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PRERECEPTOR COLOUR VISION DISTORTIONS IN PROTANOMALOUS TRICHROMACY

BY M. ALPERN AND S. TORII*
From the University of Michigan, Ann Arbor, Michigan, U.S.A.

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SUMMARY

1. Scotopic luminosity and fundus spectral reflexion in the protanomalous fail to confirm predictions made from the hypothesis that protanomalous photopic luminosity loss is due to an inert red-absorbing filter in his ocular media.

2. If it were supposed that the luminosity losses were due to a reduced number of normal red cones, the anomaloscope mismatches could result from a prereceptor distortion such as a reduced concentration of macular pigment or a tilt of the foveal cones. Experiments exclude these two possibilities.

3. An anomaloscope is described which makes it possible to measure colour-matching properties of the protanomalous eye by transcleral illumination. Such measurements exclude, as a class, hypotheses which attribute protanomalous colour-matching distortions to an inert filter localized anywhere between the cone outer segment and the cornea.

4. It is concluded that the absorption spectrum of at least one of the three cone visual pigments of the protanomalous eye must differ from that of the pigments of the normal fovea.

INTRODUCTION

One per cent of the male (and 0·02 % of the female) population have the congenital colour vision defect known as protanomalous trichromacy. Such people have a severe loss of luminosity in the red end of the spectrum (Wright, 1946). This loss is nearly identical to that of the protanope (who lacks the red-sensitive pigment, erythrolabe—Rushton, 1963). Furthermore, compared to the normal, the protanomalous require significantly more red in a mixture of red and green to match a yellow (Rayleigh, 1881).

* On leave from the Department of Psychology, Tokyo University of Agriculture and Technology, Tokyo, Japan.

(This measurement, carried out with the anomaloscope, provides an operational definition of the affliction.) Despite these facts, the protanomalous colour-matching functions when expressed in such a way that obviate distortions from prereceptor absorptions in the ocular media and macular pigment are surprisingly similar to those of the normal (McKeon & Wright, 1940). The simplest explanation is that the photolabile cone visual pigments of such observers are identical to those of the normal but that protanomalous eyes contain an inert filter which absorbs light in the red part of the spectrum before it reaches the visual pigments (Fry, 1965).

This hypothesis has the advantage that, while it may not explain every aspect of protanomalous vision, it does account for both the luminosity loss and the colour-matching properties. A less conspicuous prereceptor inert filter could, however, account for the colour-matching properties if the luminosity loss were due to a reduction in number of red cones, such as is occasionally found in the normal fovea (Rushton & Baker, 1964; Lee, 1966).

In the present paper a number of hypotheses of this kind have been evaluated. No evidence to support them was found. Finally, an experiment is described which makes it possible to exclude, as a class, theories of protanomalous colour-matching based on inert prereceptor colour filters. It is concluded that the colour-matching characteristics of the protanomalous must be due to an anomalous photo-sensitive pigment in at least one of the three kinds of cones.

METHODS

Absolute threshold was measured with a $\frac{1}{4}°$ test target for the 10° temporal retina of the right eye. The subject's pupil was widely dilated (using 1% tropicamide) and he was dark-adapted for 30 min before the beginning of the experiment. The light source was a 6 V, 18 A, ribbon filament focused on to a translucent white screen from behind. The subject adjusted the intensity of the neutral (Wratten no. 96) wedge for test flash threshold. Fourteen narrow band (± 3 nm) interference filters mounted in the parallel part of the light path provided monochromatic wave bands through the spectrum. The transmittances of the filters and wedges were measured with a spectrophotometer and checked in front of the light source with a calibrated photomultiplier tube (RCA IP 21). A fixation point was provided whose intensity could be varied to keep it just clearly visible with a rheostat. The subject was carefully screened from all stray light, the light source, filters, and wedge being mounted in a light-tight box on the outside of the light-tight room in which the subject was sitting. The aperture providing the test target immediately behind the translucent screen was the only opening in the wall of this room.

