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RED–GREEN BLINDNESS CONFINED TO ONE EYE

DONALD I. A. MACLEOD
Department of Psychology, University of California, San Diego, La Jolla, CA 92093, U.S.A.

and

PETER LENNIE
Psychological Laboratory, Downing Street, Cambridge CB2 3EB, England

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Abstract—We report experimental studies of an individual with different types of color vision in his two eyes. The left eye is typically deuteranomalous, with good wavelength discrimination. The right eye is typically deuteranopic, both in its wavelength discrimination and in its color matching functions. Luminosity curves of left and right eyes are indistinguishable, both being within the normal range. Binocular matches show that the colors seen with the dichromatic eye range from "orange" (610 nm) at long wavelengths to "greenish blue" (473 or 474 nm) at short wavelengths. Possible physiological and genetic mechanisms are discussed.

INTRODUCTION

The nature of the link between deuteranopia and normal color vision has been a central problem in color theory for more than a hundred years, and many experiments have attempted to clarify it. Thanks to the investigations of Pitt (1935) and others, reviewed by Nimeroff (1970), it is now possible to specify which colors deuteranopic observers confuse with which: which greens, for instance, a deuteranope will confuse with a given red or purple. But these experiments have left unanswered a still more basic question: just what color sensations does a deuteranope experience? Does he see red as green, or green as red, or both as yellow or some other color? It is useless to put this question directly to the deuteranope, for since the deuteranope knows nothing of the normal observer's color sensations, there is no guarantee that when he uses a particular color name the color sensation intended is the one to which a normal observer would apply the term. Clearly too, normal observers, lacking access to the deuteranope's experience, can never learn which of their own color sensations are available to him.

For information about the colors seen by deuteranopes, we have to rely mainly on certain rare individuals whose deuteranopia is confined to one eye, the other eye being more or less normal. For these unilateral color blinds it is a simple matter to identify, among a range of colors viewed monocularly with the normal eye, the particular color that matches a test color viewed by the color-blind eye. From the binocular matches of a unilateral deuteranope the normal individual can perhaps learn which of his own color sensations are experienced by deuteranopes.

Although the special importance of unilateral congenital red–green blindness has long been recognized (Judd, 1948), only four unilaterally dichromatic cases have been reported up to now, and probably only one of these is a deuteranope. The earliest case is the one studied by von Hippel (1880, 1881) and by Holmgren (1881) and discussed more recently by Walls and Mathews (1952). Both von Hippel and Holmgren found evidence of substantially reduced sensitivity to long wavelengths in the red–green blind eye, so this observer was probably a unilateral protanope. A second case of unilateral red–green blindness, possibly congenital, was reported by von Neipperg in 1932 but was not extensively studied. In a third case (Sloan and Wollach, 1948), the color-blind eye appears to have been truly deuteranopic: the other eye exhibited a relatively slight deutan-like deficiency. All of these unilateral dichromats, and others too (Judd, 1948), saw with their dichromatic eyes colors ranging between blue at the short wavelength end of the spectrum and yellow at the long wavelength end, and this fact has had considerable influence on the theory of color blindness (see, for instance, Judd, 1949; Graham, 1965).

The case of AHC

Currently the best-known case of unilateral dichromatism is the one investigated by Graham and his associates (Berger, Graham and Hsia, 1958; Graham and Hsia, 1958a,b,c, 1959; Graham, Sperling, Hsia and Coulson, 1961). Despite some scepticism (Walls, 1958; Cox, 1961; Weil, 1964), this case is generally regarded as an instance of unilateral deuteranopia, though perhaps somewhat atypical. Yet it is clear from the extensive and precise measurements carried out by the Columbia group that the color vision of this observer is quite unlike any known variety of congenitally defective color vision. The hue discrimination curves, for example, sufficiently demonstrate the unusual character of the defect: good or moderate wavelength discrimination in the red and in the violet are features characteristic of this observer but never found in protanopia or deuteranopia. But it is in the color matching data that the individuality of this observer is most clearly apparent. Graham and his colleagues measured the amounts of red (650 nm) and blue (460 nm) required in a red–blue mixture to match a series of monochromatic lights. These data were initially reported in the form of dichromatic coefficients, together with the comparable data

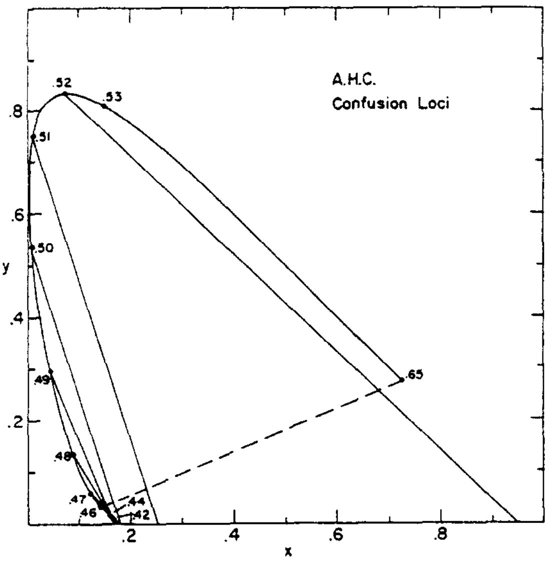

Fig. 1. CIE chromaticity diagram showing confusion loci for the unilateral dichromat AHC, from the data of Graham *et al.* (1961), Table 3.

of Pitt (1935); but the most recent paper presents a table of the untransformed energy measurements (Graham *et al.*, 1961, Table 3). This table records that to match blue-green light of 490 nm, AHC required 12 energy units of blue per unit red; to match 500 nm she required 5 energy units of blue per unit red. Pitt's deuteranopes, in contrast, matched these two wavelengths to mixtures containing, respectively, 5 and 15 times more red than blue (Wyszecki and Stiles, 1967, p. 408). So AHC here required about 60 times as much blue per unit red as did Pitt's deuteranopes. Huge though it is, this difference has received no discussion, probably because it was eliminated in the calculation of the dichromatic coefficients; these coefficients incorporate an observer-specific normalization factor, the value of which was chosen so as to bring the data for the unilateral observer into conformity with Pitt's at 494 nm. The real discrepancy between the two sets of data is illustrated in the CIE diagram of Fig. 1, in which straight lines have been drawn between the locations of various spectral lights and the purple mixtures chosen by AHC to match them. These lines clearly do not converge near Pitt's deuteranopic copoint, the approximate coordinates of which are (1·08, −0·08). Instead, some of the lines intersect near the violet corner, others near the green.

