J. Physiol. (1951) 112, 114–132 612.843.21

THE SPECTRAL SENSITIVITY OF THE CENTRAL FOVEA

By L. C. THOMSON

From the Vision Research Unit, Imperial College of Science and Technology, London, and the Institute of Ophthalmology, London

(*Received* 3 *February* 1950)

An investigation of the intensity discrimination of the centre of the central fovea (Thomson, 1949*a*) showed that at low brightness, discrimination maxima were present if the light stimuli were chosen from certain spectral regions. These regions, one at 460, another at 520 and a third between 580 and 610 mμ., correspond to those in which Granit (1947) has found modulator activity, and it was suggested that at low brightness, intensity discrimination was mainly a function of modulator response, and at higher brightness was mediated by the dominators.

Further evidence of modulator activity at low brightness should be obtained by measuring the spectral sensitivity of the foveal centre with a threshold stimulus against a dark background. Local relative increases of sensitivity might be found when the stimulus is taken from either of the three spectral regions mentioned above, because, under threshold conditions, the modulators possibly affect the sensitivity of the eye only around the maxima of their own spectral sensitivity.

Accordingly, the spectral sensitivity of the fovea has been measured by a threshold method against a background of zero luminance in five subjects; two, male, with normal colour vision; one, female, with protanomalous vision; and two, male, both protanopes.

METHOD

The measurements were made on the Wright colorimeter at Imperial College and the general experimental method was as described elsewhere (Wright, 1946; Thomson & Wright, 1947; Thomson, 1949*a*).

Briefly, the test field consisted of a small semicircle with its straight side, which subtended an angle of 15′ at the eye, downwards. This field, which was viewed against a dark surround, could be illuminated with light of any desired intensity and quality. To assist the correct positioning of the eye during the measurements, a minute point of light was provided at the centre of the straight side of the semicircle to act as a fixation dot. This dot was of such an intensity and size as to be only just sufficient to guide the eye on to the target. For the observer P.W.T. a further fixation dot was provided so that the test field could be displaced 60′ into the left visual field. All measurements were made with the rod-free area of the right eye.

Calibration. The calibration of the relative energy content of the spectrum was based upon new measurements undertaken with a multiplier photocell as described previously (Thomson, 1949*b*). No determination of the absolute energy value was undertaken.

Procedure. Since it was found that an initial period of dark adaptation made no difference to the results, observations in the central position began immediately on arrival at the colorimeter. For the observations in the 60′ position, however, observer P.W.T. undertook an initial period of 20 min. dark adaptation. Readings were taken at each 10 mμ. of wave-length from 400 to 700 mμ. For any wave-length setting the observer was asked to increase the intensity of the light until he was certain that he could just see the semicircular test field. This setting was then recorded. Then the observer altered the intensity so that he just failed to see the test patch. A further record was then made. A glance technique was used (Thomson, 1949*a*).

The mean of these settings constituted one estimate of the threshold light energy. The wave-length settings were presented in random order and the experiment continued until at least five determinations had been obtained at each wave-length. No wave-length setting was repeated during any one observing session.

Measurements with a point test field. Some measurements were made by observer L.C.T. with a test field subtending less than 1′ of arc at the eye. This field was situated 16·5′ above the fixation dot.

Threshold recovery measurements. Measurements were made of the threshold light energy during the recovery of the sensitivity of the receptors following adaptation to an intense white source. The observer undertook a period of 20 min. dark adaptation and then exposed his right eye to a circular patch of white light of a brightness of $2{\cdot}27 \times 10^4$ photons for 3 min. (Approximately standard illuminant *A*, subtending 5° at the eye and concentric with the fixation dot.) The white source was then removed and the recovery of sensitivity followed by measuring at various times thereafter the light energy necessary just to perceive the test semicircle (wave-length 580 mμ.).

Colour vision of the observers. Details of the visual performance of observers, W.D.W. and L.C.T., who have normal colour vision, have already been published. The protanomalous observer, P.W.T., makes a slightly abnormal Nagel match on wave-length 580 mμ., requiring too much red light. Her hue discrimination curve is to be published elsewhere (Thomson & Trezona, 1950). Observers G.D.P. and A.V.E., classed as protanopes with Ishihara's test plates, had their hue discrimination measured with a 1° 20′ field. The results which are expressed as $\lambda_1 - \lambda_2$ and plotted against $(\lambda_1 + \lambda_2)/2$ are shown in Fig. 1. The dotted curve gives the hue discrimination data for two observers with normal colour vision (Pitt & Wright, 1934).

Calculation. Ever since Dartnall & Goodeve (1937) pointed out the need for expressing spectral sensitivity results on the basis of an equal quantum intensity spectrum, it has been assumed that a fixed number of light-quanta per sec. are required at any wave-length to initiate a given response, such as that at the threshold of vision.

This fixed number R per sec. will only be a fraction of the total number of quanta reaching the photochemical system of the receptors; a fraction (say p_λ) (Stiles, 1948), which will depend upon the light absorbed by the photochemical pigments concerned. Thus the number of quanta required at the receptors to produce a threshold response is R/p_λ quanta per sec., where p has values for each wave-length λ dependent upon the photochemical pigments concerned. These quanta have an energy value of $Rkh\nu/p_\lambda$, where ν is the frequency of the light of wave-length λ, h is Planck's constant and k a constant which is determined by the units in which the energy is measured.