The experiment was completed on five young adult protanomalous subjects. It was repeated on one observer 5 times, on two observers 3 times, on one observer twice, and on the last only once. A given measurement was repeatable within $\pm 0{\cdot}2 \log_{10}$ units from one experimental session to the next on the same subject.

Spectral fundus reflexion. The method was described by Brindley & Willmer (1952) and the present apparatus by Alpern, Thompson & Lee (1965). Briefly, monochromatic light reflected from a subject's eye is focused by the eye's optics on to an artificial pupil after

reflexion at a glass plate. The experimenter looking into the artificial pupil sees the subject's pupil glow in monochromatic light. Light from the monochromator, reflected at the same glass plate and again by a right-angle prism, allows the experimenter a view of the monochromator exit slit. A calibrated neutral wedge in front of the prism was adjusted to obtain a brightness match between the subject's pupil glow and the image of the exit slit seen in the glass plate at each wave band in the spectrum. From this measurement, the known transmissivity of the optical components, and the size of the pupil, the spectral reflexion coefficient of the fundus can be computed directly (Brindley & Willmer, 1952). A fixation point 10° to the right of the monochromator exit slit provided fixation for the peripheral measurements (10° temporal retina for the right eye). For the fovea, the subject fixated the exit slit directly. Pupils were dilated with 1 % tropicamide and measured with a precision of $\pm 0{\cdot}25$ mm with a Broca pupillometer.

The experiment was repeated at each spectral wave-length twice, both for the fovea and the 10° temporal retina, in each experimental session. Two experimental sessions were completed on two observers; one observer completed three experimental sessions and the other completed only one.

Geometric means of the results from all sessions were obtained for each subject. In obtaining the geometric mean of the results from different subjects, the mean results for each subject were given equal weights.

The Nagel anomaloscope consists of a bipartite, 2° colour-matching field viewed through a 0·5 mm artificial pupil. There are two knobs. The left-hand one controls the ratio of red (λ = 671 nm) and green (λ = 536 nm) needed to match the yellow (λ = 589 nm). The right-hand knob varies the intensity of the yellow beam. In the standard method of administrating the test, the subject makes three 'free' matches in which he adjusts both knobs for a satisfactory match. The examiner then fixes the red/green ratio within this range of matches. The subject matches by adjusting the intensity of the yellow field or states that he cannot because the match is 'too red' or 'too green'. The examiner resets the red/green knob accordingly and the process is repeated. The procedure continues in small increments in the red/green settings, in this way measuring the limits of the range of settings in which acceptable matches are possible.

Directional sensitivity measurements. A 2° centrally fixed field of monochromatic light flickering at 30 c/s was seen in Maxwellian view through a 0·5 mm artificial pupil. The subject's pupil was widely dilated with 1 % tropicamide. The centring of the subject's pupil with respect to the artificial pupil could be varied independently in a horizontal and a vertical direction by two micrometer screw attachments to the sturdy bite bar assembly which clamped the subject's head in position. The edges of the pupil are readily determined in this method by subjective eclipse of the test field. A calibrated neutral wedge mounted in the light path was adjusted for a threshold flicker for different horizontal and vertical positions across the subject's pupil in 0·5 mm intervals. The experiment was repeated on two protanomalous subjects 5 times at a variety of wave bands in the spectrum. The identical method was also used to measure anomaloscope matches for different regions of pupillary entry.

RESULTS

Part I

Scotopic spectral sensitivity. A prereceptor pigment in the ocular media of the protanomalous subject which would account for his *photopic* luminosity curve should cause identical distortions of his *scotopic* luminosity curve. The continuous line in Fig. 1 shows the logarithm of the C.I.E. standard scotopic luminosity curve; the dashed line shows the

logarithm of the scotopic curve predicted for the protanomalous if a prereceptor inert pigment in the ocular media were to account for his luminosity losses. The open circles show the averages of the logarithms of the absolute thresholds for rod vision on five protanomalous observers at fourteen different wave bands throughout the spectrum. They fit the continuous line much better than the dashed line. This result excludes a prereceptor inert filter in the eye media common to the fovea and to the 10° temporal retina examined in Fig. 1 as the explanation for the photopic

