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CLASSICAL TRITANOPIA

BY M. ALPERN, K. KITAHARA* AND D. H. KRANTZ
From the Vision Research Laboratory and the Department of Psychology, University of Michigan, Ann Arbor, MI 48109, U.S.A.

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SUMMARY

1. A subject who has suffered from central serous chorio-retinopathy in his left eye noticed differences in the colour of a given light as perceived by each eye alone. Standard screening tests (colour order and colour matching) indicated a tritan defect in the left eye; the right eye was normal on these tests.

2. The subject was dichromatic in his left eye, trichromatic in his right. The left-eye distimulus colour-matching functions, spectral luminosity, and wave-length discrimination functions were indistinguishable from corresponding data for congenital tritanopia. Comparable right-eye data were normal.

3. Spectral dichromatic colour matches were invariant under changes of intensity and under addition of a common light to both halves of the field. (Grassmann's laws of linearity are satisfied.)

4. Increment threshold *versus* intensity (t.v.i.) curves for a blue (481·9 nm) test on a yellow background yielded the normal three branches (for $\Pi_4(\mu)$, $\Pi_1(\mu)$ and $\Pi_3(\mu)$ respectively) in the trichromatic eye. In the dichromatic eye a single mechanism was found. It had the field sensitivity of $\Pi_4(\mu)$ whether measured with the blue, or with a violet (429·5 nm) test. No trace of $\Pi_3(\mu)$ or $\Pi_1(\mu)$ was ever discovered in the tritanopic eye. Both are normal in the trichromatic eye.

5. The field sensitivities of Π_4, Π_5 and Π_3 of the normal eye are well fitted by linear combinations of the spectral colour-matching functions of the trichromatic eye. Π_4 and Π_5 of the dichromatic eye are well fitted by linear combinations of the tritanopic matching functions.

6. Colour matches made by the trichromatic eye do not match when viewed by the tritanopic eye, almost certainly because the ocular media of the two eyes have wave-length-dependent differences in absorption. For the largest difference (430 nm) the trichromatic eye transmits about 2·2 times more light than its fellow. When allowance is made for these differences, the field sensitivities of Π_4 and Π_5 of the two eyes do not differ. The field sensitivities of Π_4 and Π_5 of the normal eye, on the other hand, differ significantly from those of the average spectra obtained on four normal trichromats by Stiles, in a way that cannot be attributed to differences in transmittance of ocular media.

7. It is concluded that classical (or acquired) tritanopia is not distinguishable in its

* Present address: Department of Ophthalmology, Jikei University School of Medicine, 3-19-18 Nishishinbashi, Mimato-ku, Tokyo, Japan.

manifestations from congenital tritanopia; furthermore, tritanopia can be regarded as a reduced form of normal trichromacy, once allowances are made for absorption of the ocular media and for variations among normal trichromats.

8. Despite extensive search no evidence could be uncovered which might exclude the hypothesis that the colour vision in tritanopia depends exclusively upon absorption in only two foveal cone pigments, one long-wave-absorbing and one medium-wave-absorbing.

INTRODUCTION

It is often assumed, following a suggestion first made by Thomas Young (1807), that each of the three main kinds of dichromacy (protanopia, deuteranopia and tritanopia) arises from the absence of one of three cone photopigments hypothesized to be present in the normal trichromatic eye. This assumption has served both as a starting point for attempts to understand the colour perception of dichromats (Fick, 1873; von Helmholtz, 1896; Hecht & Hsia, 1947; Walls & Mathews, 1952; Walls, 1955) and as a tool for deducing the absorption spectra of the photopigments in normal colour vision (Maxwell, 1860; Koening & Dieterici, 1886; Wyszecki & Stiles, 1967; Vos & Walraven, 1970).

For the two forms of congenital red–green dichromacy, protanopia and deuteranopia, there is now good evidence that the above assumption is correct: protanopes lack a long-wave-sensitive cone visual pigment and deuteranopes a middle-wave pigment. This evidence comes from spectroscopic measurements of photopigments in dichromats, using retinal densitometry (Rushton, 1963, 1965; Mitchell & Rushton, 1971; Alpern, 1974; Alpern & Wake, 1977).

Similar evidence is lacking for the third main kind of dichromacy, tritanopia. Retinal densitometry is not sufficiently sensitive to detect a short-wave photopigment in the normal eye; and so the absence of such a pigment cannot be demonstrated spectroscopically in tritanopes.

Densitometer imperfection is by no means the only obstacle to the understanding of tritanopia. A second is the relative rarity of the condition. The first, and for over a half century the only, careful study of such observers with narrow-band spectral stimuli was done on nine patients whose acquired tritanopia was secondary to one retinal abnormality or another (Koenig, 1897). This was called *classical* tritanopia by Judd, Plaza & Farnsworth (1950). Indeed, until recently (Smith, Cole & Isaacs, 1973; Neuhan, Kalmus & Jaeger, 1976) it was arguable (Krill, Smith & Pokorny, 1970, 1971) that there is no other kind, although descriptions of presumed *congenital* tritanopia began to trickle into the literature about thirty years ago (Fischer, Bouman & ten Doesschate, 1951; Wright, 1952; Sperling, 1960; Cole, Henry & Nathan, 1965; Wald, 1966; Voke-Fletcher & Fletcher, 1978). It has been estimated (Wright, 1952) that one congenital tritanope is to be found among 13000 to 65000 British people.

An important question is whether tritanopia is a *reduced* form of normal trichromacy, that is, whether the metameric matches made by normal trichromats are accepted by tritanopes as well. If so, then it is probably safe to assume that the only cone pigments involved in tritanopic colour vision are ones also found in normal colour vision. Two of the tritanope's cone pigments could then be assumed to coincide with the normal middle- and long-wave pigments (since tritanopic colour discrimation is excellent in the middle to long wave-lengths). Either these would be the only two, or the normal short-wave pigment might also be present, in which case the loss of one degree of freedom would occur by convergence of quantal absorptions (or of their signals) from three pigments into only two receptor or post-receptor channels. Clearly, evaluation of the hypothesis of reduction dichromacy is a reasonable first step.

Such an evaluation inevitably confronts the difficulty that 'normal trichromacy' is only a convenient idealization. Substantial individual differences exist among normal colour matches. The best way to test the hypothesis of reduction dichromacy is to measure the spectral colour-matching functions of the dichromat and to attempt to express these as linear combinations of trichromatic spectral colour-matching functions, for an average trichromat, or for a trichromat in the 'normal range'. Koenig performed a test of this sort, and concluded that the hypothesis of reduction dichromacy could not be rejected. It is true that his data do not reject the hypothesis, but neither are they precise enough to accept it with any confidence.

One of us (Alpern, 1976) reanalysed the colour-matching functions of the congenital tritanopes published by Wright, by Fischer *et al.* and by Sperling, and showed that matches of any one of these observers could not be linear transformations of the matching functions of the average normal trichromat (defined either by the 1931 C.I.E. standard observer or by the modification of it proposed by Judd, 1951). The discrepancies are not such as can be accounted for by differences in fixed preretinal filters (e.g. differential absorption of the lens or macula pigment). Though they differ significantly from reduction dichromacies based on the standard observer, these dichromats might well be reductions from some other trichromat, or trichromats, in the normal range (Estévez, 1979).

A student of this literature is left with a variety of unanswered questions:

1. How alike are the colour visions of the two kinds of tritanopia, Koenig's classical tritanopia and the congenital tritanopia studied since by various authors (perhaps most thoroughly, and certainly in the largest number, by Wright, 1952)?

2. Is either class of tritanopia a reduction dichromacy? (One needs both to confirm the fact of *di*chromacy – a fact which may be doubted for various forms of 'tritanopia' induced in normal vision, e.g. 'small-field tritanopia' or 'transient tritanopia' – and to investigate whether the matches are reduced forms of normal trichromatic matching.)

3. Is there evidence for a mechanism with short-wave spectral sensitivity in the tritanopic eye? Can the presence of three functional cone types, with independent photopigment absorptions, be excluded?

The opportunity to deal with these questions occurred in the autumn of 1977 when a graduate student in experimental psychology appeared in the laboratory, curious about the difference in the colours as seen by his two eyes. A detailed report of ophthalmological examinations is presented in the Appendix. In brief, he is a 26-year-old white male with no previous history of visual abnormality, who, 2 years before, had an acute episode of central serous chorio-retinopathy (involving inflammation and shallow central retinal detachment) in his left eye. No treatment was initiated. Over a course of weeks the symptoms subsided, leaving visual acuity

(Snellen chart) normal in both eyes. Visual-field tests with a small red test object, however, showed a continued relative central scotoma in his left eye, about 4° horizontal by 8° vertical. Difference in the colours perceived by his two eyes are reported in detail by Alpern, Kitahara & Krantz (1983).

The present paper consists of four parts. In Part I we present the results of diagnostic tests, which established tentatively that the observer is a (classical) tritanope for vision through his left eye and a normal trichromat with his right eye. Part II confirms this diagnosis by presenting dichromatic and trichromatic spectral colour-matching functions, respectively, for his left and right eyes, and then tackles question 1 above, by comparing the colour matching, spectral luminosity, and wave-length discrimination functions of this classical tritanope with the similar measurements made on Wright's congenital tritanopes. Part III describes attempts to answer question 3 above. We tried to find evidence for three functional cone photopigments in the tritanopic eye using two different approaches: increment threshold measurements on adapting backgrounds, and tests of Grassmann's additivity and scalar multiplication laws for colour matching. Both Parts II and III also present results of various analogous observations on the right eye, showing the normalcy of that eye. Finally, Part IV addresses the question of reduction dichromacy (question 2 above), taking advantage of the trichromacy of the right eye to ask whether the distimulus colour space of the left eye can be viewed as a reduction of the approximately normal tristimulus representation of the right eye. Because of the likelihood of different preretinal wave-length selectivity in the two eyes, we approach this problem via transformations of colour-matching data to field-sensitivity action spectra, using results of Part III.

