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THE COLOUR SENSITIVITY OF THE RETINA WITHIN THE CENTRAL FOVEA OF MAN

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In 1894 König noticed that if the size of a coloured object was sufficiently reduced and that if it was observed by the eye so that its image fell upon the central fovea, all colours could be matched by a mixture of a red and a blue stimulus only, i.e. that vision under these conditions was dichromatic. König also discovered that the ability to differentiate between wavelengths in the blue-green region of the spectrum was impaired and that the type of vision was similar to that found in the tritanopic form of colour blindness.

Recently, Willmer (1944), and Willmer & Wright (1945) have confirmed and extended König's observations. Luminosity, dichromatic coefficient and hue-discrimination curves were measured and spectral mixture curves calculated for a small circular field whose diameter subtended an angle of 20′ at the eye. The image of this field lay on the retina at the fixation point within the central fovea, and vision for this field was found to be dichromatic and tritanopic. Fixation of the object could only be maintained momentarily and if fixation was imperfect the dichromatic match was at once disturbed. Hartridge (1945*a*, *b*), using as his test for dichromatic vision the fact that yellow is seen as white, has also investigated the sensitivity of the fovea with a series of small yellow-painted test objects, and compared this sensitivity with that of the surrounding retina. He concluded that if an object were sufficiently small, it would exhibit the characteristics of dichromatic vision not only at the fovea but wherever its image lay on the retina. It is clear that in his view, retinal position is of no importance, and that it is the reduction of size alone which initiates the effects described by König. He inferred from his experiments that there was no significant difference between vision at the foveal centre and that within a much larger retinal area.

The present series of experiments were designed to record the characteristics of vision for different points within the central fovea. The luminosity, coefficient and hue-discrimination curves were again recorded for a 15′ test field when viewed at 20′ and 40′ from the foveal centre and the results have been compared with the data for central fixation. For greater displacements than this, a larger test field must be used to compensate for the reduced visual acuity and no measurements of this type are reported here.

METHOD

The observing fields were of two types. In type A, Fig. 1, the test and comparison beams formed the two halves of a small circular field, the diameter of which subtended an angle of 15′ at the eye. Displacement of the field was effected by the provision of two points of light to one side of the circular field so that, if the appropriate point was fixated, the centre of the circular field would then be displaced from the fixation point through an angle of either 20′ or 40′. In type B, Fig. 1, the size of the two halves of the field was the same as that in type A, but the lower semi-circular patch *a* could be compared with any one of the three upper patches *a*′, *b*′ and *c*′, where the angular displacements of *b*′ and *c*′ from *a*′ were respectively 20′ and 40′. With an arrangement of this type it was possible, by fixating *a*, to obtain a comparison of the relative sensitivities of the central, 20′ and 40′ areas. All observations were made with the right eye and the displacements from the foveal centre brought the test fields into the nasal half of the visual field (temporal side of the retina).

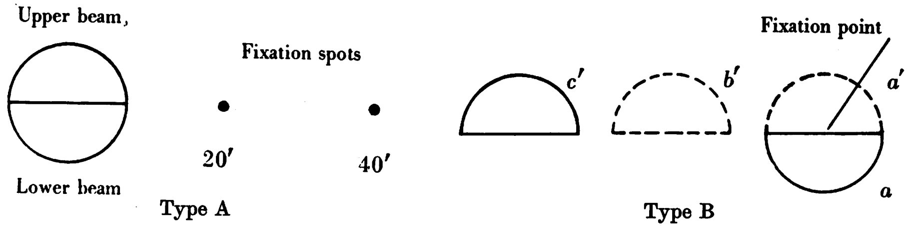

Fig. 1. The two types of observation made. This diagram of the test field will subtend an angle of 15′ if it is held at a distance of 12 ft. from the eye.

The measurements were made with the colorimeter developed by one of us (Wright, 1927, 1939) in which a wide variety of spectral lights, with independent intensity control, may be applied to each of the two halves of the circular field. Correct alinement and fixing of the head relative to the exit pupil of the instrument were obtained by biting upon a suitably placed dental impression mouthpiece. A further addition to the optical system was the introduction, immediately behind the exit pupil of the colorimeter, of a small lens with sufficient chromatic over-correction to correct for the chromatic aberration of the eye. The lens was designed to have approximately zero power for yellow light but to give +3·0 D. chromatic over-correction between the wave-lengths 0·70 μ. and 0·40 μ. The specification of the lens was as follows:

Hard crown biconvex component, $n = 1{\cdot}5190$, $v = 60{\cdot}4$.
Radius of curvature of each surface = 0·33 in.
Thickness = 0·10 in.
Diameter = 0·33 in.

Dense flint biconcave component, $n = 1{\cdot}6226$, $v = 36{\cdot}0$.
Radii of curvature of surfaces = 0·33 in. and 0·419 in.
Thickness = 0·05 in.
Diameter = 0·33 in.

Crown and flint components cemented together.

The fitting of this lens greatly increased the certainty and consistency with which observations could be made in the blue and violet region of the spectrum, since without the lens the area of retinal stimulation must vary according to the wave-length of the light and the focusing of the observer's eye. The small circular field and fixation points were produced by placing a metal plate in which suitable holes had been drilled, between the photometer prism and the eyepiece of the apparatus. The fixation points in type A experiments were thus illuminated by light from the colorimeter prism and were of the same colour and brightness (but lower intensity) as the circular field itself. An exit pupil 2 mm. in diameter was used and the field brightness in all experiments was approximately 50 photons.

