J. Physiol. (1953) 122, 332–350

THE EFFECTS ON COLOUR VISION OF ADAPTATION TO VERY BRIGHT LIGHTS

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(*Received* 9 *April* 1953)

It is conspicuous that large changes in the appearance of colours can be produced by adaptation to coloured lights without markedly changing the eye's colour-discriminating power, and without upsetting colour matches made between lights of different spectral composition; indeed Von Kries (1878), having deduced from Helmholtz's form of the trichromatic theory that no colour match should be upset by adaptation, tested matches of white against mixtures of blue and yellow or red and blue-green before and after adaptation to various coloured lights, and did not detect any alteration in the amounts or wave-lengths of the complementaries required for matching. Wright (1936), however, showed that very bright adapting lights could upset colour matches. At still higher adapting brightnesses, Burch (1898) found striking changes in colour discrimination.

Section I of the present work examines in detail the properties of the upset of colour matches found by Wright. In part the experiments were exploratory; but to a large extent they were designed to test certain definite hypotheses concerning retinal mechanisms in colour vision; for example, from section I(*a*) (discussion on p. 346) we can infer that the disturbance of colour matches by adaptation is not due to the production or destruction of a general screening pigment, and from section I(*b*) (discussion on p. 347) that, in the dichromatic red-green range of the spectrum, it can be fully accounted for if only two classes of receptor are here active, one with a spectral sensitivity curve unaffected by adaptation, the other affected as it would be if it contained a high concentration of photopigment in the unadapted state, which was partially bleached during light adaptation.

Section II describes a disturbance of colour matches on passing light eccentrically through the pupil which resembles closely the disturbance produced by adaptation; and it is suggested that it has a similar cause.

Sections III and IV examine in detail the states described by Burch and some

other analogous states. It is suggested that they provide evidence on the spectral sensitivity curves and other properties of single classes of receptors which, though not very precise, provides a useful check on inferences from other kinds of experiments.

METHOD

The apparatus used (Fig. 1) was designed by Dr E. N. Willmer for investigations on colour vision with very small foveal fields, and served for the present purpose with only minor modification.

Light for the two fields to be matched was provided by the 6 V 18 A ribbon filament lamps S_1 and S_2. Light from S_1 was focused on the entry slit of a Hilger single monochromator, whose exit

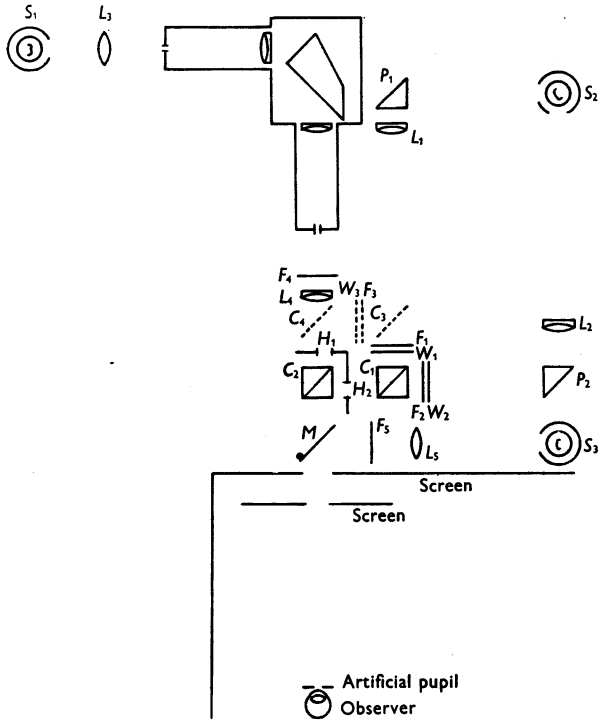

Fig. 1. Diagram of apparatus. S_1, S_2: ribbon filament lamps. S_3: spiral filament lamp. L_1–L_5: convex lenses. P_1, P_2: right-angled glass prisms. F_1–F_5: neutral or colour filters. W_1–W_3: neutral wedges. C_1, C_2: beam-splitting cubes. C_3, C_4: glass plates functioning as beam-splitters. M: mirror. H_1, H_2: stops.

slit was imaged by the lens L_4 on the artificial pupil. Light from S_2 provided a comparison field of mixed light, part coming through the prism P_1 and the lens L_1, and part through the prism P_2 and the lens L_2. L_1 and L_2 formed coincident images of the filament of S_2 on the artificial pupil, the light which passed through them being recombined in the half-silvered cube C_1. The two stops H_1 and H_2 determined the contiguous semicircular fields 1° in diameter seen by the observer, the light of the H_1 field being transmitted by the half-silvered cube C_2, that of the H_2 field reflected at it. When it was required to match a mixture of two lights against a mixture of two others, glass plates

at 45° were inserted at C_3 and C_4, performing similar functions to the half-silvered cubes and diverting some of the light from L_1 to pass through H_1.

The movable mirror M was usually out of the path of light, but could be swung into the position shown in the figure, thereby replacing the matching fields by an adapting field 3° in diameter provided by the lamp S_3, whose filament was then imaged on the artificial pupil by the lens L_5. The artificial pupil was a circle of 3 mm diameter, except in the experiments of section II, where a 1 mm pupil was used.

The wave-bands of light in pathways other than that of the monochromator were controlled by filters at F_1, F_2, and when required F_3. The intensities were controlled discontinuously by colloidal carbon neutral filters and continuously by neutral wedges at W_1, W_2 and W_3, operated by the subject by means of pulleys.

The position of the subject's head was fixed in relation to the artificial pupil by his biting on a dental impression clamped to the optical system but adjustable vertically and horizontally by screws.

The relative energy of light from the monochromator at different wave-lengths was determined from $\lambda 460$ mμ to $\lambda 680$ mμ by Dr L. C. Thomson with an electron multiplier photocell calibrated by the National Physical Laboratory, and from $\lambda 520$ mμ to $\lambda 900$ mμ with a bolometer. A smoothed curve incorporating both sets of data has been used in calculating the results.

The neutral filters and wedges used were calibrated throughout the spectrum in parallel light, the wedges by the National Physical Laboratory and the filters in Cambridge with a Hilger Uvispek photo-electric spectrophotometer. Their densities were checked in the apparatus at wave-lengths 480 and 600 mμ with an electron multiplier photocell. The values determined for parallel light were found to need no correction. The linearity of the wedges was similarly tested in the apparatus at these two wave-lengths.