METHODS

Measurements were made with monochromatic as well as with broad-band lights, many of them on apparatuses described elsewhere (Alpern, Bastian, Pugh & Gras, 1976; Alpern & Moeller, 1977: Alpern & Pugh, 1977; Alpern & Zwas, 1979). The details of design, calibration and procedure, wherever they can be found in these publications, are not repeated here. Those which were uniquely arranged for the present work are described in the appropriate part of this and the following paper just before the description of the data they yield. These experiments were carried out with the informed consent of the subject after approval of the University of Michigan Hospital Committee to Review Grants for Clinical Research and Investigation involving Human Beings, following guidelines set down by the National Institute of Health.

Part I: establishing the diagnosis

Two tests based on ordering of coloured samples (the Farnsworth–Munsell (F–M) 100-Hue and Dichotomous tests: Farnsworth, 1943) and two colour-matching tests (the Rayleigh match, using a Nagel (1907) Model I anomaloscope; and the neutral point) were used to establish the diagnosis.

Farnsworth tests

The results of these standard tests are shown in Fig. 1 (normal eye on the right, abnormal on the left; dichotomous results below, F–M 100-Hue above). The superb performance of the right eye on the latter (total error score is 16) is strong, presumptive evidence for normal colour vision with this eye. On the other hand, both the Dichotomous and the 100-Hue results on the left eye show characteristic tritan-like errors (Kitahara, 1936; Farnsworth, 1943: Judd *et al.* 1950).

Neutral point

A neutral point in the spectrum was measured for the left eye by matching a monochromatic field to the white of the xenon light source in the apparatus of Alpern

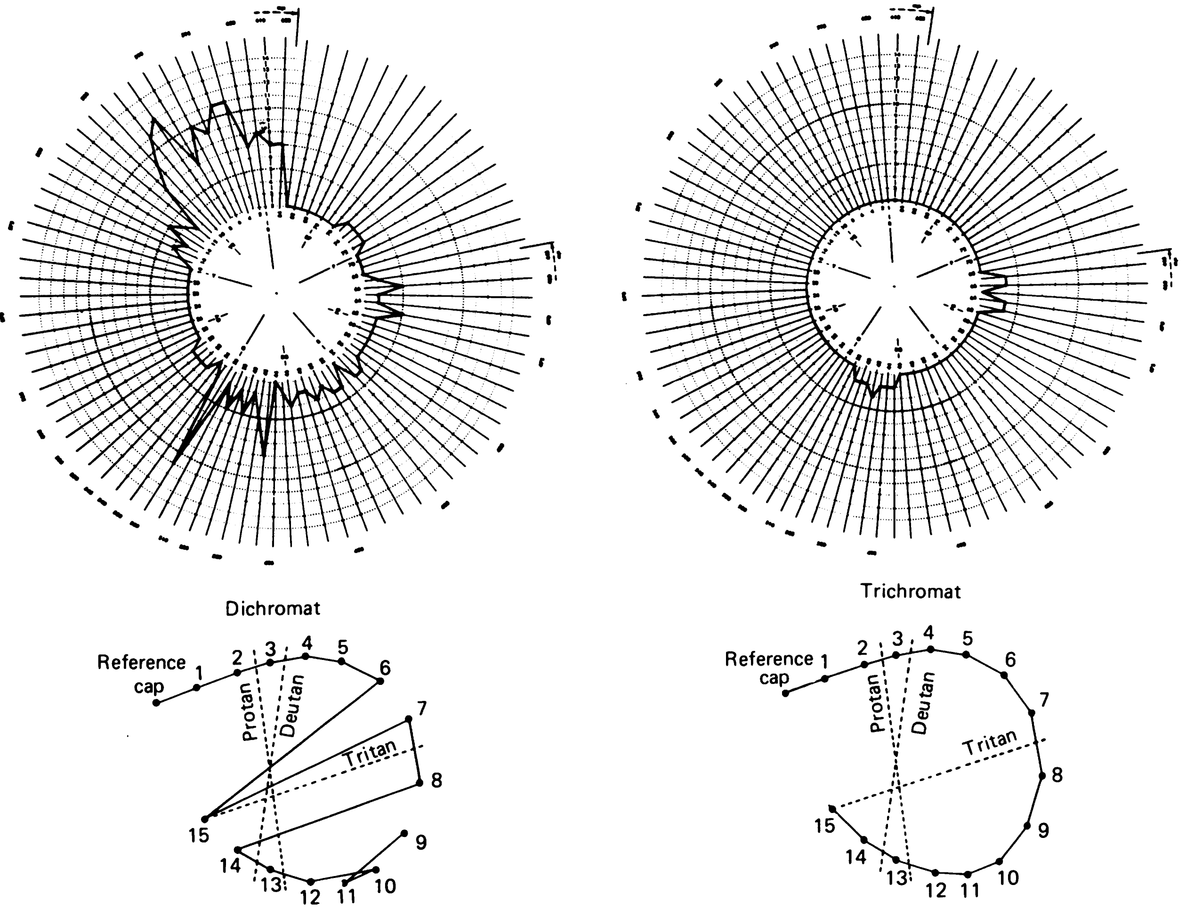

Fig. 1. Results of the Farnsworth–Munsell 100-Hue test (above) and Farnsworth Dichotomous (Panel D-15) test (below) applied to the normal eye (on the right) and to the tritanopic eye (on the left).

& Pugh (1977), the colour temperature of which was about 5200 K. On initial test the measurement yielded $\lambda_n = 563{\cdot}1$ nm; a repetition 3 days later gave $\lambda_n = 567{\cdot}5 \pm 0{\cdot}5$ nm. A second neutral point was systematically – and unsuccessfully – sought in the blue and violet end of the spectrum. The result of this test together with those shown in Fig. 1 established the tentative diagnosis for the left eye as classical tritanopia. The 'tentative' qualification was withdrawn once dichromatic colour-matching functions (see below) were established for this eye.

Nagel anomaloscope

Central serous chorio-retinopathy characteristically shows protanomalous Rayleigh matches, which becomes progressively more severe with deterioration of the condition (Kitahara, 1936; Jaeger & Noyer, 1951). The anomaloscope matches for the right eye gave (as fraction of red in the red–green mixture) $\alpha_R = 0{\cdot}522 \pm 0{\cdot}028$ (middle value ± increments to the extremes of acceptable matches) and for the left $\alpha_L = 0{\cdot}556 \pm 0.028$. Both are within the normal range of 0·4–0·6 though slightly off in the 'protan' direction from the expected middle value of 0·5 – more so in the left than the right eye.

Part II: does classical tritanopia differ from congenital tritanopia?

In this section the results of more detailed tests of the colour vision in the left and right eyes of this observer are described. Three sets of measurements are reported: spectral colour matching, step-by-step luminosity, and wave-length discrimination. Data obtained on the left eye are compared with Wright's results from similar experiments on congenital tritanopes, and those from the right eye with results on normal trichromats. It is inferred that, from data on his left eye, this observer could not be distinguished from a congenital tritanope, while as regards his right eye he falls in the range of normal trichromats.

Spectral colour matching

A *dichromat* by definition matches every foveally presented test light by adjusting the intensities of only two (rather than three) primaries (on occasion, one of the two primaries may be needed as a test desaturant). The intensities required define the *distimulus values* for the given light, relative to the two primaries selected. Dichromacy of the observer's left eye was tested by matching a series of spectral lights (about every 10 nm) with mixtures of 444·5 nm and 650·0 nm primaries. Note that this constitutes a reasonably thorough test of dichromacy, although the test was not extended to include non-spectral lights. For the right eye, a third primary (550·0 nm) was added; matches were made to the same series of spectral lights, obtaining tristimulus values.

The apparatus, matching procedures, and calibrations are described in detail by Alpern *et al.* (1976). Colour matches were made between a 1° central disk and a contiguous annular surround with 3° outside diameter. The spectral test (from a double monochromator, 2 nm half-band width (h.w.)) filled the 1° disk. Primaries were at 444·5 nm, 650·0 nm (and 550·0 nm for tristimulus matches) obtained with interference filters (10 nm h.w.). For the right-eye tristimulus matches, two of the primaries were almost always mixed in the annular surround while the third was added to the central test. The observer adjusted the intensities of these three lights to obtain a match. For left-eye distimulus matches, at most wave-lengths, the two primaries were mixed in the surround and their intensities adjusted to match the central test. (For test wave-lengths at 450·0 nm and 460·0 nm, it was usually necessary to add the 650·0 nm primary to desaturate the test in the centre, with only 444·5 nm in the surround.)

For the left eye, precise and fully satisfactory distimulus matches were possible for every test wave-length. Evidently the observer's left eye is dichromatic. For the right eye, precise and satisfactory matches required three primaries for all wave-lengths less than 550·0 nm; therefore, this eye is trichromatic.

