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LACK OF UNIFORMITY IN COLOUR MATCHING

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SUMMARY

1. The fraction of red in a red–green mixture matched to yellow increased as the intensities of the match constituents were increased sufficiently to bleach appreciable chlorolabe and erythrolabe.

2. All changes in matching found for a given normal trichromat, (i) with increase in the intensities of the matching components, (ii) as a function of time after the onset of very intense components, (iii) with change in the pupil region through which light enters the eye, and (iv) with change in the region of the retina under test, are consistent with the assumption that matching depends upon the absorption of light in three kinds of (individually colour blind) cones, each with its own visual pigment, provided that the λ_{max} densities of the latter can vary in the range 0·25–1·0 (common logarithmic units) depending upon the subject.

3. Individual differences in matching among normal (as well as among both varieties of red–green anomalous) trichromats, on the other hand, suggest that the extinction spectra of the cone pigments sensitive to long and medium wave lengths may differ from one trichromat to the next.

INTRODUCTION

Nearly every healthy human has trichromatic vision over a range of conditions including foveal and extrafoveal viewing, for light intensities extending from cone threshold to levels which bleach almost all the visual pigment. But the relative amounts of the primaries in a trichromatic match of a given light not only differ amongst observers but also differ in the same observer with such factors as the light intensity, the adaptive state of the retina, the patch of retina viewing the field and the region of the pupil through which the lights pass (e.g. Rayleigh, 1881; Wright, 1934, 1936; Brindley, 1953; Enoch & Stiles, 1961; Terstige, 1967; Ingling, 1969; Wyszecki, 1978).

The existence of this variability makes untenable the common explanation of foveal trichomacy which is that the light is absorbed by just three visual pigments each arranged in its own species of univariantly signalling (hence colour blind) cone in such a way that every molecule is similarly situated with respect to coloured materials which filter the incident light.

The simplest way of reconciling these inconsistencies with conventional trichro-

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matic theory is to suppose that not all molecules are identically situated with respect to coloured materials which filter the light because the visual pigment is itself such a material. This is the so-called 'self-screening' hypothesis. It was introduced by Stiles in 1937 to explain the change of hue that occurs as the point of entry of a monochromatic light into the eye is moved from the centre of the pupil to its edge. Brindley (1953, 1955) applied the hypothesis not only to this upset of colour matches but also to those which occur following adaptation to bright lights (Wright, 1934, 1936) and more recently, though only qualitatively (Brindley, 1970), to the possible differences between foveal and extrafoveal matches under conditions in which influences of rods and differences in absorption by macular pigment have been obviated (cf. also Pokorny, Smith & Starr, 1976). Finally, certain explanations for the 'abnormal' matches of the protanomalous (Baker, 1966; Alpern & Torri, 1968) and deuteranomalous trichromats discovered by Lord Rayleigh (1881) rely on a similar theory (Ruddock & Naghshineh, 1973). 'Self-screening' is produced by a non-negligible concentration of visual pigment in cone outer segments. Factors that affect this concentration will change a pigment's absorption spectrum and the metameric colour matches which depend upon it.

That all observed differences in matching depend upon differences in concentrations of only three chemical substances is such a simple concept that it is surprising that it has not been more generally accepted, but there is, in fact, a good deal of scepticism about it. Stiles (1960) found Brindley's explanation for the upset of a match after adaptation to bright lights difficult to reconcile quantitatively with objective pigment measurements. It was also rejected by Wright (1964) because it would then be 'surprising that some breakdown in colour match is not apparent at lower adaptation levels'. Unfortunately, neither Wright, nor anyone since, has developed a quantitative theory of self-screening which would predict, from the known kinetics of foveal cone pigments, how normal colour matches would change with adaptation level. Rather Wright (1964) proposed an undefined 'change in chemical structure of the red-sensitive pigment', while Ingling (1969) suggested that the long-wave cones contained two differently sensitive visual pigments. In Ingling's view, the more sensitive of these is the one which protanomalous subjects lack.

Nearly all current theories of anomalous trichromacy (Hurvich & Jameson, 1956; Wald, 1966; Rushton, Powell & White, 1973; Pokorny, Smith & Katz, 1973; Piantanida & Sperling, 1973*a*, *b*; MacLeod & Hayhoe, 1974; Alpern & Moeller, 1977) discard the notion that self-screening of cone pigment with normal extinction spectra accounts for abnormal matches in favour of the proposal that the extinction spectrum of at least one pigment is 'abnormal'.

This paper has three objectives, (i) to develop a realistic quantitative theory of matching based on the hypothesis that the concentration of chlorolabe and erythrolabe in the long and medium wave cones is sufficiently high for there to be 'self-screening' effects, (ii) to test this theory by studying a single colour match in one normal eye at a variety of intensities of its constituents and under different viewing conditions, and (iii) to measure individual differences in this match among normal and anomalous trichromats to test the hypothesis that every trichromat has the same three pigments.

METHODS

With one notable exception (a very recent pilot study by Wyszecki, 1978) since the first observation of the instability of colour matching by Wright (1934), the problem has been studied in the same way. First, a bright adapting field is exposed for a fixed interval, say 20 sec. Then the test field having, say, a mixture of a red (λ = 650 nm) and green (λ = 530 nm) on one side and a yellow (λ = 582 nm) on the other, is exposed at a much weaker retinal illuminance (about 200 td) for a briefer interval (say 6 sec). Following this the adapting light is turned on again and the cycle repeated. Since the test exposure is too brief for the match to be made by adjustment, the primaries are adjusted during the subsequent exposure of the adapting field. This process is repeated over and over until a match is achieved.

There is one difficulty with this method. Because of poorly understood properties of blue signalling cones, the first minute or so following the exposure of a bright adapting field is characterized by artificial 'tritanopia' (Stiles, 1949) which changes to a violet 'monochromacy' (Brindley, 1953) as the intensity of the adapting light is increased (Mollon & Polden, 1977). Matching a spectral yellow can ordinarily be completed with only two (i.e. red and green) primaries in the mixture field because the contribution made by photons absorbed in short-wave sensitive cones is negligible in this part of the spectrum. When the region of violet 'monochromacy' is reached, however, the colorimeter fields take on a violet tinge and the match becomes insensitive to the settings of red and green primaries. Unfortunately, the range of the transition from artificial 'tritanopia' to violet 'monochromacy' is precisely that required to answer the question 'are the red (or green) cone pigments of all trichromats identical?'

To obviate this difficulty, a single colour match is studied as the intensities of its constituents are increased to levels which bleach (as an upper limit) more than 80% at equilibrium. Such intensities could only be achieved with available sources by sacrificing the ability to employ monochromatic lights. Instead, broad band gelatin filters, used with a black body radiator of 3200 °K, gave red and green primaries which, when mixed together, were matched to a yellow. These primaries have dominant wave-lengths of 633, 552 and 586 nm respectively (see Fig. 1*C*). Calculations show that these broad spectral distributions reduce the range of instability by more than twice that which might have been obtained with monochromatic primaries. For example, a visual pigment density of 0·2 at the λ_{max} in red and green-signalling cones predicts a change in the log ratio of intensities of the two primaries of 0·058 (compared to 0·152 with spectral primaries). Normal observers making ten matches do so with an estimated standard deviation between 0·008 and 0·05; hence changes in matches of subjects with concentrations as low as 0·2 may barely be detected with this arrangement. Some anomalous trichromats match as precisely as the best normal subjects, but many, perhaps most, match less precisely than even the least accurate normal. This puts further constraints on quantitative confrontation of theory with measurements on anomalous subjects.

Selection of subjects

The subjects were three females and four males, ranging in age between 18 and 75 years with normal visual acuity and normal colour vision. In addition twelve colour defective male trichromats, eight deuteranomalous and four protanomalous, were also studied. All but one of the latter, a 42-year-old protanomalous, were young adults, undergraduates selected in the main from the students of the Part I physiology course at Cambridge who made abnormal matches within a reasonably small matching range with a model II version of the Nagel anomaloscope.