The filters used to determine the wave-lengths of adapting lights and of test lights other than that provided by the monochromator are described in Table 1. The 'equivalent wave-length' there given is the calculated wave-length from which the definite integral $d\lambda$ of the product of filter transmission, photopic sensitivity of the eye (C.I.E. standard curve) and energy emission of the lamp is the same up to infinite wave-lengths as down to zero wave-length (this is nearly the same as the wave-length of maximum value of this product). Each filter wave-band formed a perfect match on a 1° field with monochromatic light of its 'equivalent wave-length' when the intensities were suitably adjusted.

TABLE 1

Description of filter	Ilford catalogue no.	Wave-length of maximum transmission (mμ)	Equivalent wave-length (mμ)	Abbreviation used in text
Liquid filter of cuprammonia	—	*c.* 410	438	DV (438)
Ilford spectrum violet	601	428	454	V (454)
Ilford spectrum blue	602	469	480	B (480)
Ilford spectrum blue-green	603	492	497	BG (497)
Ilford spectrum yellow-green	605	550	550	YG (550)
Ilford spectrum yellow	606	578	578	Y (578)
Ilford spectrum orange	607	604	606	O (606)
Ilford spectrum red + infra-red-absorbing glass	608	—	658	R (658)
Ilford spectrum deep red	609	—	680	DR (680)

In all the present work the errors of calibration are small compared with the experimental errors (the calibrations having been carried out for use in other more accurate experiments) except for the determinations of the luminance of adapting fields. These latter were done by comparison with a standard field of wave-length 578 mμ produced by the monochromator, whose luminance was in turn measured by means of an S.E.I. exposure photometer calibrated against a standard lamp. For yellow adapting fields, in which the primary comparison was homochromatic, the final accuracy is about $\pm 20\%$, and for adapting fields of other colours a little worse than this.

All the experiments described in sections I–III were carried out on one subject, the author, who has normal colour vision as tested by the Ishihara (9th ed.) and Boström (1950) pseudo-isochromatic plates, and makes a normal Rayleigh match with a normal tolerance. The experiments were unpleasant in that very prolonged after-images were produced, being often very obvious 6–10 hr after repeated blue or violet adaptation. Even 8 months after the last experiment, the author's left eye, which was used throughout, showed, when looking at any moderately bright uniform field, a faint after-image reproducing the details of shape of the slightly irregular adapting field. For these reasons it was not possible to repeat on other subjects the very large number of re-adaptations required to duplicate the curves obtained with the author as subject, but a number of limited confirmatory experiments were carried out on other subjects, and are described in section IV.

RESULTS

I. *Disturbance of colour matches by adaptation*

(*a*) *Adapting conditions fixed, matching conditions varied*

The effects of adaptation to a bright yellow light on a number of colour matches are shown in Fig. 2.

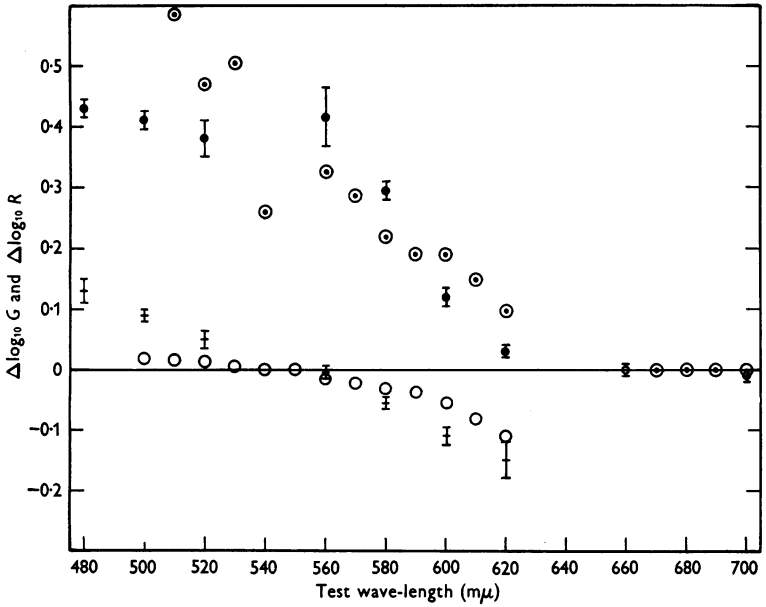

Fig. 2. Changes produced by adaptation to Y (578) at 1300 mL in $\log_{10}$(amount of red) (observed values ⧱, calculated values ⊙) and $\log_{10}$(amount of yellow-green) (observed values ⧱, calculated values ○) required to match lights of different wave-lengths.

Lights of wave-lengths 560–700 mμ were matched against mixtures of YG (550) and DR (680), with the oblique glass plates C_3 and C_4 in position and V (454) at F_3 to provide a desaturating addition to the test light. Lights of wave-length 480–520 mμ were matched against mixtures of YG (550) and V (454), with DR (680) at F_3. All these matches were made first with the unadapted eye, then after adaptation to Y (578) at luminance 1300 mL (millilamberts) for 30 sec, matching

being carried out between the 10th and 15th second after removal of the adapting field. After adaptation, for all test wave-lengths the amount of violet required became ill-defined. At 560 mμ and longer wave-lengths, formerly requiring a very small negative amount of violet, either none or a three times larger amount became tolerable. At 520 mμ and shorter wave-lengths, formerly requiring a fairly large positive amount of violet, it became possible to increase or decrease this by a factor of 1·3 to 1·6, without preventing a match and without thereby making more than a just

