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FURTHER OBSERVATIONS ON THE PROPERTIES OF THE CENTRAL FOVEA IN COLOUR-BLIND AND NORMAL SUBJECTS

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It has been previously reported (Willmer, 1949*a*, *b*) that, whereas the normal central fovea behaves as a colour-perceiving mechanism possessing only two, instead of the normal three, separate pathways, the foveal centre of red-green-blind subjects, whether they be protanopes or deuteranopes, behaves as though it possessed but a single pathway. This may be stated in another way. The normal person when limited to the central fovea only requires two primary colours, e.g. red and violet, with which to match all the spectral colours, and he can also match a wave-length in the region of 570 mμ. with white. These matches are only possible provided that the viewing fields fall on, and are maintained within, the central fovea. The size of the viewing fields should not subtend an angle at the eye of much more than 30′ or there is danger of information being obtained from regions outside the central fovea. Under the same conditions both protanopes and deuteranopes can be found who are able to match any colour with any other colour, including white. In other words, they are totally colour-blind when their vision is confined to this area.

Now, as already indicated, the red-green-blind individuals fall clearly into at least two classes. On the one hand, there are the protanopes, who can match red and green on a 2° field and whose spectrum is shortened at the red end. They make certain characteristic colour confusions (Pitt, 1944) and are generally considered to lack the red mechanism. Their photopic luminosity curve has a maximum in the region of 540 mμ. On the other hand, there are the deuteranopes; and they form a less homogeneous group. They again can match red and green on a 2° field and make other colour confusions which differ from those made by the protanopes, but their luminosity curves have been found to differ from subject to subject. In some, the curve is almost or quite identical with that of the normal observer; in others, its maximum is shifted towards the red end of the spectrum and falls outside the range for normal observers. In many, the curve is intermediate. Both protanopes and deuteranopes have a point in

the spectrum, which they can match with white. In protanopes this 'neutral' point generally lies within the restricted range between 485 and 500 mμ., but in deuteranopes the range may be extended to 520 mμ. or even further.

On theoretical grounds the position with regard to the central fovea may be stated as follows. If the normal observer possesses the pathways *A* and *B*, then the red-green blind might most simply be considered to possess either *A* or *B*, or he might possess both pathways for a limited distance along the neural path, but they combine together before reaching the centre at which colour perception occurs. In the first case, the receptors or their particular pathways may be literally absent, either congenitally or by atrophy; or the contribution which they make might be completely annulled by some inhibitory effect. Three types of red-green-blind person should on these lines be theoretically possible, represented by *A*, *B*, or *AB*. Moreover, in the *AB* type all gradations would be possible between *AB* and *A*, or between *AB* and *B* provided that fusion occurs before the colour centre is reached.

These ideas can be put to the test in two ways. First, the luminosity curve, for the foveal centre, of type *A* must differ from that of type *B*, and both would be expected to differ from the normal, but individuals should also be found, the *AB* type, whose luminosity curve might be identical with the normal. Moreover, if gradations occur between the *AB* type and either *A* or *B*, then intermediate curves should also be obtained. Secondly, if an individual possesses only one type of receptor and only one pathway in his central fovea, and if he adapts his eye to equal brightnesses (in terms of his own thresholds) of any spectral colours, then his threshold should always be raised to the same extent. In other words, the effects of adaptation on his foveal thresholds for different wave-lengths should be dependent on the brightness of the adapting light, but they should be independent of its wave-length at constant brightness. If, however, he possesses two types of receptor, but only one pathway, the effects of adaptation to different wave-lengths at equal brightness may be expected to lie between something approaching independence of wave-length to something approaching the pattern of adaptation presented by the normal subject, according to the relative numbers of the receptors of each type present.

The central fovea has therefore been critically studied from these two aspects in seven normal individuals and eleven red-green-blind subjects, all of whom except one could match red with green on a 2° field, and all of whom except two could match red with any other colour, or white, when the tests were made with central fixation on two 10′ fields, separated by a space subtending 10′ at the eye. In the exceptions noted above, the first could match red with all colours on the small field, and was 'green-blind' by every test on the Ishihara plates, but he was not satisfied that Ilford red (608) could match Ilford green (604) at any brightness on a 2° divided field. The other two could match all spectral colours between red and blue with red, but they affirmed that violet appeared

as a separate colour. In this connexion it is important to remember that the subjects were dark-adapted to a considerable, but reasonably constant, extent and, under these conditions, unless very reliable fixation is maintained, other elements than those in the central fovea may contribute to the sensation, and these exceptions may have arisen through inability to maintain complete fixation or through the encroachment of extra-foveal elements upon the fovea. All the colour-blind subjects tested therefore were considered to be very nearly, if not absolutely, colour-blind (monodic or monochromatic) in the central fovea. Many others have also been examined but found to be only partially colour-blind in the central fovea, though invariably they were far worse at colour discrimination in the central fovea than when tested on a 2° field. Moreover, several other subjects were tested in a preliminary series of experiments and their luminosity curves determined by a less exact method than has been used in the cases reported in this paper, but these earlier tests, including some on subjects who have also been tested by the more exact methods, gave substantially the same results. In the tests on adaptation described here, the subjects have been adapted separately to red and to violet and the effects on the red and violet thresholds obtained. These wave-lengths were chosen on the grounds that if there were only two types of receptor in the central fovea these were most likely to be stimulated separately by wave-lengths near the ends of the spectrum.

METHODS

Adaptation

A mirror was placed in front of the viewing fields used for matching the test colours in the apparatus already described (Willmer, 1949*b*). Normally this mirror reflected the field by which the fovea and immediately surrounding areas were adapted to lights of known intensity, but the mirror could be swung out of the way and the matching fields immediately brought into view. The adapting field consisted of the surface of a frosted electric bulb viewed through a lens by Maxwellian view. The brightness and colour were adjusted by insertion of appropriate Ilford Neutral or colour filters. For adaptation to red light an ordinary 100 W. tungsten gas-filled bulb was used, but in order to obtain the desired brightness of violet a mercury vapour bulb was used and the ultra-violet light cut out by means of a CS_2 filter and an Ilford 805 filter in addition to the Ilford violet filter (601). The red adapting light was mostly that obtained by means of Ilford Deep Red (609), but some of the earlier experiments were carried out with Spectrum Red (608). The adaptation field subtended about 4° at the eye and was centrally fixated. An artificial pupil of 2 mm. diameter has been used in all the adaptation experiments.

When a subject had been found who passed the suitable tests to show that he was either normal or completely red-green blind, and after he had received some previous training in foveal fixation and in matching colours and determining thresholds, he was subjected to the adapting lights. The procedure was as follows. He was first given 10 min. in the dark to bring the fovea to approximately its most sensitive state. He was next asked to view the adapting field which had first been reduced in area by means of a stop until it only subtended 20 min. at the eye, and then neutral filters were inserted until the field was reduced in brightness to threshold intensity, care being taken that the field was being viewed by central fixation only. When, after two or three trials, the threshold for this 20 min. field had been determined, it then became possible to provide adapting lights of different intensities by removing the filters in stages (density 1 each time) so that intensities varying from 1 to 10,000 times the foveal threshold could be obtained. Before adaptation proper started the

adapting field was restored to its full size (4°) by removal of the stop inserted for the determination of the threshold brightness.

For determining the 'absolute' threshold of the test light the adapting field consisted of four points of dim violet light arranged in a square of such a size that when the eye was directed to the middle of the square the points all just fell within the fovea and became invisible owing to the low sensitivity to violet in that area. Any slight movement brought them into view again and so the movement could be immediately checked and central fixation maintained ready for viewing the test fields. In some experiments a very dim red point (20′) was used for fixation. Of the test fields, the right-hand field (10′ diameter) was always illuminated by dim red light (Ilford 608) and served as a pilot for central fixation. As far as possible its intensity was maintained constant, but an increase was generally necessary to ensure steady fixation after the higher levels of brightness were used in the adapting field. The left-hand field (also 10′) was illuminated by the test light whose intensity and wave-length were controlled by filters and by movement of the light source along a calibrated scale. The subject was asked to fixate on the left-hand edge of the right-hand field (the pilot field). He first of all viewed the adapting field for 1½ min., fixating its centre, and thereafter the test fields were exposed for a period of 3 sec. every 15 sec., the adapting fields being again fixated in the intervals. During the 3 sec. he was asked to decide whether or not the test light was visible with central fixation. In the case of the violet test light the criterion mostly used was whether or not the test light could be made to disappear by direct fixation, since apart from its accidental disappearance due to head movement or the like it was not likely to disappear on account of inadequate fixation. Head movements were, of course, minimized throughout by the subject biting on a dental impression which was clamped to the bench in a suitable position determined with great precision. The setting of the lamp illuminating the test field was adjusted by the operator in such a way that the subject could have no idea of the changes in intensity, if any, which were made between each 3 sec. viewing period. By a process of irregular bracketing the threshold could be found with more accuracy than might be supposed (approximately $\pm 20\%$).