Technique. In making these measurements some experience was necessary before one could be certain that the correct retinal area was being used. To hold the eye rigidly in the correct position for more than a few seconds at a time was quite impossible. Measurements were therefore made in the following way. A 'bite' was taken and, by looking at the field, the head position was checked. Minor inaccuracies of head position do occur even with the bite method of fixation and it is very important to correct these by moving the head slightly on the mouthpiece, which is used as a guide to head position rather than as a rigid clamp. This done, the eye looks away for a few seconds and then returns rapidly to the desired fixation point. Adjustments of the colorimeter controls for a match are made and the eye looks away again. This glancing process is repeated until the measurement is satisfactory. Skill is soon acquired at head positioning and rapid and accurate fixation so that the period of time during which the eye is actually looking at the field can be increased somewhat with practice. If this period is allowed to become too long disturbing after-images develop which make several minutes rest an essential. A few minutes dark adaptation was allowed before any series of observations were made.

RESULTS

Luminosity curves. The luminosity curves for the three retinal positions are shown in Figs. 2 and 3. These curves, which are generally described as the equal-energy luminosity curves, record the reciprocal of the amount of energy at each wave-length required to produce a visual sensation of brightness of constant magnitude. The maximum of the curve for the central position has been arbitrarily adjusted to 100 for both observers and the curves for the other areas are shown with their ordinates adjusted to allow for the sensitivities of these areas relative to the sensitivity in the central position. The curves shown are smooth free-hand curves drawn so as to be the best fit to the means of the observations.

In the case of W.D.W. the curves were recorded using a type A field. This field was viewed centrally or in the 20′ or 40′ positions according to which curve was to be measured. The lower patch was illuminated by light of wave-length 0·530 μ. and maintained at a constant energy content throughout, while the upper patch was illuminated by various wave-lengths (λ) taken in turn through the spectrum. A brightness match between the two halves of the field was made by controlling the intensity of λ, and although there was in general a colour difference between the two patches, reasonably consistent observations were obtained. The luminosity curve was then derived by plotting the inverse of the energy required at wave-length λ for the brightness match. The relation between the curves for the three retinal areas was obtained by making a subsidiary observation with a type B field. The lower patch and one of the upper patches were illuminated by light of wave-length 0·530 μ. and brightness matches made between a and a', a and b', a and c' in turn, a being fixated in each case. From this observation the relative sensitivities of the three retinal areas to wave-length 0·530 μ. could be calculated and the relative heights of the three luminosity curves deduced. A similar type of observation was also made with 0·600 μ. and the curves again adjusted to be at the correct heights at this wave-length. These two sets of curves were very similar and from them a mean set of curves was calculated as shown in Fig. 2. The central curve is that published by Willmer & Wright (1945) for W.D.W.

In the case of L. C. T., Fig. 3, all the curves were measured with a type B field. The central curve was measured by a step-by-step method as follows: The wave-length of the lower beam was set at 0·530 μ. and adjusted to a convenient brightness. The upper beam was then set at 0·530 μ. and a brightness match made by moving the neutral wedge controlling the intensity of the upper beam. The wedge position was then recorded and with the upper beam set at wave-length 0·540 μ. three heterochromatic brightness matches were made and recorded. The wedge was then set at the mean value of these three recordings and the observer altered the lower beam in colour and brightness until equality was obtained. After this, the upper beam was set at 0·550 μ. and a further three heterochromatic matches made. Each wave-length was measured by a continuation of this process and from the mean wedge readings a figure proportional to the energy required to produce a visual sensation of constant magnitude was determined from the energy calibration curve of the instrument; the reciprocal of this energy then gives the relative luminosity.

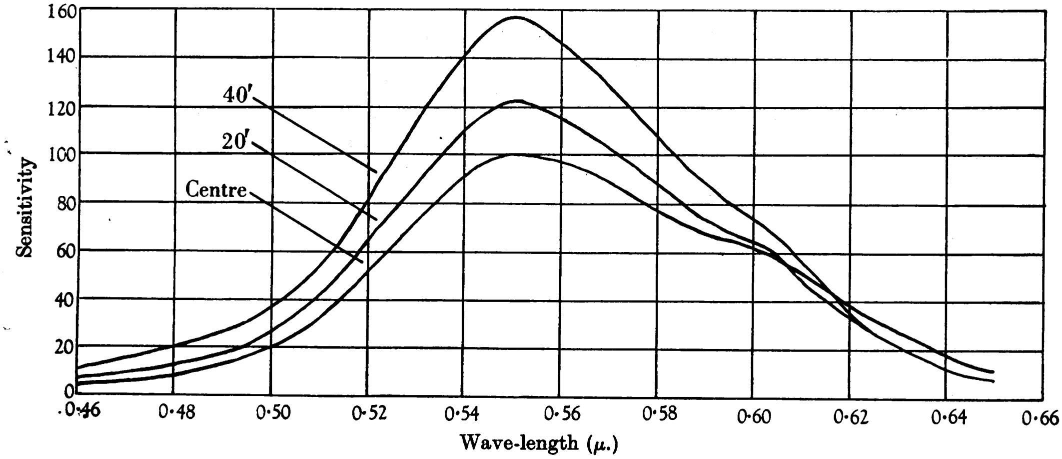

Fig. 2. Sensitivity curves for W. D. W.