It is particularly strange that 410 nm in the violet corner is confused with 500 nm, a wavelength very close to the quoted neutral point of 502 nm (Graham *et al.*, 1961, p. 18). The implication is that to this observer, 410 nm has an appearance similar to white; yet to a deuteranope, violet is of all colors the one that least resembles white. The neutral point itself raises another interesting problem. A neutral point at 502 nm is quite consistent with a diagnosis of deuteranopia. The published set of color mixture functions (Graham *et al.*, 1961, Table 3), however, is incompatible with a neutral point at 502 nm and suggests instead a much longer wavelength, well outside most estimates of the deuteranopic range of neutral points.[1] This contradiction makes it impossible to accept the 502-nm neutral point with confidence. But even if the neutral point were indeed typically deuteranopic, the evidence from wavelength discrimination and color mixture would be enough to rule out a diagnosis of deuteranopia, since the data yielded by Graham's observer in these experiments are quite different from those of every known deuteranope and bear no obvious relationship to the data of deuteranopes. Therefore among the unilaterally color-blind observers described to date, only the Sloan and Wollach observer can be confidently classified as a deuteranope.

The case of RH

We have investigated the color vision of RH, a unilateral color blind who resembles Sloan and Wollach's observer in that his left eye is deuteranomalous, while his right eye exhibits the characteristics of deuteranopia. RH was a student, aged 21, with no history of visual disturbance. A physical examination of his eyes by Dr. P. G. Watson (using the ophthalmoscope, fluorescein angiography and the Amsler charts) has shown no evidence of injury or disease. The dichromatic right eye requires a concave lens of 0·75 D; with this correction his visual acuity is as good as that of the best normal observers (20/5) with either eye, the right eye being marginally the better of the two. We know of no defects of color vision among his relatives. The Ishihara test was administered to both his parents and also to his mother's brother and father. All were apparently normal. The mother was also tested with the Nagel anomaloscope and gave normal results with each eye. She was aware of definite differences in color appearance between her two eyes. These differences were not pronounced, however, and were as conspicuous for blue as for red or green. Curiously enough, RH himself was surprised to learn that his two eyes were different.

Our investigation of RH has included a preliminary examination of each eye with an anomaloscope and with the Ishihara test, followed by experimental determinations of (1) the wavelength discrimination and (2) the luminosity curve of each eye; (3) the amounts of red and blue primaries required by the deuteranopic eye to match a range of spectral lights; and (4) the colors (viewed by the trichromatic eye) which RH matches to a wide range of monochromatic lights viewed by the deuteranopic eye. A brief report has already been published (MacLeod and Lennie, 1974).

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[1] The proof of this is as follows. Table 3 in the paper by Graham *et al.* (1961) gives r_λ and b_λ, the energies of blue and of red needed to match unit energy from various narrow wavebands spaced at intervals of 10 nm throughout the spectrum; a few gaps at long wavelengths have to be filled by interpolation. Because the color mixture functions change slowly with wavelength, a polychromatic stimulus containing unit energy in every one of these wavebands is visually equivalent to an equal stimulus. A red–blue mixture that matches the equal energy stimulus can be formed by adding together the red–blue mixtures that were found to match its various components (since matching stimuli yield indistinguishable mixtures when added to matching stimuli). The energies of red and blue in this mixture are therefore simply the sums of r_λ and b_λ, respectively, from Graham *et al.*'s Table 3.

The sums are approx 65 for red and 14·75 for blue, so red and blue are present in a ratio of 4·35 to 1. In a match to 510 nm, red and blue were present in a ratio of 0·8 to 1; it follows that the equal energy stimulus would look redder than 510 nm. It would match a wavelength close to 512 nm. The neutral stimulus used in Graham's measurement of the neutral point had a color temperature of 5000° K and would be matched to a spectral light of still longer wavelength.

PRELIMINARY EXAMINATION

Ishihara cards

In the first 21 plates of the 1969 edition, no distinction is made between anomalous and dichromatic responses. In these, both eyes of RH were shown to be red–green defective. Using his left eye he correctly read the first, "dummy" plate and six others. Using his right eye he correctly read the first plate and two others. In plates 22–27, which are intended to discriminate between mild and severe defects, and also between protan and deutan defects, RH always gave mild deutan answers when using his left eye and severe deutan answers when using his right. With both eyes open he gave the same answers as with his left eye, but then closing his right eye made it easier to read the figures.

Nagel anomaloscope

The left eye gave characteristically deuteranomalous settings, with a large greenward deviation and a matching range little greater than normal. Normal matches were rejected. When using his right eye, RH was able to match either the green or the red primary to a spectral yellow of suitable intensity. He accepted the left eye's match and also the matches of some normal observers.

APPARATUS

All the measurements to be reported here were made with the binocular Maxwellian view apparatus constructed by Dr. Paul Whittle. The apparatus incorporates three channels for each eye, originating from a single QI projector lamp and united by beam splitters. The observer's head was located by means of a dental bite which was mounted with adjustments for all dimensions of orientation and position. Artificial pupils (1·7 mm) in front of each eye guaranteed crisp Maxwellian images. Correcting lenses could be inserted just in front of each artificial pupil. Monochromators inserted into two of the left eye channels provided spectrally well-defined stimuli of bandwidth never greater than 10 nm; these are the stimuli to which all wavelength discrimination and luminosity data refer. In experiments involving the right eye alone, the head was moved leftward until the right eye came in line with the "left eye" optical system. This made it possible to use the monochromators in all monocular experiments. In the binocular matching experiments, the stimuli for the right eye were delivered through Ilford "Spectrum" filters, with bandwidths (full width at half maximal transmission) of approx 25 nm in most cases. The designations of these filters, with their wavelengths of maximal transmission as measured on a Pye spectrophotometer, were "violet" (434 nm), "blue" (462 nm), "blue-green" (485 nm), "green" (516 nm), "yellow-green" (542 nm) and "yellow" (569 nm); two short-wavelength-cutoff filters were also used—"orange" (10% of peak transmission above 574 nm) and "red" (10% of peak transmission above 633 nm).

The intensities of the beams could be reduced by inserting neutral filters, uniform in density to ±2·5% across the spectrum. Fine adjustments were made by the observer, using wedge filters uniform in density to ±5%.

RESULTS

(1) *Wavelength discrimination*

Test and comparison fields forming a vertically divided 2° circle were derived from the two monochromators. Retinal illuminations were in the range 30–100 td. RH viewed the bipartite field with either his left eye or his right eye, and carefully adjusted the intensity of the test field to make it appear as similar as possible to the comparison field. He then indicated whether the two half-fields appeared the same or different in color. When his judgment was "different", he could nearly always, if asked, correctly state the direction of the wavelength difference between the two fields. To determine the just-noticeable differences, the test field was presented several times with each of a range of comparison fields of slightly longer or shorter wavelength. The comparison field wavelengths were presented in unsystematic order. Two critical comparison field wavelengths could then be identified (one longer and one shorter than the test wavelength) which usually elicited the judgement "different", but between which the judgement was usually "same". Half of the difference between these two wavelengths is the estimated just-noticeable difference, $\Delta\lambda$. Figure 2 shows $\Delta\lambda$ as a function of test field wavelength, together with Pitt's corresponding data for normal and deuteranopic observers. As can be seen in Fig. 2, wavelength discrimination for the the left eye is well maintained across the spectrum and is as good as for Pitt's normal observer. The right eye, in contrast, discriminates keenly only near 495 nm. At that wavelength the two eyes are about equal in keenness of discrimination; but the discrimination of the right eye is greatly inferior at other test wavelengths, and fails totally for wavelengths longer than 530 nm, yielding a wavelength discrimination curve somewhat similar to those of Pitt's deuteranopes.