The energy arriving at the receptors is, however, less than the energy incident on the cornea because of the absorption of light by the ocular media (transmitting a fraction a_λ of the incident light), by the yellow macular pigment (b_λ) and by other substances such as haemoglobin ($c_\lambda \ldots$). Thus the energy incident upon the receptors will be

$$E_\lambda a_\lambda b_\lambda c_\lambda \ldots,$$

where E_λ is the energy measured at the cornea. At the threshold

$$E_\lambda a_\lambda b_\lambda c_\lambda = \frac{Rkh\nu}{p_\lambda}. \qquad (1)$$

It is usual to define the sensitivity of the eye as a whole as

$$S_W = \frac{k}{E_\lambda}. \tag{2}$$

Let us also define the *retinal sensitivity* as

$$S_{\text{ret.}} = \frac{khv}{E_\lambda a_\lambda}, \tag{3}$$

and the *receptor sensitivity* as

$$S_{\text{rec.}} = \frac{khv}{E_\lambda a_\lambda b_\lambda c_\lambda \dots}. \tag{4}$$

Further subdivision of $S_{\text{rec.}}$ might be necessary in the future because pigments which are not part of the photochemical system may be found within the receptors.

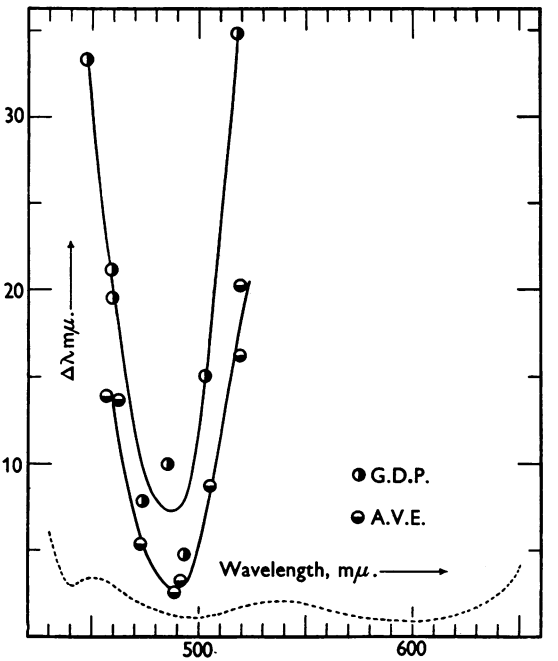

Fig. 1. The hue discrimination data for the two protanopic observers, A.V.E. and G.D.P. The results are expressed as $\lambda_1 - \lambda_2$ and plotted against $(\lambda_1 + \lambda_2)/2$. The dotted curve gives the mean data for two observers with normal colour vision (Pitt & Wright, 1934).

Clearly $S_{\text{rec.}}$ is proportional to p_λ, the light absorbed in the photochemical system (Stiles, 1948).

If the relative values of the sensitivity are alone of interest, the constant k may be given any convenient value and, at first, the values of log S_W were calculated for each wave-length and for each estimate of the threshold light energy. The mean of these values was found and the standard error of the mean calculated from the formula, $\sqrt{[\Sigma(x-\bar{x})^2/n(n-1)]}$, in which $x \equiv \log S_W$, $\bar{x}$ is the mean log sensitivity and n the number of estimates made.

RESULTS

Whole-eye sensitivity. Fig. 2 shows the values of log S_W for two observers with normal colour vision, L.C.T. and W.D.W., together with some results kindly supplied by Dr Stiles, for his observer B.H.C. The latter form the sub-

stance of Fig. 9 in his 1933 paper with Dr B. H. Crawford. They refer to a rectangular test field, the sides of which subtended 42′ and 9·5′ at the eye, and which was seen at the centre of a dark area 1·28° in diameter surrounded by a white source of 300 c./ft.^{2} of 30° in diameter. These results, although obtained against a dark background, are not strictly comparable with the present series because a large area of the peripheral retina in Stiles's experiment is light adapted. The means of the values of log S_W are shown as points on the diagram and the standard errors are shown as bars (equal to $\pm\sigma_{mean}$) above and below each.

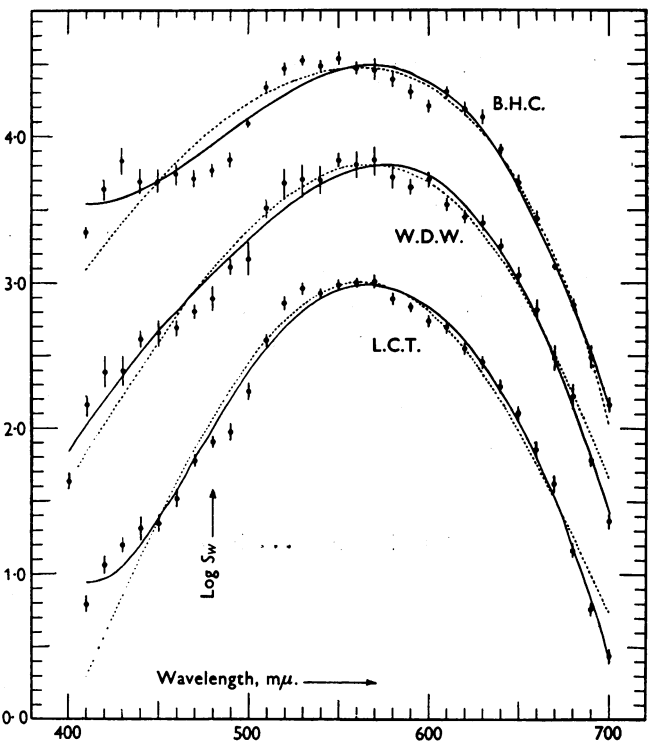

Fig. 2. The mean values of log S_W for the three observers with normal colour vision. The vertical bars indicate the magnitude of the standard error of the mean. The three sets of data have only an arbitrary relationship to each other. Dotted curves are the appropriate Pearsonian functions. Full line curves are the chosen polynomial functions.