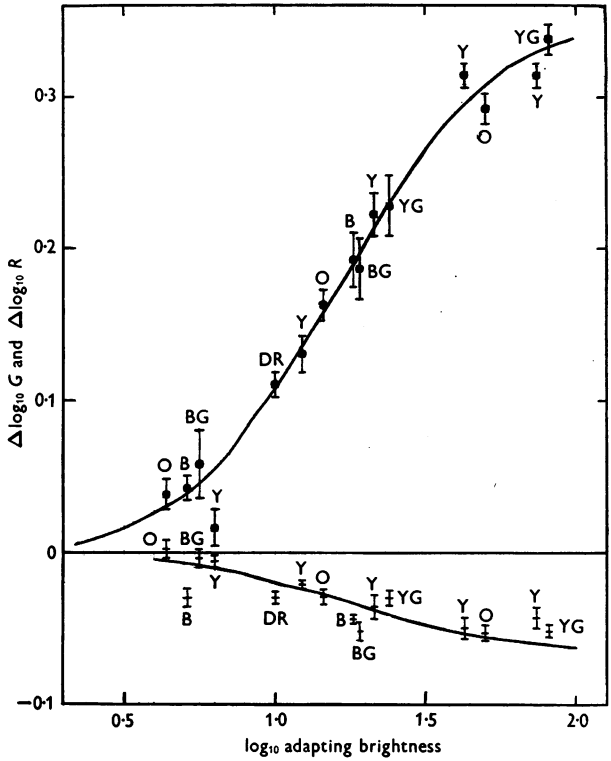

Fig. 3. Changes produced by adaptation to various lights in $\log_{10}$(amount of red) (I), and $\log_{10}$(amount of yellow-green) (I) required to match light of wave-length 580 mμ.

supraliminal change in the amounts of red and yellow-green required in it. Because of this indeterminateness, in the quantitative experiments the amount of violet in a match to be made after adaptation was fixed at the amount required for the unadapted eye, and only the red and yellow-green altered. The changes in the amounts of red and yellow-green required are shown in Fig. 2. Each point shows the difference between the means of six determinations before adaptation and six after adaptation of $\log_{10}$(amount of red) or $\log_{10}$(amount of yellow-green) in a match, and each vertical line has total length twice the standard error of the difference of means.

(*b*) *Adapting conditions varied, matching conditions fixed*

By the same technique, the effects of a number of different adapting wave-bands and luminances were tested on one colour match, that between λ 580 mμ and a mixture of DR (680) and YG (550).

Desaturating violet was omitted. A very small difference of saturation could be detected with the unadapted eye, none after any of the adaptations employed. Adaptation to Y (578) was tested at five brightness levels, O (606) at three, YG (550), BG (497) and B (480) at two each, and DR (680) at one. Each point in Fig. 3 shows the difference of the mean of six determinations in the adapted state from that of twenty-four pooled determinations in the unadapted, and once the standard error of this difference of means in each direction.

It will be seen from Fig. 3 that adapting lights of all colours and luminances increased the amount of red required in the match and decreased the amount of yellow-green, the decrease in yellow-green being roughly one-fifth of the increase in red.

If two or more different processes were concerned in the disturbance of colour matches by adaptation, e.g. if the forms of the spectral sensitivity curves of two or more classes of receptors were altered, the ratio $\Delta \log_{10} R/\Delta \log_{10} G$ would not necessarily be the same for different adapting wave-lengths; indeed we should expect it to be positive for some wave-lengths and negative for others. But if the disturbance is due to a single process with a unique spectral sensitivity curve, then the constancy of $\Delta \log_{10} R/\Delta \log_{10} G$ seen in Fig. 3 is explained. In the discussion, an attempt will be made to identify this hypothetical single process.

The sets of points for different adapting wave-bands in Fig. 3 have been shifted horizontally so that the values of $\Delta \log_{10} R$ lie as well as possible on the same curve for all adapting wave-bands, and a 0·186 time multiple of this curve has been drawn through the values of $\Delta \log_{10} G$. From the amounts of horizontal scaling required, six points on the spectral sensitivity curve of the hypothetical single process responsible were determined, and are shown as crosses on Fig. 4. To do this, it was assumed that each adapting light had the same action that a monochromatic light of its 'equivalent wave-length' would have had if adjusted in intensity to match it on visual comparison. This assumption is almost certainly valid for the orange, yellow, yellow-green, blue-green and blue adapting lights, which consisted of narrow wave-bands, and probably so even for the deep-red adapting light, consisting of a very broad wave-band.

II. *Disturbance of colour matches on passing all the light through the periphery of the pupil*

Stiles (1937) found that monochromatic light which reaches the retina from the periphery of the pupil appears of a different colour from physically similar light which reaches it from the centre of the pupil. It appears not to have been hitherto observed that two lights of different composition which match when the rays reach the retina from the centre of the pupil may not match when they reach it from the periphery. Fig. 5 shows the way in which the amounts of DR (680) and YG (550) required to match various monochromatic lights

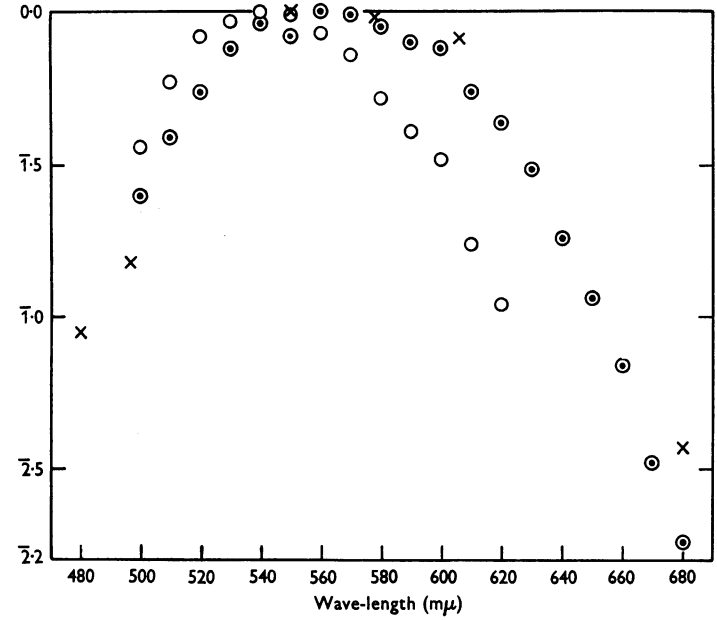

Fig. 4. ○ and ⊙ : log luminosity curves, referred to an equal energy spectrum, in states of artificial monochromacy. ○ : monochromacy following violet and red adaptation. ⊙ : monochromacy following violet and blue-green adaptation. × : values of $\log_{10} 1/E$ for adapting lights to have a constant disturbing effect on colour matches, inferred from the results of the experiment shown in Fig. 3.