The distimulus (or tristimulus) values were converted to an equal-photon spectrum by computing the ratio of photons $sec^{-1} deg^{-2}$ for each of the two (or three) primaries to the photons $sec^{-1} deg^{-2}$ of the test wave-length in a match. The results

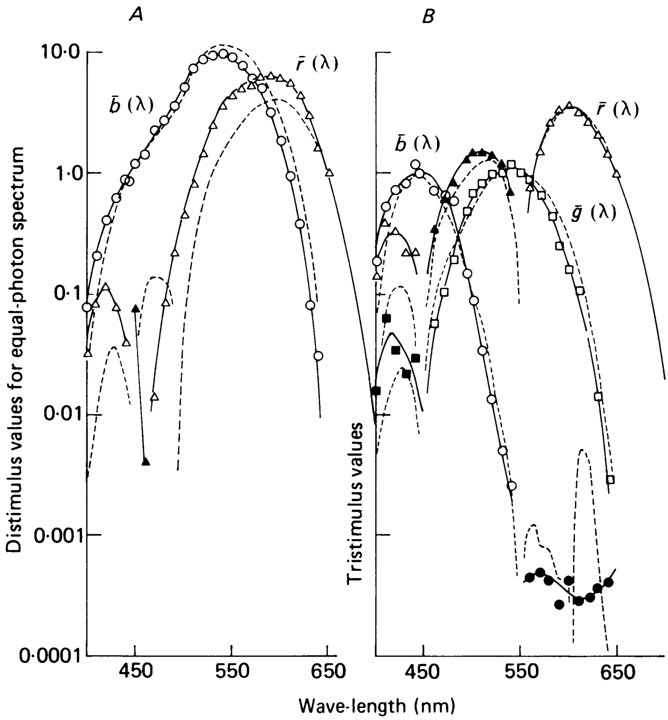

Fig. 2. Maximum-saturation spectral colour-matching functions for the dichromatic eye (*A*) and for the normal eye (*B*). In *A* all lights were matched with only two spectral primaries. The amount of the 'red' (650 nm) primary is shown by the triangles, the amount of the 'blue' (444·5 nm) by the circles (equal-photon spectrum). Continuous curves are smoothed 'eye fits' to illustrate the measurement trends. The dashed lines show the expectation if the vision of this defective eye were a reduced form of the normal colour vision of the C.I.E. standard observer. The tritanopic confusion locus on the C.I.E. chromaticity diagrams ($x = 0{\cdot}17138$, $y = -0{\cdot}01933$) was determined from these matches and the expected colour-matching functions calculated from those of the standard observer in the way described in detail by Alpern (1976). In *B* three primaries were required to match the range of spectral lights. The amounts of the primaries are shown for 'red' (650 nm) by triangles, for 'green' (550 nm) by squares, and for 'blue' (444·5 nm) by circles. Continuous curves are smooth 'eye fits' to the results; the dashed curves show the average of the ten subjects of Stiles & Burch's (1955) 2° test field 'quantized' and transformed to the present reference primaries. Filled symbols illustrate measurements in which the designated reference primary was used as a desaturant. Each plotted point is the mean of two experimental measurements obtained in different sessions on different days.

(average of two measurements on separate days) are plotted on a logarithmic ordinate scale as a function of wave-length in Fig. 2*A* for the dichromatic eye and in Fig. 2*B* for the trichromatic eye. Open symbols represent positive amounts of a given primary, filled ones represent the absolute values of negative amounts (i.e. with the primary used as a test desaturant). Triangles denote the 650·0 nm distimulus (or tristimulus) values, squares 550·0 nm, and circles 444·5 nm. In Fig. 2*B*, exactly one tristimulus value is negative (filled symbols) in each wave-length region. In Fig. 2*A*, the co-ordinates are everywhere positive except at 450 nm and 460 nm, where the filled triangles show the negative 650 nm distimulus value.

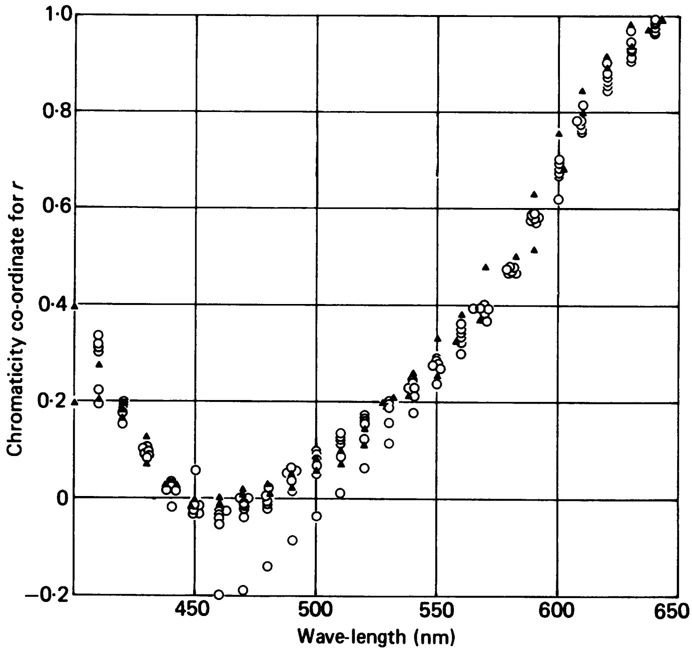

Fig. 3. Spectral chromaticity co-ordinates for dichromatic matches of tritanopic eyes for the long-wave reference primary (*r*: 650·0 nm) in the W.D.W. chromaticity chart (normalized at 582·5 nm) with the system of reference primaries used to obtain the results in Fig. 2. Open circles are individual results from the six tritanopes of Wright (1952) transformed to this set of reference primaries. The filled triangles are results obtained on the dichromatic eye of the present observer; each plotted point is the result obtained in one of the two experimental measurements made on different days.

The continuous curves drawn through these results are smoothed curves drawn by eye, constrained to pass through 1·0 at the wave-length isomeric to the given primary and through 0·0 (off the paper in this case since the ordinate scale is logarithmic) at the wave-lengths of the other primary(ies).

The dashed curves in Fig. 2*B* confirm the fact that the trichromatic matches of this observer's right eye are typical of normal observers. These dashed curves are average results on ten subjects (mean age 31) from Stiles & Burch's (1955) measurements for a 2° field, transformed to the present reference primaries and converted to an equal-photon spectrum. The disagreements are of the same order found when the matches of two different trichromats are compared (Alpern *et al.* 1976). (The logarithmic scale magnifies the discrepancies for the negative 'red' primary in the short wave-lengths and the negative 'blue' in long wave-lengths; both these measurements are very noisy on a logarithmic scale, since small, almost trivial, intensities of the negative primary are used and their admixture does not affect colour appearance very much.)

The results in Fig. 2*A* are typical for tritanopia, in that the short-wave primary is needed throughout the spectrum, including the 550–650 nm region, and the long-wave co-ordinate has a second major positive phase in the short-wave end of the spectrum. These characteristics are better depicted by a plot of the chromaticity co-ordinate for the long-wave primary, which is shown as the filled triangles in Fig. 3. (The open circles in Fig. 3 are analogous results for Wright's six congenital tritanopes, plotted for comparison.) This co-ordinate is calculated by adjusting the units of the distimulus values separately for each observer so that they are equal at some reference wave-length (582·5 nm for both Wright's data and ours) and then taking the ratio of the long-wave co-ordinate to the sum of both co-ordinates. The two filled triangles at each abscissa represent the results of the matches on two separate days. The observer made a match at 582·5 nm on each day, and the normalization of units forces the co-ordinate to be exactly 0·50 there, so only one triangle is shown. (The co-ordinate is also normalized to be 0 at 444·5 nm, where only the short-wave primary is used for an isomeric match, and to be unity at 650·0 nm where both fields are also identical; these points are not plotted.)

For a protanope or a deuteranope, a comparable graph would be nearly flat at 1·0 from 650 nm to 550 nm (where the matching is essentially monochromatic), would drop monotonically to 0 at the wave-length of the short-wave primary, and would continue monotonically downwards (increasing proportions of negative red primary) all the way to 400 nm. This observer, however, is dichromatic in every wave-length region and requires increasing proportions of *positive* red primary as 400 nm is approached; in fact, each wave-length from 400 nm to 450 nm has the same chromaticity co-ordinate as some wave-length in the 455–555 nm range; such corresponding wave-length pairs can be matched exactly in colour by adjusting their relative intensities. This characteristic tritanopic feature is precisely what Wright found in six congenital tritanopes, whose comparable data are shown by the open circles. (In Part III, these pairs of metameric wave-lengths are used to provide a simple test of Grassmann's additivity law.)

Evidently, if this classical tritanope had appeared in the survey of congenital tritanopes undertaken by Wright, he would have been indistinguishable from that group on the basis of left-eye colour matching.

In Part IV the quantitative relation between the right-eye and left-eye colour matches is discussed, with regard to reduction dichromacy. At this point, however, the distimulus colour matches can profitably be compared with the tristimulus matches of the C.I.E. standard observer.

This can be done by plotting tritanopic colour matches on a chromaticity chart, connecting points which match with straight lines. The hypothesis of reduction dichromacy means that such lines should be concurrent in a point, the 'tritanopic confusion locus'. The usual procedure (Thomson & Wright, 1953; Sperling, 1960; Alpern, 1976) is to identify from the plots of chromaticity co-ordinates (Fig. 3) pairs of wave-lengths – one on the long-wave, the other on the short-wave side of 450 nm – which have identical tritanopic chromaticities. Five such pairs were identified and following the method outlined by Alpern (1976) (which employed the C.I.E. chromaticity diagram) eight estimates of the confusion locus were obtained from the points of intersection of the five lines connecting the various matched pairs. (The results differ in detail but the essential conclusions are unchanged if the analysis is pursued on the Stiles & Burch (1955) chromaticity diagram.)

The average of these eight estimates ($x = 0{\cdot}1714$, $y = -0{\cdot}0193$) was used to generate predicted distimulus matches shown as the dashed lines in Fig. 2*A*. The failure of the prediction is obvious. The confusion lines deviate systematically from the estimated point of concurrence (this is even more obvious when the confusion lines connecting long-wave-length test fields with their two-primary matches are graphed) and this non-concurrence shows up in the systematic deviation of the continuous from the dashed lines in Fig. 2*A*. Thus the vision of this classical tritanope cannot be regarded as a simple reduced form of that of the average observer (as represented by the C.I.E. standard observer). Similar results were found for congenital tritanopes (Alpern, 1976). But such deviations could be due to variations like those of individual normal trichromats from this average normal observer (Estévez, 1979).

Wright studied two other aspects of tritanopia: spectral luminosity and wave-length discrimination. The extent to which the colour vision of classical tritanopia resembled that of congenital tritanopia in these characteristics was also examined.

Spectral luminosity

The luminosity curve was obtained by the 'step-by-step method' (LeGrand, 1957). The details of the apparatus design, construction and calibration, and of the procedures employed, are described elsewhere (Alpern & Moeller, 1977).