Apparatus

Fig. 1*A* shows the apparatus (not drawn to scale). Three separate beams from the source *S*, a tungsten-halogen lamp, provided the three primaries. In each channel identical lenses L_1 imaged the filament in the plane of an aperture stop (AS). The beams forming the red and green primaries were filtered by Ilford 205 (F_r) and 625 (F_g) gelatins respectively and brought together and reflected to fill a small central disk formed by the field stop FS_1. This stop and the image of FS_2 formed by the pellicle *P* were in the primary focal plane of an achromatic doublet L_3 (42 mm diameter, 150 mm focal length) which served as a Maxwellian lens. A neutral wedge W_r, adjusted the amount of red in the red-green mixture. The intensity balance was such that normal trichromats

matched within the range of this wedge. Protanomalous usually required further attenuation of the green, deuteranomalous of the red, beams with additional neutral filters N_g, N_r respectively. The field lenses L_2 formed an image of the uniformly illuminated face of L_1 in the planes of the field stop FS_1, FS_2. FS_1 was a metal plate with a 1·8 mm hole centred on the optical axis of the system; FS_2 had a slightly larger (2 mm) opaque disk, also centred on this axis. The two aperture stops AS_1, AS_2 were imaged by the lens L_3 in the plane of the subject's pupil. The image of AS_2 was 1·0 mm, that of AS_1 was 1·25 mm in diameter. The depth of field for the beam limited by FS_1 was very large but the field of view for the reflected beam was limited by the outer diameter of L_3 and its depth of focus was small. Subjects were accurately positioned at the image of AS_2. Inaccurate alignment along the optical axis, especially for older subjects whose pupil size is very small at high intensities was a source of artifact to be avoided. When possible

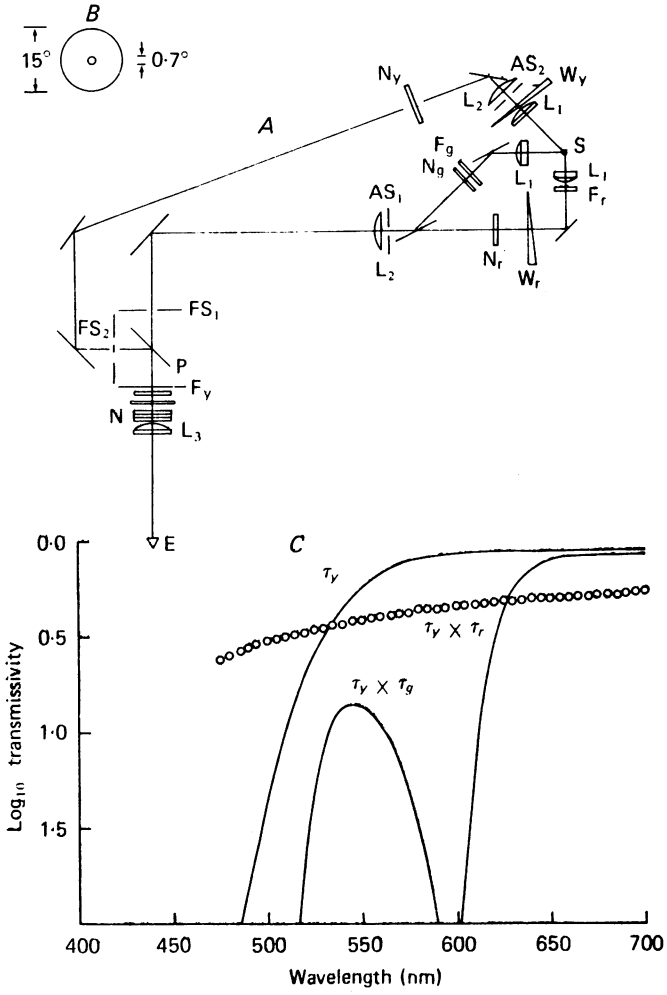

Fig. 1 *A*, line drawing of the optical arrangement seen from above. *B*, subject's view of the field. *C*, open circles: log spectral irradiance of a black body radiator with the colour temperature 3200 °K (in quanta) assumed for theoretical calculations ($E(\lambda)$ $T(\lambda)$). The continuous lines show the log spectral transmissivities of the three primary filters; τ_y is the transmissivity of F_y; $\tau_y \times \tau_g$ is the transmissivity of the filter F_y multiplied by that of filter F_g which together provide the green primary; $\tau_y \times \tau_r$ is the transmissivity of the yellow filter F_y multiplied by the transmissivity of the red filter F_r which together provided the red primary.

the subjects's pupil was dilated with one or two drops of 1 % tropicamide. In some experiments with undilated pupils, the image in the subject's pupil was monitored; a match was then discarded if made under conditions where the subject's iris eclipsed part of the light. All the results reported are believed to be free of this artifact.

The three beams passed through the gelatin filter F_y which gave the characteristic yellow colour to the surround (τ_y in Fig. 1*C*). The plot of the transmissivities of the red, and the green, filters each combined with the yellow ($\tau_r.\tau_y$ and $\tau_g.\tau_y$ respectively) are shown in Fig. 1*C*.

Subjects matched by adjusting the two wedges W_r and W_y (0·8 maximum densities). The former varied the amount of red in the red-green mixture filling the central 0·7° spot, the latter varied the intensity of the 15° surround (Fig. 1*B*). All beams could be varied together by spectrally calibrated Inconel filters in the common beam between the pellicle and L_3.

To estimate q_3, the parameter in the equation for the Stiles–Crawford brightness effect, the intensity of a light required just to detect 30 Hz flicker in the central (0·7°) field interrupted by an episcotister was measured twice, once with light entering the centre of the pupil, and again coming through the pupil edge. Centre and surround had the same colour (given by F_y) and were always equal in brightness. The difference in the logs of the average intensities of the two sets, 0·36, measures the amount of light entering the pupil 2·80 mm off centre which had to be increased for the same flicker threshold. Substituting into Stiles' (1937) equation,

$$\log I/I_{r_m} = q_3(r-r_m)^2,$$

(cf. below for the meaning of these and other symbols) gives a value of $q_3 = 0{\cdot}046$. Stiles (1939) found $q_3 = 0{\cdot}047$ for 570 nm light in his eye.

Calibration

The maximum retinal illuminance of the yellow surround field was determined by Rushton's method (Westheimer, 1966): visual photometry, with the S.E.I. metre, of the unattenuated beam falling on a white piece of paper 10 cm from the image of AS_2. The colour difference between this field filtered by F_y and the more yellow of the two S.E.I. fields was negligible; matches were precise to 0·02 log units. F_r and F_g were removed from their respective positions in the light beams and the light normally passing through the green filter was occluded. The unfiltered 'red' beam was measured by adjusting W_r to match the centre and the known surround on the paper. A similar isomeric match was made for the unfiltered 'green' central beam by occluding the 'red' beam and adjusting W_y. Since minor changes in alignment could cause small fluctuations in these values, this process was almost always repeated at the end of each experimental session.

Filters were calibrated throughout the visible spectrum with a Unicam SP 800 recording spectrophotometer. The luminous tranmissivities of the red and green filters were obtained by placing a calibrated PIN 10 (United Detector Technology, Santa Monica, California) silicon photodiode (with an optical filter yielding photometric units) in the light beam, and comparing the amount of light measured with and without each filter, in the beam. (Two infra-red absorbing filters were also added to the beam to exclude artifacts from imperfections in the design of the PIN-10 photometric filter). The accuracy of these measurements was checked by calculating (in 5·0 nm steps throughout the spectrum) the ratio of luminous transmissivities of the two filters assuming the light source was a black body radiator of colour temperature 3200 °K. The luminous transmittance of the red filter was 0·0904 log units more than the green; the calculated value was 0·117. Agreement is satisfactory.