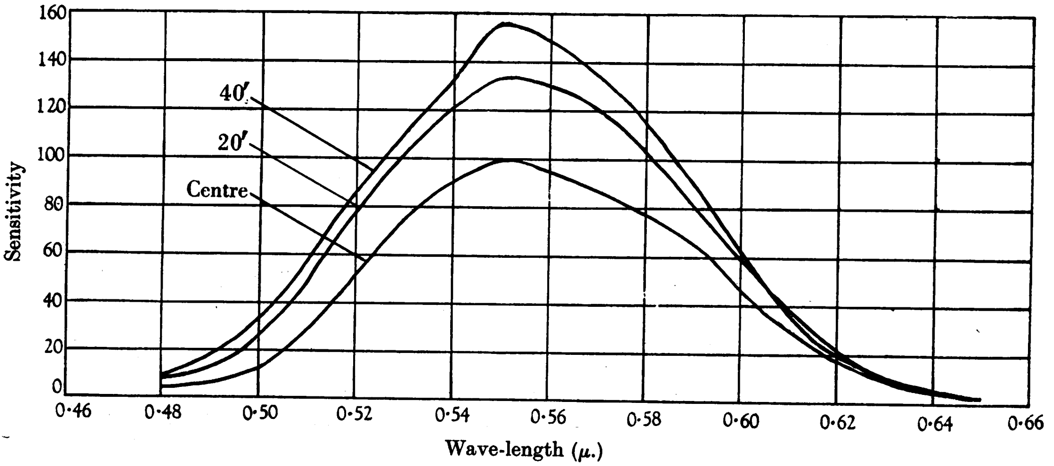

Fig. 3. Sensitivity curves for L. C. T.

In this way each wave-length was compared in brightness with an adjacent wave-length through the medium of a comparison field which did not differ greatly from it in colour. The advantage of this method over the more usual one, in which a comparison field of fixed wave-length is used, is that big differences of colour are avoided and for L. C. T., who found big colour differences very disturbing, the measurements were much improved in consistency in spite of the fact that errors of matching were cumulative and might have produced quite large discrepancies in the 'tails' of the curve unless care had been taken.

The curves for the other retinal positions were then measured by setting both the upper and lower beams to the same wave-length, and whilst the lower beam remained at the fixation point, matches were made with the upper beam situated in each of the three retinal positions. This process was continued for each wave-length, and from these measurements the brightness of the displaced beam was determined relative to the brightness of the central beam; since the ordinate of the central luminosity curve was known for each wave-length, the sensitivity curves for the 20′ and 40′ positions could be calculated.

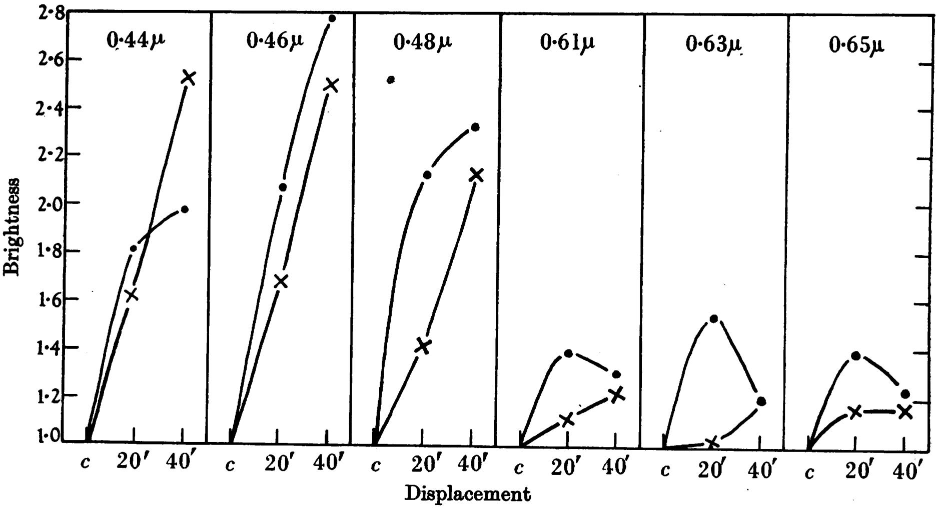

Fig. 4. The relative brightness of the test patch in the three retinal positions for six wave-lengths at the 'tails' of the luminosity curve. Central brightness adjusted to unity. Crosses, W. D. W.; dots, L. C. T.

The change in light sensitivity with displacement of the field for the two ends of the spectrum is shown in greater detail in Fig. 4. This diagram records the brightness of the test patch when viewed at the 20′ and 40′ positions in comparison with the central brightness, which has for convenience been given a value of unity for each wave-length. Results are shown for both observers, each of whom found a very marked increase in sensitivity to blue light as the patch moved away from the centre.

With regard to the accuracy of the observations, the mean of five readings, in Fig. 3, for the central curve for wave-length 0·550 μ. had a standard error of ±0·063. The standard error of the mean of the 20′ curve was ±0·035 (6 readings) and of the 40′ curve ±0·063 (6 readings). In Fig. 4 at 0·460 μ. the standard error at 20′ (L. C. T.) was ±0·168 (4 readings) and at 40′ ±0·229 (4 readings). The differences among the curves at the apices and on the blue side of the maxima in Fig. 3 are

clearly significant, but between 0·570 and 0·620 μ. there is probably no difference between the 20′ and 40′ curve, although they both differ from the central curve. Errors for W.D.W. are somewhat less than those stated above.