When interpreting the data one must decide whether the minor irregularities which disturb the main single-humped nature of the curves are significant or are merely due to experimental error. As an aid to this decision smooth curves, each belonging to the Pearsonian system (Elderton, 1927) have been fitted to the values of S_W by the method of moments. Curves from this system might be chosen by an actuary to represent single-humped data on the assumption

that the minor irregularities are of no significance and due to experimental or observational error. Thus the calculation of the appropriate curve for each set of points should provide smooth functions from which the points themselves might or might not deviate significantly. If the deviation of the points from the curve was greater than could have been expected from the known experimental error, some at least of the minor irregularities must be significant.

The spectral sensitivity curve has been regarded (Houstoun, 1932) as a smooth single-humped function of Gaussian or near Gaussian form. Thus the choice of a member of the Pearson system as a basis from which to test for irregularities would seem particularly appropriate since these curves are all modifications of the normal form. Calculation of the constants supports this choice, since the values obtained do not differ very greatly from those of the Gaussian curve itself.

The calculated curves for the normal observers are shown in Fig. 2 as dotted lines.

Owing to the smaller weight given by the fitting procedure to the values at the ends of the spectrum, the fit is here less good than it should be. Since the magnitudes of the standard error of the mean are similar throughout the spectrum, an accurate test of the significance of the residual variation should be based on a curve which has been calculated by a method giving equal weight to each mean point. A regression line of polynomial form is such a curve and the appropriate line for each set of data has been calculated and is shown as the continuous line in Fig. 2.

By using orthogonal polynomial functions (Fisher & Yates, 1943) curves of the form

$$y = a + bx + cx^2 \ldots + px^r$$

may be successively calculated, each one approaching more nearly to the experimental points as a further term, containing the next higher power of x, is included in the calculation.

For the present data most of the variation is accounted for by fitting curves of the second degree, i.e. curves of the form

$$y = a + bx + cx^2.$$

Carrying the procedure to higher powers of x, although improving the fit slightly, usually introduced inflexions into the line so that it could no longer be regarded as a smooth single-humped function and was thus of less value when testing for the presence of irregularities in the experimental results.

The procedure of fitting was thus carried to that curve which showed some secondary inflexion or to the fifth degree, whichever was reached the sooner, and the significance of the residual variation then assessed by using Fisher's z test.

The chosen polynomial curves, together with the values of z, and the probability of this value arising as the result of experimental error, are given for each set of data in Table 1. For the results for the three normal observers given in Fig. 2 the irregularities are clearly significant.

TABLE 1. Type of polynomial curve and significance of the residual variation

Observer	Curve degree	z	Probability
L.C.T.	5th	0·797	<0·001
W.D.W.	5th	0·353	<0·01
B.H.C.	4th	0·777	<0·001
G.D.P.	5th	0·778	<0·001
A.V.E.	4th	0·565	<0·001
A.V.E.	5th	0·035	>0·2
P.W.T. central	5th	0·861	<0·001
P.W.T. 60′	5th	0·778	<0·001

An attempt was made with the results for observer L.C.T. to obliterate the significance of the residual variation by carrying the process of fitting to higher degrees than the fifth. Significant deviations from a curve of ninth degree were, however, found (probability level 0·05) indicating the complexity of shape of this series of data.

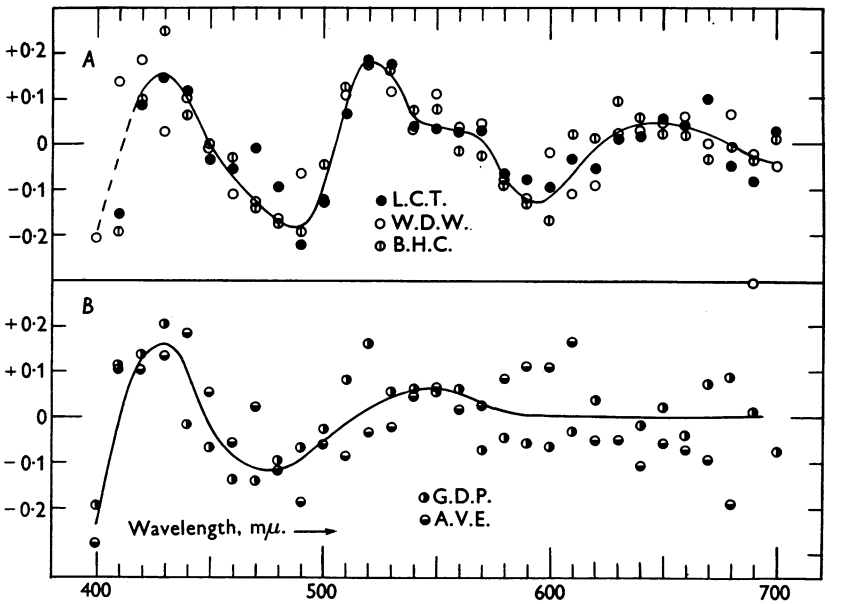

Fig. 3. The difference between the means of the observations for each observer and the appropriate polynomial function. *A*, observers with normal colour vision; *B*, observers with protanopic vision.

Fig. 3*A* shows the difference at each wave-length between the mean sensitivity and the value given by the chosen polynomial curve. In the normal subjects the major relative sensitivity increases may be seen from this figure

and Fig. 2 to be confined to three spectral regions: one at 420 mμ., another at 520 mμ. and a third between 620 and 660 mμ. Although the results for observer B.H.C. refer to an eye in which a large part of the retina, outside the test area, is light adapted (conditions markedly different from those maintained in these experiments) there is a remarkable similarity between the deviations from the polynomial curve for B.H.C. and similar deviations for the other normal observers. One might suggest that the surround has merely altered the general single-humped nature of the data and left the minor irregularities unaffected.