Procedures

Subjects aligned in the apparatus practiced adjusting the intensity of the red primary controlled by W_r (with the left hand) and simultaneously (or successively) the intensity of the surround controlled by W_y (with the right hand) for an exact match. After four or five practice matches the actual experiment began, the subject adapting to the dimmest levels of the matching field (usually somewhere from 10 to 100 td). When ten successive matches had been made at this level, the intensity of all beams was increased together by removing a 0·3 or 0·6 neutral filter from the common beam. The subject adapted again and then made ten matches at this new level. This procedure was followed until the retinal illuminance was around 10,000 td.

Because substantial proportions of the chlorolabe (and erythrolabe) are bleached by lights as bright as this, the procedure was modified. Subjects viewed the field continuously neither closing

their eyes nor allowing gaze to wander outside the field, even between matches. Beginning with the start of viewing, a time record was kept of the moments when matches were completed. Matches followed one after the other until at least ten measurements fluctuated about some equilibrium level. Ten minutes usually sufficed; it never required more than 15. At the end of this interval subjects closed their eyes and relaxed for 10 min or so before the process was repeated with a 0·3 neutral filter removed from all beams. The experiment proceeded in the same way until the brightest lights were reached. At the end of these last matches a 3·0 density neutral filter was, on some occasions, suddenly added to the common beam, the subject continuing to match (closing his eyes between measurements) for another 10 min.

PART I THEORY

Let

j = 1, 2, 3 identify the red, green and yellow light beams, respectively,

$\tau_j(\lambda)$ = the transmissivity of jth filter,

$E(\lambda)$ = the quantized spectral irradiance of the light falling on the retina but without correction for losses in the eye media (photons nm^{-1} sec^{-1} cm^{-2} of retina),

$\chi(\lambda)$ = the extinction spectrum of the medium wave sensitive cone pigment, chlorolabe. It is the product of the area of the chromophore (cm^2) and the probability that a photon of wave-length (λ) striking the chromophore will be absorbed.

$\epsilon(\lambda)$ = the extinction spectrum of the long wave sensitive cone pigment, erythrolabe. analogously defined,

c = concentration (chromophores cm^{-3}) of chlorolabe (and of erythrolabe) in the outer segments,

c_0 = c in the dark,

p_ϵ = c/c_0 the fraction of unbleached erythrolabe,

p_χ = c/c_0 the fraction of unbleached chlorolabe,

θ = position of the test in the visual field in degrees of visual angle from the fixation point,

r = the distance from the geometrical centre to the point of entry of the light in the observers' entrance pupil (mm) along a horizontal traverse at the height of maximum Stiles–Crawford brightness effect,

r_m = r for maximum luminous efficiency,

$l(r, \theta)$ = length of light-path in cone outer segments (cm); it depends upon r and θ but not upon wave-length,

$D'(r, \theta)$ = the λ_{max} optical density (common logarithmic units) of chlorolabe

$= \chi(\lambda_{max})\, c_0 l(r, \theta)\, (\log_{10} e)$,

$D'(\lambda, r, \theta) = \chi(\lambda)\, c_0 l(r, \theta)\, (\log_{10} e)$,

$D(r, \theta)$ = the λ_{max} optical density (common logarithmic units) of erythrolabe

$= \epsilon(\lambda_{max})\, c_0 l(r, \theta)\, (\log_{10} e)$

$D(\lambda, r, \theta) = \epsilon(\lambda)\, c_0 l(r, \theta)\, (\log_{10} e)$,

U_j = the wave-length independent factor by which the light intensity is reduced by wedge and neutral filters in the jth beam, as measured by the product of their respective transmissivities,

$V(\lambda)$ = the C.I.E. photopic luminosity curve,

$T(\lambda)$ = the transmissivity of the ocular media,

γ = the number of chromophores changed per photon absorbed,

J_j = the photons in the jth beam sec^{-1} cm^{-2} of retina absorbed by erythrolabe. According to the Beer–Lambert Law:

$= U \int E(\lambda) T(\lambda) \tau_j(\lambda) \{1 - \exp[-\epsilon(\lambda) c_0 l(r, \theta) p_\epsilon]\}\, d\lambda$

$= U_j A_j(p_\epsilon, r, \theta)$, in which

$A_j(p_\epsilon, r, \theta)$ = The photons $\sec^{-1}$ cm^{-2} absorbed by erythrolabe from the unattenuated light in the jth beam,

$= \int E(\lambda)T(\lambda)\tau_j(\lambda)\,[1-10^{-D'(\lambda,r,\theta)p_\epsilon}]\,d\lambda.$

$B_j(p_\chi, r, \theta)$ = the photons $\sec^{-1}$ cm^{-2} absorbed by chlorolabe from the unattenuated light in the jth beam.

$= \int E(\lambda)T(\lambda)\tau_j(\lambda)\,[1-10^{-D'(\lambda,r,\theta)p_\chi}]\,d\lambda,$

I_j = the intensity of the retinal illuminance (td) of the jth beam.

$= U_j k \int [E(\lambda)/\lambda]\,\tau_j(\lambda)V(\lambda)d\lambda$, in which k is a constant (cf. Wyszecki & Stiles, p. 216),

q_j = the parameter of the Stiles–Crawford brightness equation

$= -1/(r-r_m)^2 \log [I_{j_{r_m}}/I_{j_r}]$, where

I_{j_r} = the intensity of retinal illuminance (td) of the jth beam entering the eye pupil at the point r, needed to produce a constant visual effect,

I_0 = the retinal illuminance (trolands) needed to bleach half the foveal erythrolabe at equilibrium ($r = r_m$),

t_0 = time constant of the regeneration of erythrolabe.

(A) *Colur matching*

It is assumed that a colour match is achieved when (i) the photons absorbed in the long wave sensitive cones from the red-green mixture are identical in number to those absorbed in the long wave cones from the yellow, i.e.

$$U_1A_1 + U_2A_2 = U_3A_3,$$

and (ii) the quanta absorbed in the medium wave sensitive cones excited by the mixture are equal in number to those absorbed in the medium wave cones from the yellow,

$$U_1B_1 + U_2B_2 = U_3B_3.$$

Solving these two equations for the ratio U_1/U_2 (which is independent of U_3), converting to trolands, and taking logarithms gives

$$\log \frac{I_1}{I_2} = \log \frac{B_2A_3 - A_2B_3}{A_1B_3 - B_1A_3} + \log k_1 \quad \text{(td)}, \tag{1}$$

where

$$k_1 = \frac{\int [E(\lambda)/\lambda]\tau_1 V(\lambda)d\lambda}{\int [E(\lambda)/\lambda]\tau_2 V(\lambda)d\lambda}.$$

(B) *Cone pigment kinetics*

Rushton (1958, 1963, 1965) showed that the kinetics of bleaching and regeneration of chlorolabe and erythrolabe were so nearly identical that, with a broad spectral distribution (such as the one used here), a single differential equation describes the changes of both as if only a single visual pigment were involved ($p_\epsilon = p_\chi = p$). Consider the bleaching effect of the yellow beam (subscript 3), the equation derived in the Appendix is

$$t_0 \frac{dp}{dt} = (1-p) - KI_3A_3(p, r, \theta). \tag{2}$$

K is a constant which depends upon wave-length but not upon p, r or θ. Ripps & Weale (1964) found that light entering through the edge of the pupil was less effective in bleaching foveal cone pigment than light entering the centre. This result was confirmed by Coble & Rushton (1971) who showed moreover that the intensity of a light entering at any point r required to bleach 50% at equilibrium follows the Stiles parabola,

$$I_3 = I_0\, 10^{q_3(r-r_m)^2}, \tag{3}$$

in which the parameter q_3 is here assumed wave-length independent. Substituting these values in the steady-state form of eqn. (2) gives

$$K = 1/2\, I_0\, 10^{q_3(r-r_m)^2} A_3\,(0{\cdot}5, r, \theta), \tag{4}$$

and, therefore

$$t_0 \frac{dp}{dt} = (1-p) - \frac{I_3 A_3(p, r, \theta)}{2 I_0 10^{q_3(r-r_m)^2} A_3(0{\cdot}5, r, \theta)}. \quad (5)$$