In most cases, increasing stages of adapting brightness were used, but occasionally the experiment was performed in the reverse order, and a few subjects were tested only at zero brightness of the adapting field and at 1000 times threshold brightness. Minor modifications of this technique have been necessary or desirable from time to time, but the method described has been the usual one followed. Frequent rest periods were given and very few sittings lasted for more than 1 hr. at a time, since the requisite steadiness of fixation becomes too difficult to maintain after that time. Many unknown factors must naturally enter into work of this type, such as the degree of previous light adaptation, the degree of freshness or tiredness of the subject, and, above all, the attention he is prepared to give to the work. In spite of these difficulties, however, the results to be described will be seen to be fairly precise.

Luminosity curves

It was necessary to determine the luminosity curves for the central fovea in all the colour-blind subjects, and the threshold method was considered to be the most suitable, but, of course, this necessitated that great care be taken that strict central foveal fixation was maintained. For this purpose the subject's head position was again controlled as closely as possible by his biting on a dental impression clamped in a suitably adjustable holder. When his head was in position he could see through a 1 mm. artificial pupil a small red fixation point subtending about 2′. This point was near the centre of a small square of blue points of such intensity that they were invisible on the foveal area but they became visible as soon as central fixation was lost. The test light was then made to appear (or not) in $\frac{1}{10}$ sec. flashes at a point about 5′ away from the red fixation point and to its left. Owing to the chromatic aberration of the eye it was necessary in fixing the position of the subject's head to fix it first with a violet test light (continuously visible) and then with a red test light. If his head position was correct the field did not change its position with respect to the fixation light, but if he was not adequately centred then the two fields were found to change their positions; by changing back and forth between red and violet test lights the head position could be fixed in a reliable manner.

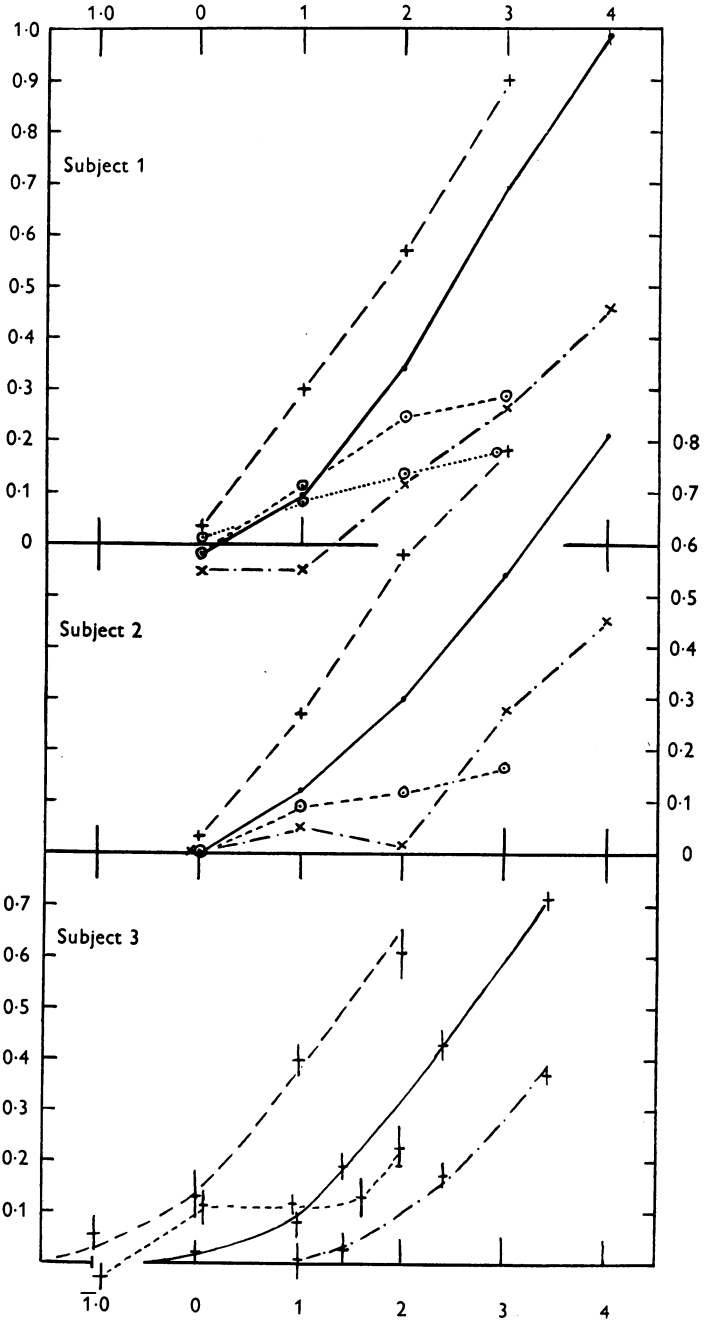

Fig. 1. For explanation of figure see p. 427.

The test lights were seen by Maxwellian view, and the field was delimited by a stop whose aperture subtended an angle of about 8′ at the eye. The field was illuminated by means of a Hilger Monochromator, and the light source was provided by a ribbon filament lamp (6 V. 18 A.) run at 4·4 V. from batteries which were being simultaneously charged. Intensity control was carried out by calibrated neutral filters, and a pair of polaroids placed in the exit beam. The calibration of the energy of the spectrum and the transmission of the polaroids was kindly carried out by Dr L. C. Thomson by means of a calibrated electron multiplier photocell. The duration of the flash, which was 12 msec., was determined by an adjustable rotary pendulum shutter, and has remained constant in these experiments. This short flash was used because it was hoped that by this means there would be no possibility of any eye movements as the result of the flash, so that if the subject's eye was well fixated there was no possibility of the test light falling outside the so-called rod-free area.

The subject was in complete darkness during the experiment and no readings were taken until he had been in the dark for 15 min. Each session lasted about an hour and for each curve the points were repeated four or five times, and the scatter of the points indicated a variation in the determined value of the threshold equivalent to a factor of about 2. The readings taken during the first session nearly always indicated a lower sensitivity than those found subsequently; some sharpening of the criterion for visibility always occurred. It also seemed to be evident that some of the later variation was due to an actual change in sensitivity of the eye from day to day. It must, however, be remembered that errors in centration and the Stiles-Crawford effect (Stiles & Crawford, 1933) may also contribute to the variability.

The curves were plotted between 480 and 700 mμ. Only a few readings were taken at wavelength shorter than 480 mμ. because the variable quantities of macular pigmentation in different subjects make estimation of the sensitivity in that region of doubtful value as an index for the sensitivity of the receptors.

RESULTS

Adaptation

All the experiments described here concern the manner in which the thresholds for lights from the spectral extremes are changed by adaptation to the same light as the test light or to the opposite light. The effects of red adaptation on red violet thresholds, and of violet adaptation on violet and red thresholds, have been determined. If, as seems fairly clear now, the foveal centre of a normal subject only possesses two receptors, then these lights from the spectral extremes might be expected on general principles to stimulate one receptor considerably more than the other, at least at low intensities, though it is possible that at one

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Fig. 1. Diagrams showing the extent to which the thresholds for red and violet are altered by adaptations to different intensities of red and violet, in three normal subjects 1, 2 and 3. +----+, effect of violet adaptation on violet threshold; ·————·, effect of red adaptation on red threshold; ⊙.....⊙, effect of violet adaptation on red threshold; ×—·—·—×, effect of red adaptation on violet threshold. Ordinates: logarithm of the multiples of the original threshold with no adapting light. Abscissae: log intensity of the adapting light; 0 = intensity of the adapting light corresponding to the threshold for a 20′ centrally fixated field. At this intensity the field appears coloured. At intensity 1·0 the violet field (4°) became almost colourless. The red field was below threshold at this intensity. In subject 3 the vertical strokes indicate the standard error of the mean of about thirty readings for each point. The technique of finding the threshold in subject 3 was slightly different from that in the other two subjects. The subject (E.N.W.) altered the intensity himself and judged the threshold within 20 sec. of removing the adapting light, after an adaptation time of 3 min.

end of the spectrum the two receptors might have similar sensitivities and so be stimulated more or less equally.