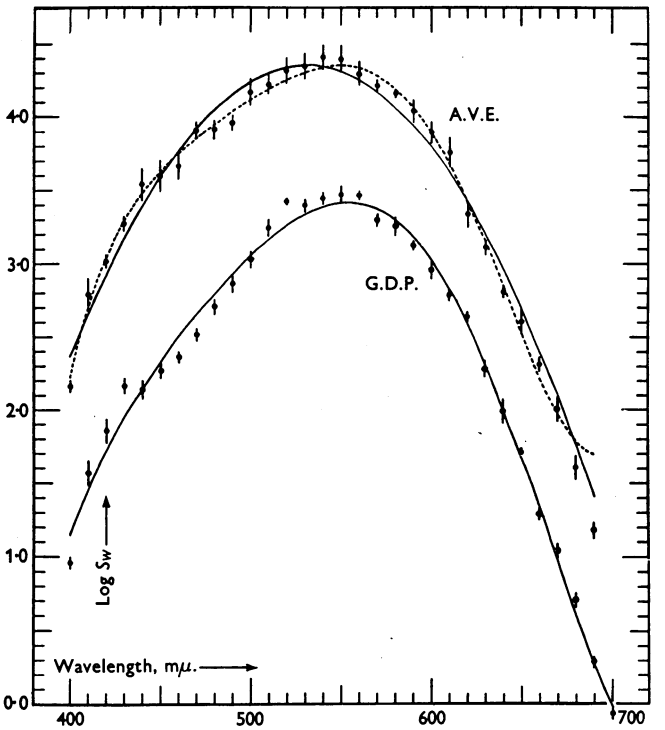

Fig. 4. The mean values of log S_W for the two protanopic observers. The two sets of data have only an arbitrary relationship to each other. Full line and dotted curves are polynomial functions.

In Fig. 4 the results for two protanopic observers are given. The fifth degree curve for observer A.V.E. does destroy the significance of the residual variation, but since the regression line has a maximum around wave-length 560 mμ. and a secondary shoulder at 440 mμ., there must be, even in this observer, some deviation from the single-humped form. For observer G.D.P. the test showed that the results (probability level 0·001) were significantly irregular.

The deviations from the mathematical curves are shown in Fig. 3*B* and only appear of any magnitude in the blue region of the spectrum.

Fig. 5 shows the results for an observer with protanomalous vision. The lower curve was obtained in the usual way from the centre of the central fovea. The upper curve was measured with the test patch displaced 60′ into the left visual field. Irregularities are in both cases significant.

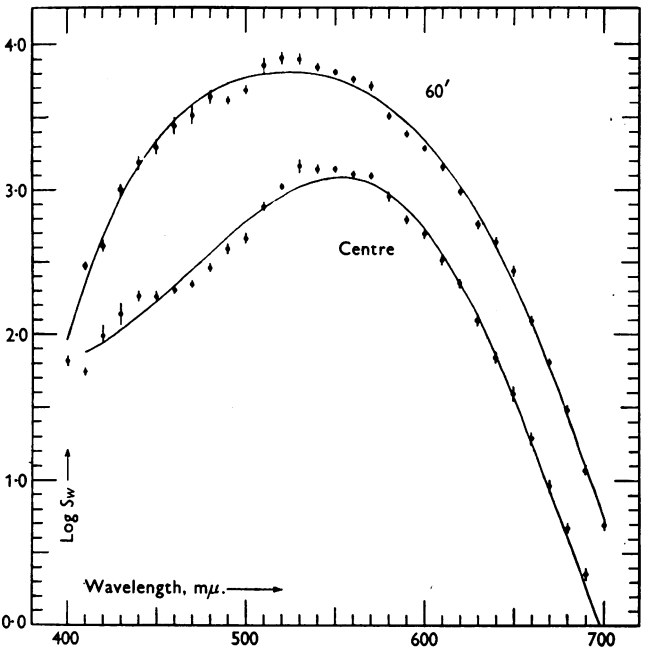

Fig. 5. The mean values of log S_W for observer P.W.T. Upper curve, 60′ position; lower curve, centre. The single value at 400 mμ. refers to the 60′ position. Two sets of data have only an arbitrary relationship to each other. Full-line curves are the appropriate polynomial functions.

Since inflexions appear in the regression line for most observers and since the deviations from these inflected lines are still significant, one can say with confidence that the spectral sensitivity of the centre of the central fovea cannot be a smooth single-humped function.

DISCUSSION

Calculation of the retinal sensitivity. From equation (3):

$$\log S_{\text{ret.}} = \log S_W + \log h + \log \nu - \log a_\lambda.$$

Log h may be neglected if only relative values of log $S_{\text{ret.}}$ are of interest. The values of a_λ given by Ludvigh & McCarthy (1938) have been accepted, and in Fig. 6 the results for observer L.C.T. with the 15′ field are given with log $S_{\text{ret.}}$ as ordinates.

Two further series of results measured with a point source of light (see above) are also shown. For one set of measurements the fixation dot was illuminated by wave-length 600 mμ., and for the other, by 540 mμ. The line shown joins the means of all readings at each wave-length.