A variety of estimates (Rushton, 1958, 1963, 1965; Rushton & Henry, 1968; Alpern, Maaseidvaag & Ohba, 1971; Hollins & Alpern, 1973; Alpern & Wake, 1977) converge on the value of $t_0 = 2{\cdot}0$ min used here. I_0 has also been measured in these studies, as well as by Coble & Rushton (1971), and Shevell (1977). These results together with a fair number of unpublished measurements on other subjects in my laboratory lead to a value of log $I_0 = 4{\cdot}43$ log td. In theory I_0 (the retinal illuminance of a light needed to bleach 50% of erythrolable at equilibrium ($r = r_m$)) will depend upon l_{r_m} which cannot be directly measured. The difficulty about using a single value for I_0 in eqn. (5) and applying it to all subjects (who were unavailable for long enough periods to measure it directly) is that this estimate was made from results on different subjects very likely with different (and unknowable) values of l_{r_m}. Nevertheless this assumption is made in a theoretical formulation which for other reasons can only be regarded as an approximation. Substituting this value in the equilibrium form of eqn. (5) after taking logarithms gives

$$\log I_3 = \log 2(1-p) + 4{\cdot}43 + q_3(r-r_m)^2 + \log \frac{[A_3(0{\cdot}5, r, \theta)]}{[A_3(p, r, \theta)]} \quad \text{(td)}. \quad (6)$$

The open circles (at the top) in Fig. 5 are the means (bound on either side by vertical lines which terminate at the limits provided by 1 S.E. of the mean) of the fraction of erythrolable (as measured with the Hood & Rushton (1971) retinal densitometer) bleached by various intensities of lights on the one normal subject (R_e) who was available for a sufficient period to be studied in this way. The continuous curve is defined by eqn. (6). ($r = r_m$, $\theta = 0$) with density D obtained from the psychophysical experiment. The agreement is reasonable.

To solve eqn. (1) the following assumptions have been made.

(i) That $R(\lambda) = (1-10^{-D(\lambda)})/(1-10^{-D})$ is given by the 'red' (Koenig type) fundamental tabulated by Wyszecki & Stiles (1967, p. 414) expressed in quanta.

(ii) That $G(\lambda) = (1-10^{-D'(\lambda)})/(1-10^{-D'})$ is given by the 'green' fundamental in that same Table.

(iii) That $E(\lambda)\,T(\lambda)$ is given by a black body radiator of colour temperature 3200 °K (circles, Fig. 1*C*).

(C) *Applying theory to results*

Assuming values for D' and D, the optical densities of chlorolabe and erythrolabe at their respective λ_{max}, one calculates

$$D(\lambda) = \{-\log [1 - R(\lambda)\,(1-10^{-D})]\},$$

and

$$D'(\lambda) = \{-\log [1 - G(\lambda)\,(1-10^{-D'})]\}.$$

The values for $D(\lambda)p_\epsilon$, $D'(\lambda)p_\chi$ can be substituted directly into eqns. (1) and (5) and log I_1/I_2 determined for any value of I_3, t, r, θ. Unfortunately, eqn. (5) has no explicit solution. A PDP11 computer was programmed (i) to carry out the necessary integration in 5 nm steps in the spectral range 495–690 nm for a large variety of values of D and D' and (ii) to solve eqn. (5).

(1) *Equilibrium matches* ($r = r_m$, $\theta = 0$). First, eqns. (1) and (6) were used to fit these results, obtaining values of D, D' which best describe the changes in log I_1/I_2 as a function of log I_3. A purely *ad hoc* adjustment of the theory allowed vertical displacement of the entire curve as might be required if the assumption made about $T(\lambda)$, the transmissivity of the ocular media, were inappropriate for a given observer. These shifts were always small, never exceeding 0·12 log units.

(2) *Changes in matches as a function of time.* The value of D obtained from step 1 was substituted into eqn. (5); it was solved for $p_\epsilon(t)$ [$= p_\chi(t)$] in 0·1 min intervals by Euler's method for the relevant initial condition. Each value of p_ϵ and p_χ was then substituted into eqn. (1) obtaining log I_1/I_2 as a function of time after the onset of given set of matching conditions. In order to be certain that this interval was sufficiently small, the predictions made with it were compared with those obtained with an interval of 0·025 min under the most intense field intensities (where an inappropriately chosen interval size is most likely to prove misleading). Agreement was good.

(3) *Equilibrium matches made with the parafoveal retina* ($r = r_m$, $\theta \neq 0$). All differences

between these and foveal matches were assumed to be due to the path-length in paraforeal cones being smaller than in the foveal cones. The justification for this is the histological observation that the outer segments of foveal cones are longer than those of parafoveal cones. An appropriate reduction in path-length, l, was selected to predict parafoveal matches at low intensities from eqn. (1) given the values obtained from step 1 for this subject. All other parafoveal matches were then completely, and uniquely, determined by the theory.

(4) *Foveal matches* ($\theta = 0$) *made at equilibrium with lights passing through the periphery of the observer's pupil* ($r \neq r_m$). Following Brindley (1953), it is assumed that the path-length through the cones is shorter than for lights which enter the eye through the centre of the pupil. There is no histological justification for the assumption in this case as there is for matches of the parafoveal retina but in other respects the calculation is the same. A smaller value of l, the path length, is applied to the parameters obtained from step 1 for this subject to approximate the matches made at pupil entry point r at low intensities. Once this change in path-length has been assumed, the values of $\log I_1/I_2$ for all other values of $\log I_3$ are once more completely, and uniquely, determined.

(D) *Limitations*

In several respects the theory is unrealistic. (i) The spectra of the long and medium-wave sensitive cones $R(\lambda)$, $G(\lambda)$, are no doubt modified by unknowable absorption by the ocular media which distort the extinction spectra calculations. These distortions are unlikely to be large in the red–green part of the spectrum of concern here. (ii) More serious is the assumption that all normal subjects have identical $R(\lambda)$, $G(\lambda)$ action spectra rather than the more likely one that all have identical $\chi(\lambda)$, $\epsilon(\lambda)$ extinction spectra. Since neither is likely to be exactly true (Alpern & Pugh, 1977) and there is a dearth of explicit information available that would allow of a more realistic approximation, the above approach has been taken in a theoretical analysis primarily concerned with matches of the same individual. Interpretation of individual differences in normal matches in this theoretical frame must, therefore, be guarded. (iii) It is assumed that the intensity I_3 is constant following any given initial condition, while, in fact, I_3 was a time dependent variable. Perhaps because of the limited range of W_y, the variability of these settings was always very small (the standard deviation rarely exceeded 0·1 log units even for imprecise observers). The error introduced by this complexity can, therefore, safely be neglected. (iv) Contributions from short-wave sensitive cones have been assumed negligibly small. However reasonable this may be for low intensity red–green matches entering through the pupil centre, it is not necessarily so more generally even for this part of the spectrum (Enoch Stiles, 1961). These contributions are expected to be more substantial at higher field illuminances than at lower ones (where the green as well as the red and yellow primaries will be subthreshold for the blue cones). Indeed, at the onset and offset of the most intense fields this assumption is untenable and the theory inapplicable in these circumstances (cf. below). Under all others it was found that the matches were always crisply made by adjusting the intensities of only two primaries, so that these contributions were not then sufficiently large to contradict the simple first-order theory developed here. This result is consistent with those of Wyszecki (1978) matching three primaries to white; only the relative amounts of the red and green primaries changed with intensity. There was no change in the ratio of blue to white radiances for the match.