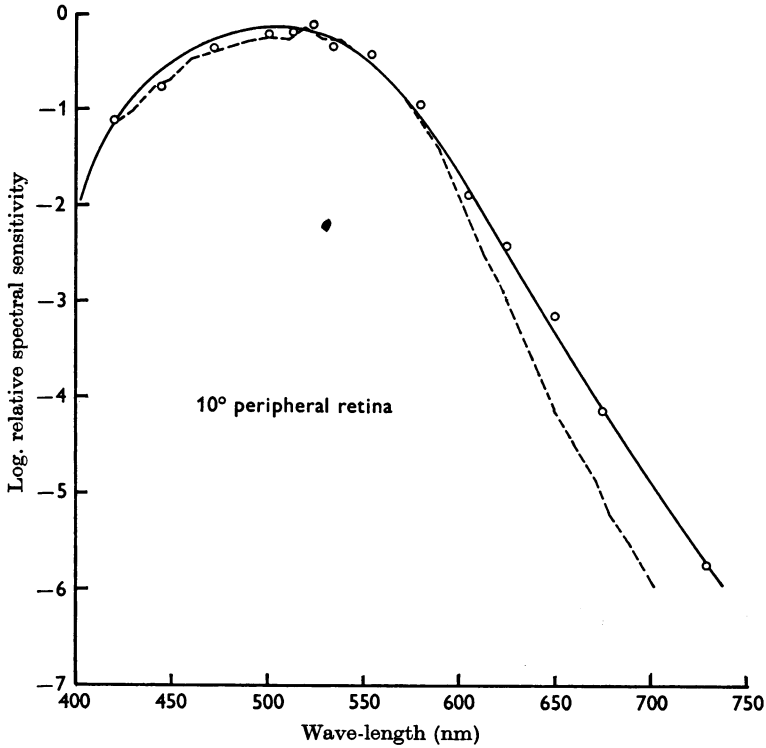

Fig. 1. Logarithm of the relative scotopic spectral sensitivity curve for (¼°) test target 10° temporal retina of the right eye of five protanomalous observers (open circles). The continuous line shows the logarithm of the C.I.E. scotopic luminosity curve. The dashed line is the protanomalous measurement predicted if a prereceptor filter would distort the scotopic curve in the same way as the mean protanomalous photopic luminosity curve is distorted.

luminosity loss. On this basis, one excludes as a possible site for such a filter the cornea, aqueous humour, lens, and at least the anterior part of the vitreous body and uniform distribution throughout the remainder of the vitreous and the transparent layers of the retina. To obtain information about a non-uniform distribution in the posterior part of the eye, measurements of the spectral reflexion coefficients of the fundus are of some value.

Fundus reflexion. Two possibilities can be considered: (1) that the prereceptor pigment in the protanomalous fundus is uniformly confined to the posterior vitreous or to the retina around the fovea and is not found at