In brief, a 1° monochromatic central disk was matched in 'brightness' to a contiguous annular surround with 3° outside diameter. The surround wave-length distribution was determined by one of twelve narrow-band interference filters, distributed through the spectrum; each central wave-length was quite similar in colour to the two or three nearest surround distributions, so that the small colour difference could be readily ignored. Successive surround distributions were equated in brightness relative to each other by using both a slightly heterochromatic and a nearly homochromatic match to the same central wave-length. The relative spectral luminosity for each central wave-length is the inverse of the photons $\sec^{-1} \deg^{-2}$ required to match this constant brightness level.

The open circles in Fig. 4*A* give results of measurements on the normal eye of this subject while the filled circles illustrate the spectral luminosity of his tritanopic eye. The latter shows a small systematic loss in the short-wave end of the spectrum. Fig. 4*B* shows results obtained by Wright (1952) in congenital tritanopia. The filled circles are the average results from seven dichromats; the open circles are results obtained on Wright's own eye representing normal data with his apparatus and procedures (flicker photometry from 500 nm to the red end of the spectrum and direct matching from 500 nm to the violet spectral extremity). The quantitative similarity between these two comparisons of tritanopic and normal luminosity is clear from Fig. 4*A* and *B*.

It is a mistake to infer that such data necessarily imply the functional (much less the structural) absence of short-wave-sensitive cones in either classical or congenital tritanopia. While it is true that the abnormalities of the tritanopic luminosity curves in Fig. 4 are qualitatively consistent with the 'loss' hypothesis, they are generally

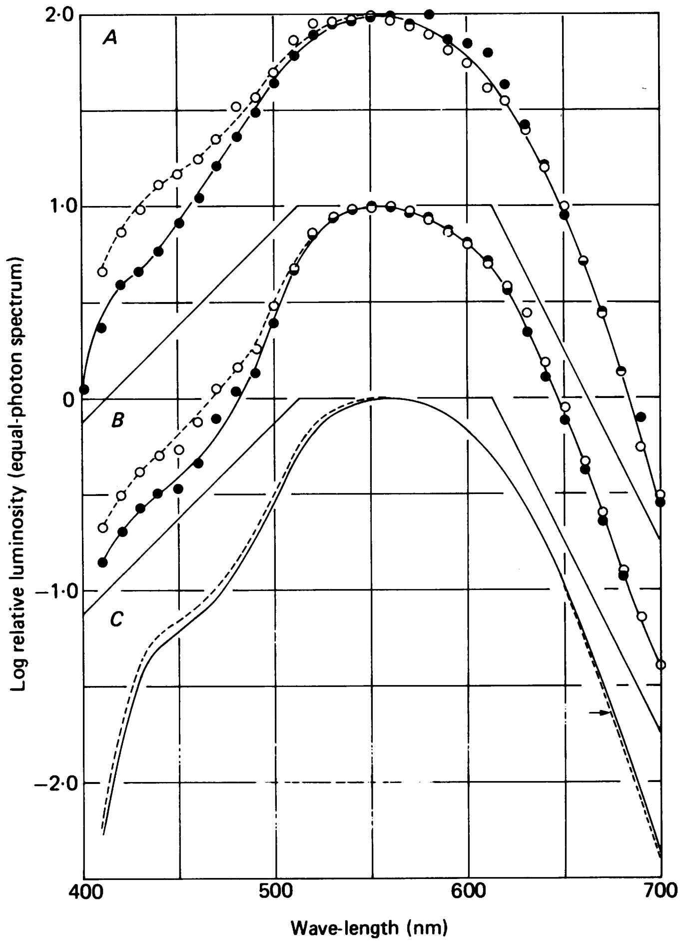

Fig. 4. Relative luminosity curve for spectral lights measured on the fovea and normalized to unity at the peak (555–560 nm). *A*, measurements obtained with the step-by-step method. Filled symbols and the continuous curve show results measured on the dichromatic eye; open symbols and the dashed curve show measurements on the normal eye. *B*, data of Wright (1952). The continuous curve and filled circles show the average of seven tritanopes; the dashed curve and open circles show results on Wright's eye as a representative normal trichromat, following the same procedure on his apparatus. *C*, step-by-step luminosity curves at the high-intensity asymptote predicted from the Stiles line-element using the cone action spectra of Stiles (1946*a*). The dashed curve is the normal (eqn. (21) on p. 52 of Stiles, 1946*a*), the continuous line is the expectation if blue cones were missing in the tritanope retina so that $B(\lambda)$ in that equation is unity.

too large when compared with the discrepancies expected using Stiles' (1946*a*) line-element theory to calculate tritanopic luminosity according to this hypothesis (Fig. 4*C*). Uncertainties about the transmissivities of the media of the eyes concerned, about the absorption spectra of the medium- and long-wave-sensitive cones, the absence of a compelling physiology for line-element theory and the rather low measurement precision all preclude a strong inference of this kind. Instead, it is concluded only that the classical tritanopic eye of this study has an abnormal loss of luminosity in the short-wave part of the spectrum which is similar to the abnormality measured for the 'average' congenital tritanope studied by Wright.

Wave-length discrimination

The final test employed in Wright's study of congenital tritanopia was wave-length discrimination. The apparatus arrangement is shown in Fig. 5*A* of Alpern & Moeller (1977) though the testing procedure was less complex – and briefer – than the one used in that study.

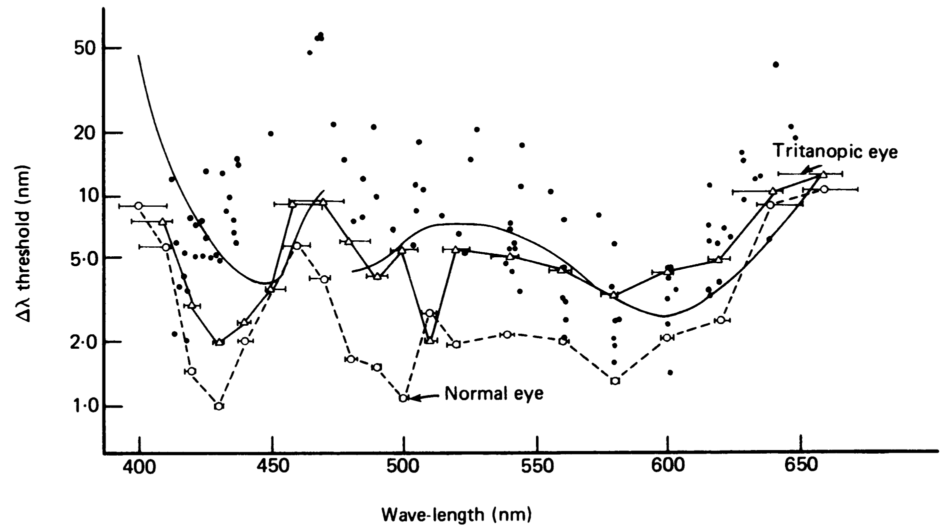

Fig. 5. Wave-length discrimination in tritanopia. Ordinates give thresholds of just-noticeable differences in wave-length (logarithmic scale) as a function of wave-length. Triangles connected by a continuous line give results for the tritanopic eye, circles connected by a dashed line are data obtained with the normal eye. Each of these symbols shows the mean $\Delta\lambda$ plotted at the wave-length of the comparison standard. The horizontal line through it connects the abscissa extremes defined by $\lambda + \Delta\lambda$ (upper) and $\lambda - \Delta\lambda$ (lower) which are marked by small vertical lines. The dots are data obtained on four congenital tritanopes by Wright. The continuous smooth curve is the theoretical prediction of the Stiles (1946*a*) line-element, if short-wave-sensitive cones made no contribution to this discrimination (obtained by setting $B(\lambda) = 1$ in his eqn. 23).

On each trial the experimenter set the wave-length of both the standard and the comparison fields. The observer then adjusted the intensity of the comparison field in an attempt to achieve both a brightness and a colour match. This was almost always possible when the comparison wave-length was identical ('catch' trials), or very close, to the standard wave-length; but when the difference was sufficiently great, the task became impossible. The experimental measurement was the estimated wave-length difference between standard and comparison which would result in report of failure of an exact match on 50% of these adjustment trials. The experimenter first used some large wave-length steps (interspersed with 0 steps, for 'catch' trials) to obtain a rough estimate of the transition from exact match to failure, and then obtained a more exact estimate using comparison wave-length steps of 0·2–0·5 nm.

The comparison field was the 1° central disk, and the standard was the 3° annular surround, as in *B* above; however, in this experiment, both wave-length distributions were controlled by identical Bausch & Lomb double monochromators. The comparison field was fixed at an intensity of 10 trolands above 460 nm, but the maximum intensity available in the apparatus dropped off below 460 nm, down to $4\cdot5\times10^{-3}$ trolands at 400 nm.

For each standard wave-length, estimates were made of $\Delta\lambda$ for comparison wave-lengths both higher and lower than the standard. Both $\Delta\lambda$ estimates were made for one eye, then for the other; then a new standard was introduced, etc. The entire spectrum was traversed in this way in two experimental sessions (each approximately 3 h in duration).

The results are plotted in Fig. 5. The abscissa is the standard wave-length and the ordinate is the mean of the $\Delta\lambda$ estimates in both directions. The asymmetry of these estimates is shown by a horizontal range bar, connecting $\lambda+\Delta\lambda$ (upper) with $\lambda-\Delta\lambda$ (lower). The results for the tritanopic eye are shown as triangles with a continuous line connecting successive values of λ, mean $\Delta\lambda$, while analogous data for the trichromatic eye are plotted as circles connected with a dashed line. The latter are in reasonable accord with previous findings on normal eyes (Alpern & Moeller, 1977) but the maximum at 460 nm suggests somewhat lower sensitivity in this part of the spectrum than is often found. The extent to which this is a functional abnormality, a residual of an old resolved serous detachment of the retinal pigment epithelium barely visible in the ophthalmoscopic examination of this retina (see Appendix) remains undetermined. If so it is the only anomaly of function detectable in exhaustive study of the vision of this eye.