PART II DIFFERENCES IN A GIVEN COLOUR MATCH MADE BY THE SAME OBSERVER

(A) *Time course of match* ($r = r_m$, $\theta = 0$)

Below 10,000 td no systematic change was found in the red–green settings as a function of time after a half a minute or so of adaptation to the field. This was also the case for the adjustment of the yellow, not only at those levels, but all others. However, at illuminance levels which bleach substantial amounts of pigment, there was a systematic change in red wedge settings in time after the onset of the bright field. Fig. 2 is a plot of the log of the retinal illuminance of the red primary minus

that of the green primary of such matches, as a function of time (min) after the subject began viewing. The results are for the five most intense fields. (The ordinate scale is correct for the lowest set of results only; plots for each successively brighter field have been placed 0·1 $\log_{10}$ unit above those obtained with the immediately dimmer field.)

The onset of bright lights which bleach up to about 50% of cone pigments at

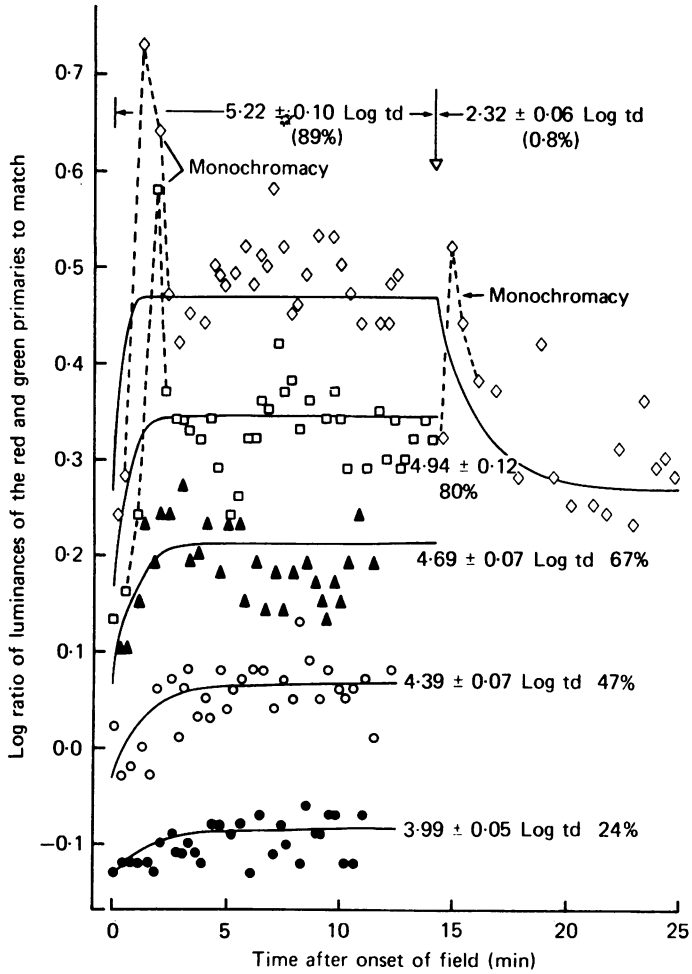

Fig. 2. Matches in time after starting to view the test field at the five highest intensities (single experimental run). The intensities of the red and green primaries whose log ratio at the match are plotted on the ordinate scale are given in trolands. The parameter is the average intensity of the yellow field. The ordinate scale is appropriate for the filled circles (I_3 = 3·99 ± 0·05 log td). Open circles (4·39 ± 0·07 log td) have been displaced up 0·1 log units, filled triangles (469 ± 0·12 log td) have been displaced up 0·2 log units, squares (4·94 ± 0·12 log td) have been displaced up 0·3 log units, and diamonds (5·22 ± 0·1 log td for the first 15 min, 2·32 ± 006 log td thereafter) have been displaced up 0·4 log units. The continuous curves are theoretical (i.e. the solution to eqns. (1) and (5) with appropriate initial conditions) assuming $D' = D = 0·8$. Dotted lines connect settings made during the interval of artificial 'monochromacy'. The fraction of pigment bleached at equilibrium by each average field intensity is indicated on the graph.

equilibrium is followed by a gradual increase in the amount of the red required in the mixture compared with dimmer lights. The matches tended to settle to a new steady (and more protanomalous) level after some 3 min of continuous observation. For brighter lights, the transition between the two states included a period in which any setting of the red wedge in the available range (0·8 $\log_{10}$ units) provided an equally satisfactory match (in the examples illustrated in Fig. 2 these were mainly even more protanomalous than the steady level but in other instances the reverse was true and, in fact, the setting of the red wedge was quite incapable of upsetting the match during this interval). This transition state following the onset of a very bright yellow field disappears within about 3 min and the range of positions of the red wedge for an acceptable match then becomes as sharply defined around the new (protanomalous) level as was the case with less bright matching fields.

A sudden dimming of a bright field (viewed long enough for the matches made with it to become precise) is associated with a similar transient 'monochromacy'. The diamonds in Fig. 2 (beginning at 15 min) illustrate results of one experiment of this kind. For about 2 min after dimming the field, the match was once more independent of any position of the red wedge. This is similar to the violet 'monochromacy' observed by Brindley (1953) from 5 to 45 sec following adapting to a yellow field (dominant wave-length 578 nm) of 315,000 td for 10 sec.

Alpern, Rushton & Torii (1970) showed that long and medium-wave foveal cones saturate when exposed to very bright lights for intervals so short that no appreciable bleaching occurs. No doubt the transitory violet 'monochromacy' found at the onset and offset of these bright yellow lights is related to this cone saturation, although a quantitative formulation of the relationship has yet to be made.

The ratio of red/green needed for a match as a function of time after the onset of each *average* field intensity (supposed invariant with time) was calculated from eqns. (1) and (5), assuming only that $D = D' = 0{\cdot}8$. The continuous lines in the Figure show these theoretical curves. Even neglecting matches made during the transient 'monochromatic' intervals, these curves provide only approximate descriptions of the results. *Ad hoc* adjustment of the photosensitivity of erythrolabe and/or other constants in the general kinetic equation, would improve the fit. However, curve fitting of this degree of precision seems unjustified in view of the uncertainties of the assumptions about the absorbances and concentrations of chlorolabe and erythrolabe for the subject concerned.

Approximate as it is, the agreement is sufficiently good to meet Wright's (1964) objection that, according to the self-screening hypothesis, 'it is surprising that some breakdown does not occur at lower...levels'. No expectation of this kind follows from the theory.

No further attempt has been made to analyse matches made during the transition periods at the onset and offset of lights which bleach appreciable amounts of photopigments. Only results obtained at least 3 min after the onset of the light, at which time matches were always precisely made, are now considered. In later experiments matches made during the first 3 min were not recorded.

(B) *Equilibrium matches as a function of field intensity* ($r = r_m$, $\theta = 0$)

Fig. 3*A* illustrates three sets of matches made in three separate experimental runs on different days. The ordinate in the Figure shows the logarithm of red to green

ratio required for the match (at equilibrium) as a function of the logarithm of the intensity of the fields. The widths and heights of the rectangles in this (and subsequent) figures enclose means by a distance of one standard deviation in each of the four directions.