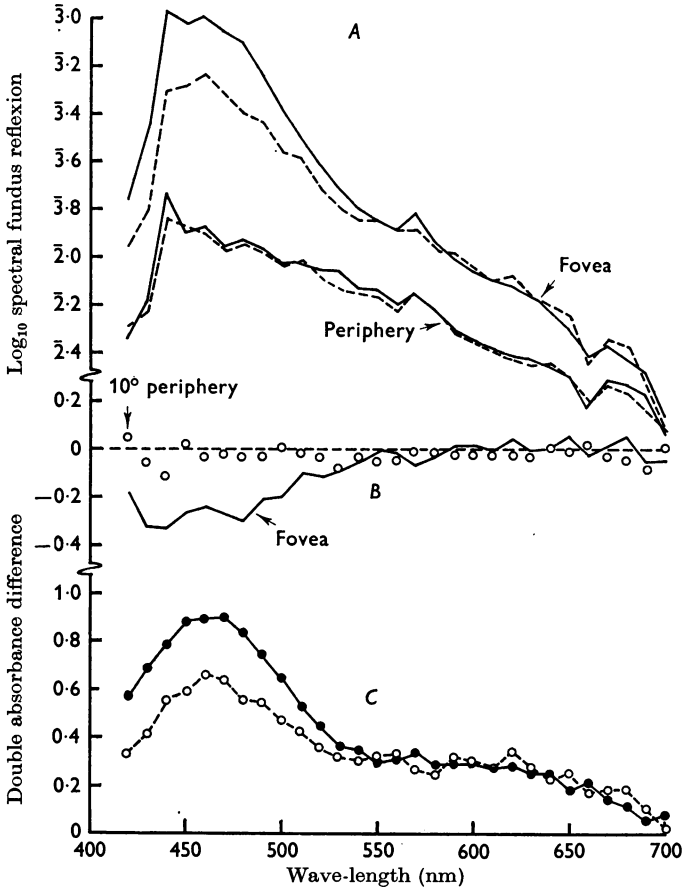

Fig. 2. *A.* Spectral reflexion coefficient of the fovea and 10° temporal fundus in four young normal subjects (continuous line) and four young protanomalous subjects (dashed line). *B.* Differences between the normal and protanomalous curves illustrated in *A*: fovea (continuous line); 10° temporal fundus (open circles). *C.* Differences between the fovea and peripheral measurements illustrated in *A*. Filled circles, continuous line for the normal; open circles, dashed line for the protanomalous.

all in the vitreous and/or the retina in the 10° temporal retina, and (2) that the prereceptor pigment is confined uniformly to all the protanomalous cones (foveal and peripheral) but not to the 'protanomalous' rods.

The mean results of measurements on four normal and four protanomalous eyes are shown in Fig. 2. If possibility (1) were correct and a

red-absorbing pigment were situated in front of the fovea (but not 10° away as we have seen), then near the fovea the protanomalous fundus will show much less reflected red light than the normal fundus.

If possibility (2) were valid and a screening pigment were placed in front of cones (but not rods), then, since the cone population is densest near the fovea, so this red-screening pigment will be densest there. Consequently, we should expect the same result as with possibility (1)—the protanomalous fundus will reflect less red light than the normal fundus, and this reflexion deficit will be more conspicuous near the fovea than 10° away.

Experiment verified neither possibility. Contrary to (1), the reflexion coefficients of the fovea and peripheral retina are almost identical in the red part of the spectrum in the protanomalous (as in the normal) retina. A difference of 2·0 absorbance at 700 nm is expected on the basis of the luminosity deviations.

This conclusion can be verified by another experiment which is easily performed by anyone who examines the fundus of a protanomalous eye with an ophthalmoscope. If a red filter, such as a Wratten no. 92 gelatin, is introduced into the light path, the macular area—according to possibility (1)—would stand out as very black against the red of the surrounding retina, since the prereceptor pigment must absorb about 100 times as much light of 700 nm as the peripheral retina. In fact, the protanomalous (as the normal) fovea and periphery are virtually indistinguishable in red light. Still a third way of excluding this possibility is to show that protanomalous colour matches in the 10° temporal retina are at least as anomalous as his foveal matches. This is an invariable finding.

The second possibility—that all protanomalous cones have red-absorbing 'oil droplets'—is also not confirmed by fundus reflexion. By it, the normal retina should reflect more red light than the protanomalous fundus. It is difficult to be certain of how much more, since we do not know how much of the light in the reflexion coefficient measurements has passed through the retina but passed around the prereceptor pigment. Rushton (1965) has treated a similar problem theoretically as it relates to retinal densitometry. Using this theroetical treatment permits a conservative estimate, that all other things being equal, if as little as 10% of the measurement light passes twice through a filter which could explain the protanomalous foveal luminosity curve, this increased absorbance of the protanomalous fovea in the red part of the spectrum could be easily detected. In fact, however, the protanomalous foveal fundus reflects about 0·06 $\log_{10}$ units more—not less—light at 700 nm than the normal fovea.