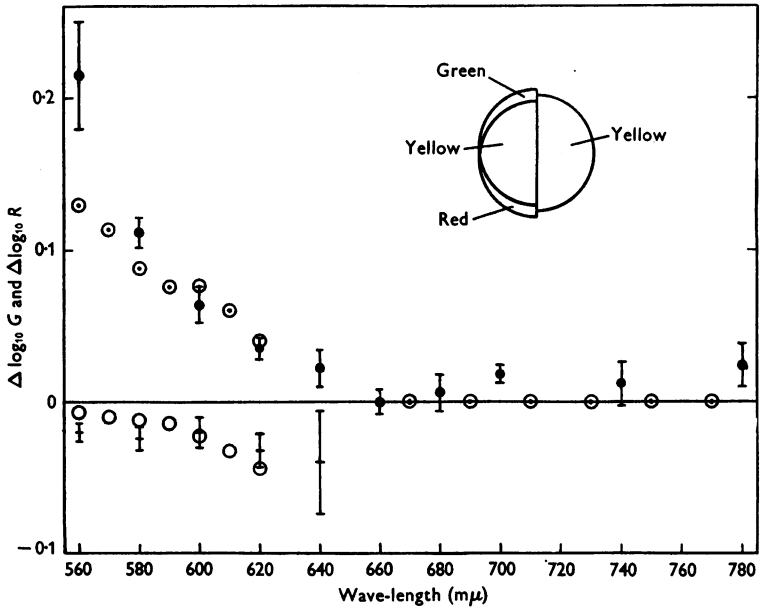

Fig. 5. Changes, produced by 3 mm decentring of the eye on the artificial pupil, in $\log_{10}$ (amount of red) (observed values ⊺, calculated values ⊙) and $\log_{10}$ (amount of yellow-green) (observed values ⊺, calculated values ○) required to match lights of different wave-lengths. Inset: appearance of matching fields with the eye decentred.

altered when the author's homatropinized eye was moved in relation to the artificial pupil (which was 1 mm in diameter), so that the light, which had all been passing through the centre of the pupil, came to pass through a region about 3 mm above the centre. Owing to chromatic aberration at the cornea, this decentring caused a slight separation of the red and green components of the mixed field. The appearance is shown in the inset to Fig. 5.

An attempt was made to see whether a colour match already disturbed by adaptation was further disturbed by decentring to the same or a greater or less extent than a match made by the unadapted eye. The combined technical difficulties and the low apparent brightness of the fields when both decentring and adaptation were introduced made it impossible to get satisfactory results by matching; but by using single 1° fields of monochromatic light at greater luminance it could be seen that the apparent hue change on decentring was completely abolished by adaptation to Y (578) at 14,000 mL (1 mm artificial pupil for both adapting and test light), although a change of actual wave-length corresponding to the apparent hue change on decentring the unadapted eye could for wave-lengths 490, 580 and 600 mμ be detected by an eye which was both adapted and decentred.

III. *The effects of brighter adapting lights*

Burch (1898) described the appearance of a spectrum after adaptation to very bright coloured lights. He found that for a short time after adaptation to violet followed by green, or a mixture of violet and green, only the part of a spectrum from the *A* Fraunhofer line (760 mμ) to midway between the *G* and *F* lines (about 500 mμ) remained visible, and all of this appeared of one colour, an unsaturated red. After adaptation to a mixture of violet and red, the spectrum was visible from the *C* line (656 mμ) to the *G* (431 mμ), and all appeared of an unsaturated green. His descriptions of the effects of other adapting lights made it seem likely that besides these states of reduction of the light-discriminating power of the eye from three degrees of freedom to one (intensity only), states in which there were two degrees of freedom remaining could also be produced.

These findings and suggestions are here confirmed, and quantitative characteristics of the 2-chromatic and 1-chromatic states given.

(*a*) *Adaptation to violet: artificial 'tritanopia'*

After adaptation for 30 sec to DV (438) at brightness 1100 mL, any monochromatic light could be exactly matched on a 1° field with a mixture of red and blue. Discrimination between such mixtures was good, the tolerance never exceeding twice that of the unadapted eye, and the dichromatic matches could be easily and accurately reproduced from day to day. The duration of this dichromatic state varied considerably with the brightness of the test field,

the period of absolute dichromacy being followed by one in which dichromatic matches could still be made at low brightnesses, but broke down at high. With test fields of brightness 2 mL, dichromatic matches could be made for about 40 sec after adaptation. Spectral mixture curves referred to an equal-energy spectrum, using B (480) and DR (680) as primaries, with test fields of luminance between 1·3 and 2·8 mL (this was not kept exactly constant because the amount of light from the monochromator could be varied only discontinuously by means of neutral filters) are plotted in Fig. 6. Each point is the mean of four determinations, two at each wave-length having been made on each of 2 days.

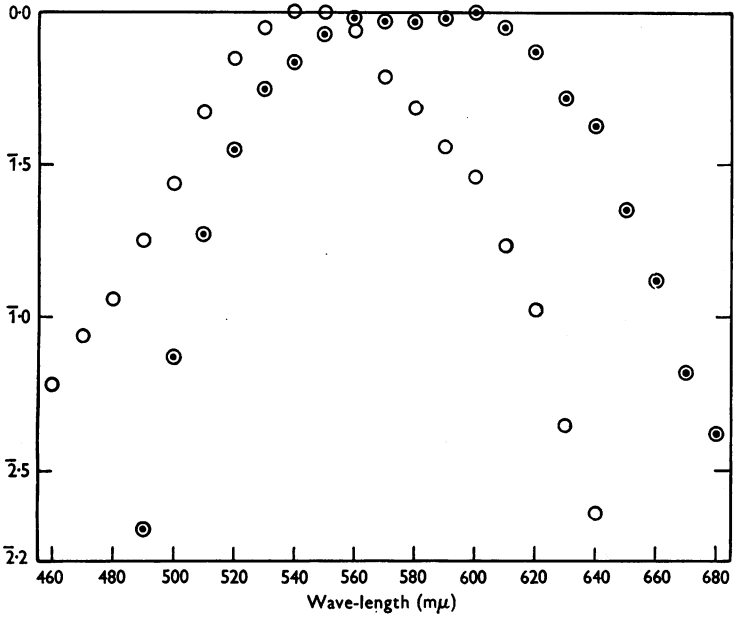

Fig. 6. Log spectral mixture curves referred to an equal-energy spectrum in the state of artificial tritanopia. ○ : $\log_{10}$(amount of B (480)). ⊙ : $\log_{10}$(amount of DR (680)).