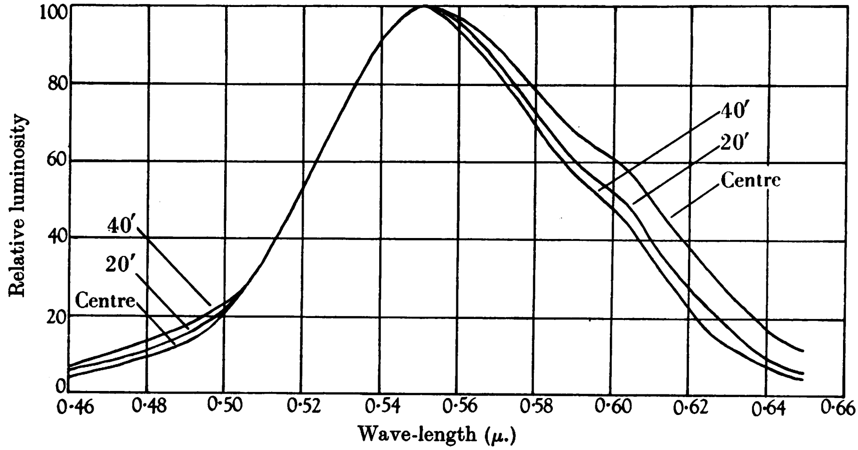

Fig. 5. W.D.W. Relative luminosity curves for the three retinal areas adjusted so that the maximum ordinate of each is 100.

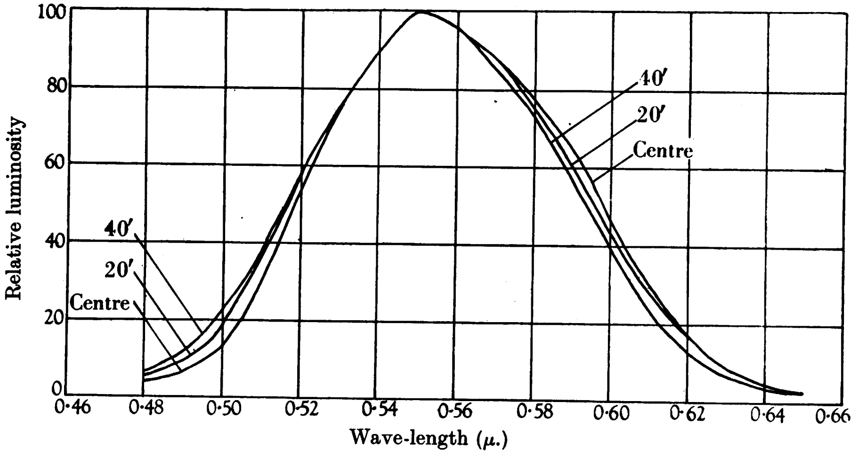

Fig. 6. L.C.T. Relative luminosity curves for the three retinal areas adjusted so that the maximum ordinate of each is 100.

Even though these two sets of curves have been measured by different methods, the similarity of shape between them is remarkable, as may be seen by comparing Figs. 5 and 6 which show the curves of Figs. 2 and 3 plotted so that the maximum ordinate of each curve is 100. Moreover the general shape does not greatly alter with displacement of the beam to the 20′ and 40′ positions and the small hump at 0·600 μ. in W.D.W.'s central curve is reproduced in his two other curves. When, however, the 20′ and 40′ curves bear their correct relation to the central curve as in Figs. 2 and 3 it can be seen that fairly large increases in sensitivity are obtained at most wave-lengths when the beam is displaced; the greatest changes being in the blue region of the spectrum where the sensitivity in the 40′ position for both observers at 0·460 μ. is about 2·75 times the central value. It was this sensitivity change which was one of the most striking features of the whole investigation.

It will be noticed that in Fig. 2 the luminosity of the red wave-lengths appears to fall when the beam is displaced, and that in Fig. 4 it appears to rise. Both these sets of measurements are consistent among themselves and are similar except in so far as the first set was made in July and the second set in October. Errors of this kind are inseparable as yet from work with small fields and they serve to show that other factors, at present uncontrolled, may be affecting the matches. Further, changes of sensitivity with displacement as measured with the upper patch displaced (as in these experiments) are not entirely the same as the changes which occur when the measurements are made by displacing the lower patch. All the results quoted here refer to the former arrangement. The differences are not large and may be due to the fixation point being somewhat displaced from the anatomical centre of the fovea.

Dichromatic coefficients. With a type A field, colour-matching experiments have shown that for both observers and for each of the three retinal positions examined, vision is dichromatic and thus any colour can be matched by a mixture of two matching stimuli only. In these measurements the upper beam (the matching field) consisted of a mixture of red and blue radiations (wave-lengths 0·650 and 0·460 μ. respectively), the proportions in the mixture being controlled by means of neutral wedges; the lower beam (the test field) was illuminated by light of the wave-length to be matched. Matches in colour and brightness were then made between the two halves of the field and the proportions of the red and the blue stimuli required in the mixture were recorded. The units of the stimuli were so chosen that equal amounts of the red and the blue were required in the match on a monochromatic yellow of wave-length 0·5825 μ. and the values for the red (r) and blue (b) dichromatic coefficients in any match were adjusted to bring $r+b=1$. The values of r and b through the spectrum for each retinal position are given by the coefficient curves for W.D.W. in Fig. 7. It should be noted that the units for each retinal position were based on a 0·5825 μ. match made in that position; hence all the curves have coefficients of 0·50 at the wave-length 0·5825 μ. Similar curves for L.C.T. were also obtained.

The advantage of evaluating the coefficients in this way has been discussed elsewhere (Wright, 1929; Pitt, 1935); the main advantage, however, is that the coefficients as measured on this basis are independent of macular pigmentation. The differences in the curves of Fig. 7 can therefore be attributed to differences in the sensitivity of the receptor processes themselves.

The white point (i.e. the wave-length which could be matched with white) for each of the three retinal positions was measured. The result for the central position for W.D.W. was 0·578 μ.; for 20′, 0·575 μ.; and for 40′, 0·572 μ. The corresponding values for L. C. T. were, centre 0·577 μ.; 20′, 0·576 μ.; and for 40′, 0·571 μ. The white standard S_B was used, colour temperature, 4,800° K.