A comparison of the continuous line joining the triangles (threshold wave-length discrimination of the tritanopic eye) and the dashed line (that of the normal eye) in Fig. 5 shows that near the long-wave (650 nm), and again at the short-wave (450–400 nm) spectral extreme, discrimination of the two eyes is about the same. Elsewhere in the spectrum in the blue, green and yellow-green regions (and especially in the spectral range 455–480 nm) the tritanopic eye is conspicuously less sensitive than is the trichromatic eye. (The loss in discrimination at 455–480 nm is even more pronounced if it is compared not with the performance of its trichromatic fellow (which as noted above is also rather poor here) but with that of other normal trichromats (e.g. Alpern & Moeller, 1977) in this spectral region.)

That these anomalies in wave-length discrimination of acquired tritanopia are qualitatively similar to the abnormalities found in congenital tritanopia can be seen by comparing the triangles in Fig. 5 with the black dots in that Figure, the data from the four congenital tritanopes obtained by Wright. These results, too, show fair discrimination in the violet and red parts of the spectrum but even more severe losses in the blue. Measurements on congenital tritanopia by Fischer *et al.* (1951) and more recently by Voke-Fletcher & Fletcher (1978) yielded losses somewhat between the triangles and the black dots in the spectral range 455–480 nm. Smith's (1973) results, on the other hand, with colour naming are even better than those reported here in this part of the spectrum. Part of these differences may be due both to differences in methods and in the subjects' experience as observers at the time measurements were obtained.

The smooth curve in Fig. 5 shows results predicted by Stiles' line-element theory assuming that the short-wave-sensitive cones make no contribution to wave-length discrimination and that the action spectra of the middle- and long-wave cones are those used by Stiles (1946*a*). Following Wright's practice the curve has been interrupted in the range 470–480 nm, indicating that in this spectral range 'there is no perceptible change in appearance' with change in wave-length (W. D. Wright, personal communication).

While the triangles are in reasonable accord with the line-element expectation if short-wave-sensitive cones make no contribution to wave-length discrimination, the dichromatic eye under study here shows considerably better discrimination in the spectral range 450–480 nm than Wright found. Whether this discrepancy is to be explained solely by lack of experience of Wright's subjects remains in question.

Conclusions

With the quantitative (albeit not the qualitative) difference noted in the immediately preceding paragraph as the sole possible exception, the vision of the present subject's left eye cannot be distinguished from the colour vision of congenital tritanopia by any test or combination of tests used in previous studies of tritanopes. The remaining parts of this paper describe studies not previously undertaken in any tritanope, classical or congenital. We adopt the most parsimonious assumption, until further experimental results exclude it, that all tritanopes (classical and congenital) are physiologically the same, without resurrecting the controversy over the aetiology of tritanopia. (The ophthalmological studies of Smith *et al.* (1973) and Neuhan *et al.* (1976) on congenital tritanopes make a convincing case that tritanopia can occur without other retinal or optic nerve pathology.)

Part III: do tritanopes have a short-wave-sensitive cone pigment?

Since the purely chemical methods now available cannot answer the question of whether tritanopes have a short-wave-sensitive cone pigment, one is confined to inferences from psychophysical experiments. The fact that tritanopes' colour matching is dichromatic in the spectral range above 540 nm, where short-wave cones have negligible sensitivity, suggests that they, like colour-normal trichromats, have two different cone pigments with middle-wave to long-wave sensitivity. But it is conceivable that they also have functional cones with a short-wave-sensitive pigment, and that the limitation of their vision to two colour dimensions is based on the convergence of three more or less normal cone outputs into only two neural channels. This would be strongly suggested if there were psychophysical data that could not be accounted for in terms of mechanisms involving just the two pigments with peak sensitivity in the long and middle wave-lengths. This section reports two different attempts to obtain such data: one based on additivity of colour matching and the other based on Stiles' two-colour increment threshold method. The latter also provides the groundwork for a third attempt to reject the two-pigment hypothesis, reported in Part IV. All three attempts turned out negative; we emerge with no grounds for rejecting the view that the short-wave-sensitive pigment is missing in tritanopia.

Grassmann's additivity laws

If dichromatic colour matching is based on just two distinct photopigments, then Grassmann's additivity laws are necessarily valid (for intensities where no appreciable pigment is bleached), regardless of any non-linearities introduced subsequently by neural mechanisms. This is true because any colour match, by hypothesis, is a match

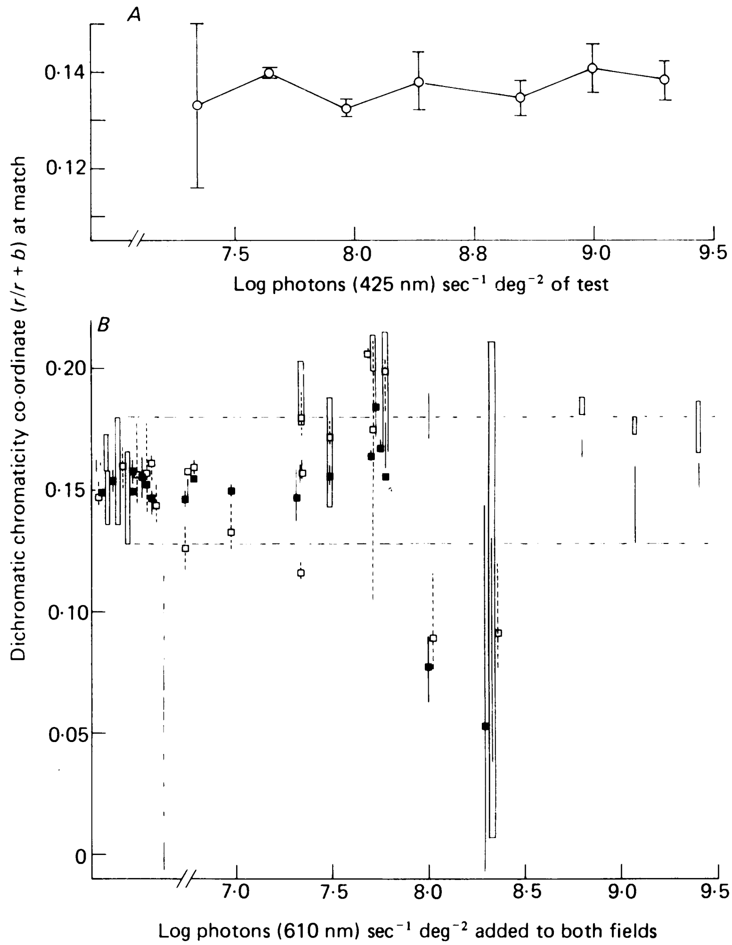

Fig. 6. Tests of Grassmann's laws of scalar multiplication (*A*) and additivity (*B*) as applied to the colour matches of the dichromatic eye. *A*, the chromaticity co-ordinate of a distimulus (long-wave primary, *r*, 650 nm; short-wave primary, *b*, 444·5 nm) mixture, matching a 425 nm light is shown as a function of intensity (photons (425 nm) sec^{-1} deg^{-2}) of the latter. Plotted points represent the means of five matches; error bars show one standard deviation on each side of the mean. Scalar multiplication is clearly applicable to this dichromatic match. *B*, the chromaticity co-ordinate (from Fig. 3) of the monochromatic light which matched a monochromatic light at 421·8 nm. The abscissa is the log radiance of an orange (610 nm) light added identically to both the test and the matching fields. Open symbols represent metameric matches, filled symbols isomeric matches. The lines and rectangles show the extremes of the acceptable ranges, when the observer adjusted only the intensity of the centre field. The squares show the averages bounded on either side by the extreme settings (short dashed lines for metamers, continuous lines for isomers) when he adjusted both the intensity and the wave-length of the central field.

for each of the two photopigments, and each photopigment produces a signal proportional to the rate of photon absorption. Since absorption is additive, colour equations are additive. But if the alternative three-pigment but two-channel hypothesis were true, there would necessarily be colour matches which were not matches for each pigment separately. In such a case neural non-linearities might or might not be such as to produce a breakdown of additivity for colour equations. Thus, a violation of additivity would be strong evidence that the two-pigment hypothesis is false; but confirmation of additivity is consistent with both the two-pigment hypothesis and certain versions of the three-pigment but two-channel hypothesis.

Despite the power of this test to reject the conventional view that dichromats have only two cone pigments, Grassmann's additivity law has been tested on dichromats only by Starr (1978). He obtained no violations of additivity in two protanopes and two deuteranopes. We carried out limited tests of additivity on the tritanopic eye of this observer.

Scalar multiplication law. The scalar multiplication law (Krantz, 1972, 1975) states that a metameric match remains so when both sides are altered by a scalar multiple, i.e. the intensity at each wave-length is multiplied by the same factor. To test this, dichromatic matches to 425 nm were obtained using primaries at 444·5 nm and 650·0 nm, just as in Part II, but varying overall intensity by rotating a sectored disk, at a rate considerably above the fusion frequency, in the final common light path of the colorimeter. Seven different intensity levels were used, as shown in Fig. 6*A*. Matches were made in a single session, going from the brightest to the dimmest level, after allowing time for full adaptation to each, taking five matches per level. The results in Fig. 6*A* plot the dichromatic chromaticity co-ordinate for the match as a function of the intensity of the 425 nm test light. The error bars show clearly that the null hypothesis of a horizontal trend (validity of the scalar multiplication law) cannot be rejected; moreover, there is no hint of any other trend in the results.

It is doubtful that violation of scalar multiplication would be found for any other colour match, since the one tested here was chosen as a most likely candidate for producing a violation (being far from a match in the three normal cone photopigments).

Addition law. The addition law states that a metameric match remains so when both sides are altered by admixture of the same addend light. To test this, we took advantage of the fact that below 550 nm there are two distinct wave-lengths corresponding to each value of the chromaticity co-ordinate, one above 450 nm and one below (see Fig. 3). We could thus study the invariance of a metameric match between two widely separated wave-lengths, when a third wave-length was added to both sides of the match.