Even allowing for the fact that the ordinates at 550 mμ. in each series have been equated in value, the agreement between the two point series and the 15′ sensitivity curve is very close. If the point on the retina used for fixation of the eye differs for each wave-length (Hartridge, 1946, 1947; Thomson, 1946), the two sensitivity curves for a point source should relate to different portions of the foveal retina. Since the distribution of the various receptors is probably

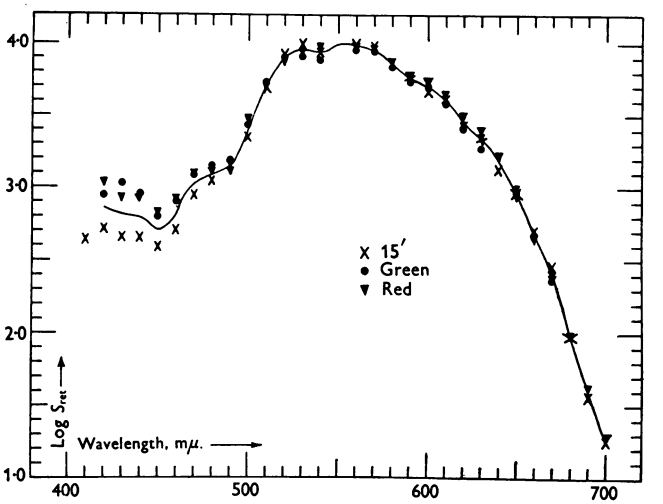

Fig. 6. The mean values of log $S_{ret.}$ for observer L.C.T. and for three types of observing conditions. *X*, 15′ semicircular field viewed at the centre of the fovea; ●, a 'point' field viewed at 20′ above a green fixation dot. ▼, a 'point' field viewed at 20′ above a red fixation dot. The full line joins the means of all the observations.

governed by chance, the sensitivity curves obtained from these two different retinal areas should show some differences of shape. In fact, the two curves are almost identical and if there is a variation of fixation point one cannot detect it by this method.

Absolute relationship. The relative values for the constant *kh* for each observer were measured by threshold determinations at wave-length 550 mμ. under similar observing conditions. Fig. 7 shows the results with ordinates correctly related to those for observer L.C.T. To some extent the differences between the curves must be due to lack of knowledge of the value for a_λ in each individual eye, but it is interesting to note that the sensitivity of both protanopic eyes (G.D.P. and A.V.E.) is greater than normal in the blue and green region of the spectrum; a result which differs from that of Hecht (1949). This difference cannot at present be accounted for by absorption of light by the yellow macular

pigment, and it seems more likely that this increased sensitivity is achieved by some regrouping of the receptors in the protanopic eye.

The usual loss of sensitivity in the red for the protanopic eye is well shown, and the protanomalous subject has a protanopic sensitivity in the red and orange region of the spectrum and a normal one in the blue. No technical defect could be found for the very low blue sensitivity of observer L.C.T. Such low values are probably not abnormal, since his sensitivity, when

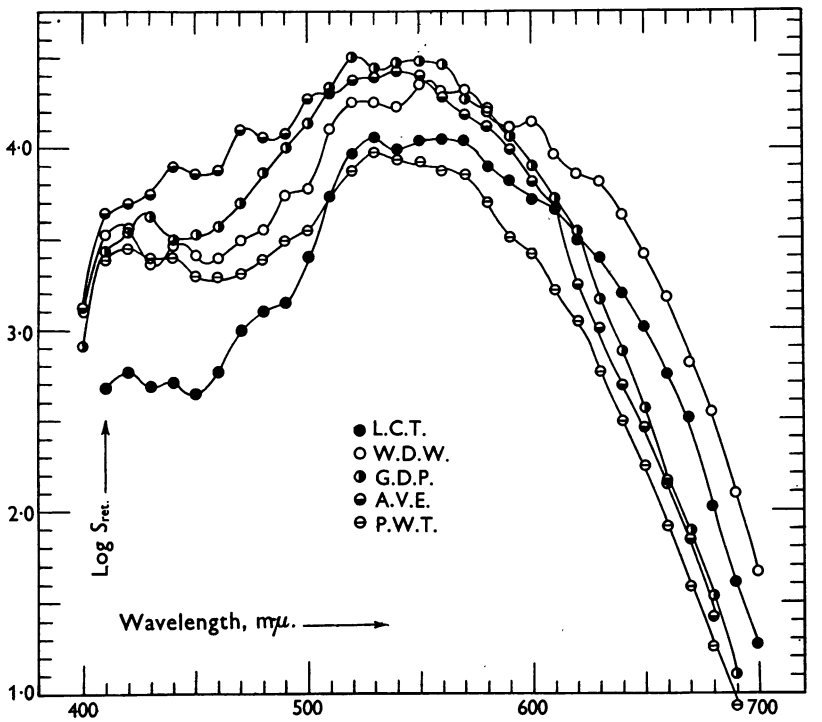

Fig. 7. The mean values of log $S_{ret.}$ for all observers with ordinates correctly related to those for observer L.C.T.

measured with a 1° 20′ field (Thomson, 1949*b*) agrees with the lowest figures given by Gibson & Tyndall (1923–4), being almost coincident with Tyndall's own curve.

Yellow foveal pigmentation. Wald (1945, 1949) has obtained an estimate of the density of the yellow macular pigment by comparing the sensitivity of the eye as measured at the fovea with that as measured outside the foveal area. The assumption was made that log $S_{rec.}$ was similar in magnitude for both retinal areas. An extract of pigment from human maculae revealed the presence of lutein or leaf xanthophyll, and Wald gives the density (which is the best fit for his visual estimate) of the crystalline substance dissolved in chloroform for each 10 mμ. of wave-length.