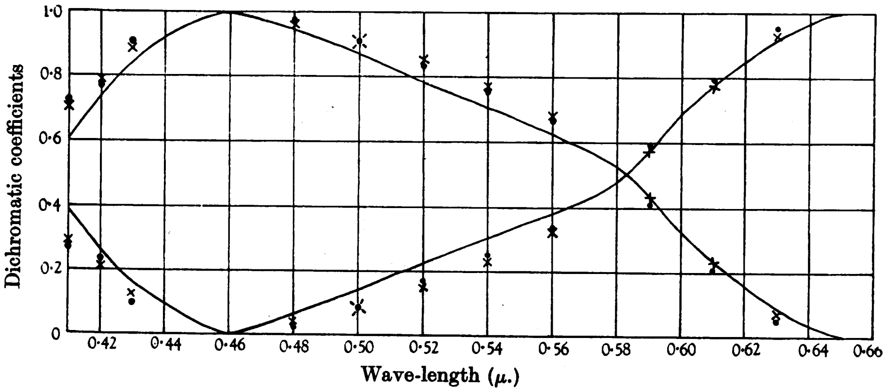

Fig. 7. W.D.W. Dichromatic coefficients. Full curve, central; crosses, 20′; dots, 40′.

Relative luminosities of the matching stimuli. The relative luminosities, L_R and L_B, of unit amounts of 0·65 and 0·46 μ. (that is, the amounts required in the colour match of 0·5825 μ.) were obtained by direct brightness matches made between each matching stimulus in turn against a fixed comparison beam. Red, yellow and blue radiations were used in different experiments for this comparison beam and while significant differences were obtained by one of us (W.D.W.) according to which colour was used, the results given in Table 1 are the averages for all the observations.

TABLE 1. Relative luminosities of matching stimuli. (Units of matching stimuli based on 0·5825 μ. match for W.D.W. in each retinal position, and for L.C.T. in central position only)

	L_B/L_R Retinal position		
Observer	Centre	20′	40′
W.D.W.	1·37	1·47	2·00
L.C.T.	1·30	1·93	2·93

Spectral mixture curves. The unit dichromatic equation for wave-length λ is given by

$$C_\lambda = r_\lambda R + b_\lambda B,$$

where r_λ and b_λ are the dichromatic coefficients for that wave-length. The equality match between C and the R, B mixture can also be expressed in luminosity units by applying the relative luminosity values of R and B as given in the previous section. Thus

$$L_\lambda C_\lambda = r_\lambda L_R R + b_\lambda L_B B,$$

where L_λ is given by $$L_\lambda = r_\lambda L_R + b_\lambda L_B.$$

The ordinate F_λ of the equal-energy luminosity curve at wave-length λ can be divided into two parts representing the amounts in luminosity of 0·65 and 0·46 μ. which are equivalent to the amount of λ present in the equal-energy spectrum. These amounts can be calculated as follows:

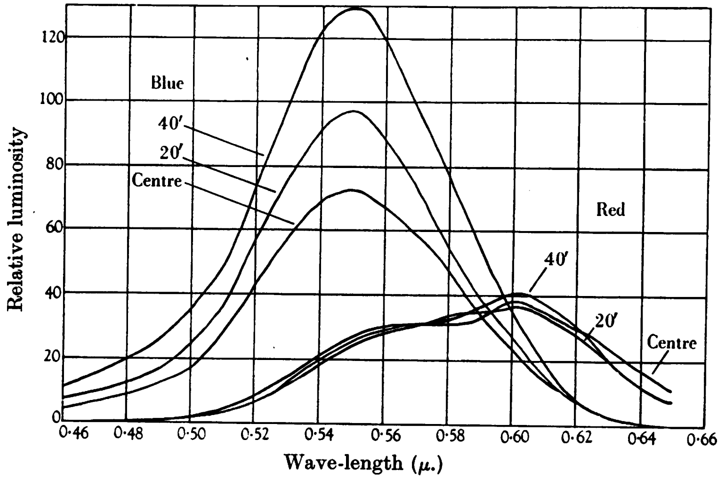

Fig. 8. W. D. W. Spectral mixture curves.

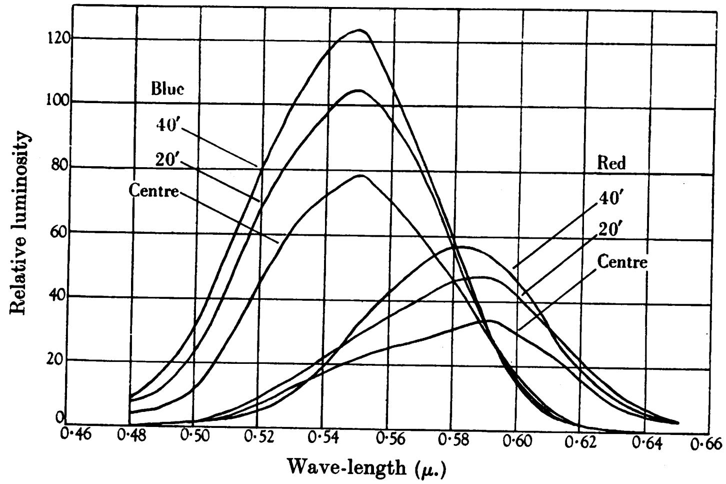

Fig. 9. L. C. T. Spectral mixture curves.

$$\text{Amount of } R = \frac{F_\lambda}{L_\lambda} r_\lambda L_R,$$

$$\text{Amount of } B = \frac{F_\lambda}{L_\lambda} b_\lambda L_B.$$

If these values are worked out for various wave-lengths through the spectrum, the results can be plotted to give the mixture curves shown in Figs. 8 and 9. These curves were derived from the luminosity curves of Figs. 2 and 3, and therefore include the effect of the change in light sensitivity with retinal position.