The superior performance of the trichromatic eye for wavelengths near 495 nm is probably a practice effect: measurements on the dichromatic eye were completed before measurements on the trichromatic eye were begun. In informal tests conducted later to investigate this point, RH viewed a 495-nm test field alongside comparison fields of slightly different wavelength alternately with left and right eyes. He judged these color differences equally noticeable with the two eyes.

(2) *Luminosity curves*

Luminosity curves for left and right eyes were obtained by flicker photometry, using a 1° square test field and a dark surround. The standard was a light of 530 nm; its intensity varied with test wavelength within the range 9–30 td, but was usually greater than 20 td. At each test wavelength the standard used was the same for both eyes. The flicker frequency was 12 Hz. Energy measurements employed a UDT PIN 10 photocell, the spectral sensitivity of which had been determined by comparing it with a silicon photocell calibrated by the National Physical Laboratory.

Luminosity curves for left and right eyes were virtually identical (Fig. 3). The differences (open triangles, Fig. 3) are irregularly distributed across the spectrum and probably originate from random matching error. Within the red–green spectral range there is good agreement with Pitt's deuteranopic curve, also shown in Fig. 3. One normal observer was tested under the same conditions as RH. He yielded a curve

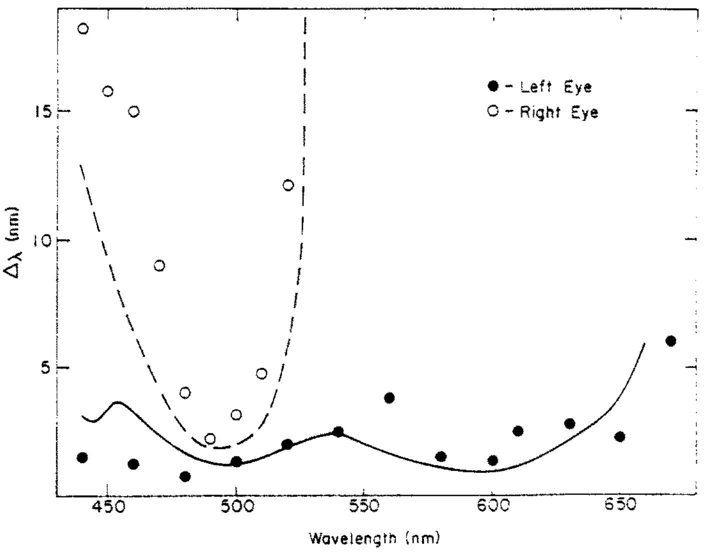

Fig. 2. Wavelength discrimination of RH: filled circles, left eye: open circles, right eye. Continuous line, normal observer; dashed line, deuteranopic observer (Pitt, 1935).

that agrees with those of RH throughout the spectrum, as is shown by the filled triangles in Fig. 3. These results agree with those of previous studies. The observer of Sloan and Wollach resembles RH in being fully sensitive to all wavelengths. The unilaterally EDA observer of Bender, Ruddock, DeVries-DeMol and Went (1972) showed a short wavelength loss but it was common to both eyes.

(3) *Color matching by the dichromatic eye*

For these measurements, the test field was filled with monochromatic light from the spectral range 460–650 nm. The comparison field contained a mixture of blue (460 nm, from a second monochromator) and red (Ilford Spectrum filter 608). For each monochromatic light, RH was able, using his right (dichromatic) eye, to find some mixture of primaries that was visually indistinguishable from the test light so that the bipartite field appeared uniform in color. For test lights of 530 nm and longer wavelength, the blue primary was not required. Unfortunately the amounts of the primaries chosen varied considerably from session to session with this technique. More consistent results were obtained when the experimenter fixed the amounts of the red and blue primaries, with RH setting the wavelength and intensity of the test light. Each session also included a flicker photometric match between the primaries, and this made it possible to specify the relative luminances (for RH) of the primaries in the dichromatic matches. Figure 4 shows the mean wavelength of the wavelengths chosen to match a range of red–blue mixtures; the vertical axis

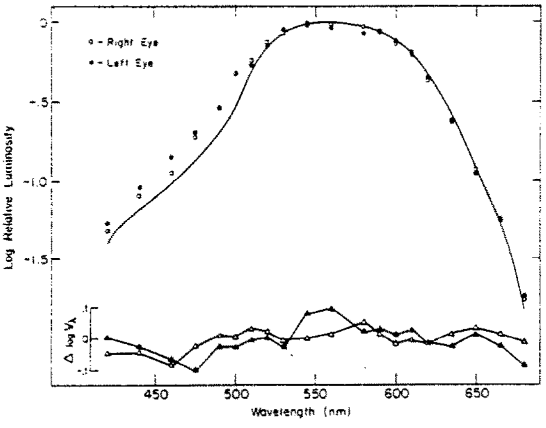

Fig. 3. Luminosity curves for RH. Filled circles, left eye; open circles, right eye. Curve is Pitt's average for deuteranopes. Below, open triangles show the ratios of right eye (dichromatic) to left eye (trichromatic) luminosities. Filled triangles show the ratios of right eye luminosities to those of a normal observer, PL.

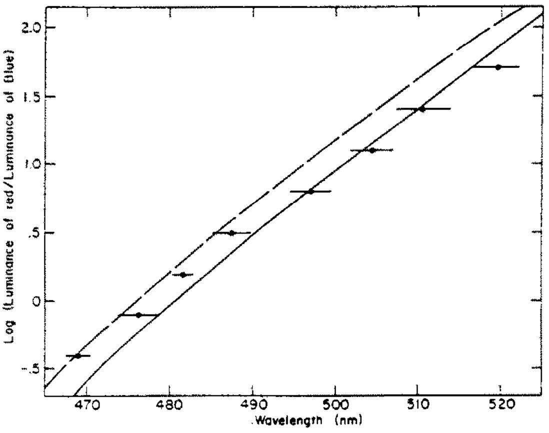

Fig. 4. Circles show colors confused by the dichromatic eye of RH; the horizontal lines subtend twice the standard error of the wavelengths chosen to match the purple mixtures (standard errors based on variation between sessions). The dashed line shows results corresponding to a copoint of (1·08, −0·08) in the CIE diagram. The continuous line shows results correcponding to a copoint of (1·54, −0·54) (Nimeroff, 1970). The ordinate represents relative luminance of red and blue as defined by the flicker photometric matches of RH.

