathrm{d}\lambda}$$

a jagged theoretical wave-length discrimination curve is bound to occur when using unsmoothed experimental points. This puts constraints on wave-length discrimination as a test of the accuracy of a given observer's putative $R(\lambda)$ and $G(\lambda)$. Jagged theoretical curves make decisions about the accuracy of prediction difficult, while smoothing risks confusing valid irregularities in the spectra with measurement error. Under these circumstances pressing the curve fitting process further appears unproductive and we have elected not to try to improve the agreement of data and theory by any of a number of smoothing strategies which come to mind.

Although the solid line is not a satisfactory description of *W.*'s wave-length discrimination, given the restrictions imposed by line element theory, the spectra used to generate it cannot be excluded by the admittedly approximate fit. The theory does make one further prediction, which apparatus limitations have not yet allowed us to evaluate: *W.*'s wave-length discrimination for lights one order of magnitude brighter, will show further improvements in the red relative to the rest of the spectrum.

Until such time as this expectation can be explored, three aspects of the present analysis of *W.*'s wave-length discrimination are notable. The assumed spectral distributions alone suffice to predict in at least a rough quantitative way: (i) the measured poorer wave-length discrimination of *W.* in the range $520 \leqslant \lambda \leqslant 630$ when he is compared with two normal subjects studied under identical conditions, (ii) the wave-length of *W.*'s poorest discriminability, and (iii) the *superiority* of *W*.'s wave-length discrimination at the red end of the spectrum when it is compared to that of either normal subject. This last is a very surprising experimental result. The fact that line element theory correctly predicts it, is some justification for continuing to believe that the spectra used to generate the prediction may be on the right lines.

In summary *W*.'s wave-length discrimination is at least consistent with our identification of the spectra of his long and medium wave sensitive cone visual pigments. But the test is by no means strong because of the jagged theoretical prediction so sensitive to

$$\frac{\mathrm{d}\ln[G(\lambda)/R(\lambda)]}{\mathrm{d}\lambda}$$

in Stiles' line element theory, and the results therefore are not very compelling.

Hence it seemed important to obtain a further test of *W*.'s cone spectra which obviated this difficulty. Specifically we sought a measurement of his colour vision in which (i) theory would not require derivatives of the action spectra with respect to wave-length and (ii) the uncertainty of the action spectrum of *W*.'s short wave sensitive cones could not appreciably influence the theoretical predictions in the red-green spectral range. We found it in his step-by-step luminous efficiency curve.

(*c*) *Step-by-step luminous efficiency curves.* The procedure for these measurements was identical to that followed on deuteranopes and described in detail in Part II. The results of the four spectral traverses measured on *W*. on two separate days were analysed separately and the means of the log luminous efficiency ± 1 S.D. are plotted in Fig. 7 after normalizing for minimum scatter.

The retinal illuminance of the test in these experiments was 16 td, i.e. somewhere between the low level asymptote in the Stiles line element which has the form,

$$V_\lambda^2 = C\left\{\left[\frac{R(\lambda)}{\rho}\right]^2 + \left[\frac{G(\lambda)}{\gamma}\right]^2 + \left[\frac{B(\lambda)}{\beta}\right]^2\right\},$$

and the high intensity asymptote,

$$\log(V\lambda) = \left(\frac{1}{\rho}\right)^2 \log[R(\lambda)] + \left(\frac{1}{\gamma}\right)^2 \log[G(\lambda)] + \left(\frac{1}{\beta}\right)^2 \log[B(\lambda)] + k_1.$$

The wave-length independent constants C and k_1 alone are arbitrary. Because we have no certain knowledge of the form of $R(\lambda)$ and $G(\lambda)$ for $\lambda < 520$ nm, the analysis is confined to the red-green part of the spectrum in which case