Normal subjects. The curves expressing the pattern of adaptation in three normal subjects are shown in Fig. 1, where the extent to which the threshold is raised by adaptation to lights of increasing intensity is plotted against the logarithm of the intensity of the adapting light, in terms of the threshold intensity for the subject. The method used for one of the three subjects was slightly different, and either because of that, or for some other reason, the effects of the adapting lights seem to start at lower intensities, but essentially the same pattern is obtained.

There are several points of interest about this pattern, though it is not the purpose of this paper to discuss their possible significance. In the first place, though the red and violet adapting lights were of the same strength to the subject, as determined by foveal fixation on a 20′ field, yet the violet affected the violet threshold to a greater extent than the red affected the red threshold. In fact the violet light seemed to affect the violet threshold at intensities below the foveal threshold. It is, of course, important to remember that 'foveal threshold' is a variable quantity according to the size of the field and may be well above the actual threshold for the receptors, which, however, may not be able to evoke an adequate sensory response unless considerable summation occurs. It has been shown elsewhere (Willmer, 1950) that the relationship between area and brightness is the same for red as it is for violet within the foveal area, so that it does not appear likely that the difference between red and violet is to be sought along these lines. Another point to remember is that the subjective impression, when comparing the brightness of the 4° adapting fields, is that the violet field is very much the stronger, at least when it is first compared, but this apparent brightness is very largely due to the stimulation of the parafoveal rods and the Purkinje shift. It is also possible that the stimulation of the peripheral rods may contribute to the factors determining foveal thresholds. Nevertheless, in a few experiments where the red and violet adapting lights were equalized in intensity at a higher level by direct heterochromatic matching the violet adaptation produced the greater effects.

It is clear that the effect of the violet adapting light on the threshold for violet is, at all intensities, greater than that of violet on red, or of red on either violet or red. The three curves expressing the effects of violet on violet, red on red, and red on violet are in all probability much the same curves, but shifted along the intensity axis. At least, this seemed to be so in the case of the author's eye where the curves are based on a much greater number of observations. The curves for observer 3, in Fig. 1, are all the same curve and it is seen that they satisfy the data reasonably well. On the other hand, the curve showing the effect of violet adaptation on a red test light seems to be somewhat different. Roughly speaking it has about half the slope of the other curves and in some

observers there is even some suggestion of an early rise, a plateau and a second rise. The meaning of this difference is at present obscure and must await further research, but the important conclusion now is that in the normal subject there is a definite pattern of the effects of adaptation to red and to violet lights and that this pattern supports the view that the normal fovea possesses two receptors, one of which is more stimulated by violet light than it is by red light, and the other more by red than by violet. This may not be all that can be deduced from the shapes of these curves but it is the essential point for the present argument.

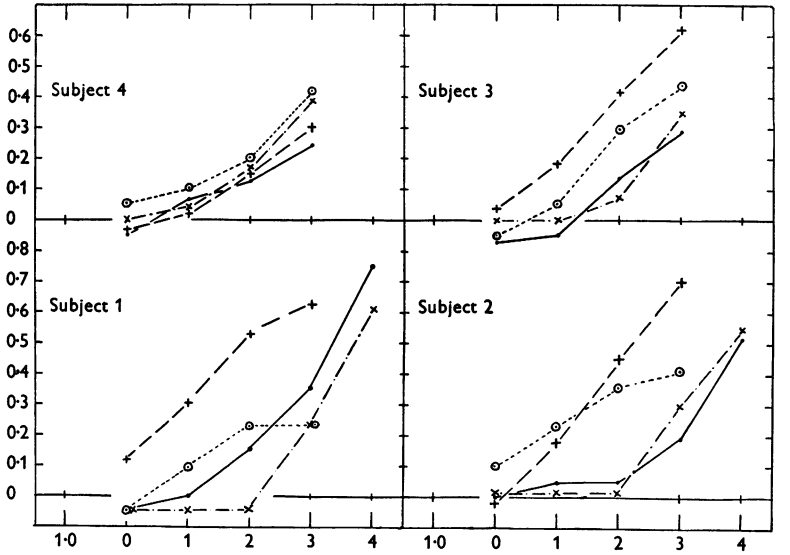

Fig. 2. Diagrams showing the extent to which the thresholds for red and violet are altered by adaptation to different intensities of red and violet, in four deuteranopes. All conventions as in Fig. 1. Note that subject 1 has a pattern indistinguishable from the pattern for the normal subject (see Fig. 1). In subject 4, however, it is doubtful whether the differences between the curves are significant.

Deuteranopes. If now the same tests are performed on the red-green-blind subjects who show no insensitivity to red, i.e. on the deuteranopes, the results are sometimes very different from, and sometimes they are closely similar to, those obtained on the normal observer. Fig. 2 shows a series of sets of curves obtained on four different observers, and, besides those shown, other intermediate types have also been obtained, so that there is clearly a graded series from observer 1 to observer 4. Observer 1 could not be distinguished from the normal observer on the basis of this test, yet he is totally colour-blind in the foveal centre. On the other hand, observer 4, also totally colour-blind in the foveal centre, shows a pattern of adaptation in which the curves cannot be distinguished from each other. For this subject and within the limits of experi-

mental error, red and violet lights at the same brightness seem to have the same capacity for raising the threshold for both red and violet.

These results clearly point to the conclusion that observer 4 is totally colour-blind in the foveal centre because he only possesses one type of receptor and one pathway. At the opposite end of the scale, observer 1 shows evidence of possessing the same receptors and perhaps even the same pathways as the normal person, but somewhere the paths must fuse before they reach the 'colour centre'. Among the deuteranopes therefore there are many different grades which extend on the one hand from observers whose pattern of adaptation is indistinguishable from the normal (deuteranopes, type I), to those, on the other hand, whose pattern of adaptation suggests the presence of but a single type of receptor (deuteranopes, type II). In other words, if the normal eye possesses receptors A and B which transmit their effects along two pathways a and b, the eyes of the deuteranopes tend towards one of two extremes in which, on the one hand, these receptors have a common path (ab) or, on the other hand, one of the receptors and its pathway is missing (say B and b). These two extremes may be conveniently labelled deuteranope type I, in which the adaptation pattern is nearly normal, and deuteranope type II in which the adaptation pattern suggests a single type of receptor.

Table 1 shows the extent to which the thresholds are raised for various observers by adapting lights of one thousand times the threshold intensities as determined for the respective subjects. The figures include some for observers in whom it has not been possible to obtain full curves at different intensities, and it will be seen that the 'pattern' for the deuteranopes conforms to the one deduced from the observers for whom full curves have been obtained.

Protanopes. Table 1 also includes figures for two protanopes, i.e. red-green-blind individuals who are relatively very insensitive to red. Now these observers again show a characteristic pattern. In them, the red threshold is raised to approximately the same extent by either red or violet, and similarly the violet threshold is raised equally by red or violet adapting lights, but the extent to which the two thresholds are raised is somewhat different, and this difference, though small, has been noted rather constantly and is probably outside experimental error. It is difficult to see how such an effect could be brought about, but it could occur if the adaptation, or some of it, is in the nerve pathway as well as in the receptor. Thus it is possible to imagine that there are two receptors present in the protanope, one mainly sensitive to the longer wave-lengths and the other sensitive to the blue end of the spectrum. If the latter showed some degree of photochemical adaptation while both receptors produce adaptation in the neural pathway, then the neural adaptation should be caused equally by the red and violet adapting lights, but photochemical adaptation in the 'violet' receptor would raise the threshold to violet more than to red, though presumably violet would be more effective in causing the photochemical adaptation than

red and this does not seem to be so. The fact, however, that red and violet adapting lights produce equal effects on the threshold for red, and equal effects on the threshold for violet suggests very strongly that there is only one neural pathway though there may be more than one receptor. This, of course, agrees with the finding that the protanopes are completely colour-blind in the foveal centre. Of the two tested here, one was completely colour-blind in the foveal centre, the other could distinguish violet from other colours, but these other

TABLE I. The effects of adapting to red or violet on the central foveal thresholds for red or violet. 'Red on violet', etc., means the effect of adaptation to *red* light *on* the *violet* threshold.