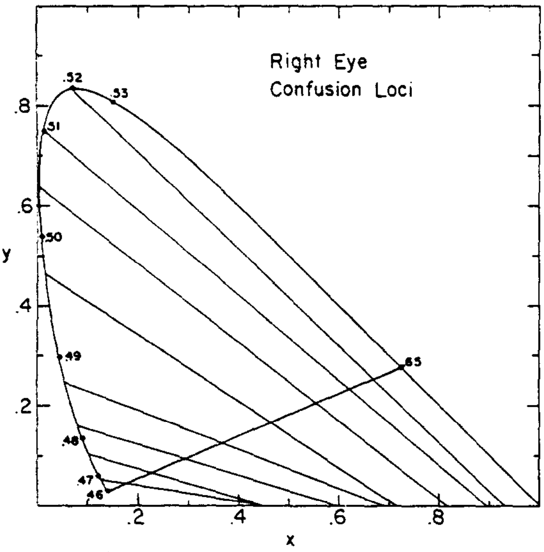

Fig. 5. The CIE chromaticity diagram showing the confusion lines of RH, replotted from the circles in Fig. 4.

is the ratio of red to blue, expressed as a multiple of the ratio required by RH for a flicker photometric match and converted to the decimal logarithm. The data are seen to be in rough agreement with Pitt's (1935) and Nimeroff's (1970) results for deuteranopes.

To estimate the color matching functions of RH in terms of physically defined units, we referred to the luminosity curves of Fig. 3 to find the relative energies of two monochromatic lights, 650 and 460 nm, which respectively would have matched unit luminance of the red and blue primaries. This made it possible to express the amounts of the red and blue primaries in terms of equivalent energies of 460 and 650 nm primaries, and hence to determine the CIE chromaticities of the red–blue mixtures. Thus transformed, the mean data from Fig. 4 appear in the CIE chromaticity diagram of Fig. 5, where straight lines link each spectral light to its indistinguishable purple. Most of these confusion lines meet the extension of the long wavelength spectrum locus at points within the range characteristic of deuteranopic color matching: copoints estimated for bilateral deuteranopes vary from (1·08, −0·08) to (1·70, −0·70) (Nimeroff, 1970).

In other experiments, RH first used his left eye to establish trichromatic matches for yellow or white test lights; two primaries were used, and for the white test light the necessary third degree of freedom was provided by allowing RH to choose the wavelength of the short-wavelength primary. When he was satisfied with the match, RH then viewed the matched fields with his right (dichromatic) eye. The dental impression was used throughout to ensure central pupil entry. In every case, the matches made by the anomalous left eye were acceptable to the dichromatic right eye. Sometimes, indeed, matches established with the left eye appeared even better when viewed with the right eye. This suggests that the pigments of the dichromatic eye are found also in the anomalous eye. But RH with his dichromatic eye also accepted the matches (to yellow light) of the normal observer PL. Hence, the pigments of the right eye must be common to deuteranomalous and normal eyes. In studies of color matching by bilateral deuteranopes, Mitchell and Rushton (1971) and MacLeod and Hayhoe (1974) show similarly that the pigments of deuteranopia are shared by normal and deuteranomalous eyes. It is hard to avoid the conclusion that the right eye of RH is typically deuteranopic.

(4) *Binocular matching*

The binocular Maxwellian view apparatus made it possible to stimulate separately the left and right eyes, without the observer's knowing which eye was actually generating the sensation experienced. To find out about the sensations generated by RH's dichromatic eye, we presented a test field to the dichromatic eye and a comparison field, adjustable in color, to the trichromatic eye. The object of the experiment was to find which stimuli were required by the trichromatic eye to mimic the appearance of the test stimuli as viewed by the dichromatic eye.

Each eye viewed a 1° field with a dark surround. In binocular viewing, the two fields appeared one above the other, separated by a 30′ dark horizontal strip. At the center of the horizontal strip was a dim orange binocular fixation spot, introduced to obviate vergence difficulties. Test lights for the dichromatic right eye were defined in their spectral composition by Ilford "Spectrum" narrow-band filters. The comparison patch viewed by the trichromatic left eye could be illuminated by two monochromators. Except where noted, variation of intensity and wavelength was enough to attain a match, no desaturating light from the second monochromator being required.

For protection against the effects of chromatic adaptation, we used a trial and error procedure in making the measurements. We began by continuously exposing in the comparison field a stimulus which was clearly too red or too green to match the test field; RH adjusted its intensity for a brightness match. The wavelength of the comparison field was then changed progressively (at about 1 nm/sec) and the wavelengths noted at which the test and comparison fields began to look similar in hue and at which, later, they began to look different again. The average of these two wavelengths was the starting point for the next trial: its intensity was adjusted for a brightness match, and by progressively changing wavelength, the wavelengths which seemed just too green or just too red were determined once again. The midpoint of the new matching range served as the starting point for the next trial, and within a few trials a stable matching range emerged, demonstrably independent of the initial starting point.

Long wavelength test stimuli (green, yellow-green, yellow and red) viewed by the dichromatic eye were all matched to a spectral orange viewed by the trichromatic eye. The averages of the midpoints of the matching ranges were 610·7 nm for the green test stimulus, 609·4 nm for the yellow-green test stimulus, 608·9 nm for the yellow test stimulus and 610·5 nm for the red test stimulus. The slight differences between these values could easily be due to experimental error, and a value of 610 nm can be considered representative.

With short wavelength stimuli, binocular matches were possible over a wider range of wavelengths (470–480 nm) in continuous viewing. More exact results were obtained when the test fields were exposed in brief flashes of 100 msec duration. Under these conditions, violet was matched to 473 nm and blue to 474 nm. With brief flashes, the matches to 610 nm at long wavelengths remained valid.

When asked to produce lights (100-msec flashes) that looked not at all reddish or greenish, RH (using his deuteranomalous trichromatic eye) selected the two wavelengths, 466 nm (±4 nm) and 589 nm (±4 nm); pure green (neither yellowish nor bluish) was at 515 nm. RH described the colors seen by the dichromatic eye as a definitely greenish blue and a definitely reddish yellow or orange. He thus presents us with a clear exception to the rule that blue and yellow are the only colors perceived by the red–green blind.

The blue-green test light differed from the others in that it could not be matched by any spectral light viewed by the trichromatic eye, owing to its desaturated appearance. Nor could it be matched by any mixture of 610 and 474 nm. But when a third degree of freedom was made available by allowing RH to adjust the wavelength of the short wavelength primary, acceptable matches were obtained using a short wavelength primary of 482 nm.

With his dichromatic eye, RH could find a region of the spectrum which he would describe as achromatic or neutral in color. His settings of this subjectively neutral point had a mean of 499·3 nm (S.E. 1·2 nm). This agrees with previous results on deuteranopes, both bilateral (Bailey and Massof, 1974) and unilateral (Sloan and Wollach, 1948). However, there is some doubt as to whether this stimulus appeared totally achromatic, since RH tended to describe it as greenish but never described it as reddish.