At wave-lengths less than 460 mμ, it was necessary to widen the entry slit of the monochromator to obtain enough light, and to add a filter to cut out stray light of longer wave-lengths. In these circumstances the energy values for light from the monochromator became uncertain, so that no mixture coefficients for an equal-energy spectrum can be given. Fig. 7 gives the dichromatic coefficient curves for the spectrum, using units of the primaries based on a match on λ 582·5 mμ, and includes values for wave-lengths less than 460 mμ.

The mixture curves and dichromatic coefficient curves show a close resemblance to those of the dichromacy of very small central foveal fields (Willmer & Wright, 1945; Thomson & Wright, 1947) and to those of tritanopic subjects (Wright, 1952).

(*b*) *Adaptation to red: artificial 'protanopia'*

Adaptation for 20 sec to R (658) at 12,000 mL produced for about 10 sec a state in which (i) sensitivity to red was diminished in comparison with sensitivity to green, (ii) lights of wave-lengths from 540 to 620 mμ were indistinguishable from each other when their intensities were suitably adjusted, all appearing of an unsaturated blue-green, and (iii) all monochromatic lights of wave-lengths from 440 to 620 mμ could be matched by mixtures of V (454) and O (606). This state, which in these three features resembles protanopia, could never, by varying the conditions, be made to complete its resemblance

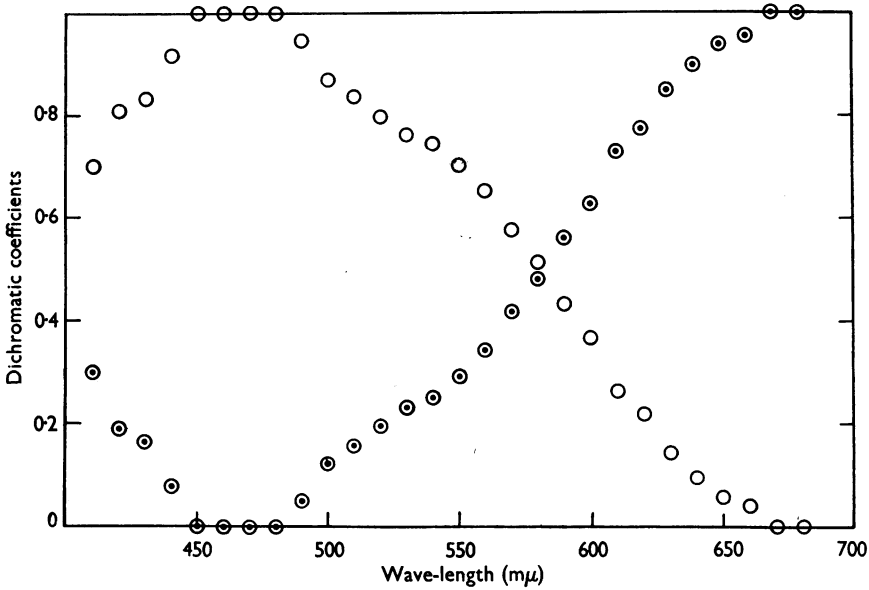

Fig. 7. Dichromatic coefficient curves for the spectrum in the state of artificial tritanopia. ○ : amount of B (480). ⊙ : amount of DR (680). Units based on a match on λ 582·5 mμ.

by including wave-lengths over 630 mμ in the dichromacy; these always appeared redder than any mixture of V (454) and O (606). The exact wave-length above which the dichromacy broke down varied with conditions. With bright test fields or adaptation periods less than 20 sec it extended only to about 600 mμ, but with dimmer test fields and 20 sec adaptation it could always be made to extend to 620 mμ and often to 630 mμ.

In marked contrast to the state of artificial 'tritanopia', in artificial 'protanopia' it was very difficult to obtain consistently reproducible colour matches. In part this was due to the brief duration of the state, but principally to the large tolerance for changes in the amount of violet in a colour match.

No conditions of adaptation were discovered which would produce a third type of dichromacy analogous to deuteranopia.

(c) *Artificial monochromacies*

The first two of the three states described in this section have been qualitatively described by Burch (1898), and the present observations do not conflict with his. The third state has apparently not been previously described.

Monochromacy following violet and blue-green adaptation. After 20 sec adaptation to DV (438) at 1100 mL followed immediately by 10 sec adaptation to BG (497) at 3500 mL, it was possible to match exactly, intensity alone being adjusted, any monochromatic light between 500 and 700 mμ with Y (578). This state lasted for about 10–15 sec, and it was not difficult during this time to make fairly accurate and reproducible matches. Fig. 4 shows the luminosity curve, referred to an equal-energy spectrum, obtained in this state with test fields varying in luminance for different wave-lengths between 2·5 and 5·4 mL. Each point is the mean of four determinations, two on each of 2 days, the order of wave-lengths being opposite on the 2 days.

Lights of wave-length less than 500 mμ could not be matched exactly with Y (578); they always appeared bluer.

Unlike the sensation produced by red light after *moderate* brightnesses of blue-green, which is more saturated than that of red as seen by the unadapted eye, in the present conditions of adaptation (as in Burch's description of a similar state) the sensation due to red light (or light of any other wave-length over 500 mμ) was a very unsaturated red or pink.

Monochromacy following violet and red adaptation. Adaptation to DV (438) at 1100 mL for 20 sec followed by R (658) at 12,000 mL for 10 sec produced for about 10–15 sec a state in which light of any wave-length between 480 and 620–630 mμ could by adjusting intensity alone be exactly matched with Y (578), both fields appearing of an unsaturated blue-green. As with the dichromacy produced by adaptation to R (658) alone, lights of wave-length above 630 mμ always appeared redder than lights within the range of monochromacy.

The luminosity curve, referred to an equal-energy spectrum, obtained in this state at a field brightness varying between 2·5 and 4·7 mL is shown in Fig. 4.

'Violet' monochromacy. The two states just described were very similar to each other in duration, in the ease and reproducibility of intensity matching, in the unsaturated quality of the sensation, and in that visual acuity appeared to be as good in the adapted as in the unadapted eye. By adaptation to Y (578) at 14,000 mL for 10 sec, a third kind of monochromacy could be produced with strikingly different properties. Lights of all wave-lengths between 400 and 500 mμ could be exactly matched with V (447), both fields appearing of a very saturated violet, substantially more saturated than any spectral violet as seen by the unadapted eye. The appearance of this very saturated violet on changing the test wave-length gradually to or from the

range in which it could be obtained was sudden: just outside the range the sensation was a very unsaturated blue-green, and only over a very small range of intermediate wave-lengths were intermediate degrees of saturation seen. The disappearance of the very saturated violet as the adaptation wore off was similarly sudden.