If Wald is correct, the sensitivity curves reported here should be affected by the absorption of light by leaf xanthophyll, and an attempt to check Wald's estimate has been made in Fig. 8. Here the lowest curve of each set which, like its fellows, is merely a smooth curve drawn through the calculated points, gives

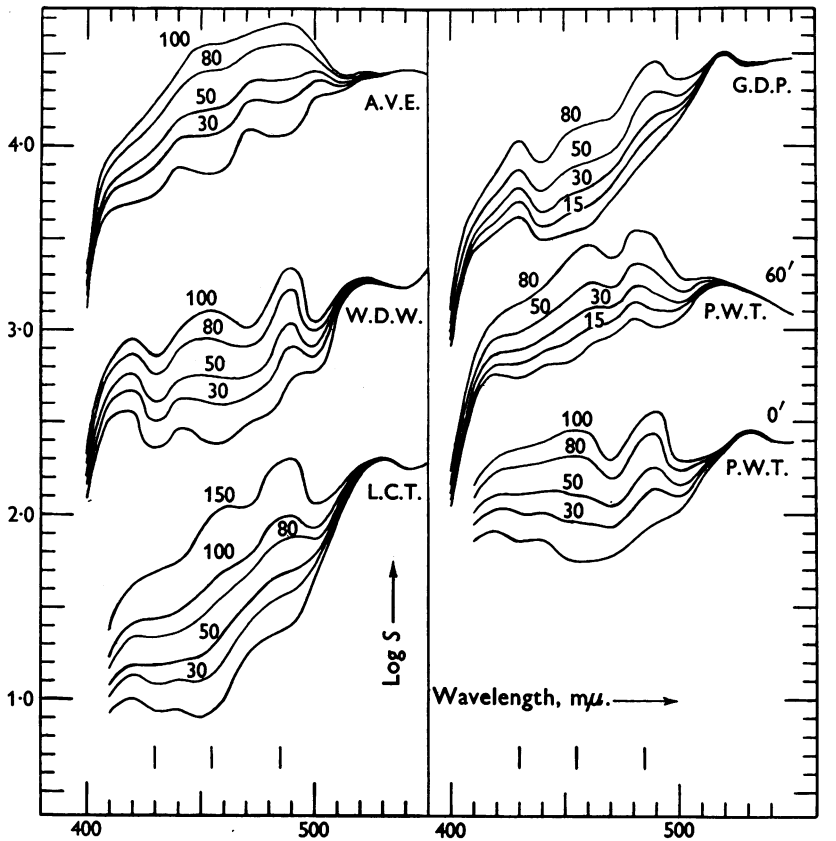

Fig. 8. Correction for the absorption of light by the yellow macular pigment. By applying various percentages (shown by the numbers against each curve of a set) of Wald's estimate for the density of the foveal pigmentation, the values of log $S_{rec.}$ have been determined for each observer. The smooth curves shown join the calculated values at each 10 mμ. of wave-length.

the values for log $S_{ret.}$, and at the foot of the figure three vertical bars indicate the wave-lengths of maximum absorption by leaf xanthophyll. There is some evidence that the values of log $S_{ret.}$ for observers A.V.E., W.D.W., L.C.T. and P.W.T. have been affected by the absorption of light by this pigment, since small depressions occur in the curves at wave-lengths corresponding to the maxima of absorption by leaf xanthophyll. These depressions are most clearly shown at wave-lengths 430 and 455·5 mμ.

An attempt has been made to calculate log $S_{rec.}$ by using Wald's estimate of macular pigmentation.

Since, from equation (4),

$$\log S_{rec.} = \log S_{ret.} - \log b_\lambda$$

and

$$D_\lambda = \log 1/b_\lambda,$$

where D_λ is the estimated density of the leaf xanthophyll at the fovea, the values given by Wald may be added directly to log $S_{ret.}$ to give log $S_{rec.}$ which is plotted as the curve marked 100 in each set of data in Fig. 8. Wald's estimate is, however, too great, because after its use the minima become maxima and the values for log $S_{rec.}$ are impressed by the peaks of the leaf xanthophyll absorption spectrum.

Since $D_\lambda = \epsilon_\lambda Cl$, where ϵ_λ is the absorption coefficient of leaf xanthophyll, C, the concentration of the pigment in the retinal tissues and l, the thickness of tissue through which the light must pass, $D_\lambda \propto C$, l being approximately constant. By applying to the data various percentages of Wald's correction the effect of differing concentrations of the pigment may be gauged. The intermediate curves in Fig. 8 show such a correction. If the 'smoothest' curve of each series be chosen as the one in which the absorption by leaf xanthophyll has been correctly gauged, the values for each observer are; L.C.T., 50%; W.D.W., 30%; A.V.E., 50%; G.D.P., 15% or less; P.W.T., central 30%; P.W.T. 60′, 15%. Since the value of l at 60′ is about three times that at the centre, the concentration of the pigment in the lateral position must be even less than 15% of Wald's estimate. The value for L.C.T. indicates an approximate concentration of leaf xanthophyll in the tissues of 200 mg./l. If $\epsilon_{max.} = 2{\cdot}55 \times 10^2$ (Zscheile, White, Beadle & Roach, 1942) and $l = 0{\cdot}007$ cm. Wald's estimate of b_λ would appear to be somewhat too large. This may be due to his neglect of differences of receptor sensitivity between the foveal and extrafoveal regions. The present results indicate that the blue insensitivity of the foveal centre is due partly to absorption of light by this pigment and partly to a lower receptor sensitivity to blue light, provided always that further yellow macular pigments do not exist.

Too much reliance cannot be placed upon the result for observer A.V.E., since in this case a fifth degree polynomial destroys the significance of the residual variation.