The intensities required to establish the binocular matches did not suggest any difference in sensitivity between the two eyes. To test this more exactly, we measured the intensity of light of 610 nm required by RH at his left (trichromatic) eye to match another orange light (Ilford Spectrum Orange filter) at the right eye, and compared the mean intensity settings with those of a bilaterally deuteranomalous observer. The settings of the two observers agreed within 4%, a difference well within the likely range of error in the binocular comparisons.

DISCUSSION

Is RH a unilateral deuteranope?

Before considering the implications of our results in relation to the problem of deuteranopia, we must deal with various objections to the assumption that RH is in fact a unilateral deuteranope.

First, it may seem surprising that we found no deuteranopic or deuteranomalous relatives. But this pedigree is hardly relevant to the point at issue. With one eye apparently deuteranopic and the other deuteranomalous, RH almost certainly inherited an abnormal gene of one kind or the other (DA or D) at the deutan locus; and if he did so, there would still be about a one-in-four chance that the defect would not be manifest in any of the relatives we tested. Much heavier odds than these would be required to render plausible the alternative hypothesis, the RH's deuteranomaly and his deuteranopia represent two different corruptions of genetically normal vision. We must therefore assume that RH inherited a gene for either deuteranomaly or deuteranopia.

But this does not explain why his two eyes are not the same. Is it possible for a genuinely congenital dichromacy to appear in one eye only, or must the red–green blindness of RH's right eye be attributed to the action of some unknown disease or injury on a constitutionally deuteranomalous eye? Once again, the pedigree of RH is not sufficient to decide the issue; but there does exist evidence that unilateral color defects in males can have a genetic basis. The unilaterally deuteranomalous observer studied by Von Kries (1919) had a deuteranomalous daughter (Trendelenburg, 1941) and must have been himself genetically deuteranomalous. Yet one of his eyes was practically normal. It may also be relevant that monozygotic twins may occasionally have different types of color vision (Francois, 1961, p. 417). The interpretation of a unilateral defect as congenital cannot be dismissed as unreasonable on genetic grounds.

Finally it is odd, if his condition is congenital, that RH failed to detect the red–green blindness of his own right eye. Yet the same remarkable lack of awareness is a feature of the four cases studied by von Hippel (1880), Sloan and Wollach (1948), Graham and Hsia (1958c) and von Kries (1919); it may therefore be a characteristic feature of congenital unilateral deficiencies.

The alternative interpretation, that the right eye of RH is basically deuteranomalous and has been rendered red–green blind by disease or injury, is strongly contradicted by several lines of evidence. First there is the stability of the condition. Acquired dichromacy, according to Koellner (1929) always appears as just one stage of a continuously developing condition, but the visual capacities of the right eye of RH have not discernibly changed during 8 months of experimental investigation or during the 5 yr for which we have remained in contact with him. Second there is the absence of any clinical symptoms of disease, either currently present or recollected. Third, in our measurements, visual functions other than red–green discrimination are quite unimpaired even though the red–green loss is total. Visual acuity is normal for both eyes although according to Koellner (1929) acuity in acquired red–green blindness may be expected to be only 1/6 or 1/10 of normal. The binocular color matches suggest that the dichromatic eye has lost nothing in brightness sensitivity or in blue–yellow sensitivity. No known acquired abnormality so closely mimics congenital deuteranopia. Consequently, although we have no definite proof that RH's condition has a genetic basis, we will proceed on the assumption that it does.

Does the dichromatic eye lack a green-sensitive pigment?

If RH is indeed a unilateral deuteranope, our results can help to answer some fundamental questions about the physiological basis of deuteranopia. For instance, are deuteranopes dichromatic because they possess only two visual pigments, one sensitive to long wavelengths and one to short wavelengths? If they are, then the deuteranomalous eye of RH must contain a green-sensitive pigment absent from his right eye, and the luminosity curves of the two eyes should reflect that difference. The prediction is not fulfilled: the two curves are the same (Fig. 3). To make the hypothesis of pigment loss consistent with this result, the postulated "green-sensitive" pigment in the anomalous eye must be undetectable by luminosity measurements, either because it contributes weakly to brightness in all parts of the spectrum or because it is quite similar in spectral sensitivity to the red-sensitive pigment that mediates vision at long wavelengths in the dichromatic eye. This "hidden pigment" interpretation is supported by experiments in which the spectral sensitivity of the anomalous eye was examined under adaptation to differently colored backgrounds. A flicker photometric equation between 530 and 650 nm was disturbed by less than 0·05 log units by exposure to either red or green backgrounds of 1000 td. Since in these experiments a constant long wavelength luminosity curve is observed for the anomalous eye under conditions which should significantly alter the green-sensitive pigment's contribution to brightness, a similar curve could be characteristic of the deuteranopic eye even if that pigment were entirely absent from it. Each curve could then be approximated by the spectral sensitivity of the red-sensitive pigment alone in the red–green spectral range.[2]

A related difficulty for the pigment loss theory is that neither the anomalous eye nor the dichromatic eye shows any appreciable loss of sensitivity for green, by comparison with the normal observer PL. Nevertheless it is reassuring that recent estimates of the spectral sensitivity of the red-sensitive pigment in normal vision (Vos and Walraven, 1971; Smith and Pokorny, 1972; MacLeod and Hayhoe, 1974) do not differ much from the luminosity curves of RH at long wavelengths. Observer variation in the *in situ* spectral sensitivity of the red-sensitive pigment may be sufficient to obscure the presence or absence of a green-sensitive pigment, in comparison between different observers.

We conclude that although the evidence from RH is against a unilateral pigment loss, the possibility cannot be excluded.

Does the dichromatic eye possess a green-signalling receptor?

To permit trichromatic vision, the receptors housing the red-, green-, and blue-sensitive pigments must differ in functionally important ways in their action on more central neurons. To express this, and to help distinguish between neural and photochemical interpretations of color blindness, it is convenient to classify receptors in accordance with their central effects, as red-, green- or blue-signalling. Since the dichromatic eye of RH may lack green-sensitive pigment, it is worth considering the possibility that it also lacks the associated receptor, and that only the blue- and red-signalling receptors are present.

In previous discussions of unilateral color blindness, it has been argued that on this "receptor loss" hypothesis, the colors seen by the deuteranopic eye should be limited to a series of purples, those which a normal observer would experience if a light stimulated only his blue- and red-signalling receptors. Our results contradict this: deuteranopic colors RH ranged between orange and greenish-blue. According to theory, then, the green-signalling receptor must be present and functional in the deuteranopic eye, even though it may contain only the red-sensitive pigment (Aitken, 1872; Leber, 1873).