$$V^2(\lambda) = C\{[R(\lambda)/\rho]^2 + [G(\lambda)/\gamma]^2\},$$

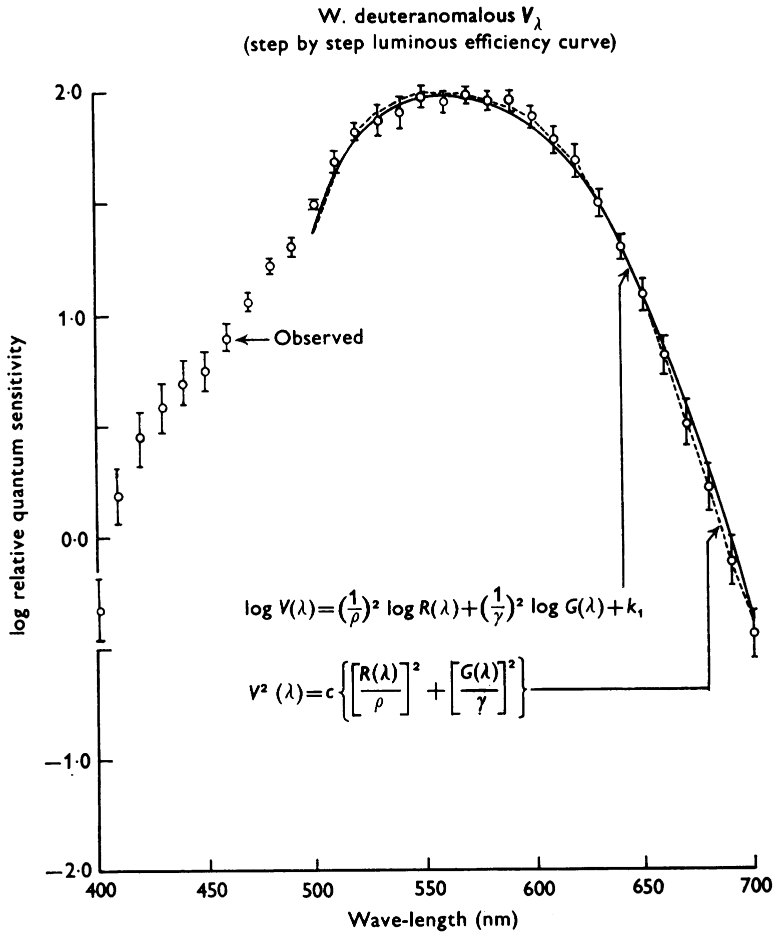

Fig. 7. Small step luminous efficiency curve of deuteranomalous subject *W*. The error bars include the mean ± S.E. of four experimental repetitions on two separate days. The continuous line is theoretical prediction from $R(\lambda)$ and $G(\lambda)$ from the bottom set of points in Fig. 4 from the high intensity asymptote of the Stiles (1946) line element. The interrupted line is the curve predicted from the low intensity asymptote. The actual level (16 td) falls somewhat between these two asymptotes.

and

$$\log V(\lambda) = \left(\frac{1}{\rho}\right)^2 \log [R(\lambda)] + \left(\frac{1}{\gamma}\right)^2 \log [G(\lambda)] + k_1,$$

are reasonable approximations. The line element equation has no formal solution between these two forms, but the discrepancies in predictions are so small it was unnecessary to obtain the exact curve. Instead in Fig. 7 predictions from the two asymptotic equations are plotted (the high level asymptote with a continuous, the low level with an interrupted line), and the reader may see for himself the course a curve somewhere between would follow. The agreement is good enough to substantiate the identification of *W.*'s long and medium wave sensitive cone action spectra, in the red-green spectral range.

DISCUSSION

In two previous papers (Alpern & Wake, 1977; Alpern & Pugh, 1977) the concept of a single erythrolabe common to all deuteranopes and to the long wave sensitive cones of all normals was rejected. A distribution of long wave sensitive cone visual pigments was found only one of which was common to long wave sensitive cones of a given normal. While the evidence on the middle wave sensitive cone pigment of protanopes is less certain, preliminary measurements (B. Bastian, unpublished) indicate that chlorolabe spectra are analogously distributed (nothing is known about the short wave sensitive cone visual pigment cyanolabe; even whether or not it is absent in tritanopia is uncertain (Alpern, 1976)). A normal trichromat in this new view is an observer whose long wave sensitive cone visual pigment has an action spectrum from among the erythrolabe cluster and whose middle wave-length cones have a spectrum from among the chlorolabe cluster (leaving open the question of a cyanolabe cluster).

The present study shows: the action spectrum of the medium, as well as the long, wave sensitive cones of one deuteranomalous may each be identical with that of the long wave sensitive cones of different deuteranopes. These spectra differ in peak wave-length and in shape in a way consistent with this deuteranomalous' colour matches and luminosity curve and not inconsistent at least, with his wave-length discrimination. Hence, the visual pigments in this deuteranomalous' medium and his long wave sensitive cones are both from the same (erythrolabe) cluster. This is quite different from the usual view that deuteranomalous have two (i.e. cyanolabe and erythrolabe) 'normal' and one (the deutanolabe of Piantanida & Sperling, 1973) 'abnormal' cone pigments.