Part II

The above experiments exclude a scheme which would account for both luminosity losses and colour-matching functions of the protanomalous on the basis of a prereceptor inert filter. However, some normal eyes show

a protanomalous luminosity curve (Lee, 1966), presumably because the number of red-sensitive cones in their foveas are reduced (Rushton & Baker, 1964). The protanomalous might also have a greatly reduced number of red-sensitive cones (accounting for their luminosity loss) *and* a prereceptor inert filter (accounting for their colour matches). The colour of such a filter could be much less obvious than that excluded by the experiments in Part I. The fundus reflexion measurements of Part I suggest one possibility, namely, that the protanomalous fovea is deficient in macular pigment.

Macular pigment. Since the macular pigment absorbs a certain amount of green light, the reduced amount of protanomalous macular pigment illustrated in Fig. 2*C* could account for protanomalous anomaloscope matches. Indeed, normal eyes make more protanomalous matches (1) when they view the anomaloscope with a part of the retina outside the area covered by the macular pigment, and (2) when the absorbance of the macular pigment is rendered neutral by viewing through a filter whose spectral transmittance opposes that of the macula (Wratten no. 80B). To test this possibility further, we sought to find how much macular pigment would need to be added to the protanomalous fovea in order to obtain normal colour matches.

The skins of fresh carrots were scraped into a mortar and ground fine in the presence of chloroform. The contents were filtered and poured into a 1 cm cuvette. When the absorbance at 450 nm was about 0·5, the absorption spectrum of this solution agreed well with the most recent measurements of that of the macular pigment in the retinas of enucleated human eyes (Wald & Brown, 1965). By varying the volume of chloroform, solutions with a variety of different absorbances were obtained. The colour matches of protanomalous observers looking through a cuvette containing the solution were obtained by mounting it immediately behind the exit pupil of the anomaloscope.

The results of one of such experiment are illustrated in Fig. 3. The ordinates show the anomaloscope settings—100 representing pure red, 0 representing pure green—and the abscissa gives the absorbance at 450 nm of the solution. The three horizontal lines in the figure show the middle and the range of acceptable 'normal' settings. The plotted points are the mid points and range of acceptable matches for this protanomalous subject. If his anomaloscope mismatches were due to a lack of macular pigment, the measurements of his fundus reflexion indicate that the amount of this deficiency would be completely compensated by less than 0·3 absorbance at 450 nm of the solution. This very dilute solution scarcely alters his anomaloscope settings at all, and it requires a solution with one whole order of magnitude larger absorbance at 450 nm to obtain a reasonably normal match. Since this represents a 500-fold error in transmittance at 450 nm over that predicted theoretically, it is evident that this hypothesis

is quite unsatisfactory. (The protanomalous, unlike the deuteranomalous (Walls & Mathews, 1952), usually experience little difficulty in viewing Maxwell's spot which has been described as an entoptic demonstration of macular pigment.)

Directional sensitivity of protanomalous cones. An alternative hypothesis is that the foveal cones in the protanomalous fovea are tilted with respect to the centre of the pupil. It is well known that the normal eye makes more

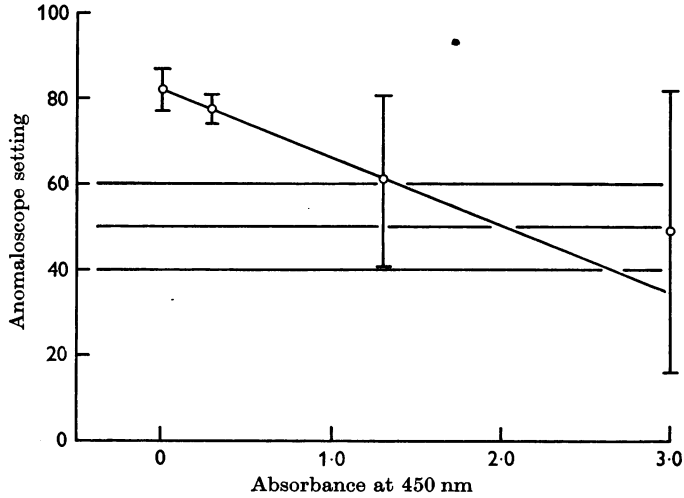

Fig. 3. Anomaloscope settings of a protanomalous observer looking through various concentrations of carrot skin chloroform solution in a 1 cm cuvette mounted directly behind the exit pupil of the anomaloscope. The absorption spectrum of a solution with absorbance of 0·5 at 450 nm is nearly identical with Wald & Brown's (1965) measurements of the absorption spectrum of human macular pigment. The open circle is the mid-point of the setting; the solid line shows the range of acceptable matches. The abscissa shows the absorbance at 450 nm of the different concentrations of solution. The fundus reflexion measurements indicate a deficiency in absorbance at 450 nm of about 0·3 for this subject.