This refutation of the simple receptor hypothesis of color blindness has been the main contribution of unilateral color blindness to the theory of color vision (see, for instance, Judd, 1949; Graham, 1965). Consequently, it is important to notice that the argument has a serious logical weakness: it tacitly assumes that a binocular match is a match for the receptors. Such a correspondence between receptor activity and sensation can be guaranteed only if the afferent pathways from the two eyes are functionally similar. For normal observers there is no reason to doubt this assumption of bilateral symmetry, but with a unilateral dichromat the situation is quite different. If dichromatism involves an abnormality of the afferent pathways, then the pairs of stimuli chosen in binocular matching by a unilateral dichromat may be mismatches at the receptor level, chosen so that they elicit similar sensations by their action on the dissimilar afferent pathways from left and right eyes. The following discussion will show that afferent abnormality is not merely a possibility but is actually a necessary part of any explanation of the binocular matches of unilateral dichromats. Consequently the colors seen by a unilateral dichromat may be a misleading clue to his endowment of receptors.

Are the receptors of the trichromatic eye served by a normal trichromatic afferent system?

Experiments with selective bleaching (for instance, Miller, 1972) strongly suggest that both protanopes and deuteranopes possess only two of the normal observer's three pigments. This accounts for their

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[2] If this interpretation is correct, the luminosity curves of bilaterally deuteranomalous observers should be identical with those of deuteranopes. The available evidence is consistent with this, but in most comparisons the anomalous and dichromatic eyes have belonged to different people and observer variation has been so large that it is not too surprising that the results of different investigators point to different conclusions. Some investigators report that when anomalous observers are compared with deuteranopes, the anomalous observers are relatively more sensitive to green (Copenhaver and Gunkel, 1959; Richards and Luria, 1968). The results of Collins (1959, 1961) tend to confirm this at absolute threshold but show no clear difference in photopic critical fusion frequency. Pitt's results (1935) point in the opposite direction, with deuteranomalous observers less green-sensitive than deuteranopes. Boynton and Wagner (1961) with 12 observers, and Wald and Brown (1965; Wald, 1966) with 20 observers, find no clear difference between deuteranomalous observer and deuteranopes. Verriest (1971) demonstrated an impressively exact agreement between 24 deuteranopes and 27 deuteranomalous observers, with differences less than 0·04 log units throughout the spectrum at each of two luminance levels. Kinnear (1974) with 15 deuteranopes and 52 deuteranomalous observers found only one statistically significant difference in the red–green spectral range.

dichromacy and it is not necessary to postulate any neural impairment in addition. Nevertheless, it is not implausible that the afferent pathway from a dichromatic eye might be affected in its development by the absence of a particular pigment or class of receptors from the retina, or vice versa: in other contexts (Gaze, 1970, p. 184), surgical experiments have revealed developmental contingencies that would allow congenital abnormalities to propagate from one afferent stage of the visual system to another in this way. And even if all the genetic requirements for normal afferent organization are present, the visual system's plasticity could create an abnormal afferent organization in response to the impoverished stimulus history resulting from the dichromacy of the receptor stage, much as the distribution of orientational selectivity in monocularly driven simple cells is biased in favor of the orientations to which the corresponding eye is preferentially exposed (Hirsch and Spinelli, 1970).[3]

One feature of RH's results provides evidence that the afferent pathways from the two eyes do behave differently and contradicts the simplistic view that his binocular matches are matches for the receptors. The binocular matches showed that stimuli of 474 or 610 nm looked the same to each eye, but blue-green lights, presented to the dichromatic eye, appeared greener that any mixture of these invariant stimuli at the trichromatic eye. This might suggest that the right eye is not strictly dichromatic; yet it easily passed a much stricter test of dichromacy, the monocular matching of blue-green to purple. Taken as a whole, the data imply that although it should indeed be possible to represent the whole range of sensations from the right eye as a single locus in a chromaticity diagram constructed for the trichromatic eye, this locus is not a straight line but is bowed toward the green corner. Thus, mixing the invariant blue-green and orange produces greener sensations in the dichromatic eye than in the trichromatic eye. A similar breakdown of binocular additivity was noted for the observer of Sloan and Wollach. Now, on the simplistic view, a binocularly invariant stimulus is one that equally excites receptors of the same class (red-, green-, or blue-signalling) in left and right eyes. In any mixure of the invariant stimuli, these equalities of excitation must be preserved, and so the mixtures too should be invariant, if it is true that the matches are matches for the receptors.[4] The fact that the mixtures were not binocularly invariant suggests that the binocularly matched fields created different signals at the receptor stage and that their similar appearance came about by the action of these dissimilar inputs upon dissimilar afferent pathways from left and right eyes.

The same conclusion may be reached by considering the colors seen at the ends of the spectrum by dichromatic eyes. In all known cases of unilateral red–green blindness, it appears that two binocularly invariant spectral stimuli could be found, one of short wavelength (blue or blue-green) and another one of long wavelength (yellow or orange), each of which looked the same to the trichromatic eye as to the dichromatic eye. To explain the perception of yellow at long wavelengths it is usual to assume that both green- and red-signalling receptors are present in the dichromatic eye, but contain the same normal pigment (or mixture of pigments), so that spectrally dissimilar lights which match for the red-signalling receptors match also for the green-signalling receptors. Suppose that a short-wavelength invariant stimulus and a long-wavelength invariant stimulus are matched, by intensity adjustments, for the red-signalling receptors of the dichromatic eye. They will also, then, have indistinguishable effects on the green-signalling receptors of that eye, though they will of course differ in their effects on the blue-signalling receptors. Now consider the effects of these two binocularly invariant stimuli on the trichromatic eye. Each is matched binocularly to itself; therefore if the binocular matches are matches for the receptors, the two invariant stimuli must be indistinguishable to the red- and green-signalling receptors of the trichromatic eye, just as they are indistinguishable to the corresponding receptors in the dichromatic eye. All such pairs of stimuli are confused by tritanopes, dichromats whose two fundamental spectral sensitivities are those of the normal red and green receptors. Thus the short- and long-wavelength binocularly invariant stimuli of the red–green blind must be indistinguishable to tritanopes. But this prediction is sharply contradicted by experiment: tritanopes confuse blue only with blue-green or violet, and they do not confuse yellow with any shorter wavelength (Wright, 1952; Sperling, 1960). When taken together with the evidence from tritanopes, the color perceptions of unilateral color blinds are therefore quite inconsistent with the type of theory that was evolved to account for them! The only escape from this impasse (leaving aside the implausible *ad hoc* postulate that dichromats might have some blue-sensitive pigment in their green-signalling receptors) is to abandon the assumption that the binocular matches of unilateral dichromats are matches for their receptors and admit instead the existence of a unilateral afferent abnormality. A similar afferent abnormality must exist bilaterally in ordinary dichromats if they have the same genetic origin as the unilateral conditions. Consequently the color perceptions and color difference thresholds of normal and dichromatic observers may not be related in any simple way.

More explicit statements of the above arguments may be found in the Appendix.