In the case of W.D.W. the increase of total luminosity with displacement of the test beam apparently develops from an increase in height of the blue mixture curve, the red curve being hardly affected. For L.C.T., on the other hand, part of the increase is derived from some absolute increase in red sensitivity.

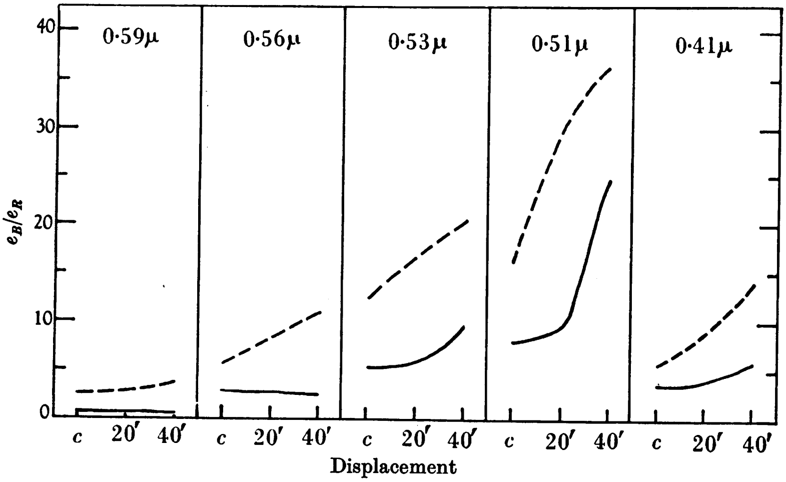

Fig. 10. Ordinate: the energy ratio e_B/e_R of the blue stimulus to the red stimulus required to match the test colour, when the mixed field is viewed always in the central position. Abscissa: displacement of the test field. Dots, W.D.W.; full curve, L.C.T. For explanation, see text.

The change in colour sensitivity with foveal position can also be expressed in terms of the energy ratio e_B/e_R of the blue stimulus to the red stimulus required to match the test colour, when the mixed field is viewed always in the central position, while the test beam is viewed in turn in the central, 20′ and 40′ positions. The change in this ratio with retinal position of the test field is illustrated in Fig. 10 for various wave-lengths of the test field; these curves have, however, been derived by calculation from the data in Figs. 2, 3, 7, 8, 9 and Table 1, and not by direct observation. This method of expressing the results has the advantage that the change in colour of the test field is shown in terms of matching stimuli viewed on the same area of the retina in all cases, so that the matching stimuli are of constant light and colour quality. The very striking increase in the e_B/e_R ratio, particularly at 0·51 μ., was the quantitative counterpart of a subjective change in the test field with change in retinal position; thus, 0·51 μ. viewed centrally looked green but in the 40′ position turned blue.

Hue discrimination. The hue discrimination of both observers was measured with a type A field. The upper beam was set at wave-length λ and the lower beam adjusted to wave-length $\lambda \pm \Delta\lambda$ until a just noticeable difference of colour could be seen. Owing to the very large wave-length difference recorded in many of the observations, it was frequently convenient to measure the step on one side of λ only, the step generally being observed towards the yellow part of the spectrum. The intensity of the lower beam was fixed at a suitable level and equality of intensity between the two beams was maintained throughout the observations by adjusting the neutral wedge in the upper beam. The ability to discriminate between neighbouring wave-lengths is inversely proportional to $\Delta\lambda$, and in Figs. 11 and 12 $\Delta\lambda$ is plotted against $\lambda \pm \frac{1}{2}\Delta\lambda$. $\Delta\lambda$ is always considered as positive. The central curve for W.D.W. is slightly modified from the curve published by Willmer & Wright (1945).

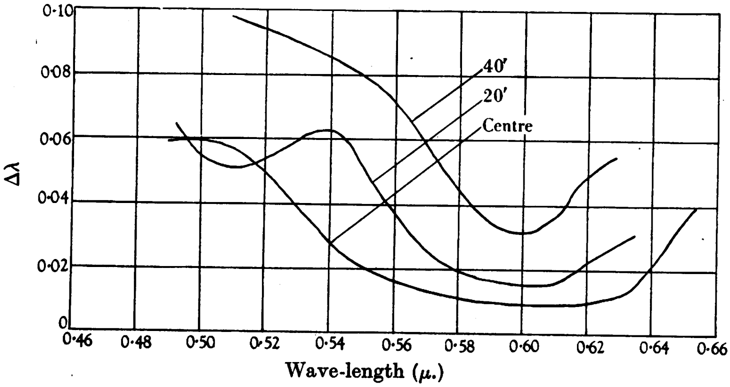

Fig. 11. W.D.W. Hue-discrimination curves.

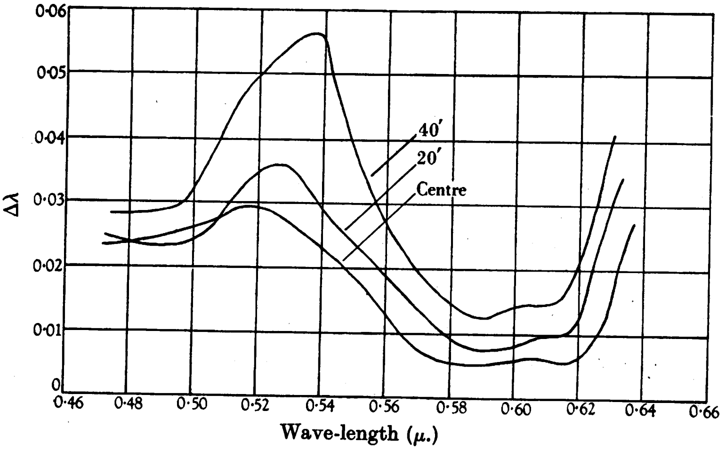

Fig. 12. L.C.T. Hue-discrimination curves.