In the colorimeter described in Part II, the 3° outside diameter annulus was used to present a light of narrow wave-band (10 nm h.w.) centred at 421·8 nm, with or without various intensities of a 610 nm addend. The 421·8 nm annulus and a monochromatic isomer in the central disk (2 nm h.w.) could be matched with high precision: the matching wave-length ranged from 421·5 nm to 422·2 nm. With his tritanopic eye the observer could also make a metameric match using a wave-length around 523 nm in the central disk to match the 421·8 nm annulus.

For the additivity test, isomeric 610 nm lights were added to both the central disk and the surrounding annulus. These lights were obtained with the use of two nearly identical (Baird-Atomic 10 nm h.w.) interference filters, mounted in the two other channels (one for the centre, one for the surround) of the colorimeter. Very careful isomeric matches between the 610 nm lights in these two channels were made at each intensity to be added in a given experiment, and then the intensity settings required for the isomeric match in a particular session were used in the additivity experiment.

For any one trial, the experimenter set the mixture in the surround (421·8 nm alone or combined with some intensity of 610 nm) and set the matching intensity (if non-zero) for the 610 nm light added to the centre field. The subject then attempted to match the two fields by adjusting the remaining beam in the centre field. Either the subject was allowed to adjust both the wave-length and intensity of this beam, to obtain an exact colour match, or, on some trials, the experimenter set its wave-length and the subject adjusted only its intensity, reporting whether or not an exact colour match could be attained. (This is very similar to the use of two-knob and one-knob matches in screening observers with the Rayleigh match in the anomaloscope.)

Each trial was either an *isomeric trial*, in which the experimenter initially set the wave-length control near 422 nm or a *metameric trial*, in which the experimenter initially set the wave-length control near 525 nm. Even with two adjustments available, the observer almost never wandered into the opposite range: the initial setting was close to a match, and it was easy for him to see whether a moderate wave-length adjustment made it worse or better.

For a trial on which the subject controlled both knobs, five matches were required, and the mean wave-length and the end-points of the range were converted to chromaticity (using Fig. 3) and plotted as a square (mean) and a range bar through the square in Fig. 6*B*. The metameric trials are shown by open squares (and dashed lines between the extremities), the isomeric by filled squares (and lines). For a trial in which the subject controlled only the intensity, the experimenter's wave-length settings were chosen (as in the wave-length discrimination study reported earlier) to discover the transition points between exact matching and failure to match. These transition wave-lengths were also converted to chromaticity using Fig. 3. The range between these transition points is shown by an open bar (metameric trial) or a thin line (isomeric trial) in Fig. 6*B*.

The results are plotted as a function of the intensity of the 610 nm addend. The numerous results at the left of Fig. 6*B* show the repetitions, over all five sessions, of the isomeric and metameric matches without any addend. These results demonstrate that metameric matches are somewhat noisier, but even isomeric matches show day-to-day fluctuation which may reflect criterion shifts for the matching across the boundary between disk and annulus. Around 8·0 log photons sec^{-1} deg^{-2} of the 610 nm addend there is a clear departure from invariance, but the isomer shifts at least as much as the metamer, and we are inclined to the view that this is simply a larger than usual criterion shift. Problems in maintaining a match criterion may be exacerbated because of the shift of the colour at the match end-point by the bright addend. Once again, the null hypothesis of additivity – a horizontal trend – cannot be rejected.

Increment threshold mechanisms

Another way to reject the two-pigment hypothesis would be to demonstrate a short-wave action spectrum in the tritanopic eye. The basic method for isolating a short-wave mechanism is to measure the threshold for a short-wave test light presented as an increment on a middle- or long-wave adapting background. It is important, however, to carry out such tests systematically, so that the limiting thresholds of various detection mechanisms are determined. To accomplish this, we first repeated some of Stiles' basic threshold *versus* intensity (t.v.i.) curves for both the normal and the tritanopic eye; we then used the various branches of the t.v.i. curves to obtain field action spectra $\Pi_3(\mu)$, $\Pi_4(\mu)$ and $\Pi_5(\mu)$ (Wyszecki & Stiles, 1967).

The first step was to measure t.v.i. curves for monochromatic lights on various backgrounds. Some of these curves were obtained with test and background at the same narrow wave-band (centred at either 429·5 nm, 481·9 nm or 651·1 nm). In other instances the test was narrow-band (either 429·5 nm or 481·9 nm) while the background had a broad spectral distribution, either the unfiltered 'white' of the 150 W xenon arc-light source, or the same filtered by a Wratten no. 22 filter (metameric with 596 nm).

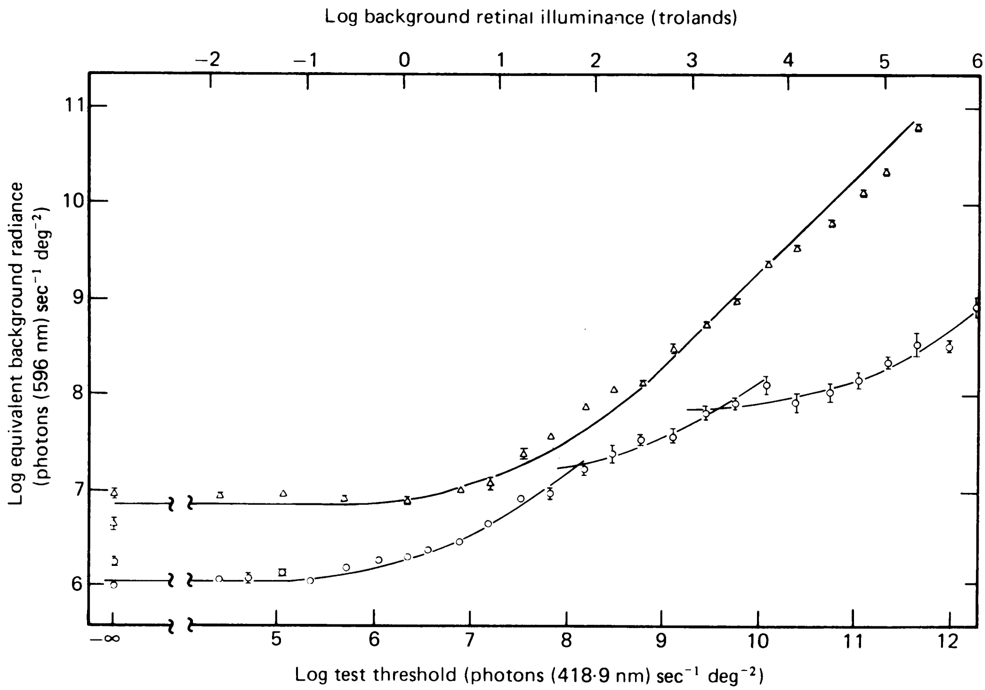

Fig. 7. Threshold *versus* intensity (t.v.i.) curves for a 481·9 nm test on a yellow background; circles for the normal eye, triangles for the dichromatic eye. Each symbol represents the mean of five measurements; the error bars give the limit specified by one standard error on either side of the mean (whenever they were large enough to be plotted). Measurements on one eye were all obtained in the same experimental session. The ζ template of Stiles defines the curves through the circles and the triangles.

Threshold *versus* intensity curves were measured for a 1° diameter circular test superimposed in the centre of a 5° circular background field. Two tiny fixation lights, one slightly above, the other just below the test, directed fixation to its centre. The apparatus was the three-channel Maxwellian view optical system of Alpern & Zwas (1979). Narrow-band (10 nm h.w.) interference filters provided the test fields or increments, the radiances of which were determined with a calibrated PIN-10 silicon photodiode. The test field or increment was exposed for 200 msec every second, following the procedure of Stiles (1978). For a measurement, the subject adjusted the intensity of the flashing increment to 'threshold' (after he had adapted to the background for a sufficient interval – a minimum of 1 min plus whatever additional time was needed for the measured results to become stable). Stiles'(1946*b*) practice of making measurements with short-wave test lights only between 4 and 12 min in the dark (when cones have fully recovered but rods are still considerably less sensitive than the cones) was initially followed to obviate testing rods. Subsequent measurements showed that the subject controlled his fixation so accurately that this precaution was unnecessary to ensure that the test flash studied cones at thresholds, and the practice was discontinued.

The t.v.i. curves obtained for a 481·9 nm test on the yellow background provided by filtering the xenon light with Wratten no. 22 filter are illustrated in Fig. 7, in which the ordinate gives the log test intensity at threshold while the abscissa specifies the background radiance. The circles with error bar limits show the mean ± 1 S.E.M. of five measurements, all obtained with the trichromatic eye in a single session; the triangles are comparable results measured with the dichromatic eye 1 week later.

Stiles (1939, 1953) found that the two-colour t.v.i. data with this test–background combination were divisible into three parts each separated in its turn from the others by a 'change in law'. For each component a single template curve (the ζ function: Wyszecki & Stiles, 1967) describes the elevation in threshold with increase in background intensity. This is the pattern followed in fitting the smooth curves through the open circles in Fig. 7. For Stiles' subjects the lowermost curve is attributed to Π_4, the middle-wave cone mechanism, while the upper two define Π_1 and Π_3, two short-wave mechanisms. The same is no doubt true for the trichromatic eye of the present observer although our measurements on the short-wave mechanisms are limited.

The analysis of the dichromatic t.v.i. data in a similar way is made difficult by the less conspicuous 'changes in law' shown by the triangles in Fig. 7. This was the most extensive set of increment thresholds obtained from the dichromatic eye, an exact repetition of the experiment on the trichromatic eye carried out 1 week before. Six other, less extensive curves, some covering a similar range of radiances but with fewer background intensities, using either 481·9 nm or 429·5 nm tests were obtained. None of these other measurements showed 'changes in law'; all are well described by the single ζ template. Thus the deviations of the triangles from this template are probably measurement errors, though the possibility of another mechanism, with greatly reduced sensitivity compared with the trichromatic eye, cannot be excluded with data using 481·9 nm as the test.

The next step was to measure the field-sensitivity action spectra of individual Π mechanisms. To this end a test wave-length (λ) was identified for each mechanism and the intensity of the background required to elevate this test threshold by a factor of 10 was estimated for each of thirty-six monochromatic background wave-lengths (μ) in a single experimental session about 2 hr long.