protanomalous anomaloscope matches when the light enters the foveal cones at an oblique angle of incidence (Brindley, 1953; Enoch & Stiles, 1961) than matches made when light strikes the cones with normal angle of incidence.

No evidence to support this explanation for protanomalous colour matches was found. Measurements of directional sensitivity on the protanomalous (as on the normal) are fitted well by the (Stiles, 1937) parabola

$$\log_{10} I/I_0 = \alpha(r - r_0)^2,$$

in which I represents the luminance required to eliminate 30 c/s flicker, r is the point of pupil entry (mm), and the subscript 0 refers to these

respective values at the point of maximum effectivity. In our experiments constants α and r_0 are measured with a precision of $\pm 0{\cdot}001$ and $\pm 0{\cdot}025$ mm, respectively. For the protanomalous, each of these constants is well within the limits of the values obtained on the normal fovea. Furthermore, we have had protanomalous subjects make anomaloscope matches when the light pencil (0·5 mm in diameter) enters different parts of the widely dilated pupil, but we could never find a point of pupil entry where the anomaloscope matches were at all within the normal range nor any suggestion that such a position would be found if the angle of incidence of the anomaloscope beam could have been made even more oblique than that permitted by the margin of the iris. Taken together, these experiments make the hypothesis that receptor misalignment is responsible for the anomaloscope mismatches of the protanomalous quite improbable.

The transcleral anomaloscope. The experiments just described exclude two possible ways of explaining the colour matches of the protanomalous, assuming their photolabile cone pigments were exactly normal. They are, however, by no means the only possible mechanisms that can be imagined. It is of some value therefore to exclude as a class all explanations of protanomalous colour matches based on an hypothesized inert filter residing somewhere between the outer segments of the protanomalous foveal cones and the cornea. This is achieved by the following experiment, a modification of one described by Brindley & Rushton (1959).

Light from two separate sources orthogonally polarized was brought together by a mixing cube and focused on to the entrance port of an optical fibre bundle mounted in the wall of a light-tight room. One of the beams was red, obtained by a glass filter transmitting only light of wave-lengths greater than 650 nm; the other was green, provided by a very narrow band interference filter with peak transmittance 552 ± 3 nm. The proportion of red and green light in the mixture was varied by a rotating polaroid in the common beam. The other end of the optical fibre bundle was fitted with a glass rod with a smooth, well-rounded tip which either the subject or the examiner placed firmly against the temporal sclera as the eye (the right) turned to the left. A piece of glossy white paper was taped against the nose, and monochromatic light (589 nm) from a Bausch & Lomb grating monochromator was focused on to it. This image of the exit slit, about 1 mm^2 in area, was seen by the subject in the usual way through the pupil. Its intensity was varied by the subject, who adjusted the current to the monochromator light source with a rheostat.

The tip of the glass rod was pressed against the subject's temporal sclera. The subject, with fully dilated pupil (two drops of 1% Mydriacyl), saw the image produced by the light which transilluminated the sclera as a bright spot immediately adjacent to the yellow field on the glossy white paper illuminated by the monochromator. His task was to vary the intensity of the yellow comparison standard to obtain a match of the yellow spot with the bright spot produced by the red/green mixture which transilluminated the sclera from behind. The proportion of red/green in the mixture was set at a specific value, and if the subject could not match, he indicated whether this was because the mixture was 'too red' or 'too green'. The proportion was changed accordingly and the subject again attempted a match. The process was repeated until the range of values which gave satisfactory matches was determined.