Intensity discrimination, which in the other two monochromacies was good, and allowed fairly accurate luminosity curves for the spectrum to be obtained by matching, was in this 'violet' monochromacy exceedingly bad; if two violet or blue fields which matched for the unadapted eye were examined after yellow adaptation, no difference between them could be detected on increasing the intensity of either by a factor 4.

The boundaries of the two test fields, as seen in this state, were conspicuously less well-defined than those of the same fields, or even of fields of much lower brightness, as seen by the unadapted eye. This observation suggested the measurement of visual acuity in the state of 'violet' monochromacy.

To eliminate the possibility that any apparently low acuity might be due to failure to accommodate correctly, all the measurements were carried out in full cycloplegia produced by homatropine, with an artificial pupil 3 mm in diameter and a spectacle lens placed 4 cm from the eye correcting vision for the working distance (54 cm) at the wave-length used in the test. The power of spectacle lens required was determined by trial with the unadapted eye. Acuity was measured by means of a series of thirteen gratings inserted to replace the stop H_1 in the apparatus. Each grating was a square of linear dimensions approximately 1·24 times those of the next smaller member of the series, and each contained seven opaque and eight transparent strips of equal width. A circular stop within the monochromator limited the viewing field to 1° 13′ at 404·7 mμ, 1° 18′ at 470 mμ, and 1° 22′ at 560 mμ, so that only the smaller gratings were seen entire, and of the largest of all (11·9, 12·6 or 13·3′ according to wave-length) only three transparent bars separated by two opaque were visible. The magnification due to the spectacle lens used at each wave-length was determined by measuring a grating viewed under the experimental conditions by the left eye against a scale viewed in white light at 27·5 cm by the right, and acuity is given as the width of one black bar of the finest grating resolvable in units of 1′ of arc (0·080 mm) of the scale.

Table 2 shows the results for the unadapted eye and three states of light adaptation at λ 470 mμ, and for the unadapted eye and one state of light-adaptation at 560 and 404·7 mμ. It will be seen that whenever the appearance of the test field is that characteristic of the 'violet' monochromacy, the visual acuity falls to about 12′, and that this low value is maintained for the same state of adaptation over a hundred-fold variation in test luminance, whereas in the unadapted eye or in states of adaptation not producing 'violet' monochromacy, there is never so much as a tenfold range of test luminances for which the acuity is in the neighbourhood of 12′.

IV. *Confirmatory experiments on other subjects*

The experiments of section III were repeated qualitatively on three other subjects, all of whom have normal colour vision. All the states described in that section could be produced by similar adapting conditions with these subjects. Some details of their observations are given in Table 3.

TABLE 2. Visual acuity in minutes of arc, determined on the fifth second after a 30 sec period of light adaptation

Test wave-length (mμ)	Log test luminance*	Adaptation: None	Y (578) 14,000 mL	Y (578) 1300 mL	B (480) 900 mL
560	5·24	0·8	0·8	—	—
	4·20	0·8	1·3	—	—
	3·17	0·8	1·7	—	—
	2·13	1·3	Invisible	—	—
	1·07	2·6	Invisible	—	—
	0	>13·3	Invisible	—	—
470	4·21	0·7	12·6†	1·6	1·2
	3·17	0·9	12·6†	10·0†	Invisible
	2·18	1·6	12·6†	12·6†	Invisible
	1·10	3·3	Invisible	12·6†	Invisible
	0	>12·6	Invisible	Invisible	Invisible
404·7	2·40	1·1	—	11·9†	—
	1·21	1·9	—	11·9†	—
	0	>11·9	—	Invisible	—

* Test luminance is given in arbitrary units different for the three wave-lengths. The unit is approximately 1·0 μL for 560 and 470 mμ, 1·5 μL for 404·7 mμ.

† Indicates that the field had the very saturated violet appearance characteristic of the 'violet' monochromacy.

TABLE 3. Summary of observations on four subjects

	G.S.B.	E.W.B.	M.L.	E.N.W.
Artificial tritanopia:				
Approx. duration (sec)	40	120	30	40
Range of 2-chr.	Whole spectrum	Whole spectrum	Whole spectrum	Whole spectrum
Artificial protanopia and 1-chr. following violet and red adaptation:				
Approx. duration (sec)	10–15	18	14	14
Sensation	Unsaturated blue-green	Pale green	Pale green	Dirty yellow
Range (mμ)	500–620	520–615	520–615	500–620
1-chr. following violet and blue-green adaptation:				
Approx. duration (sec)	10–15	20	10	14
Sensation	Unsaturated red	Pinkish orange	Pink	Dirty yellow
Range (mμ)	500 to extreme red	520 to extreme red	520 to extreme red	500 to extreme red
'Violet' 1-chr.:				
Approx. duration (sec)	5th–20th	10th–45th	5th–20th	10th–30th
Sensation	Very saturated violet	Intense violet	Very deep blue	Very saturated violet
Range (mμ)	500 to extreme violet	510 to extreme violet	500 to extreme violet	500 to extreme violet

The agreement between different subjects is quite good. That E.N.W. saw the fields as dirty yellow after both violet+red and violet+blue-green adaptation, though the other subjects saw them in one case as pale green and in the other as pink, is not so striking a disagreement as it appears, since the hue was not very easily named in the presence of a marked after-image, and without any standard for simultaneous comparison. All subjects agreed on

the very high saturation in the 'violet' monochromacy and the very low saturation in the other two monochromacies, and on the poor definition of the fields and poor brightness discrimination in the 'violet' monochromacy.

DISCUSSION

Disturbance of colour matches by adaptation

As von Kries (1878) pointed out, if only three kinds of receptors are active in photopic vision, and the form of the spectral sensitivity curve of each is uninfluenced by adaptation, then colour matches which hold for the unadapted eye must hold also in any state of adaptation. Since they do not, we must conclude either that the form of the sensitivity curve of at least one of the three kinds is altered by the adaptation, or that more than three kinds are active. Hartridge (1949), having reached the latter conclusion on other grounds, has used Wright's (1936) observation that colour matches can be upset by adaptation to support it. But the findings of the present detailed examination of the manner in which they are upset are much more easily explained on a basis of changes in sensitivity curves than on a polychromatic hypothesis.