Despite variability in matches made on successive days, the same general trends are found in each experimental run and (with minor differences, considered below)

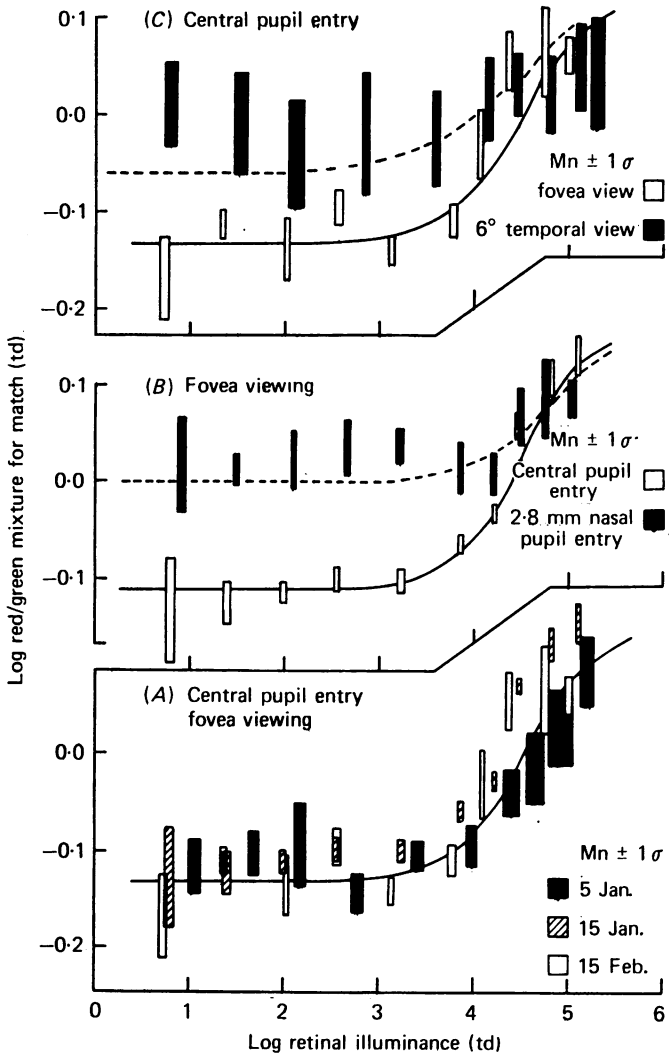

Fig. 3. For legend see facing page.

in every similar experiment carried out on seven normal subjects. At levels of retinal illuminance bleaching only very small amounts of pigment, the matches are more or less stable, independent of the field intensity. Somewhere between 1000 and 10,000 td, equilibrium matches become protanomalous, i.e. more of the red primary is required that at lower levels. With higher retinal illuminances this trend is accentuated until

at levels which at equilibrium bleach 80 % (i.e. roughly 100,000 td) matches approach a limiting value.

The continuous curves in this and Fig. 4 are derived from the theory. In Fig. 3*A* this curve has been shifted vertically up 0·0963 $\log_{10}$ units and the values assumed for $D = D' = 0{\cdot}9$. The agreement is reasonable, though there is a suggestion that the change towards protanomalous matches occurs at higher, and approaches the limiting value at lower, intensities than expected from this simple theory.

The results in Fig. 3*A* were obtained on separate days, the light entering through the centre of the pupil ($r = r_m$) with foveal viewing ($\theta = 0$). Additional experiments shown in Fig. 3*B* and *C* were done on two of these days. On 15 January, the experiment was repeated with foveal viewing, the light entering the pupil 2·8 mm nasal, and on 15 February, with the subject viewing the colorimetric field with a patch of retina 6° temporal to the fovea along the horizontal meridian ($r = r_m$). These additional results are displayed as filled rectangles in Fig. 3*B* and *C* respectively along with those from the appropriate 'control' experiment (i.e. $r = r_m$, $\theta = 0$) as open rectangles.

(C) *The effect of peripheral pupil entry on equilibrium colour matching* ($r \neq r_m$, $\theta = 0$)

The colours of monochromatic lights change (Stiles, 1937) as do the relative amount of primaries required to match them (Brindley, 1953; Enoch & Stiles, 1961) with change in the point of pupil entry of the light into the eye. According to the self-screening hypothesis (Stiles, 1937; Brindley, 1953; Walraven & Bouman, 1960; Enoch & Stiles, 1961; Walraven, 1966), rays entering the edge of the pupil are absorbed by less dense pigments so that the colour matches are more protanomalous than those made with lights passing through the centre of the pupil.

Fig. 3. Log ratio of retinal illuminance of the red and green primaries at the equilibrium match plotted as a function, of field retinal illuminance for the right eye of subject Ma (56 y) (units of both scales, td.) The width and height of each rectangle in this and in the following Figure represent the limits of two standard deviations usually of ten measurements) one on either side of the mean. *A*, three repetitions of the main experiment ($r = r_m$, $\theta = 0$) on separate days. The filled rectangles (5 January) are average results of the equilibrium matches individual settings of which are plotted in Fig. 2. The rectangles with oblique lines (15 January) and unfilled (15 February) are also plotted as open rectangles in Fig. *B* and *C* respectively. *B*, filled rectangles, results on 15 January, taken for foveal viewing ($\theta = 0$) with the lights entering the eye pupil 2·8 mm nasal to its centre ($r - r_m = 2{\cdot}8$). *C*, filled rectangles, results on 15 February with light entering the centre of the pupil but viewing so that the centre of the field fell on a patch of retina 6° temporal to the fovea ($\theta = 6°$, $r = r_m$). The curves are theoretical (eqns. (1) and (6)). The continuous curve refers to results for $r = r_m$, $\theta = 0$. In *A* and *C*, it has been vertically shifted 0·0963 log units and the densities of chlorolabe and erythrolabe at their respective λ_{max} have been assumed equal to 0·9. In *B* it has been shifted vertically 0·116 log units and the densities of chlorabe and erythrolabe at their respective λ_{max}. has been assumed to be 1·0. The dashed curve in *B* is the theoretical expectation when the point of pupil entry is displaced 2·8 mm nasal to the centre. It has been calculated from the continuous curve in this same Figure with the assumption that the length of the light path through the cone outer segment is 0·527 of the path when the light enters the centre of the pupil. The dotted curve in *C* is the theoretical expectation for parafoveal viewing ($\theta = 6°$) calculated from the continuous line in this figure with the assumption that the outer segment length of the parafoveal cones is 0·603 that of foveal cones.

The results in Fig. 3*B* are consistent with this explanation. The continuous curve is similar to that in Fig. 3*A* with slightly different *ad hoc* constants (0·116 for the vertical shift, $D = D' = 1{\cdot}0$) that describe the control results on this particular day (although this day-to-day variability remains unexplained). The dashed curve is the theoretical expectation if the light passing through the pupil at $r = 2{\cdot}8$ mm nasal to its centre, passes through a column of visual pigment in the cone outer segments only 0·527 as long as the path of light passing through r_m. Note that theory predicts, and measurements confirm, a shift toward *deuteranomalous* matching with change in the points of pupil entry from centre to edge when the lights are bright. This change, opposite to that found at low light levels, is small: at 5·2 log td (which bleaches 88% of the pigment passing centrally through the pupil and 75%, 2·8 mm nasal to its centre) 'edge' matches are predicted to be only 0·008 log units more deuteranomalous than 'centre' matches. Measurements at nearly this intensity yield a log red/green ratio of $0{\cdot}088 \pm 0{\cdot}019$ (mean $\pm$ 1 S.D.) for 2·8 mm nasal pupil entry and $0{\cdot}128 \pm 0{\cdot}021$ for central entry. This difference is larger than expected but perhaps not unreasonably so given the sensitivity of the theoretical prediction to the measurement of q_3 the parameter in the directional sensitivity equation, the approximate character of the theory and the measurement precision.

This small effect would scarcely be worthy of note if its physiology were less instructive. At low levels where bleaching is small, matches made with light coming through the edge of the pupil are protanomalous because the rays are absorbed by pigment having about half the density of that absorbing central light. But as the field illuminance is increased, light through the centre begins to reduce (by bleaching) the concentration of its absorbing pigment at a light level which (because of the Stiles–Crawford brightness effect) causes light entering through the edge of the pupil to produce little of no change in pigment concentration. Hence the change in concentation with increase in the amount of light is greater for that entering through the centre of the pupil, than through the edge. For the subject whose results are plotted in Fig. 3*B* the densities of pigments absorbing light entering the centre and edge of the pupil are about the same at about 50,000 td and at still higher levels the light passing through the edge of the pupil is actually absorbed by pigments in greater density (however, dilute) than that absorbing the light passing through the pupil centre.

Although this effect is small in Fig. 3*B*, it would be increased if spectral primaries were used, if the images in the pupil were made very small and if the subjects were young enough for their pupils to be widely enough dilated to permit the light to enter say 4·0 mm off centre.