The numbers in columns 3 to 6 indicate the logarithm of the number of times the threshold is raised by adaptation to a light of intensity 1000 × threshold, i.e.

$$\left[\log \frac{\text{Threshold after adaptation to red (or violet) light at } 1000 \times \text{threshold}}{\text{Threshold after adaptation to darkness}}\right].$$

In columns 7 and 8, if the violet and red receptors were one and the same, then one would expect the differences to be zero. Note that for deuteranopes of type II this is approximately true.

(1) Type of subject	(2) Subject no.	(3) Red on red	(4) Red on violet	(5) Violet on red	(6) Violet on violet	(7) Difference between red on red and red on violet	(8) Difference between violet on violet and violet on red
Normal	1	0·62	0·30	0·35	0·90	0·32	0·55
Normal	2	0·31	0·01	0·18	0·45	0·30	0·27
Normal	3	0·47	0·35	0·04	0·64	0·12	0·60
Normal	4	0·43	1·92	0·16	0·38	0·51	0·22
Normal	5	0·44	0·15	0·08	0·59	0·29	0·51
Normal	6	0·59	0·27	0·17	0·79	0·32	0·62
Normal	7	0·63	0·26	0·30	0·71	0·37	0·41
	Mean	**0·50**	**0·18**	**0·18**	**0·64**	**0·32**	**0·46**
Deuteranopes Type I	1	0·29	0·00	0·24	0·45	0·29	0·21
	2	0·34	0·10	0·25	0·71	0·24	0·46
	Mean	**0·32**	**0·05**	**0·25**	**0·58**	**0·27**	**0·33**
Intermediate	3	0·21	0·23	0·32	0·67	−0·02	0·35
Intermediate	4	0·50	0·46	0·30	0·82	0·04	0·52
Intermediate	5	0·43	0·57	0·55	0·74	−0·14	0·19
Intermediate	6	0·30	0·36	0·43	0·63	−0·06	0·20
	Mean	**0·36**	**0·40**	**0·40**	**0·72**	**−0·04**	**0·32**
Type II	7	0·24	0·40	0·42	0·30	−0·16	−0·12
Type II	8	0·44	0·39	0·41	0·43	0·05	0·02
Type II	9	0·33	0·38	0·37	0·30	−0·05	−0·07
	Mean	**0·34**	**0·39**	**0·40**	**0·34**	**−0·05**	**−0·06**
Protanopes	1	0·29	0·52	0·43	0·59	−0·23	0·16
Protanopes	2	0·27	0·40	0·23	0·34	−0·13	0·11
	Mean	**0·28**	**0·46**	**0·33**	**0·46**	**−0·18**	**0·13**

colours could all be matched among themselves, and with white, providing that the brightnesses were made equal. Further work is, therefore, clearly needed in order to determine exactly how the protanopes behave with respect to these adaptation tests. So far as the available results show, protanopes behave

differently from the normal observer and probably differently from the deuteranopes of type II, though it is not possible to say definitely that only one type of receptor is present.

Luminosity curves

Protanopes. Further information on the properties of the foveal centre can be obtained from the luminosity curves for this area. If, for example, as the

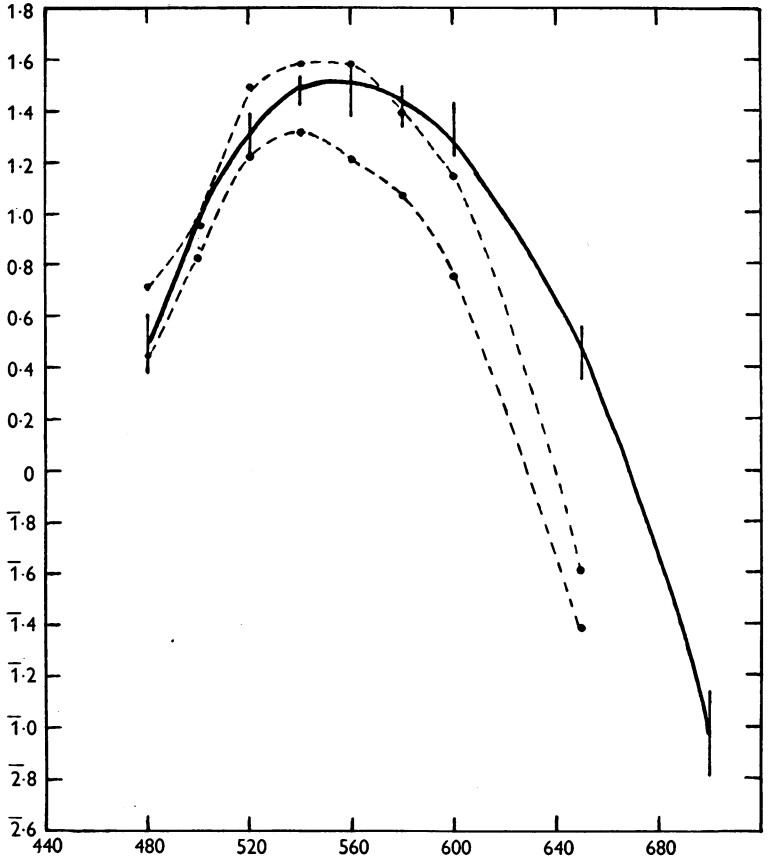

Fig. 3. Luminosity curves for the central fovea of the normal subject, and for two protanopes. Equal energy spectrum. ————, normal luminosity curve (mean for five observers). – – – – –, luminosity curves for the protanopes. The vertical lines on the normal curve indicate the range of variation among the normal subjects. The curve for each subject is the mean of five readings for each point, each of the five readings being taken on a separate day. Ordinates: logarithm of luminosity (arbitrary units). Abscissae: wave-lengths (mμ.).

experiments on adaptation indicate, some of the colour-blind subjects have only one type of receptor in the foveal centre, then the luminosity curve for this region of such subjects must measure the spectral sensitivity of the single type of receptor. When this curve is determined for the protanopes, it differs greatly from that of the normal foveal centre. It has its maximum at about

540 mμ. and indicates a conspicuous loss of sensitivity to all wave-lengths towards the red end of the spectrum as compared with the normal (Fig. 3). From a series of preliminary observations on a group of protanopes previously investigated it appears that there is very great variation in the shape of the