Does a similar situation describe all four varieties of red-green defective colour vision transmitted recessively on the X chromosome? Are the visual pigments of both the long, and the medium, wave-length sensitive cones of all deutans to be found somewhere in the erythrolabe cluster and those of all protans in the chlorolabe cluster? Are red-green dichromats merely deutans (or protans) in whom the long wave-length cones have the same pigment as the medium wave-length cones and anomalous trichromats subjects in whom the spectra of these pigments (always from the same cluster) differ, if only ever so slightly?

Such speculations transcend the data by a good margin and we would hesitate to present them were they not sensitive to straightforward testing. In particular they suggest a way of dealing with one aspect of abnormal colour vision which the usual theoretical frames either ignore or treat in terms that defy experimental exclusion. Measurements on deuteranomalous (Pitt, 1935; Nelson, 1938) and protanomalous (McKeon & Wright, 1940) subjects emphasize that within each of these anomalous groups are individuals with widely different wave-length discrimination abilities. The colour matching functions in Fig. 1 exclude the possibility that all deuteranomalous have cone visual pigments with identical action spectra. The suggestion that two deuteranomalous differ from each other because their long (and their medium) wave-length cone visual pigments are represented by different members of the erythrolabe cluster leads to the expectation that their wave-length discrimination curves will differ in a manner not unlike that actually found by Pitt (1935) and Nelson (1938). It is, for example, not too difficult to find other pairs of deuteranopes whose long wave sensitive foveal cone action spectra when used respectively as $R(\lambda)$ and $G(\lambda)$ in eqn. (1) roughly predict the wave-length discrimination of one or the other of these deuteranomalous subjects with no reference to 'nerve connexions' as required in other theories (for example, Hurvich & Jameson, 1956). Though the fits are still relatively crude, the idea has the advantage of explaining individual colour vision differences on the basis of action spectra differences alone. Whether this simplification will survive a more rigorous analysis of individual differences in deuteranomalous colour vision remains to be shown.

The suggestion that dichromats have long and medium wave sensitive cones with the same visual pigment is not new. It was made in the same form that the present results have led us, by von Helmholtz (1896) and it is one interpretation (Hecht & Hsia, 1947; Walls & Mathews, 1952) of the 'fusion' hypothesis of Fick (1879) and Leber (1873). Without a pedantic discussion as to what Fick and Leber may, or may not, have meant, it is important to distinguish between this variant of the fusion hypothesis and one proposing a fusion of the red and green signals in a dichromat having all three normal cone pigments (Wyszecki & Stiles, 1967). Modern retinal densitometric analysis (Rushton, 1965; Mitchell & Rushton, 1971*a*; Alpern & Wake, 1977) shows no evidence of two red-green photolabile pigments in the foveas of deuteranopes in the way predicted by the latter version of 'fusion'; but expectation of the former (abnormally high amount of long wave pigment in deuteranopes) has yet to come to crucial densitometric test. Using flicker photometry to assess the spectral sensitivity of the long wave cones (King-Smith, 1973*a*, *b*) is reasonable enough for deuteranopes, but not for the normals with whom they must be compared. The difficulty (accurate assessment of the fraction of stray light entering into the measurements in the normal and deuteranope being compared) is formidable, but not insurmountable, and the matter remains open.

This form of fusion was rejected by Hecht & Hsia (1947) who expected it to result in no over-all loss of luminosity in deuteranopia. They found, instead, that deuteranopes' spectral sensitivity at foveal threshold was reduced by 40% compared to normal. Walls (1958) criticized this on the grounds that foveal absolute threshold was not a valid measure of 'luminosity' and cited Heath's (1958) critical flicker study on six deuteranopes in support of the position that deuteranopes show, not losses, but gains, in photopic 'luminosity'. To modern readers both ignore the crucial issues, namely, the validity of the assumptions which underlie the theoretical views of luminosity and the way one is led from them to an exact expectation as to how photopic luminosity (however operationally defined) is to be altered in this variant of the fusion hypothesis. In summary, an adequate psychophysical test of these ideas on dichromats awaits, if not a more rigorous theory of the physiology of luminosity, then at least an explicit theory of the relation between the number of cones in a given receptive field all with the same pigment and say, the intensity required for threshold flicker detection at a given wave-length.

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