To illustrate the procedure consider the lowermost mechanism, $\Pi_4(\mu)$, for the trichromatic eye, indicated by the circles in Fig. 7. First the absolute (dark-adapted) threshold was measured for the 481·9 nm test alone. A given background wave-length (μ) and intensity were then selected and the observer adapted to this combination for 1 min or whatever additional time was required for the threshold to settle to a steady level. Five (sometimes ten) settings of the wedge were then made by the subject (method of adjustment) to obtain the threshold. It was essential that the value of these measurements always remained less than 7·15 log photons (481·9 nm) sec^{-1} deg^{-2}, the asymptotic (i.e. absolute) threshold for the next most sensitive mechanism (Π_1) for the 481·9 nm test. To some extent the choice of background intensity for any given μ was arbitrary, subject only to the constraints that it should be large enough to raise the test significantly (preferably, more than 0·4 $\log_{10}$ units) above the absolute threshold but weak enough not to raise test threshold to, or above, the absolute threshold of Π_1. If initially the estimated background raised the threshold outside this range, the process was repeated as often as needed to obtain the desired results, which almost always could be achieved with a single repetition. Within this limitation the value of the log photons sec^{-1} deg^{-2} of the test at threshold as well as that of the background on which it was obtained are all that is needed to calculate field sensitivity, $\Pi_4(\mu)$, for this background: the Stiles ζ template was fitted through the point plotting this threshold on a graph and from the template curve the log field intensity (log photons (μ) sec^{-1} deg^{-2}) required to elevate the 481·9 nm test 1 log

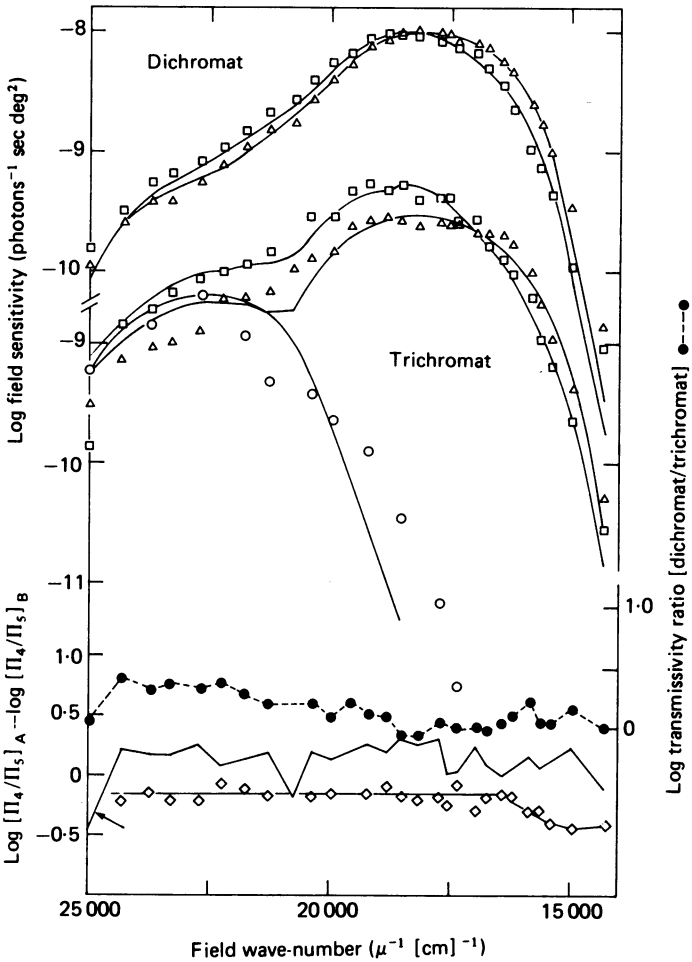

Fig. 8. Field-sensitivity action spectra for the dichromatic eye (above) and for the trichromatic eye (middle). The latter set are results of a single experimental determination (average of about five individual measurements), while the former are averages of four (squares) or of three (triangles) experimental determinations (each determination an average of about five individual measurements) spaced out over a 12 month interval. The smooth curves are linear combinations of the smooth curves through the dichromatic and trichromatic colour-matching functions from Fig. 2*A* and *B* respectively. Symbols: triangles, $\Pi_5(\mu)$; squares, $\Pi_4(\mu)$; circles, $\Pi_3(\mu)$. The circles have been shifted up to 0·73 $\log_{10}$ units to obviate confusion with the results of calculations illustrated at the bottom of this Figure. Below, the jagged continuous line shows $\log[\Pi_4(\mu)/\Pi_5(\mu)]$ measured on the trichromatic eye (*A*) minus $\log[\Pi_4(\mu)/\Pi_5(\mu)]$ measured on the dichromatic eye (*B*). The results are, within the margin of experimental error, independent of wave-length. The diamonds show $\log[\Pi_4(\mu)/\Pi_5(\mu)]$ of the average observer of Stiles (*A*) minus $\log[\Pi_4(\mu)/\Pi_5(\mu)]$ of the trichromatic eye of the present observer (*B*). Note the systematic departure from constancy at the long-wave end of the spectrum. Ordinate scale for both these comparisons is to the left. Filled circles connected by a dashed line show the plot of $\log\{[\tau'(\mu)/\tau'(700)]/[\tau(\mu)/\tau(700)]\}$ calculated as discussed in the text (ordinate scale to the right).

unit above its absolute threshold read from the graph. The same procedure carried out at every other field wave-length defined the field-sensitivity action spectrum, $\Pi_4(\mu)$, plotted as the squares in Fig. 8 in the middle set (trichromat).

These $\Pi_4(\mu)$ results were obtained in a single experimental session of about 3 hr duration. In a separate session the middle set of triangles shown in Fig. 8 was obtained by using a 651·1 nm test and confining the background intensities to those which elevated the test threshold in the range 0·76–0·98 $\log_{10}$ units. The background intensity required to raise the 651·1 nm test 1·0 $\log_{10}$ unit above its absolute threshold calculated from these measurements by means of the Stiles ζ template yields the $\Pi_5(\mu)$ field-sensitivity spectrum of the trichromatic eye shown by this set of triangles. Finally the open circles in Fig. 8 were measured on the trichromatic eye following similar procedures with a 481·9 nm test and the help of an auxiliary background sufficiently intense (10·38 log equivalent photons (596 nm) sec^{-1} deg^{-2}) to raise the test threshold onto the Π_3 branch, upon which main backgrounds were then added to elevate the test significantly above the absolute threshold of Π_3.

The continuous curves fitted to the Π_3, Π_4 and Π_5 measurements are linear combinations of the trichromatic colour-matching functions (Fig. 2*B*); this will be discussed in Part IV.

In applying a similar strategy to the field sensitivity of the dichromatic eye, a single ζ template was fitted to the absolute threshold and to the increment threshold on each background field. This procedure attributes the apparent cusps in the dichromatic t.v.i. curve in Fig. 7 to measurement error since they were not repeated on any other t.v.i. curve on this eye. The radiance of the background field was set by guessing the value required to elevate the λ = 481·9 nm threshold in the range 0·8 to 1·1 $\log_{10}$ unit. The ζ template was fitted to both the measurements of the absolute and increment thresholds, and this template was used to estimate the background radiance elevating the test 1·0 $\log_{10}$ unit above absolute threshold. The initial guesses were not invariably accurate and an increment threshold anywhere in the range 0·688–1·567 $\log_{10}$ units above absolute threshold was used in practice for the template fit. Given this wide range, the fact that a repetition 10 months later yielded essentially the same action spectrum suggests that this approach is not grossly misleading.

The failure of these experiments to reveal any trace of a short-wave mechanism in the dichromatic eye precipitated a further search, measuring the background radiance necessary to elevate a 429·5 nm test 1 $\log_{10}$ unit in a similar way; in normal eyes this procedure yields the action spectrum of Π_1 or Π_2. No Π_2–Π_1 change in law appears in the t.v.i. curves measured with this test, which were well fitted by a single ζ template. The results of two determinations of the field-sensitivity spectrum, separated by 10 months, were again nearly identical. In fact none of the four spectra differed from the others beyond the precision of the measurement and all are averaged together and shown as squares at the top in Fig. 8. The triangles at the top of this Figure are the average of three repetitions of the measurement of the field sensitivity of $\Pi_5(\mu)$. The continuous curves drawn through these results are linear combinations of the dichromatic colour-matching functions shown in Fig. 2*A*; they are discussed below.

The essential finding of all these experiments on the dichromatic eye is that the short-wave-sensitive cone mechanism is either entirely absent or very disproportionately reduced in sensitivity. The data are not extensive enough to exclude the possibility that a short-wave mechanism mediates thresholds at very high background radiances. The similarity of the t.v.i. curves and the action spectra derived from the

429·5 nm and 481·9 nm test lights indicates that thresholds at low to moderate backgrounds are mediated by a middle-wave-sensitive mechanism, identified as the tritanope's Π_4.

Part IV: receptor absorption spectra and reduction dichromacy

Are the visual pigments that contribute to the dichromatic vision of the tritanopic eye normal? The traditional way of addressing this issue is to determine whether tritanopia is a reduced form of the trichromatic vision of some representative normal eye. If the latter is the C.I.E. standard observer, then the discrepancies between the experimental points in Fig. 2*A* and the dashed lines provide a clear negative answer. Alpern (1976) showed that applying the same tests to each one of Wright's (1952) congenital tritanopes yields a similar negative answer. A more interesting question is whether the tritanopia is a reduced form of the normal vision of the same observer's trichromatic eye. This question has a direct empirical answer: one gets the subject to inspect with his tritanopic eye the trichromatic matches completed with the 'normal' eyes. Do these matches still hold? This, too, has a crisp negative answer.

However, the latter failures of reduction dichromacy may be caused by wave-length-dependent light losses in the prereceptor media that are different in the two eyes. Differences in colour matching arising from this cause have been found (using the method of von Kries, 1899) in previous studies of defective colour vision (Alpern, 1976; Alpern *et al.* 1976; Alpern & Moeller, 1977).