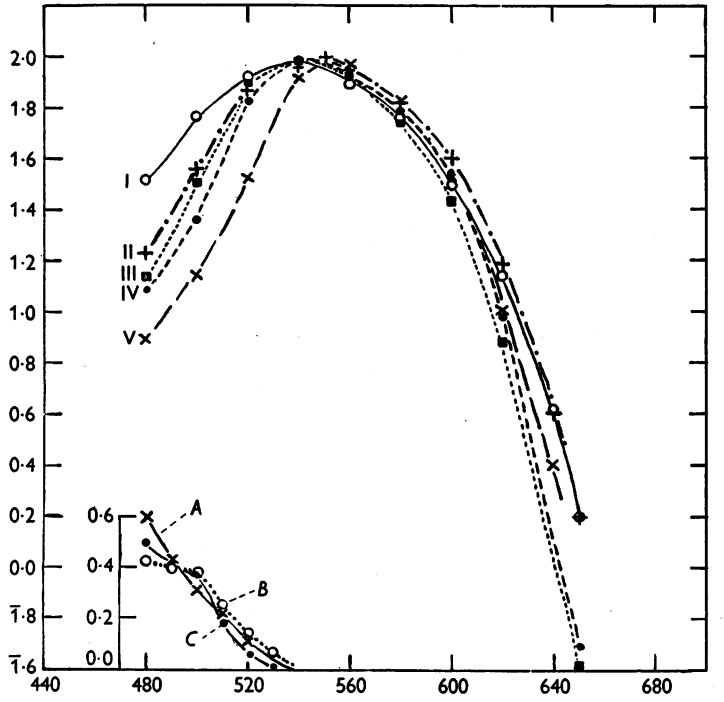

Fig. 4. Luminosity curves for five protanopes showing the comparative uniformity of the curves towards the red end of the spectrum and the diversity towards the violet end. The curves have all been shifted along the vertical axis to have the same maximum. Equal energy spectrum. Data for some of these curves supplied by Dr L. C. Thomson and obtained by a different technique. Curve I, though belonging to a subject who is not quite completely monochromatic in the central fovea, has been used as the standard curve for an estimation of the extent to which the amount of macular pigment accounts for the differences between the curves in the blue region of the spectrum. Curve *A* (× — ×) represents the density of macular pigment as determined by Wald (1945) from differences between the photopic luminosity curve for the periphery and that in the fovea. Curve *B* (○·····○) represents the density of macular pigment as deduced by subtracting the mean of the four curves (II–V) from curve I. Curve *C* (● – – ●) represents the density of macular pigment as deduced by subtracting the ordinates of the mean curve for the two protanopes whose curves are shown in Fig. 3 from the visual purple curve, as determined by Donner & Granit (1949) for the cat, but moved along the spectrum to fit the protanope's curve. (Both curves corrected for quanta.) (See Text, p. 441.)

curve in the blue part of the spectrum (Fig. 4). Sometimes the sensitivity is considerably above that of the normal observer (Dr Thomson has reported a case to me in which the sensitivity was nearly ten times greater than the normal at 450 mμ.), and in others the sensitivity is normal or even rather

below the normal. How far these observations are due to actual differences in the sensitivities of the receptors, and how far they are due to variations in the distribution of macular pigment, or to the encroachment of low threshold rods into the foveal area, or merely to inadequate fixation it is at present difficult to decide. The position of the maximum and the shape of that part of the curve which extends from the maximum to the red end is much less variable, and can be regarded as correct with some degree of certainty. If in Fig. 4, where the curves have all been brought to the same maximum, the highest curve in the blue (curve I) region may be regarded as representing the greatest sensitivity because the observer has least macular pigment (an assumption for which there is no direct evidence) and the other curves indicate lowered sensitivity because of greater amounts of macular pigment, then the loss in sensitivity can be estimated for the different subjects by taking the difference between this curve and the other curves of Fig. 4. These differences will represent the density of the supposed macular pigment. The density of the pigment, deduced by subtracting the ordinates of the mean of the four lower curves from those of curve I, is shown in Fig. 4, where the values are compared with the densities of macular pigment as deduced by Wald (1945) for the corresponding region of the spectrum. Wald's figures were obtained in a similar manner by comparison of cone sensitivity (photopic luminosity curve) in the periphery of the retina with that in the fovea. Clearly the two sets of figures based on different data are of the same order of magnitude and follow much the same trend. Wald found that the absorption by macular pigment in different subjects may vary between 0 and 90% at 436 mμ., so the agreement is well within the bounds of probability and it may be tentatively concluded that the differences in the form of the sensitivity for the different protanopic observers in this region of the spectrum is at least partly explained by differences in pigmentation. In addition to this there are, of course, the absolute differences of sensitivity between different observers to be explained. These differences are not so apparent in Fig. 4 where all the curves have been arbitrarily given the same maximum. Fig. 3, however, indicates the order of magnitude of the variation which may occur between observers.

Deuteranopes. In general, the luminosity curves for the deuteranopes differ less from the normal than do those of the protanopes. In fact, some are indistinguishable from the normal. In Fig. 5 three curves are plotted. One is for five normal observers. The second is for three deuteranopes in whom the red adaptation light produced almost the same effects on red and violet thresholds, and in whom violet adaptation also produced equal effects on the two thresholds, i.e. for those deuteranopes (type II) in whom the adaptation pattern most clearly differed from that of the normal. This curve confirms some preliminary observations (Willmer, 1949*a*) and shows a maximum between 570–580 mμ. with a significant difference from the normal towards the blue end of the spectrum. The difference between the curves for the deuteranope type II

and the normal subject conceivably might be due to differences in pigmentation in the retina and ocular media, but such evidence as that of Wald (1945) and the earlier work of Abney (1895) and Sachs (1891) all suggest that such effects

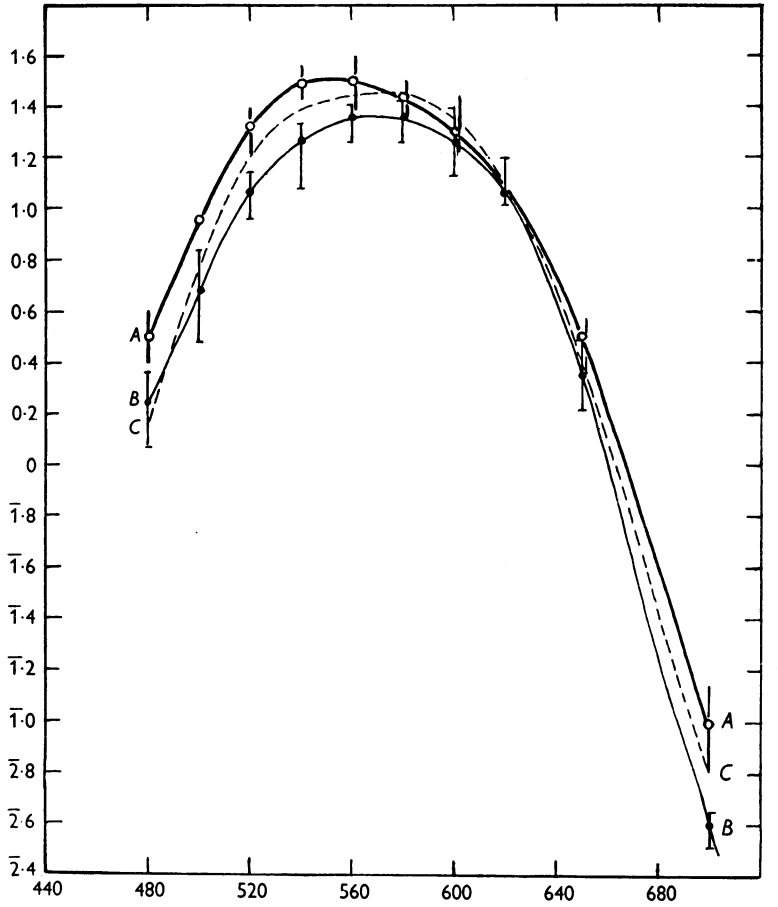

Fig. 5. Luminosity curves for normal and deuteranopic subjects. Equal energy spectrum. *A*, mean normal luminosity curve. The vertical lines show the range of the mean curves for five observers. *B*, mean luminosity curve for three deuteranopic observers for whom the adaptation pattern is like that shown in Fig. 2, no. 4, i.e. observers in whom the foveal centre apparently possesses but one type of receptor. The vertical strokes indicate the extremes. *C*, mean luminosity curve for three deuteranopic observers for whom the adaptation pattern is like that shown in Fig. 2, no. 3. Ordinates: logarithm of sensitivity—arbitrary units. Abscissae: wave-lengths (mμ.).

become very small or negligible at wave-lengths longer than 520 mμ., while the difference between these two curves does not disappear till about 580 mμ. The third (dotted) curve is for three deuteranopes in whom the adaptation pattern was similar to that in Fig. 2, no. 3. These observers can be considered as

tending towards deuteranopes of type II, but there is still an indication of another receptor. In other words, they are 'intermediate', and this adjective could also be applied to the position of their luminosity curve between that of the normal and that of the deuteranopes, type II. The luminosity curves for