Experiments on parafoveal vision, where rods as well as cones are involved, have yielded supportive

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[3] Weak evidence for a plasticity of the monocular pathways in color vision may be found in a report by McCollough (1965). McCollough reported a small interocular difference in color appearance after wearing red and green filters side by side over one eye only for more than a month. One of us has worn for 3 days monocular goggles which admitted only red light to the left eye; this experiment yielded no evidence of plasticity, for, when the goggles were removed, binocular matches became once again stable and accurate within about 3 min. Other evidence against plasticity was obtained by Peterson (1962): ducks reared in monochromatic light retained the capacity to distinguish colors.

[4] The argument made here proceeds on the assumption that receptors of the same sort in left and right eyes do not differ in the way that their signals depend on stimulus intensity (apart from the possible differences in sensitivity due to a change of pigment). See Appendix for further details.

(but not conclusive) evidence of abnormal afferent organization in bilateral deuteranopes. With the availability of an additional visual pigment, rhodopsin, the deuteranope might be expected to become trichromatic; but in experiments to test this (MacLeod and Varner, unpublished), deuteranopes have remained dichromats in mesopic vision (Nagel, 1909, however, came to the opposite conclusion). It is therefore likely that the deuteranope's afferent pathway is organized for dichromatic vision only, for instance by the elimination of the red–green opponent system (DeValois, 1960; Hurvich and Jameson, 1962). This would make it easy to understand why the sensations from the dichromatic eyes of previously reported unilateral dichromats have ranged from a subjectively pure yellow to a subjectively pure blue, with little or no trace of redness or greeness. Unfortunately for this simple view, the dichromatic sensations of RH are reddish at long wavelengths and greenish at short wavelengths. Moreover, RH resembles Sloan and Wollach's observer in choosing as subjectively neutral a wavelength that is perceived by the trichromatic eye as blue-green and not as pure green.

To summarize, RH poses difficulties for all the simple interpretations of deuteranopia that have been considered. Loss of a green-sensitive visual pigment (with or without substitution) is somewhat difficult to reconcile with the experimental luminosity curves, but it cannot be ruled out. The binocular matching data cannot be explained simply, either on the hypothesis of loss of a green-signalling receptor, or on the hypothesis that the red- and green-signalling receptors are both present but with the same spectral sensitivity. The one thing to emerge clearly is that whatever the condition of the pigments and receptors, an afferent abnormality must in any case be present. But it cannot be simply a loss of the red/green chromatic system since the sensations from the dichromatic eye can be reddish or greenish.

Genetic mechanism

Unilateral deutan or protan defects, like bilateral defects, seem to be more common in males (Holmgren, 1881; von Neipperg, 1932; Trendelenburg, 1941; Sloan and Wollach, 1948; Nimeroff, personal communication; Bender *et al.*, 1972), and RH confirms this trend (but cf. Graham and Hsia, 1958; Hayes, 1911). Presumably, and certainly for Trendelenburg's observer, the genes involved are the same as those responsible for the bilateral defects. The possible genetic mechanisms are of two sorts. One possibility is that a unilateral observer may have inherited an allele for dichromacy and another allele for trichromacy at the same locus of two different X chromosomes. The allele for trichromacy could be absent (if the individual were an X chrosome mosaic) or fail to express itself in the dichromatic eye. Such an interpretation is difficult to reconcile with the preponderance of males among the sample of unilaterals. The alternative is that just one X chromosome is inherited, and that left and right eyes have different alleles as a result of a mutation either in the maternal germ cell or early in embryogenesis. A mutation from DA to D or vice versa at the deutan locus could account for all the characteristics of RH's color vision. The only difficulty with the hypothesis is that mutations are quite rare, statistically, with frequencies less than one in 10^5 at most loci (Vogel, 1970). Moreover, not all mutations could give rise to unilateral defects, but the incidence of unilateral retinoblastoma (Vogel, 1967) suggests that the fraction that may do so is quite substantial. Unlikely though it may be, mutation is the only attractive genetic explanation for the condition of RH. The alternative of X-chromosome mosaicism can be excluded on the following grounds. Both the parents of RH were normal so not more than one gene for a deutan defect can have been present in his genetic background. Hence if RH were a mosaic it would be a mosaic of normal and defective vision, not a mosaic of deuteranomalous and deuteranopic vision.

Curiously enough, all the male cases cited above exhibited atypical minor red–green defects in their "good" eyes. Perhaps the search for more unilateral color blinds should concentrate on individuals who are color defective to some degree when tested with binocular vision.

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APPENDIX: EVIDENCE FOR A NEURAL ABNORMALITY IN UNILATERAL RED–GREEN BLINDNESS

Red–green blindness can be attributed to a photochemical change or other abnormality affecting those receptors which in the normal eye distinguish red from green. Such an abnormality could abolish differences in spectral sensitivity between those receptors, either by rendering some of the receptors unresponsive to light or by giving them the same spectral sensitivity as the rest of the receptors that are excited by red or green light. If this sort of explanation for red–green blindness is adopted (as it usually is), there is no need to associate any abnormality of nervous organization with red–green blindness; the abnormality within the receptors is enough to account for the loss of discrimination. The conclusion arrived at in the Discussion above, that the colors seen by unilateral red–green blinds cannot be accounted for on such a simple view, and that they imply an afferent abnormality in addition to any changes within the receptors, appears to call for some amendment to the prevailing conception of red–green blindness. The arguments that led to that conclusion will here be stated more explicitly, in the interests of clarity and rigor.

The hypothesis called in question is that the afferent pathways from the dichromatic and trichromatic eyes are similar (or more exactly, that they are related by bilateral symmetry). The attempt to test that hypothesis by binocular matching experiments presents special problems, which may be avoided by discussing an idealized version of the experimental situation. It will be assumed that the stimuli compared are delivered successively to the central foveas, that is to corresponding points with a common visual direction, so that the resulting sensations are indistinguishable unless they differ in color. Because the two foveas are also corresponding points in the sense implied by bilateral symmetry, it is almost self-evident that similar signals from the receptors of the left and right foveas will elicit indistinguishable sensations, if it is true that the afferent pathways from the left and right eyes are similar. (Complications arising from differences between nasal and temporal hemiretinas are practically insignificant for small subtense stimuli.) Self-evident or not, this psychophysical linking hypothesis will be taken for granted in the following examination of the hypothesis of afferent similarity. Afferent similarity, then, will be taken to imply that if two stimulus presentations, one to the left eye and one to the right eye, equally excite the receptors of each class in their respective eyes, the resulting sensations will be indistinguishable. The converse proposition, that a binocular match is a match for the receptors, will also be true. [Since just three pigments are the basis of normal foveal color matching (Brindley, 1970), it must be possible, using three suitable primaries, to find one trichromatic match for a given test light which is a match for all the pigments, hence also a visual match. Since experimentally no other visual matches can be achieved using the same test light and primaries, all visual trichromatic matches must be matches for the pigments and for the receptors that house them. The example of trichromatic matches is enough to show that any mismatches for the receptors are in principle visually apparent.]