A hypothesis that there are more than three kinds of receptors active, and that the trichromacy of vision as a whole results from their convergence on to only three classes of neurones at some more central level in the visual pathway, leads to the conclusion that any adaptation which depresses the sensitivity of different classes of receptors to different extents will change the form of the spectral sensitivity curves at the 3-class level determining trichromacy, and hence upset colour matches; and if lights of different wave-length have different relative adapting actions on the various classes of receptors, then they must alter the form of the spectral sensitivity curves at the 3-class level differently and hence upset colour matches differently. This is contrary to the results described in section I(*b*) (Fig. 3); and a polychromatic hypothesis postulating a 3-class level to explain trichromacy can only be reconciled with them if either: (i) none of the receptors are altered in sensitivity by adaptation to bright lights, and the upset of colour matches is due to some other process; or (ii) the activity curves for different wave-lengths in depressing receptor sensitivities are the same for all receptors; or (iii) only one class of receptors is influenced by light adaptation; or (iv) there is a mechanism which compensates for the disturbance of colour matches by differential adaptation of receptors, but introduces a disturbance of its own.

A polychromatic theory such as that of Hartridge (1949), which denies the existence of a 3-class level and leaves the experimental fact of trichromacy unexplained, appears to require one of the same four *ad hoc* additional hypotheses, though the vagueness of Hartridge's theory concerning colour

matching makes the argument (on the same lines as before, but replacing 'spectral sensitivity curves at the 3-class level' by 'the three functions of the receptor activities which determine whether two lights shall match') more abstract and less certainly exclusive of alternatives.

None of the four reconciling hypotheses is at all readily acceptable; the second and third conflict directly with the results of section III of the present paper, and the first and fourth are very uneconomical, the more so since the 3-receptor explanation to be put forward here explains also the disturbance of colour matches on decentring, which on a polychromatic explanation would require further *ad hoc* hypotheses.

If we set aside the polychromatic explanation, we must accept that the form of the spectral sensitivity curve of at least one class of receptor is altered by adaptation. Concerning two possible mechanisms for such alteration, the present data provide information.

Suppose first that the only relevant action of adaptation is to produce or destroy somewhere in front of the receptors a pigment which screens all receptors to an equal extent from incident light. Then in a match of any light against a mixture of red and green, the change after adaptation in the ratio of red to green required in the colour match depends only on the changes in the absorption of the red and green lights by the screening pigment, and hence is independent of the nature of the other light that is being matched. Hence $(\Delta \log_{10} R - \Delta \log_{10} G)$ must in the experiment of section I (*a*) (Fig. 2) be constant. Since it is not, the hypothesis must be false. This argument, though different in form, is in essence the same as that by which Wright (1936) drew the same conclusion from his results.

A second conceivable mechanism, analogous to that suggested by Stiles (1937) to explain the change of hue on passing light through the periphery of the pupil, is the following. If the optical density of pigment in a receptor is for some wave-lengths high, then the form of the sensitivity curve will, if Beer's law is obeyed, vary with the pigment concentration according to the law

$$K_\lambda = \frac{K'_{\lambda\text{max.}}}{D'_{\lambda\text{max.}} \log_e 10}\left(1 - 10^{-D_{\lambda\text{max.}} \frac{K'_\lambda}{K'_{\lambda\text{max.}}}}\right) \qquad (1)$$

where K'_λ is the sensitivity at wave-length λ when the maximum pigment density has the very low value $D'_{\lambda\text{max.}}$ and K_λ the sensitivity at wave-length λ when the concentration is such that the maximum pigment density is $D_{\lambda\text{max.}}$.

The monochromatic states described in section III appear to be states in which all but one of the classes of receptors are so reduced in sensitivity by adaptation that they contribute no information whereby lights of different wave-length can be distinguished. If so, the spectral sensitivity curves for the eye in these states are spectral sensitivity curves for classes of receptors.

Since they are obtained in states of adaptation more extreme than those known to disturb colour matches, they are certainly not the same spectral sensitivity curves that these receptor classes have in the normal eye; but on the present hypothesis they are simply related to them, being the spectral sensitivities K'_λ for very low pigment concentration. If then we assume values for the peak densities of the 'red' and 'green' receptor pigments, we can use the data of Fig. 4 to calculate the values of $\Delta \log_{10} R$ and $\Delta \log_{10} G$ which should have been obtained in the experiment of Fig. 2, for

$$\left.\begin{aligned}\Delta \log_{10} R &= \log_{10} \frac{(a_r b_g - b_r a_g)\,(A_\lambda B_g - B_\lambda A_g)}{(A_r B_g - B_r A_g)\,(a_\lambda b_g - b_\lambda a_g)} \\ \Delta \log_{10} G &= \log_{10} \frac{(a_r b_g - b_r a_g)\,(A_\lambda B_r - B_\lambda A_r)}{(A_r B_g - B_r A_g)\,(a_\lambda b_r - b_\lambda a_r)}\end{aligned}\right\}, \tag{2}$$

where A_r, A_g and A_λ are the sensitivities of the 'red' receptors and B_r, B_g and B_λ those of the 'green' receptors to DR (680), YG (550) and the test light respectively, and the corresponding small letters their sensitivities after adaptation. These sensitivities can be calculated for the assumed peak densities using Eqn. (1).

The points shown as ⊙ and ○ in Fig. 2 give the calculated values of $\Delta \log_{10} R$ and $\Delta \log_{10} G$ for a peak density of red-receptor pigment in the unadapted eye of 0·5, and a negligible peak density of green-receptor pigment (0·1 would be low enough for this; alternatively, the assumption that the amount of green-receptor pigment is not substantially altered by adaptation would lead to the same conclusion). The discrepant point at 550 mμ on the presumed red-receptor curve has been adjusted from $\bar{1}$·92 to $\bar{1}$·96 in making the calculation. Other irregularities in the curves are untouched. The differences between the observed and calculated values of $\Delta \log_{10} R$ and $\Delta \log_{10} G$ are greater than the experimental errors of the observed values; but in view of the great dependence of the calculated values, especially for wave-lengths less than 550 mμ, on small inaccuracies in the curves of Fig. 4, they may be regarded as satisfactorily small.