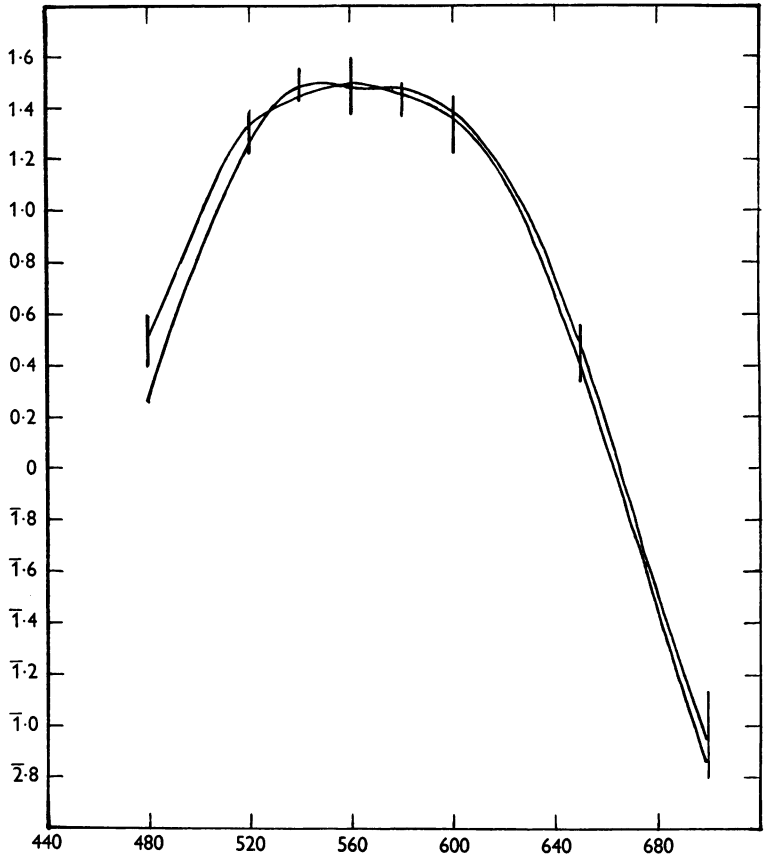

Fig. 6. Luminosity curves of two deuteranopes (type I) whose pattern of adaptation does not differ significantly from that of the normal observers (see Fig. 1, no. 1). The vertical lines indicate the range of variation among the five normal observers. Equal energy spectrum. Ordinates: logarithm of sensitivity—arbitrary units. Abscissae: wave-lengths (mμ.).

two observers in whom the adaptation 'pattern' did not differ appreciably from the normal (deuteranopes, type I, see Fig. 2, no. 1) are not significantly different from the normal luminosity curve (Fig. 6).

It appears, therefore, that just as the adaptation patterns tend towards two extremes, so the luminosity curves also divide the deuteranopes in a similar manner.

There appears to be no consistent difference in general sensitivity between deuteranopes and normal observers. While some deuteranopes, belonging to

both types, have been found with very low sensitivity as compared with the normal, in others, again belonging to both types, the sensitivity may be well within normal limits and in some cases even slightly above. Thus there is no clear support for the view that deuteranopes are necessarily less sensitive to light than normal observers, though in many cases they undoubtedly are. An important experimental error may easily creep into determinations of this type, for it has been found that when a subject first begins to determine thresholds he invariably obtains higher values (indicating lower sensitivity) than he will subsequently do. Owing to the difficulty of obtaining colour-blind observers for unlimited tests it is often necessary to take only a few series of readings, whereas the readings so obtained are often compared with those of a normal observer well trained in the technique. This comparison may introduce quite a considerable error.

Subjective colour impressions

Although very little weight can be attached to the data acquired in this way, there are some interesting observations which are worth recording with regard to the names given to the colours seen, or imagined, during the determination of the luminosity curve by the flash method. All the flashes were made very near to the threshold level and the subject was unaware of the wave-length employed. Under such conditions most of the colour-blind subjects reported all the flashes as colourless or very pale blue, or pale blue-green. A few when tested on violet reported it as violet, though this generally occurred in those subjects who found it possible to distinguish violet from other colours on the small field. One deuteranope (in the terminology of earlier days, 'green-blind') reported all the flashes as green! Since, however, he could match green and white this was obviously not very significant. It became quite clear that the colour-blind subjects were unable to distinguish the colours in these short flashes and they behaved in a manner consistent with vision by one pathway only. They behaved as the normal person does when his vision is restricted to the rods in twilight vision.

An interesting point thus emerges. When the observer has only one receptor and one pathway, as the deuteranope of the second type appears to have, that receptor, which in this case might be described as the red receptor, does not give him the sensation of red, but a sensation of 'no-colour'. Similarly, when the other type of pathway found in the deuteranope of type I is responding alone, then, again, only a 'colourless' sensation is perceived. Presumably, colour sensations must derive from differences in response between two or more pathways, and not as the result of the response along a single pathway when this cannot be compared with the response along another or other pathways.

In this connexion the colour impressions obtained by the normal observer are also worthy of note. Colours at the red end of the spectrum were mostly reported as red, but as the wave-length became shorter, a number of flashes

were reported as colourless. In the orange region a few flashes were reported as green. In the region from 570 to 590 mμ. flashes were reported as orange, colourless, and green, in proportions varying with the wave-length. From 570 to 480 mμ. green or blue-green was the answer which preponderated more and more first over orange and then over colourless. Now the normal person matches a wave-length in the region of 570 mμ. with white under conditions of foveal fixation. Thus the colourless sensation here again probably depends on there being no difference of response in the two pathways. Under the 'flash' conditions, perhaps in accordance with Hartridge's cluster theory (Hartridge, 1947), the stimulus may sometimes be more effective in initiating impulses in one receptor type rather than in the other, and these unbalanced responses give rise to the two 'coloured' sensations, green or orange, which the normal observer may receive from a flash of light which should be colourless. The degree of unbalance will presumably be reflected in the saturation of the flash.

DISCUSSION

The experimental observations recorded in this paper are consistent with the view expressed in the introduction and which may be summarized as follows. The central fovea of the normal subject possesses two types of receptor and two independent pathways. It should be noted, however, that the two pathways need not necessarily each correspond to the sensitivity of one of the receptors, but either or both of them might pass on effects set up by both receptors in different proportions. Indeed, some such idea may have to be invoked in order to account for the characteristic adaptation 'pattern' to red and violet displayed by the normal observer (see Fig. 1). For example, if the receptors themselves are labelled A and B, then the pathways may relay from A and B separately, but more probably they relay from some combination like AB and B. Exactly how the effects combine in AB can only be determined by further research; but it is possible that AB may represent pathways in which A adds its effects to B, in which A detracts from the effects of B, or vice versa. All such arrangements would be consistent with a dichromatic fovea, for these different pathways would not be independent pathways—they would all essentially depend on the sensitivities of the two primary receptors A and B.

If now the protanope is truly monochromatic or monodic in his central fovea, and if B be considered as the receptor covering the red end of the spectrum, he might very well not have this separate pathway, but rely on the A, or more probably the AB receptor pathway only. This would be consistent with his lower sensitivity in the red; moreover, the complexity of his adaptation pattern suggests that his single pathway is not a simple one, so that it is more likely to be AB.

The deuteranope whose adaptation pattern resembles the normal pattern and whose luminosity curve is indistinguishable from the normal must clearly

have the same receptors as the normal and it must be supposed that their effects are combined together before reaching the 'colour' centre. In other words, if the normal observer possesses *AB* and *B*, then this type of deuteranope possesses these receptors also, but the pathway gives 'pooled' information (*AB* and *B*) only. This is consistent with Pitt's (1944) observations and deductions from colour mixing data from which he suggests that deuteranopes have their red and their green pathways fused.

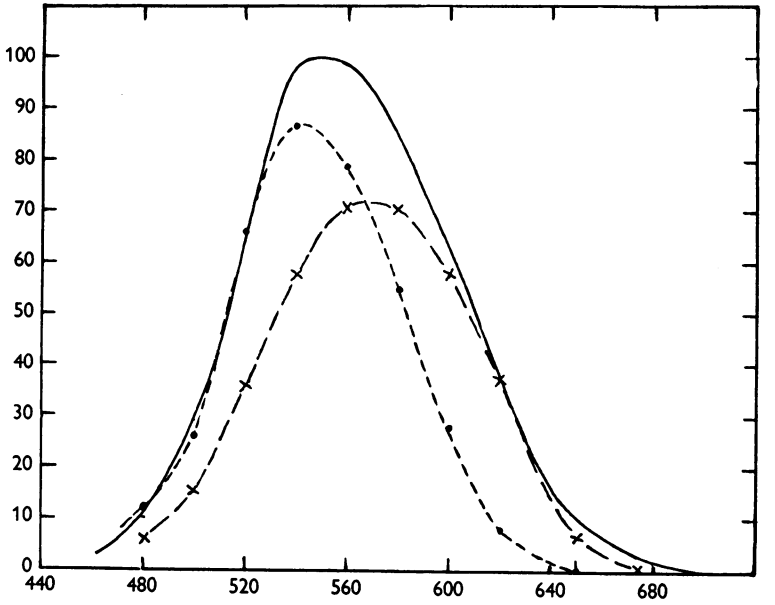

Fig. 7. Luminosity curves for the central fovea of normal subjects. (————), deuteranopes, type II (— — —), and protanopes (- - - - -). Equal energy spectrum. Ordinates: sensitivity, as percentage of the maximum. Abscissae: wave-length (mμ.).