(D) *The effect of parfoveal viewing* ($r = r_m$, $\theta = 6°$)

The filled rectangles in Fig. 3*C* are the log red/green intensity ratios required for the match at various field intensities when the centre of the field fell upon a patch of retina 6° temporal to the fovea. They were two or three times less precise than foveal matches.

At modest illumination levels parafoveal matches are more protanomalous than those made foveally. This is in rough agreement with expectation if the parafoveal cones contain the same visual pigments as the corresponding foveal cones but in outer segments 0·6 as long. This would happen if the length of the outer segments of parafoveal cones were about 20 μm shorter than that of fovea cones (assuming from the microspectrophotometric measurements of monkey cones of Bowmaker, Dartnall, Lythgoe & Mollon (1978) that the specific density of erythrolable in both

parafoveal and foveal cones is $0{\cdot}013 \pm 0{\cdot}002\ \mu m^{-1}$ and that of chlorolabe is $0{\cdot}015 \pm 0{\cdot}004$). If that were the case, the change in the log red/green settings as the test field intensities approach bleaching levels should be much smaller in the parafovea than in the fovea (Brindley, 1970, p. 221). The results in Fig. 3*C* qualitatively confirm this prediction. However, *quantitative* agreement with theoretical expectation (dotted line) is not very exact. Perhaps this is not too surprising given that both theory and measurements are only rough first order estimations.

Comment

The results described so far were obtained from a single observer. Agreement between theoretical expectation and measurement is by no means exact. Moreover, unanalysed (albeit very slight) *ad hoc* adjustments to density and eye media transmissivity are needed in order to account for results obtained on different days. Nevertheless, the variations in the colour matches of this observer are quite consistent, and in reasonable quantitative agreement with the self-screening hypothesis applied to a single extinction spectrum of chlorolabe and a single extinction spectrum of erythrolabe. No additional hypotheses are required to provide a qualitative and (at least approximate) quantitative account of all the differences in matching made by this subject. To what extent is this true for differences between subjects?

PART III INDIVIDUAL DIFFERENCES

(A) *Normal trichromats*

Repeating the experiment giving the data in Fig. 3*A* on six other practised normal trichromats yielded the results in Fig. 4. All make more protanomalous matches at levels which bleach significantly compared to those made at levels which do not. The size of this change differs remarkably between subjects in a way perhaps related to age. (Each subject's results are placed in the Figure according to age, those for the oldest (75 yr) at the top, youngest (18·5 yr) at the bottom). In theory these differences may be explained by the differences in pigment density. This sample is, however, too small to allow anything more than the suggestion that cone outer segments may be growing longer as subjects grow older.

Some observers tend to make more protanomalous matches at the very lowest intensities compared with those made around 1000 td. The explanation is unclear. It may be related to an inclination in dim fields to allow fixation to wander away fromt the target (as though by recruiting rods into the observation, the clarity of the target might improve). Where such tendency occurs the theoretical curve gives less emphasis to the low intensity matches.

There is no general trend for the differences in matches among normal trichromats to be appreciably smaller at very high light levels. The small sample size again precludes strong inference from this fact, but the suggestion remains that the residual differences can best be accounted for by some combination of individual difference in cone pigments and eye media transmission. (There are other, albeit less likely, possibilities.) Since transmission losses in this part of the spectrum are normally small (perhaps less so in older subjects), the weight of available evidence is in favour of there being cone pigment differences. The point is noteworthy only because repeating

the experiment with monochromatic lights at several different wave-lengths, as in Wyszecki's (1978) experiment, does allow an unequivocal distinction between these alternatives to be drawn, in a way that it is not possible with the results in Fig. 4.

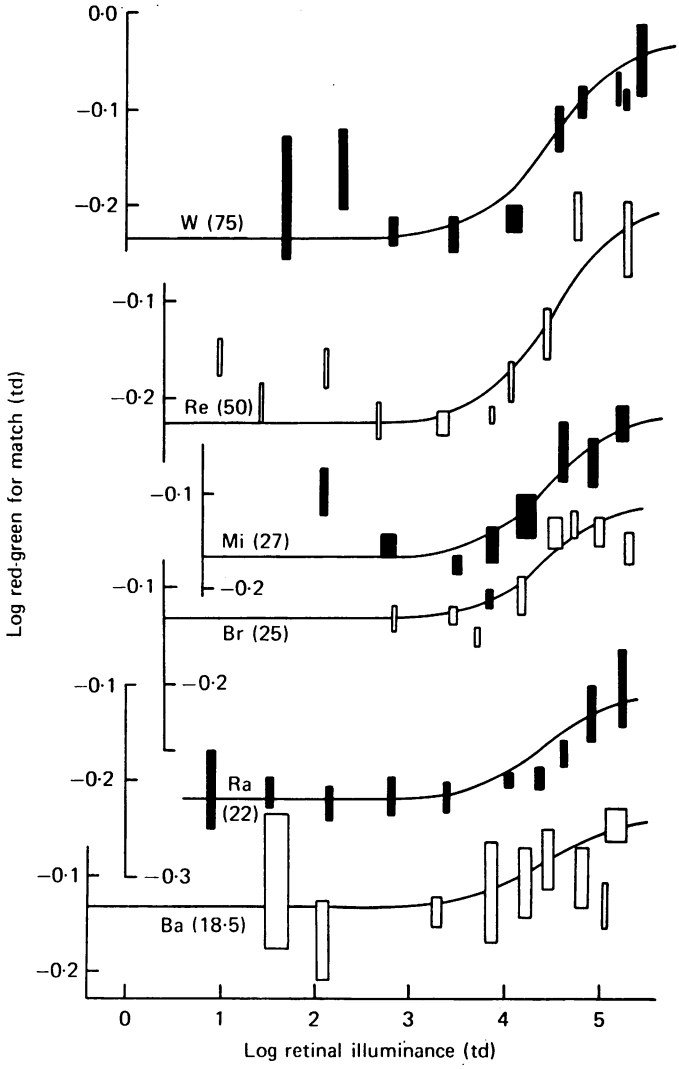

Fig. 4. Equilibrium colour matches at different intensities ($\theta = 0, r = r_m$) for six other normal trichromats. The curves shown by the continuous line are derived from the theory as in Fig. 3. The constants D' and D used in the derivation of these curves are respectively for Ba: 0·32, 0·25; Ra: 0·4, 0·3; Br: 0·5, 0·4; Mi: 0·5, 0·5; Re: 0·8, 0·8; and W: 0·7, 0·7. The age of each subject is given on the Figure. Note that the position of a subject's result is determined by his age, and that according to the theory subjects appear to have pigments of higher and higher density according to their age.

(B) *Anomalous trichromats*

Anomalous trichromats match considerably less precisely than normals. Estimates of the standard deviation from ten measurements of their matches varied in the range between 0·012 to 0·23 compared with 0·008 to 0·05 found among normal trichromats.

Variances this large qualify interpretation of the results (and preclude illustration in the figures).

Despite this qualification there is little to suggest that all anomalous matches converge into the normal range when lights are bright enough to cause significant bleaching as would be expected from the Ruddock–Naghshineh (1974) hypothesis. This is readily seen in Fig. 5 in which the average individual matches for seven normals (points connected by dashes lines), four protanomalous (filled symbols) and eight deuteranomalous (open symbols) are all brought together. Though one protanomalous (M) very nearly and one deuteranomalous (J) very clearly does match normally at the brightest level, Fig. 5 shows that this is by no means the rule.