Actually there are many carotenoid pigments, all with trident-like absorption in the blue region of the spectrum, and it might be possible to find one which more nearly fitted the data (see Karrer & Jucker, 1948). Further, the effect of changing the solvent may be to change the wave-length of maximum absorption. Other computations on this basis could no doubt be attempted, but until one knows for certain the nature of the yellow pigment in the macula, Wald's data are the only ones which can reasonably be used.

Absorption by haemoglobin. On viewing a 5° field evenly illuminated with violet light, P.W.T. was able to see the shadows of the blood corpuscles in the retinal vessels, and she confirmed that these shadows passed over and around the retinal area occupied by the test field when displaced 60′ into the left visual field. This is in accordance with Wolff's (1948) description of the retinal capillaries and also with Weale's estimate for the foveal area devoid of retinal vessels (quoted by Dartnall & Thomson, 1949.)

Thus the results for observer P.W.T. (60′) must be affected by absorption of light by haemoglobin, and an attempt has been made to estimate the magnitude of this absorption.

Some specimens of the perifoveal capillary bed injected with indian ink were examined. From these the largest reasonable estimate for the thickness of the haemoglobin film in front of the receptors was 10 μ. About 50% of the light would pass between the capillaries and thus suffer no absorption, so that it was decided to calculate the effect upon the values of log $S_{\text{ret.}}$ of a solution of 10 μ. thickness covering 50% of the test area, containing 15 g./l. of a mixture of 70% oxy- to 30% reduced haemoglobin. The density of this solution was calculated from the results (kindly supplied by Dr I. G. Wootton) of a new determination at each 10 mμ. of wave-length of the density of a 1 cm. layer of both oxy- and reduced haemoglobin.

The amount of light absorbed by this solution can be calculated, and if it is assumed that its effect on the visual response is equivalent to another solution absorbing the same amount of light, but uniformly spread over the retina, the transmission of the equivalent solution, c_λ may be calculated from the original density D_λ by the relation:

$$c_\lambda = 1 - m\,(1 - 10^{-D_\lambda}),$$

where m is the fraction of the total area covered by the original solution.

Thus for observer P.W.T. in the 60′ position,

$$\log S_{\text{rec.}} = \log S_{\text{ret.}} - \log b_\lambda - \log\,(1 - m\,(1 - 10^{-D_\lambda})).$$

The most appropriate values (15%) for b_λ were chosen from Fig. 8, and the values obtained for log $S_{\text{rec.}}$ are shown as the upper full curve in Fig. 9. The lower full curve gives the values for the same quantity when measurements are made in the central position, and with b_λ 50% of Wald's estimate. The absolute relationship between the curves is shown correctly. The lower dotted curve gives log $S_{\text{ret.}}$ for the 60′ position and the upper dotted curve, similar values when the space correction factor m is neglected and $-\log c_\lambda = D_\lambda$. This latter curve is clearly overcorrected.

Thus the correction for absorption of light by haemoglobin is of minor importance in all spectral regions except that around wave-lengths 410–430 mμ., and although the values for log $S_{\text{ret.}}$ dip in the green and yellow region of the spectrum, the depressions cannot be wholly due to absorption of light by

haemoglobin because the magnitude of the correction required to smooth them leads to a large over correction of the values in the region of the Soret band at 420 mμ.

The two full curves are of similar shape, but with a remaining absolute discrepancy, which cannot at present be explained on the basis of retinal pigmentation. The difference may well be due to the greater sensitivity of the receptors in the 60′ position, i.e. the value of R (see above) may be different for each retinal area.

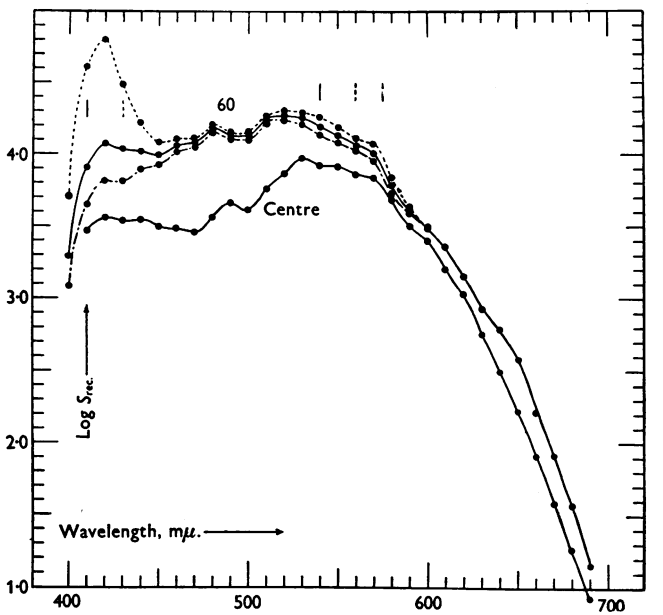

Fig. 9. The mean values of log $S_{rec.}$ for observer P.W.T. for the 60′ and central retinal positions. (Full curves.) Dotted curve: the values when the space correction factor is neglected; dot and dash curve: the values of log $S_{rec.}$ with the leaf xanthophyll correction alone applied. Vertical solid bars: maxima of oxy-haemoglobin. Vertical dotted bars: maxima of reduced haemoglobin.

Rod contribution. It might be argued that some of the discrepancy noted above may be due to stimulation in the 60′ position of a proportion of rod receptors, which are more sensitive to light than the cones, and which would thus lower the threshold for the test area used. To test this possibility, the recovery of sensitivity following adaptation to white light was followed for 20 min. (see Method section). Wave-length 580 mμ. was chosen as test stimulus because it should produce a double curve in which the upper part is usually attributed to the cones and the lower to the rods (Hecht, 1937). As may be seen from Fig. 10, which shows the values of log E_λ plotted against the time in the darkness, there is no 'knee' to be seen anywhere in the curve for any

observer, and so it was concluded that the rod receptors played no part in this investigation.