If any substantial change in the density of green-receptor pigment is assumed to be produced by the adaptation, the fit of calculated to observed values becomes much worse. The fact that these data are best fitted by assuming that the sensitivity curve of only one class of receptors is altered by adaptation agrees well with the similar inference made from independent data in section I(*b*) (i.e. from the finding that adapting lights of different wave-lengths upset matches similarly). The spectral sensitivity curve inferred in section I(*b*) (crosses on Fig. 4) for the process affected by adaptation gives further support to the conclusion that it is the red receptors that alone are affected, for it agrees within experimental error with the presumed red-receptor curve.

Disturbance of colour matches by eccentric passage through the pupil

Stiles (1937) suggested that the hue changes on passing lights eccentrically through the pupil were not due merely to a difference in magnitude of directional sensitivity of different classes of receptors, but to a difference in form of the spectral sensitivity curves for different directions of incidence, on the grounds that the former mechanism would require improbable spectral sensitivity curves. The present finding that colour matches can be upset by decentring very strongly supports this suggestion.

The upset of colour matches observed was not due to the slight difference in obliquity of incidence of the right and left fields, for the same upset was found on decentring to the right as to the left, in which cases the differences in obliquity were opposite; nor to the minute difference in obliquity of incidence of the red and green components of the mixed fields, due to chromatic difference of refraction at the cornea, for on decentring vertically (as was normally done, in order to preserve the sharp boundary between the two fields) the upper and lower parts of the mixed field were alike in hue and brightness, despite a greater difference of obliquity than that between the red and green components in any one part of the field.

As with the upset of colour matches by adaptation, the fact that the curves of $\Delta \log_{10} R$ and $\Delta \log_{10} G$ are not parallel excludes explanation in terms of a general screening pigment, e.g. a difference in absorbing properties between the centre and periphery of the lens. The effect can therefore only be a retinal one, and, if there are only three classes of receptors concerned, must be a difference in the form of the spectral sensitivity curve of at least one class of receptors for different directions of incidence, either intrinsic to the receptors or due to structures related to them individually. The high density of pigment postulated in red receptors to explain the upset of colour matches by adaptation provides a mechanism for just such a difference, along lines suggested by Stiles (1937).

Light which reaches the receptors obliquely will pass through a smaller total density of pigment than light which travels along their axes, and hence the spectral sensitivity curves for it will approximate to those found after adaptation to bright lights. The circles in Fig. 5 show the results of calculating $\Delta \log_{10} R$ and $\Delta \log_{10} G$ assuming that the effective peak density of red-receptor pigment falls by 0·2 for oblique incidence. They agree satisfactorily with the observed values, if the errors of both are taken into account.

The finding (section II) that a degree of adaptation sufficient to produce by itself a large upset of colour matches (on the present hypothesis because it markedly reduced the red-receptor pigment density) abolished the apparent hue change on decentring fits in with the above explanation, and gives some further support to the view that the upsets by decentring and by adaptation are connected.

The properties of the 'violet' monochromacy

The low brightness discrimination found in the 'violet' monochromacy can hardly be a characteristic of the 'violet' or 'blue' pathway of trichromatic theory under normal conditions, for if so, then at every point in brightness-colour space there would be one direction (that corresponding to change in blue-pathway activity only) along which the discrimination step was very much greater than at right angles to it, and this is not observed.

The low visual acuity found in the 'violet' monochromacy seems likely to be connected with that which Stiles (1949) observed for blue flashes under difference-threshold conditions against backgrounds of other colours, and if so may well be a general character of the blue-receptor mechanism. Such low acuity might be explained either as (1) secondary to the low brightness discrimination, but this would not so well explain the low acuity under Stiles's difference-threshold conditions; or (2) due to scarcity of blue receptors; or (3) due to the convergence of many receptors on to each ganglion cell in the blue-receptive pathway.

Either (2) or (3) would also explain the tritanopia found with small foveal or parafoveal fields, but if scarcity of blue receptors were the cause, then there should be tritanopic confusion for some positions of a pair of small fields on the fovea (if no blue-receptors happened to be illuminated), but not for others. A search for this phenomenon failed to reveal it, and an attempt to see whether a circular field 10′ in diameter under conditions of 'violet' monochromacy appeared to flash on and off as it was moved across the fovea also yielded negative results. Hence convergence is at present a more acceptable explanation of the low visual acuity than scarcity.

SUMMARY

1. Colour matches can be upset by adaptation to bright lights. The way in which a match of yellow against red+green is upset is independent of the wave-band of the adapting light.

2. Colour matches made with light passing through the centre of the pupil are upset when the light passes through the periphery of the pupil. The direction of upset is the same as that produced by adaptation, but the magnitude less.

3. States resembling tritanopia and protanopia, and also states in which, over large ranges of the spectrum, no colour differences can be detected, can be produced by adaptation to certain very bright lights. Some quantitative characteristics of these states have been determined.

4. All the present experimental results and some other published observations, can be explained if (i) three classes of receptors are active in foveal photopic vision; (ii) the 'red' receptors have a maximum optical density of

photopigment about 0·5, which is decreased by adaptation to bright lights; (iii) in the foveal 'blue' pathway many receptors converge on to each ganglion cell.

This work was done while I held a Research Studentship from the Medical Research Council. I am very much indebted to Dr E. N. Willmer for his advice and criticism.

REFERENCES

BURCH, G. (1898). On artificial temporary colour-blindness, with an examination of the colour sensations of 109 persons. *Phil. Trans.* B, **191**, 1–34.

HARTRIDGE, H. (1949). The polychromatic theory. *Docum. ophthal.* **3**, 166–193.

VON KRIES, J. (1878). Beitrag zur Physiologie der Gesichtsempfindungen. *Arch. Anat. Physiol., Lpz., (physiol. Abt.)*, 503–524.

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

STILES, W. S. (1949). Increment thresholds and the mechanisms of colour vision. *Docum. ophthal.* **3**, 138–163.

THOMSON, L. C. & WRIGHT, W. D. (1947). The colour sensitivity of the retina within the central fovea of man. *J. Physiol.* **105**, 316–331.

WILLMER, E. N. & WRIGHT, W. D. (1945). Colour sensitivity of the fovea centralis. *Nature, Lond.*, **156**, 119–125.

WRIGHT, W. D. (1936). The breakdown of a colour match with high intensities of adaptation. *J. Physiol.* **87**, 23–33.

WRIGHT, W. D. (1952). The characteristics of tritanopia. *J. opt. Soc. Amer.* **42**, 509–521.