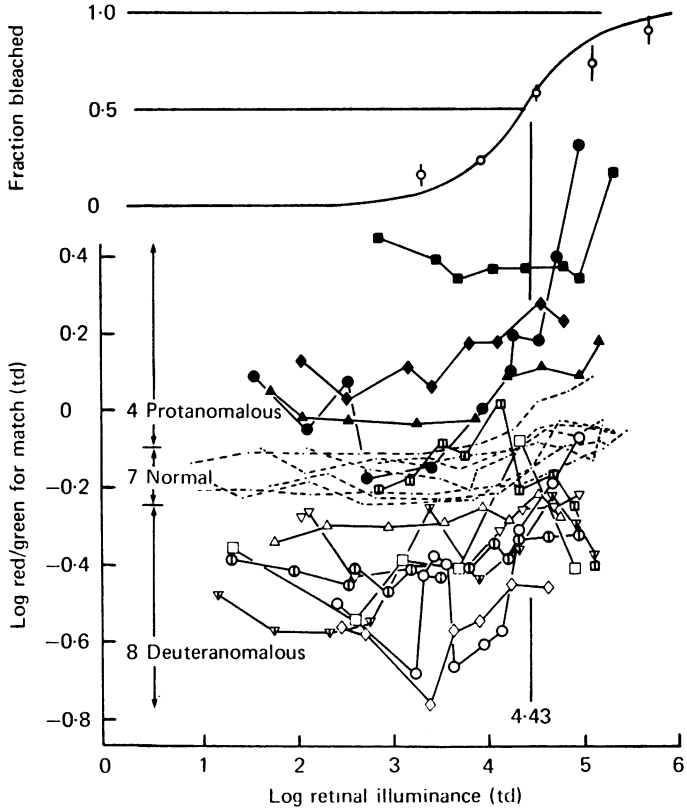

Fig. 5. *Above*: fraction of cone pigment bleached at equilibrium on the fovea of a normal subject Re. Error bars enclose the mean ± S.E. of mean; the curve is defined by eqn. (6) $D = 0{\cdot}8$ appropriate for this subject (cf. Fig. 4). 4·43 log td bleach 50 % at equilibrium. *Below:* average matches of all nineteen trichromats of this study. Points connecting by dashed lines represent normals. Each filled symbol indicates results from a different protanomalous (circle (W), diamond (N) square (H) and triangle (M)). Each open symbol indicates the average matches of a different deuteranomalous (base up triangle, D; square, T; base down triangle, B; diamond, R; square with a vertical line, Pa; circle with a vertical line, P; triangle with a vertical line, A; circle, J). Note that the matches of deuteranomalous J very clearly and of protanomalous M very nearly, fall in the normal range at the highest light level.

DISCUSSION

These results suggest that, excluding contributions of rods and regional differences in transmission of eye media, all changes in matching of a given trichromat are consistent with there being only three visual pigments each in its own cone species so long as it is assumed that the concentrations of such substances are not dilute. Neither an unspecified chemical change in structure of erythrolabe at high levels (Wright, 1964), nor the introduction of an unidentified second photolabile pigments in the long wave cones (Ingling, 1969) nor any other theory (e.g. wave guides) provide as satisfactory quantitative explanation for the changes measured here as does the simple 'self-screening' hypothesis. The optical densities (at λ_{max}) of chlorolabe and erythrolabe required by this theory fall in the range 0·25–1·0. These estimates are close enough to those found by other psychophysical (Brindley, 1955; Enoch & Stiles, 1961; Miller, 1972) and densitometric (King-Smith, 1973*a*, *b*) experiments to have some claim to validity.

The specific density of chlorolabe and erythrolabe in monkey cones found by Bowmaker *et al.* (1978) can be used in conjunction with present estimates of total density to calculate the length of cone outer segments. The results (17–75 μm) bracket the range of estimates from histology (36–40 μm for human; 42–67 μm for monkey) (Polyak, 1941; Dowling, 1965). Allowing for individual differences and inaccurate shrinkage correction, the agreement is close enough to infer that the 'self-screening' hypothesis is consistent with modern microspectrophotometric measurements of pigment density in outer segments of single cones.

The results in Part III, on the other hand, are most consistent with theories of anomalous trichromacy suggesting that the spectrum of at least one of the three species of cone pigments in anomalous trichromats is 'abnormal'. They are quite consistent with Alpern & Pugh's (1977) view that the spectrum of erythrolabe (say) in different normal trichromats also differs, though they do not rigorously exclude the (less likely) alternative that differences in *normal* matching of bright lights, are due to differences in eye media. This matter requires further study.

Nor is the possibility that an occasional anomalous trichromat may have three cone pigments all with 'normal' extinction spectra excluded. Indeed, the matches of one deuteranomalous fell into the middle of the normal range at the highest level. To make the argument compelling even in this case, however, it should be shown that his matches are normal everywhere in the spectrum at these levels. This point (the extent to which deuteranomalous trichromats belong to a homogeneous group) is important and requires further examination matching spectral lights at levels which bleach a major fraction of normal cone pigments, as in the experiments of Wyszecki (1978). Such experiments would also draw an unequivocal distinction between variability of matches related to differences in eye media and those due to differences in pigment extinction spectra.

APPENDIX

The kinetic equation for bleaching and regeneration of erythrolabe

Rushton (1958, 1965), Rushton & Henry (1968), Alpern *et al.* (1971) have shown that because regeneration of erythrolabe in the living eye proceeds quite independently of bleaching, its time rate of change is simply the difference between the bleaching rate and the regeneration rate. The former is given by

$$\frac{dc}{dt} = -\gamma J / l_{r_m},$$

in which $l_{r_m} = l_{r_m}, 0$. Since $p = c/c_0$,

$$\frac{dp}{dt} = -\gamma J / c_0 l_{r_m}.$$

The latter has the form

$$\frac{dp}{dt} = (1-p)/t_0.$$

$$t_0 \frac{dp}{dt} = [1-p] - \frac{\gamma t_0}{c_0 l_{r_m}} U_j \int E(\lambda) T(\lambda) \tau_j(\lambda) \{1 - \text{expt}[-\epsilon(\lambda) c_0 l(r, \theta) p]\} d\lambda,$$

which can be converted to td and written more simply as

$$t_0 \frac{dp}{dt} = (1-p) - \frac{\gamma t_0 I_3 A_3(p, r, \theta)}{c_0 l_{r_m} k \int [E(\lambda)/\lambda] V(\lambda) \tau_3(\lambda) d\lambda}.$$

This is text eqn. (2) in which,

$$K = \frac{\gamma t_0}{c_0 l_{r_m} k \int [E(\lambda)/\lambda] V(\lambda) \tau_3(\lambda) d\lambda}.$$

K is wave-length dependent but independent of p, r, and θ. The fact that K depends upon l_{r_m} is noteworthy because it follows from text eqn. (4) that I_0 the intensity of retinal illuminance required to bleach half of the erythrolabe at equilibrium is also dependent upon l_{r_m}. Thus the suggestion that l_{r_m} varies with subject's age is inconsistent with the assumption that log I_0 is fixed at 4·43 log td independent of the subject. However, this estimate of log I_0 has been made from converging results from different measurements made in different laboratories on different subjects; it appears to be a good first order approximation for the subjects in this experiment (for whom neither l_{r_m} nor log I_0 could be directly measured) in a relatively simple theory, heuristic in the main for the way it deals with non-uniformities in the colour matches of the same subject. Insofar as the theory is applied to non-uniformities of matching between subjects, the constraints imposed by the unrealistic assumption that $R(\lambda)$ and $G(\lambda)$ are appropriate for all subjects has already been noted in the text.

The experiments were carried out in the laboratory of W. A. H. Rushton at Cambridge while on sabbatical leave from the University of Michigan. I am grateful to Professor Rushton for suggesting the test of the Ruddock–Naghshineh hypothesis, for the design and construction of the apparatus, for assisting in the experiments and providing the oldest eye recorded in Fig. 4. The work was assisted by Grants G976-425-N to Professor Rushton from the Medical Research Council, and EY-00197-19 from the National Eye Institute to me. I thank J. G. Robson for introducing me to his PDP 11 computer. Programming was performed at various stages by

Dr Robson, by Dr Norma Graham or by Mr Dennis Pelli, whomever I could corner when the need arose. Clive Hood gave valuable technical assistance. Professor David Krantz of the University of Michigan suggested several improvements on previous versions of this manuscript.

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