Under the hypothesis of afferent similarity, then, the binocular matches of unilateral color blinds are matches for their receptors. The observations discussed below show that the binocular matches are not matches for the receptors, and suggest that the hypothesis of afferent similarity must be rejected.

(1) *Non-additivity of binocular matching in the unilaterally red–green blind*

Suppose that a stimulus with spectral energy distribution $E_1\ (\lambda)$ in the right eye is matched to a stimulus with spectral energy distribution $E'_1\ (\lambda)$ in the left eye, and that a stimulus $E_2\ (\lambda)$ to the right eye is matched by a stimulus $E'_2\ (\lambda)$ in the left eye. It will be shown that if these binocular matches are matches for the receptors, the matches will be additive, that is, the mixed stimulus $E_1\ (\lambda) + E_2\ (\lambda)$ in the right eye will be binocularly matched to $E'_1\ (\lambda) + E'_2\ (\lambda)$ in the left eye. Suppose that the receptors of each eye have been classified in accordance with the color sensations they produce; on the hypothesis of afferent similarity each class of receptor will be represented with equal frequency in the left and right eyes. The signal generated by each receptor will depend on the pigment it contains. The natural expectation that each receptor contains only a single pigment is supported by microspectrophotometry; but doubts may remain in the case of deuteranopic vision (Fick, 1896; Le Grand, 1968), so for generality it will only be assumed that the signal from each receptor is a monotonic function (perhaps different from one class of receptor to the other) of a weighted sum of the fractions of molecules isomerized in each of the three visual pigments. (The weights may be regarded as expressing the amount of each pigment in the class of receptor in question.) The signals generated by receptors of classes *a*, *b*, *c*, *d*, etc. in the right eye in response to the stimulus $E_1\ (\lambda)$ may then be expressed as

$$a_1 = f_a(m_{a1})$$
$$b_1 = f_b(m_{b1})$$

etc., where m_{a1}, m_{b1}, etc. are the weighted sums of the fractions isomerized for each class of receptor and f_a, f_b, etc. are the monotonic functions appropriate to each class of receptor. If the binocular matches are matches for the receptors, the same set of signals a_1, b_1, etc. must be generated by the corresponding receptors of the left eye in response to the matching stimulus $E'_1\ (\lambda)$. If the functions f_2, f_b, etc. are the same for left and right eyes, it follows that the fractions isomerized are also the same for corresponding receptors in left and right eyes, when $E_1\ (\lambda)$ is matched binocularly to $E'_1\ (\lambda)$. When $E_2\ (\lambda)$ is matched to $E'_2\ (\lambda)$ the fractions isomerized are again the same in the two eyes, being equal to m_{a2}, m_{b2}, etc.

If the mixed stimulus $E_1\ (\lambda) + E_2\ (\lambda)$ is presented to the right eye and the stimulus $E'_1\ (\lambda) + E'_2\ (\lambda)$ is presented to the right eye, the fractions isomerized will once again be the same in one eye as in the other, being equal to $m_{a1} + m_{a2}$, $m_{b1} + m_{b2}$, etc. The signals generated by the receptors will also be the same, being $f_a(m_{a1} + m_{a2})$, $f_b(m_{b1} + m_{b2})$, etc., so that the two mixtures will constitute a binocular match if the binocular matches are matches for the receptors.

Experimentally this prediction is clearly contradicted, both for the Sloan and Wollach observer and for RH. In the case of AHC there is even a suggestion that monocular additivity fails (see footnote 1). These failures of additivity show that purely photochemical interpretations of the red–green blindness of these observers are inadequate.

(2) *Relation between binocular matches of the unilaterally red–green blind and tritanopic confusions*

The simplest explanation for the perception of yellow (or orange) at long wavelengths by an apparently deuteranopic eye would be that the red-sensitive pigment of normal vision has replaced the green-sensitive pigment in the normally green-sensitive receptors. But it has been equally popular to explain deuteranopia by supposing that in the deuteranope the red- and green-sensitive pigments are mixed together in a ratio that is the same for all receptors (Fick, 1896). For the present purpose these two possible mechanisms need not be distinguished. What is important is that both theories imply that lights of different spectral composition which are indistinguishable by some of the deuteranope's receptors (by virtue of their relative intensities), are also indistinguishable by his other receptors sensitive in the red–green spectral range and are distinguished, if at all, only by the blue-sensitive receptors which are not sensitive in the red–green spectral range. Such a pair of lights can always be produced by intensity adjustments only.

If binocular matches are matches for the receptors, a binocularly invariant stimulus, which looks the same to the one eye as to the other, will be one that equally excites receptors of the same class in the dichromatic and trichromatic eyes. If two such binocularly invariant stimuli (one, say, of short wavelength and another of long wavelength) are of intensities such that they match for the receptors of the dichromatic eye that are sensitive in the red–green spectral range, they must then also be indistinguishable in their effects upon the corresponding receptors in the trichromatic eye. When such a pair of stimuli is viewed by the trichromatic eye, they will be distinguishable only by the blue-sensitive receptors of that eye just as they are by the blue-sensitive receptors of the dichromatic eye. When viewed by a tritanopic eye they should therefore match, since a tritanope lacks functioning blue-sensitive receptors.

This prediction too is contradicted by experiment. The invariant stimuli for unilateral deuteranopes are blue and yellow (or in the case of RH, orange and blue-green). The yellow of most unilateral deuteranopes is not confused by tritanopes with any shorter wavelength greater than 400 nm. The blue of most unilateral deuteranopes is confused by tritanopes only with nearly adjacent spectral wavelengths. In tritanopia, blue-yellow confusion is quite uncharacteristic.

The most natural way to resolve the contradiction is to abandon the hypothesis that binocular matches are matches for the receptors, and with it the hypothesis of afferent similarity. Alternatives exist, however: the spectral sensitivities of the receptors sensitive in the red–green spectral range in the dichromatic eye could be assumed to differ at short wavelengths by admixture of a blue-sensitive pigment not sensitive in the red–green spectral range; or the receptor or pigment loss hypothesis of tritanopia could be abandoned. The latter alternative is not attractive, since the color matches made by normal observers in a condition of artificial tritanopia (Brindley, 1970) are accurately similar to those made by congenital tritanopes.

A more valid objection to this argument, in its application to bilateral red–green blindness, is that no unilateral case has yet been found in which the trichromatic eye was totally normal and the dichromatic eye typically protanopic or deuteranopic. RH may be the "cleanest" case from this standpoint, since he appears to be affected by typical congenital deuteranomaly in one eye and by deuteranopia in the other. Of course, the red–green anomaly in his trichromatic eye makes it unfair to compare his invariant colors with those confused by tritanopes whose red and green receptors are normal. But we have determined the color matching functions of another typically simple deuteranomalous observer in artificial tritanopia, and the confusions made (yellow with deep violet, blue-green only with adjacent wavelengths) left the two invariant colors of RH still clearly distinguishable.