A small dental mirror held by the subject at the medial canthus against his nose allowed him to view the eye of a (normal) observer looking into the mirror. By rotation of the mirror, the subject found it possible to superimpose the 'spot' of light (seen by transcleral illumination from the glass rod) on the observer's pupil. The observer then saw the subject's pupil glowing from the transcleral illumination. The proportion of red and green in the transcleral mixture required for the normal observer to match the yellow reflected off a white piece of paper taped to the subject's nose was determined in a similar way.

It proved impractical for the subject and observer to make matches in the same run. However, subjects did estimate whether or not matches made by the examiner were satisfactory to them.

It is difficult to be certain about the precise region of the retina tested under these conditions, and undoubtedly it varied from one subject to the next and probably also on the same subject from one observation to the next. An attempt was made to get the glass rod as far back on the sclera as possible (by wedging it in the temporal fornix), but this rarely, if ever, reached the macular area. The more usual region was in the temporal retina about 22° from the fovea.

This test is useful if, and only if, protanomalous observers are still protanomalous in the region of the retina excited by the test lights. We have made measurements with the usual anomaloscope (i.e. light entering the eye in the normal way) in the relevant part of the peripheral retina in several protanomalous subjects. In some instances foveal protanomalous subjects are protanopic in the region of the retina tested by the transcleral anomaloscope, a feature which excluded them from the test. Two protanomalous subjects whose colour matches were not very different in the peripheral retina compared with the fovea did succeed in making satisfactory matches with the transcleral anomaloscope, and the results which follow are based on their observations.

Consider two possible explanations of protanomaly: (*a*) that there is an abnormal pigment in one class of cone, (*b*) that the cone pigments are normal but some abnormal stable screening pigment is situated in front of the cones. The Rayleigh match is made not only in the usual way with lights entering through the pupil, but also with the red + green mixture entering the eye through the sclera and passing through the retina from behind, matched against a yellow light projected against the side of the nose. With this arrangement there are two kinds of match: (i) that made by the protanomalous himself, (ii) that made by a normal investigator who matches the yellow light on the nose of the protanomalous against the red + green mixture emerging from his pupil.

In comparing these measurements with those made upon a normal subject, expectations depend sharply upon whether possibility (*a*) or (*b*) is adopted. With (*a*) (the abnormal cone pigment), the *protanomalous* will make the same deviation from the normal match whether the light passes from behind or in front; but the *investigator*, matching the mixture emerging from the pupil, will make the same setting for protan as for normal (the cone pigments forming so dilute a screen).

With (*b*) (the dense screening pigment in front of the cones), on the other hand, the protanomalous will make the same match as the normal when light passes from behind, since now the screening pigment is not inter-

posed. But it *is* interposed in the light that leaves his pupil to be matched by the (normal) investigator. Consequently in comparing the light emerging from the protanomalous eye with the normal eye, the investigator will require the same red excess for his match that the protanomalous did for *his* match, made with light entering through the pupil in the ordinary way. For in both cases the same screening pigment is interposed.

TABLE 1. Anomaloscope matches
Fraction of red ($\lambda \geqslant 650$ nm) in a red/green ($\lambda = 552 \pm 3$ nm) mixture needed to match yellow ($\lambda = 589 \pm 3$ nm).

Subject	Normal illumination			Transcleral illumination: As matched by a normal observer looking through the subject's pupil			Transcleral illumination: As matched by the subject		
	N	$\frac{R}{R+G}$	Range	N	$\frac{R}{R+G}$	Range	N	$\frac{R}{R+G}$	Range
Protanomalous:									
R.G.	10	0·830	±0·043	10	0·134	±0·052	5	0·587	±0·044
G.D.	10	0·736	±0·038	6	0·104	±0·082	5	0·577	±0·044
Normal:									
M.A.	5	0·519	±0·033	11	0·179	±0·163	5	0·147	±0·068
							5	0·138	±0·030
L.G.	5	0·500	±0·009	10	0·117	±0·043	10	0·231	±0·108
S.T.	10	0·416	±0·031	Palpebral fissure too narrow to match			5	0·215	±0·031
							6	0·203	±0·017