On the other hand, the deuteranope of the other type has his maximum sensitivity moved towards the red end of the spectrum (see Fig. 7), and his adaptation pattern is simple, all lights of equal brightness to him exerting equal effects, so that it is tempting to believe that the limit in this direction is reached when receptor *B* alone is present. If this is so, then it means that the luminosity curve for this type of deuteranope represents the spectral sensitivity of receptor *B*. In this connexion it is interesting to observe its resemblance to the curve expressing the sensitivity of the red mechanism according to Stiles (1939) and that the curve has a very similar form to that of visual purple, but is displaced along the spectrum towards the red (Fig. 8). Krause (1942) has called attention to the fact that when the length of the conjugated chain is increased in certain dyes, similar in structure to the carotenoid of visual purple, then the absorption spectra of the resulting dyes may remain unchanged in form but

shifted towards the red end of the spectrum. The sensitive substance of receptor *B* may therefore be a similar modification of visual purple. Moreover, the spectral sensitivity of receptor *B* is not very different from the curve recorded by Granit (1942) as the sensitivity of the photopic receptor (cone) in the pigeon, and its maximum lies in the same region as the probable maximum for the one photo-sensitive pigment which has been extracted from cones, namely

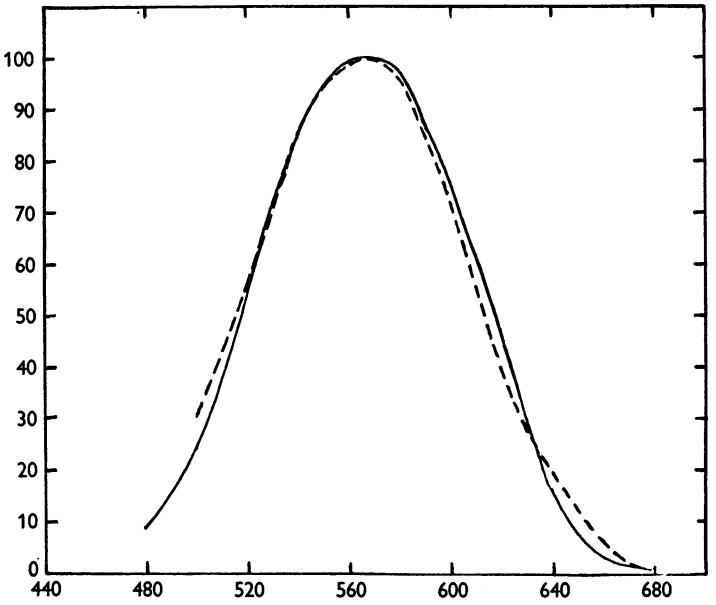

Fig. 8. Luminosity curve for the deuteranope, type II (————), compared with the luminosity curve for the visual purple receptors in the cat's retina as recently determined by Donner & Granit (1949) (- - - - - - - -). Both curves corrected for quanta, and the visual purple curve moved along the spectrum to have the maximum at 570 mμ. Ordinates: sensitivity as percentage of the maximum. Abscissae: wave-length (mμ.).

iodopsin, the pigment extracted from the retina of the chicken by Wald (1937) and also by Bliss (1946). All these observations may perhaps point to the idea that receptor *B* is none other than the human cone.

If this is so it remains to be seen whether receptor *A* is another variant of visual purple, or is visual purple itself. All that can be said at the moment is that if the protanope depends on receptor *A* only, then receptor *A* is not solely dependent on visual purple because the protanope has his maximum sensitivity at 540 mμ. and not near 507 mμ. But if, as seems probable, the second receptor of the normal observer, and the remaining receptor of the protanope, is a composite receptor then *A* may well contain visual purple. Although insufficient data are at present available, it is interesting that the form of the protanope's sensitivity curve again resembles that of the visual purple absorption curve, though differing in its position in the spectrum, and being somewhat too low in

the short-wave end of the spectrum. This resemblance to the visual purple curve could arise either if the receptor again depended on some simple chemical modification of visual purple which caused its absorption curve to be shifted along the spectrum towards the red end, or if the sensitivity curve resulted from the combined action of two receptors each of which depended on a substance whose sensitivity curve had the same shape as that of visual purple, but each of which had a different point of maximum sensitivity. Porphyropsin, the receptive substance found in certain fishes, is almost certainly a modification of rhodopsin, and it has its maximum sensitivity at about 522 mμ. It is, indeed, conceivable that the receptor of the protanope might be sensitized by this substance, but its maximum is not at the right point nor is there as yet any evidence either for its occurrence in the mammalia, or for the presence of the related substance vitamin A_2 in man or mammals.

It has been pointed out that the protanope's sensitivity curve differs from the visual purple curve in a systematic way in the blue part of the spectrum. This difference begins at about 530 mμ. and steadily increases towards the blue, and this is exactly the sort of change in sensitivity which would occur in a receptor dependent on a visual purple variant (max. 540 mμ.) if it were screened by macular pigment. Now it has already been shown that much of the variability of protanopic sensitivity in the blue could be explained in terms of differing quantities of macular pigment. So it is relevant to see whether the differences between the protanope's curves and the visual purple curve indicate the same spectral distribution of absorption by macular pigment as is indicated (1) by the variability among the protanopes themselves and (2) by the difference between peripheral and central cone sensitivity which was used by Wald to estimate the absorption by the pigment. Now when the protanope's luminosity curve is plotted on a logarithmic scale, and the visual purple curve is superimposed and given the same maximum, then the difference between these curves should give, if the foregoing reasoning is sound, the 'density' of the macular pigment. The result is plotted in Fig. 4, curve *C*, and is clearly of the same kind as curves *A* and *B*, which are the previous estimates of the absorption by macular pigment. Thus, allowing for macular pigment, there are strong indications that the spectral sensitivity curve of the protanope's receptor is fundamentally similar to that of a visual purple receptor, but shifted along the spectrum towards the red, and in this way it resembles the spectral sensitivity curve for the deuteranope, type II, but it is not displaced so far. For this there seem to be two possible explanations. The curve for the protanope would result either if the receptor depended on a chemical variant of visual purple, or if the curve were itself the result of combined activity of two receptors such as a visual purple receptor and the receptor *B*. For example, it is possible that the response from a ganglion cell might be an average response of the two or more receptors which play upon it. Now the response from a single receptor is

roughly proportional to the logarithm of the intensity of the light acting upon it. Therefore, the response of the receptor to different wave-lengths is roughly proportional to the ordinates of its spectral sensitivity curve when this is plotted on a logarithmic scale. The ordinates may thus be looked upon as a measure of the nerve impulses set up at the different wave-lengths by