As regards the accuracy of the observation, for wave-length 0·490 μ. and for L. C. T., the standard error of the mean of observations taken at the centre was ±0·0021 λ. (6 readings). For the 20′ position the error was ±0·0036 λ. (6 readings), and for the 40′ position ±0·0034 λ. (6 readings). From these figures it might be argued that the difference between the central and 20′ curve shown at this point is not significant, but these errors are mainly produced by day-to-day variations in the results as a whole and these curves have been judged significantly different by an examination of their relationship within the results of each day. The day-to-day variations are probably due to a variable interpretation of the words 'just noticeable difference' and this is also the probable explanation of the fact that any step made by L. C. T. is approximately half that made by W. D. W. under similar conditions. Nearer the minimum of the curve the standard error is only ±0·0005 λ. for the 20′ curve.

These curves again show the minimum of hue step (maximum discrimination) in the region of 0·610 μ. which was noticed by Willmer & Wright (1945) for the central position and in addition show that this minimum is reproduced in the 20′ and 40′ curves. A further minimum is shown in the region of 0·490 μ. which is most marked in the 20′ curves for both observers, and also in the 40′ curve for L. C. T. The hue discrimination in this region of the spectrum for the 20′ position is actually better than that for the central position and as yet there is no complete explanation for this. On the whole, discrimination becomes more difficult the further the beams are displaced from the fixation point and is in any case far more difficult than discrimination of hue when using larger fields (Willmer & Wright, 1945).

DISCUSSION

Visual sensations. It is important to emphasize that the luminosity and colour matches reported here represent stimulus equations in which we have had no concern with the quality of the sensations produced by the stimuli apart from establishing equality between the two halves of the field. We shall not, for example, discuss whether the 0·46 μ. matching stimulus gives rise to a blue or a green sensation, or possibly to one sensation under one condition and another under a different condition, and although our results may be related to the spectral sensitivity of the receptor mechanisms in the retina, no study of the sensations aroused by the activity of these receptor mechanisms has been made. If it is true that there are two receptor processes active within the central fovea (Willmer & Wright, 1945), the further problem arises of how the various colour sensations can be stimulated with only two such processes responding in any small retinal area. Before this question can be settled, a different type of experiment from that described in this paper is required, in which the quality of the sensation is studied for various intensities and wave-lengths of the light stimulus, for various sizes of test spot and retinal position and, most difficult of all, for various conditions of fixation, e.g. momentary fixation, prolonged fixation, no fixation, etc.

Anatomy. Since special steps have been taken in this investigation to neutralize the chromatic aberration of the eye, a great increase in the precision of retinal stimulation has been achieved and some account of the anatomy of the central fovea is necessary in order to interpret the results. All the facts and the outlines of Fig. 13 have been taken from Polyak (1941). The figure, which represents a cross-section of the central fovea, shows the relationship between the image of the circular field and the receptors. Linear measurements can be judged from the scale of μ. below the diagram and the scale of minutes below this shows the visual angle to which the linear measurement corresponds. The positions and extent of the image of the circular field in the photoreceptor layer correspond to the positions shown at the foot of the figure.

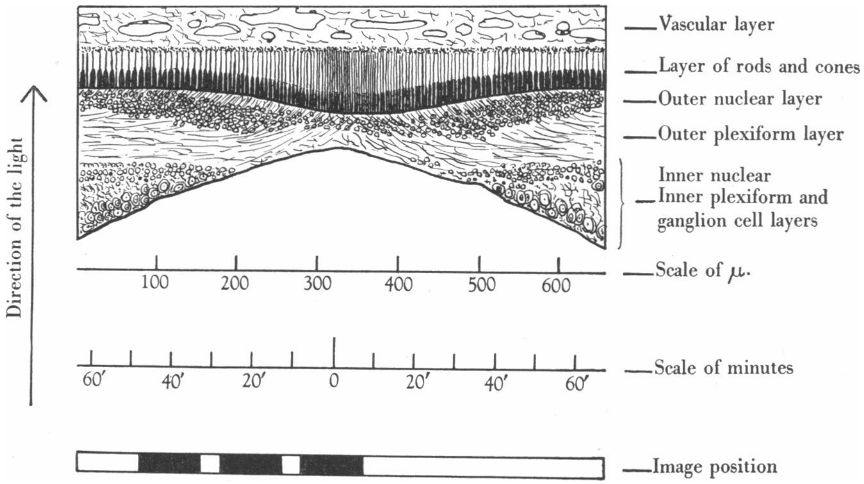

Fig. 13. The relationship between the image of the test patch and the photoreceptors of the retina. (The diameter of the more lateral cones has been somewhat exaggerated.) (Modified from Polyak.)

The thinning and disappearance of the ganglion and inner nuclear and plexiform layers, which occur in this region, can be seen and also the increase in length of the cones at the foveal centre. This increase in length is associated with a decrease in the diameter of the inner segments of the cones and in the foveal centre this diameter is 1·5 μ. as compared with 2·5 μ. in the more lateral positions. The yellow macular pigment is confined to the ganglion and inner nuclear layers and is, therefore, most evident in the foveal slopes where these layers are increased in depth. The foveal centre contains little or no pigment.