Suppose that the absorption spectrum *in situ* for the *i*th photopigment is $a_i(\lambda)$ in one eye and $a_i'(\lambda)$ in a second eye. Let $\tau(\lambda)$, $\tau'(\lambda)$ respectively denote the transmission spectra of the prereceptor media in these two eyes. Then the hypothesis in question asserts that

$$a_i(\lambda)/\tau(\lambda) = a_i'(\lambda)/\tau'(\lambda)$$

for each photopigment. If one divides the above equations for two different photopigments, say a_i and a_j, then one obtains

$$\frac{a_i(\lambda)}{a_j(\lambda)}\Big/\frac{a_i'(\lambda)}{a_j'(\lambda)} = \text{constant (independent of } i, j \text{ and } \lambda).$$

To test this extended form of the reduction dichromacy hypothesis, we require linear transformations of the colour-matching functions for each eye which yield photopigment absorption curves. (This is unnecessary for cases where it can be assumed that the linear equations relating the photopigment absorptions to the matching functions are the same for the two eyes, except for constants expressing differential prereceptor absorptions at the wave-lengths of the colorimetric primaries; for then it can be shown that the ratios of any two colour-matching functions are proportional in the two eyes. But this simplification obviously cannot apply to a trichromatic and dichromatic eye, where necessarily the linear transformations involved are distinct, one being 3×3, the other 2×2.)

Unfortunately, there is no agreed procedure for deriving linear transformations of the colour-matching functions of an individual observer which represent that observer's *in situ* photopigment absorptions. In the face of this difficulty, we hypothesized that the field sensitivity curves $\Pi_3(\mu)$, $\Pi_4(\mu)$, $\Pi_5(\mu)$ in the normal eye, and $\Pi_4(\mu)$, $\Pi_5(\mu)$ in the tritanopic eye, are good approximations to the photopigment absorptions. This hypothesis is supported by two previous findings: (i) Pugh & Siegel (1978) found that the average field sensitivities of four subjects, tabulated by Wyszecki & Stiles (1967), are reasonably well described by a linear combination of the average of the normal small-field colour-matching functions (Stiles & Burch, 1955) (see also Estévez & Cavonius, 1977); and (ii) the average $\Pi_4(\mu)$ and $\Pi_5(\mu)$ are in good quantitative agreement with measurements made on middle- and long-wave cone pigments of rhesus monkeys (Bowmaker, Dartnall, Lythgoe & Mollon, 1978) and of man (Bowmaker & Dartnall, 1980) with a microspectrophotometer.

We tested the fit of linear combinations of this observer's normal and dichromatic colour-matching functions to the respective Π action spectra. The fit is shown by the comparison of the continuous curves with the points in Fig. 8. The linear combinations used for the continuous curves were estimated by least squares (in linear units, with constant term constrained to zero). This seemed simpler than the perhaps more appropriate logarithmic fit, and was adequate to the task. For the trichromatic eye, 97·6% of the variance was accounted for in $\Pi_4(\mu)$ and 97·0% in $\Pi_5(\mu)$; the corresponding figures for the dichromatic eye are even better, being 99·3% and 99·8%, respectively. The somewhat large deviations of the points at 700 nm from the curve (on the logarithmic scale of Fig. 8) did not enter into the least squares calculation appreciably, since predicted and observed are both near zero on the linear scale; this is just as well, because we did not actually measure colour-matching functions beyond 650 nm, and used extrapolations of the measured functions to draw the continuous curves out to 700 nm. For reasons which are unclear, the fit for $\Pi_3(\mu)$ is not especially impressive (87·5% of the variance); but this has no effect on the following calculations.

Assuming the measurements of $\Pi_4(\mu)$ and $\Pi_5(\mu)$ on the two eyes are good approximations to the *in situ* absorption spectra of the middle- and long-wave-sensitive cone pigments, we compared the ratio $\Pi_4(\mu)/\Pi_5(\mu)$ for the two eyes. The logarithm of the ratio of these ratios is plotted as the continuous jagged line in Fig. 8 (bottom, ordinate scale to the left). The result shows some differences from one wave-length to the next but no systematic wave-length dependency which cannot be attributed to measurement errors bound to be manifested in the field-sensitivity spectra of the normal eye which were each obtained in only a single experimental session.

It is concluded that differences in prereceptor transmissivity of the ocular media of the two eyes could be responsible for the failure of the tritanopic eye to accept the trichromatic colour matches made by the normal eye. With this conclusion it is possible to estimate the transmission ratio of the media of the two eyes. From the previous equations,

$$\frac{\tau'(\lambda)}{\tau(\lambda)} = \frac{a_i'(\lambda)}{a_i(\lambda)},$$

where now τ, τ' are respectively the spectral transmission functions of the normal and tritanopic eye, and a_i, a_i' are the corresponding action spectra for either Π_4 or Π_5. A reasonable way to obtain a combined estimate, using both Π_4 and Π_5 ratios (Alpern *et al.* 1976), is first to normalize the estimates at one wave-length (700 nm was used) and then to take the weighted average, using the relative magnitudes of normal Π_4 and Π_5 at any given wave-length as weights. That is, at wave-length μ estimate:

$$\frac{\tau'(\mu)/\tau'(700)}{\tau(\mu)/\tau(700)} = \left(\frac{\Pi_4(\mu)}{\Pi_4(\mu)+\Pi_5(\mu)}\right)\frac{\Pi_4'(\mu)/\Pi_4'(700)}{\Pi_4(\mu)/\Pi_4(700)} + \left(\frac{\Pi_5(\mu)}{\Pi_4(\mu)+\Pi_5(\mu)}\right)\frac{\Pi_5'(\mu)/\Pi_5'(700)}{\Pi_5(\mu)/\Pi_5(700)}.$$

The logarithm of this estimate is plotted as a function of wave-length by the filled circles connected by a dashed line in Fig. 8 (ordinate scale to the right). From this graph it is clear that the maximum difference occurs around 420 nm, at which wave-length the ocular media of the dichromatic eye absorb about 2·2 times more light than the media of the trichromatic eye. Perhaps this curve represents the absorption spectrum of a residual scar from the period 2 years before when the central serous retinopathy was active.

Finally, it is of interest to ask how 'normal' the colour vision of the trichromatic eye is. The anomaloscope matches and the measurements in Figs. 1, 2, 4, 5 and 7 attest the acute, sensitive, colour discrimination characteristic of normal trichromacy. Still, the $\Pi_4(\mu)$ and $\Pi_5(\mu)$ field-sensitivity spectra of this eye are distinctly different from those of the average observer of Stiles (Wyszecki & Stiles, 1967). This is shown by the ratio of the ratios at each wave-length of these quantities for these two observers, illustrated as a function of wave-length by the diamonds at the bottom of Fig. 8 (ordinate scale to the left). A clear wave-length dependency of this ratio documented by the systematic, however gradual, change in this ratio for $\mu \geqslant 620$ nm suggests that these differences cannot be dismissed by the trivial interpretation that the prereceptor media differ. In this comparison the hypothesis that the cone pigments which underly $\Pi_4(\mu)$ and $\Pi_5(\mu)$ in the normal eye of our subject are identical to those of the average observer of Stiles is excluded. Evidently, the visual pigments in either or both the long- and middle-wave-length-sensitive cones of different normal trichromatic eyes differ from one another in much the same way that Alpern & Pugh (1977) have already noted for the visual pigments of long-wave-sensitive cones of different deuteranopes.

This paper concerns the colour vision of the two eyes of a single observer whose right eye is normal while the left has classical tritanopia. We have documented the details of this dichromacy and demonstrated that in every way that congenital tritanopia has been studied, it is indistinguishable from classical tritanopia. We conclude tentatively that the tritanope has long-and middle-wave cone pigments in the normal range and has no functional short-wave-sensitive cone pigment. But what colours does a tritanope see? That question is answered in the following paper (Alpern *et al.* 1983).

APPENDIX

Report of Ophthalmologic Examinations

This 24-year-old white male was initially seen at the University of Michigan Medical Center in September 1975, with a history of metamorphopsia and blurred vision in his left eye of several weeks' duration. His past ocular and medical histories were unremarkable. He took no medications except occasional antihistamines for seasonal rhinitis.

His visual acuity was recorded as 6/4·5 (+0·75 sph.) in his right eye and 6/9 (+1·50 sph. +0·25 cyl axis 120) in his left eye. Amsler grid testing defined a sepia-toned relative central scotoma with metamorphopsia in his left eye. The results of the anterior segment and slit-lamp examinations were normal. Ophthalmoscopic examination of the right eye revealed a few scattered areas of retinal pigment epithelial atrophy and clumping, compatible with old resolved serous detachments of the retinal pigment epithelium. The sensory retina was flat and normal out to the ora serrata. In the left eye a shallow serous detachment of neuroepithelium covered an elliptical zone, about two and one-half disk diameters around the macular area centred on the umbo. There were several isolated and minute zones of pigment clumping and atrophy scattered throughout this eye of the same kind as were present in the right eye. The remainder of the peripheral retina to the ora serrata appeared normal.

Intravenous fluorescein angiophotography of the left eye indentified a focal leak of dye with a classical 'smoke-stack' appearance, arising from the pigment epithelium under the foveal avascular zone and filling the secondary retinal detachment. No treatment was initiated.

Over the subsequent 8 weeks the metamorphopsia and blurred vision in the left eye cleared, resulting in a final visual acuity of 6/4·5. Ophthalmoscopy showed the neuroepithelium reattached, an excellent umbo, and only minor residual pigment clumping in the foveal area.

At the time studies reported here began, i.e. 2 years after the initial exacerbation, examination of the left fundus showed only residual macular pigment clumping in an otherwise quiescent retina. The visual acuity in the right eye was then 6/6 +2, that in the left 6/6 −2. Visual field measured on a tangent screen at 1 m was normal for the right eye, but showed an ellipsoid relative central scotoma $8° \times 4°$ across (i.e. elongated vertically) for a 2 mm red test object for the left eye.

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