The results of such experiments, summarized in Table 1, completely confirm alternative (*a*). Protanomalous subjects require more red in the mixture to match a yellow compared with normal subjects, whether the red/green mixture enters the eye from in front through the pupil or from behind through the sclera. Presumably (cf. below) this is due to difference in the absorption spectra of anomalous pigments in the red- (and/or green-) sensitive cones. It cannot be due to a prereceptor colour filter because a normal observer looking through the protanomalous pupil at the red/green mixture transilluminated through the sclera makes essentially the same settings in matching it to a yellow (seen next to the pupil) as he does for a similar experiment on normal eyes. The normal subject whose eye is illuminated through the sclera accepts the matches made by the normal examiner looking through his pupil at the mixture as 'about right', but the protanomalous examined in the same way finds them unsatisfactory. (He requires much more red.)

DISCUSSION

These experiments exclude the possibility that the protanomalous colour matches can be explained merely by the existence of an inert prereceptor pigment in the anomalous eye which alters the absorption spectra

of normal photolabile visual pigments. In the normal, colour vision depends upon three different kinds of photolabile pigments, each in its own kind of cone (Marks, Dobelle & MacNichol, 1964). If, as is almost certainly the case, the response of each kind of cone is univariant, then the linearity of Grassman's three laws follows directly. Accordingly, the results of the experiments described in this paper lead to the important conclusion that to explain protanomalous colour matches the absorption spectrum of at least one of their three cone visual pigments must be different from that of the cones of the normal fovea.

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REFERENCES

ALPERN, M., THOMPSON, S. & LEE, M. S. (1965). Spectral transmittance of visible light by the living human eye. *J. opt. Soc. Am.* **55**, 723–727.

BRINDLEY, G. S. (1953). The effects on colour vision of adaptation to very bright lights. *J. Physiol.* **122**, 332–350.

BRINDLEY, G. S. & RUSHTON, W. A. H. (1959). The colour of monochromatic light when passed into the human retina from behind. *J. Physiol.* **147**, 204–208.

BRINDLEY, G. S. & WILLMER, E. N. (1952). The reflexion of light from the macular and peripheral fundus oculi in man. *J. Physiol.* **116**, 350–356.

ENOCH, J. M. & STILES, W. S. (1961). The colour change of monochromatic light with retinal angle of incidence. *Optica Acta* **8**, 329–358.

FRY, G. A. (1965). Mechanisms subserving color vision. *Am. J. Optom.* **42**, 271–287.

LEE, G. B. (1966). Luminosity curve differences among subjects with normal color vision. *J. opt. Soc. Am.* **56**, 1451.

MARKS, W. B., DOBELLE, W. H. & MACNICHOL, E. F., JR (1964). Visual pigments of single primate cones. *Science, N.Y.* **143**, 1181–1183.

MCKEON, W. M. & WRIGHT, W. D. (1940). The characteristics of protanomalous vision. *Proc. phys. Soc.* **52**, 464–479.

RAYLEIGH, LORD (1881). Experiments on colour. *Nature, Lond.* **25**, 64–66.

RUSHTON, W. A. H. (1963). A cone pigment in the protanope. *J. Physiol.* **168**, 345–359.

RUSHTON, W. A. H. (1965). Stray light and the measurement of mixed pigments in the retina. *J. Physiol.* **176**, 46–55.

RUSHTON, W. A. H. & BAKER, H. D. (1964). Red/green sensitivity in normal vision. *Vision Res.* **4**, 75–85.

STILES, W. S. (1937). The luminous efficiency of monochromatic rays entering the eye pupil at different points and a new colour effect. *Proc. R. Soc.* B **123**, 90–118.

WALD, G. & BROWN, P. K. (1965). Human color vision and color blindness. *Cold Spring Harb. Symp. quant. Biol.* **30**, 345–361.

WALLS, G. L. & MATHEWS, R. W. (1952). *New Means of Studying Color Blindness and Normal Foveal Color Vision*, 172 pp. University of California Publications in Psychology, vol. 7, no. 1. Berkeley: University of California Press.

WRIGHT, W. D. (1946). *Researches on Normal and Defective Colour Vision*, p. 308. London: Henry Kimpton.