Polyak states that the area containing the slender cones at the centre of the fovea usually occupies a visual angle of 10′ on either side of the central point and if one assumes that the fixation point is at the centre, the circular field in its central position would lie wholly on the slender cones, and it has been estimated that the image of each half of the circular field would then stimulate as few as 700 of these cones. The 20′ and 40′ areas fall on the somewhat fatter cones of the more lateral part of the fovea and here the image of each half of the field stimulates somewhat less than 700 cones. It is unlikely that any rods are included in the 40′ area, for Polyak states that even in a small fovea, 50′ of visual angle on each side of the centre is absolutely free from rods and that even at 1° from the centre there are only a few rods. From this it would follow that all three field positions that we have used are free from the influence of the rods. It is interesting to note that the ability to resolve the field became rapidly worse as the field was displaced and that this might be due either to the introduction into the beam of the bodies of a few ganglion cells, to the increased diameter of the foveal cones which occurs in the 20′ and 40′ positions, or more probably to the less precise representation of each cone in the cerebral pattern.

Dichromatic vision. In so far as vision for all our image positions was dichromatic, these experiments confirm, for the central area, the findings of Hartridge mentioned earlier in this paper that the size of the image and not its retinal position determines whether vision shall be dichromatic or trichromatic. But although vision was dichromatic for each position (which may mean that the receptor mechanisms are similar in kind all over the fovea) very striking increases of sensitivity occur in the blue region of the spectrum with displacement of the test beam, so that, whatever the receptor mechanisms may be, they clearly function in a way which is peculiar to the retinal position. It is possible to obtain subjective confirmation of this non-uniformity of behaviour from matches made with the more extended field of a trichromatic colorimeter. There is in fact a central pip in the fovea which is markedly less sensitive to blue light than the immediately surrounding zones. This pip can be observed as a small spot of different colour when a blue-green field is being matched.

This variation of blue sensitivity may also explain the observation made by König (1894) and by Willmer & Wright (1945) that a dichromatic match was at once disturbed unless perfect fixation was maintained. Without the aid of fixation spots, the image of the test patch would only remain stationary upon the retina and so give sufficient time for a match to be made, when it lay at the foveal centre. Since no other retinal area can be steadily directed towards the test patch of light, its image would, elsewhere on the retina, be at all times on the move across a retina of varying sensitivity, so that no test for dichromasy could be made, although vision might nevertheless be dichromatic for small fields all over the retina. Our experiments indicate that this explanation might be correct; when fixation spots were provided, it was confirmed that in addition to the centre, the vision of the lateral parts of the central fovea was also dichromatic. It may be that further experiment will show that the vision of the whole of the retina is dichromatic when small fields are used.

Trichromatic vision. If any small field within the fovea gives dichromatic vision, why should a larger field be trichromatic? One answer may be that, because of the differences in the dichromatic mixture curves for different foveal positions, satisfactory colour matches at two or more points at the same time can only be secured if three matching stimuli are used. This would mean that the apparent trichromasy of the retina was an artefact due to the varying spectral sensitivity of one or both of the receptor processes across the retina. On the other hand, it may be that there are only two types of receptor at the centre and a third in the more peripheral parts of the fovea, but that owing to the poor discrimination in these regions when small fields are used, apparently satisfactory colour matches can be made with only two matching stimuli.

Foveal insensitivity to blue light. Polyak (1941) states that each bipolar cell supplying the foveal periphery has a larger number of receptors in synaptic contact with it than a corresponding bipolar cell supplying the foveal centre. The same is true for the ganglion cells, whose axons are the fibres of the optic nerve, and it might be argued that this increased complexity of connexion in the foveal periphery might enable the response of one receptor to sum with that from adjacent receptors and so produce the greater sensitivity to light noted in these experiments. An explanation along these lines, however, cannot be wholly correct because the retinal neurons are united into an anatomical whole by the presence of the horizontal neurons and, as in other parts of the central nervous system, the results of stimulation of the receptors will depend upon the properties of the synapses between the neurons. These properties are as yet scarcely investigated and it may be that when they are known, the true explanation of the increase of sensitivity will be apparent.

Another explanation of the blue insensitivity of the foveal centre is that it is not due to an alteration of the receptor sensitivity but that the yellow macular pigment preferentially absorbs the blue and violet rays. Since the pigment is concentrated in the foveal slopes, this cannot be correct: the centre in our experiments shows greater insensitivity to blue than the 40′ position and in neither is very much pigment present. If any is present, the 40′ position should be less sensitive to blue than the central position.

SUMMARY

1. Luminosity, dichromatic coefficient and hue-discrimination curves have been measured with a 15′ test field and spectral mixture curves calculated for two observers and for three retinal positions of the right eye, central, 20′ and 40′ displaced into the nasal half of the visual field. The colorimeter developed by one of us (Wright, 1927, 1939) has been used.

2. The luminosity curves are similar in shape but show that there are fairly large increases in sensitivity to blue light as well as moderate increases elsewhere in the spectrum.

3. The spectral mixture curves show that the increase of sensitivity with displacement in W.D.W. largely develops from an increase in height of the blue spectral mixture curve, whereas for L.C.T. there is also some increase in the height of the red curve.

4. All three hue-discrimination curves show a minimum hue step in the region of wave-length 0·610 μ. and the curve for the 20′ position in both observers shows a second minimum at 0·490 μ., which is below the central value for this wave-length.

5. Since steps had been taken to render the eye achromatic, the precise relationship of the image of the test patch to the retinal receptors has been discussed.

6. The nature of the vision at the central fovea is considered and it has been suggested that the normal trichromasy of foveal vision, when large fields are used, could be an artefact and that the third matching stimulus allows satisfactory matches to be made at two or more points at the same time.

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