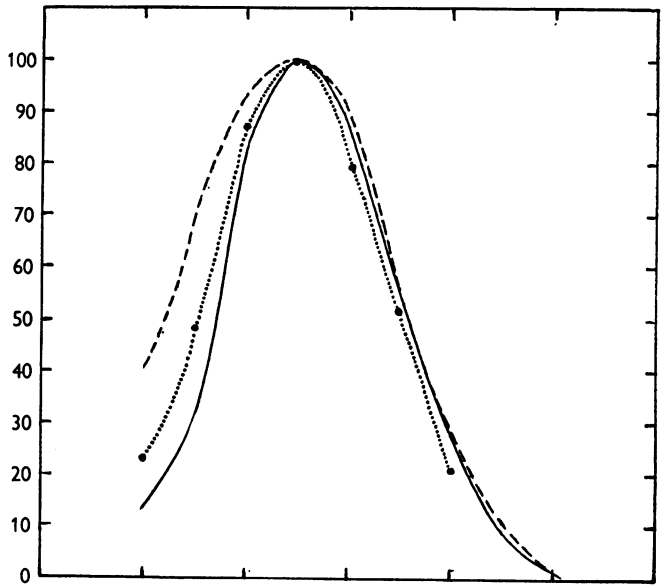

Fig. 9. Comparison between the sensitivity curve of the protanope (————), the sensitivity curve of a visual purple receptor shifted along the spectrum to have its maximum at the same point (– – –), and the curve expressing the spectral sensitivity of a ganglion cell whose response is a mean response between that of an ordinary visual purple receptor and that of a receptor having the sensitivity of those present in the fovea of the deuteranope type II. (.....). Spectrum of equal quantum intensity. Ordinates: sensitivity as percentage of the maximum. Abscissae: wave-length (mμ.).

a spectrum of equal quantum intensity. When two receptors are acting, each will therefore respond throughout the spectrum in proportion to the ordinates of its logarithmically plotted sensitivity curve, and the response from the ganglion cell at any particular wave-length would thus, on the above assumption, be the mean of these ordinates. Naturally, it might equally well be the sum, or the difference, or almost any other combination for all the direct evidence that exists, but it is perhaps significant that the curve expressing the mean between the ordinates of the visual purple curve and the sensitivity curve of the deuteranope, type II, when corrected for the absorption by macular pigmentation, is almost identical with the spectral sensitivity curve of the protanope (Fig. 9).

However this may be, the important fact remains that the sensitivity curve of the protanope may not be the result of the activity of a single receptor, but

could arise by the interaction of two or more receptors, and the experiments, with adaptation to red and violet, on the whole suggest that a composite pathway is the more likely.

A study of the 'intermediates' among the deuteranopic observers shows that there is a tendency for the adaptation effects of violet on violet, and of violet on red, to approximate to each other (see Fig. 2), and similarly for the effects of red adaptation on red threshold to become identical with those of red adaptation on violet threshold, but the effects of violet adaptation are always somewhat greater than those of red adaptation. This suggests that the violet light has more power of causing adaptation than the red light. This could arise if the violet-adapting light was for some reason actually more intense than the red, i.e. if the determination of its threshold were in some way inaccurate, or if the absolute foveal threshold had not been obtained owing to imperfect fixation. By repetition of the tests, however, no evidence has been obtained to suggest that this is the cause, but the possibility cannot be entirely ruled out. Secondly, it is conceivable that violet light works slightly differently from red light in producing the photochemical changes in the receptor. For example, Chase & Smith (1940) have observed that in the regeneration of visual purple after bleaching *in vitro*, the process is quicker after bleaching with blue than with yellow light. Another possibility lies in the nature of the change from observer 1 to observer 4. Observer 1 clearly has two types of receptor, while observer 4 only appears to have one. If this change takes place in stages, the proportions of the two types of receptor must change; then, if the numbers of receptors as well as their own sensitivities contribute to luminosity as they undoubtedly do for small areas in the fovea where the law 'intensity $\times$ area = constant' approximately holds, the receptor which is present in smaller numbers, if it is to give rise to the same sensation of brightness as the other receptors, must make up for this deficiency in number by being stimulated more intensely, while the other receptor, which is becoming relatively and perhaps actually more numerous, can give the same luminosity at a lower intensity. Hence the system of matching the strengths of the adapting lights by determination of the thresholds may lead to a more powerful effect of violet than of red, and a reduction of the effect of red. There is some evidence that this is in fact occurring. Observer 2, for example, was not completely colour-blind in the central fovea, but could distinguish violet from other colours. He shows approximation of the two curves expressing the effects of red adaptation at a low level, and approximation of those for the effects of violet adaptation at a higher level.

In the process of reduction of numbers of the violet receptor there must come a time when the receptor becomes ineffective and the intensity of violet becomes such that it stimulates the opposite (red) receptor to such an extent that this receptor now determines the threshold. As long as the violet receptor was functioning at all, one might expect that the subject would be capable of

distinguishing some colour with the foveal centre, but all those observers whose curves are more like that of observer 4 than those of observer 2 are in fact totally colour-blind, so this may not be the explanation of the effect, unless one assumes that for colour discrimination more differentiation between the receptors is needed than can be seen to exist in relation to brightness discrimination.

Another point of some interest in relation to these curves, and, if it can be shown to be a genuinely significant effect, a difficulty in the way of accepting the hypothesis that observers like observer 4 have only one type of receptor in the central fovea, is the observation that for some of these subjects there is evidence for an actual sensitization to red at the lower brightnesses of the red adapting light. This effect may be inherent in the experimental conditions and is more noticeable in some subjects than in others but, if it is true, it points to a difference between the receptors for red and those for violet, which is in exact opposition to the main trend of the experimental results. However, these are all matters which can only be elucidated by further research.

There is also a further observation which is perhaps inconsistent with the general ideas put forward in this paper: the inconsistency lies in the forms of the luminosity curves for the normal observer and for the deuteranope of the second type in the red end of the spectrum. If the deuteranope, type II, possessed cones only in his fovea one might expect him to be more sensitive in the red end of the spectrum than the normal person, but in fact the evidence, so far, points in the opposite direction, and normal observers seem to be the more sensitive in this region.

Although there are thus inconsistencies and difficulties in the interpretation of some of the results, yet it is clear that, allowing for the inaccuracy which seems necessarily to accompany work with small fields, the foveal centre is essentially a simpler part of the eye than the fovea as a whole and in the deuteranope, type II, it seems to reach the height of simplification and possess but one receptor path. It is difficult to harmonize these results with the ideas of multiple types of receptors for the normal eye.

SUMMARY

1. By adapting the fovea separately to lights of equal brightness from the two ends of the spectrum, it has been shown that the central fovea of the normal subject has its thresholds to red and to violet changed in a characteristic manner.

2. When red-green-blind subjects are treated in the same way they fall into the following classes:

(*a*) Protanopes, whose red threshold is raised equally by red and violet adaptation, whose violet threshold is raised equally by red and violet adaptation, but whose violet threshold is raised more by both red and violet than is the red threshold.

(*b*) Deuteranopes, type I, whose pattern of adaptation does not differ from that of the normal subject.

(*c*) Deuteranopes, type II, whose red and violet thresholds are raised to the same extent by both red and violet adaptation.

(*d*) Deuteranopes intermediate between types I and II and showing gradation towards type II, but with the effect of violet adaptation on violet threshold generally somewhat higher than in type II.

3. Each of these groups has a characteristic luminosity curve, thus:

(*a*) Protanopes. Maximum sensitivity at 540 mμ. and depressed sensitivity to red.

(*b*) Deuteranopes, type I. Maximum sensitivity at 550 mμ. and indistinguishable from normal subjects.

(*c*) Deuteranopes type II. Maximum sensitivity at 570 mμ. with depressed sensitivity in the blue and green and in the extreme red.

(*d*) Deuteranopes intermediate between types I and II. The curve lies between the normal and that of the deuteranopes, type II.

4. These results may be interpreted as follows:

(*a*) The protanope has a single pathway from his central fovea, but this pathway (*ab*) may be stimulated by two receptors (*AB*).

(*b*) The deuteranope, type II, has only one type of receptor (*B*) and one pathway (*b*) from his central fovea.

(*c*) The normal observer has both the receptors (*AB*) and pathway (*ab*) of the protanope together with the receptor (*B*) and pathway (*b*) of the deuteranope type II.

(*d*) The deuteranope, type I, has the same receptors as the normal subject, but his pathways fuse before reaching the 'colour centre'.

(*e*) The intermediate types of deuteranopes show a progressive elimination of the $AB \rightarrow ab$ system, eventually leaving only the $B \rightarrow b$ system of the deuteranope type II.

5. The luminosity curve for the foveal centre of the deuteranope, type II, probably represents the spectral sensitivity of the red receptor (*B*) of the normal eye. It is very similar in shape to that of a visual purple receptor, but its maximum is at about 570 mμ. instead of 507 mμ.

6. The manner in which macular pigment may function to modify the results, particularly in relation to protanopic vision, is discussed.

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