Residual irregularities. After all the above corrections have been made, certain residual irregularities, which may be related to an observer's colour vision, remain. These are shown in Table 2. P.W.T., in all except the red region of the spectrum, might be classed as a normal observer, which is in accordance with her hue discrimination data (Thomson & Trezona, 1951).

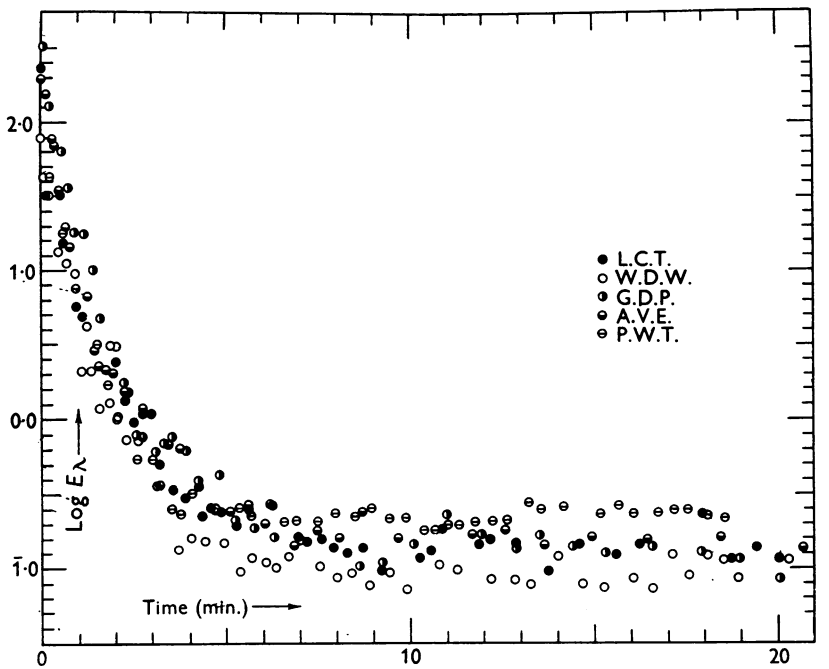

Fig. 10. The values of log E_λ for all observers plotted against the time in darkness following adaptation for 3 min. to a white source of $2{\cdot}27 \times 10^4$ photons. Note the absence of any 'knee' in the curves and that the test light used was of wave-length 580 mμ.

Some of the irregularities noted in the observers with normal colour vision appear in the results for observer B.H.C., even though these refer to a different state of adaptation. The differences in all regions of the spectrum, except the violet, between the results for normal and protanopic observers is well marked, and the minor irregularities do appear to have some relation to colour vision. One cannot, however, exclude the possibility that they are due to absorption of light by retinal or pre-retinal pigments as yet undiscovered.

The correspondence between the irregularities for observer L.C.T. and the maxima of brightness discrimination previously reported (Thomson, 1949*a*) is disappointing and the attempt to determine regions of modulator activity by the present method is not a success. However, a persistently high relative

sensitivity around wave-length 420 mμ. does, in fact, correspond with a new region of modulator activity lately described by Donner & Granit (1949). This, in its turn, corresponds with a further maximum of brightness discrimination recently found with a small test stimulus (Thomson, unpublished). The discrepancy between the raised sensitivity at 470 mμ. for observer L.C.T. and that at 490 mμ. for observer W.D.W. cannot, as yet, be explained. A raised sensitivity at 470 mμ., however, would correspond with the maximum of intensity discrimination found previously at this wave-length, which lends support to the idea that there is some relation between the intensity discrimination data and spectral sensitivity.

TABLE 2. Residual irregularities in the values of log $S_{rec.}$

Irregularity	L.C.T. 15′	L.C.T. red fixation	L.C.T. green fixation	W.D.W.	P.W.T. 0′	P.W.T. 60′	B.H.C.	G.D.P.	A.V.E.
Raised sensitivity at 600 or 610 mμ. with dip at 590 mμ.	+	+	+	+	+	+	+	−	+
Raised sensitivity at 530 mμ. with dip at 540 mμ.	+	−	+	+	+	+	+	−	−
Raised sensitivity at 630 mμ.	+	+	+	+	−	−	+	−	−
Raised sensitivity between 410 and 430 mμ.	+	+	+	+	+	+	+	+	+
Raised sensitivity at 480 or 490 mμ.	−	−	−	+	+	+	−		−
Raised sensitivity at 470 mμ.	+	+	+	−	−	−	−	−	−
Shoulder at 570 mμ.	+	+	+	+	+	+	+	−	−

In Fig. 11 the full line joins the values of log $S_{rec.}$ for observer W.D.W. when the leaf xanthophyll correction is taken as 30% of Wald's estimate. In the same figure the dotted curve gives the values for the sensitivity of the frog's dominator as measured by Granit (1947). The impression given by the values of log $S_{rec.}$ is that they result from some combination of a single broad sensitivity curve, such as the dominator, with several narrower sensitivity curves, which are responsible for the local irregularities. This view is in accordance with Granit's dominator-modulator theory, and is supported to some extent by the lack of any striking differences of the shape of the sensitivity curves as shown in Fig. 7, bearing in mind the very marked differences in the colour vision of the observers.

However, a different idea will account for the facts equally well. Fig. 11 also shows the fit which is obtained between the values of log $S_{rec.}$ and the three fundamental 'response' curves derived by Stiles (1939) from his own eye for a foveal test field. The only alterations made here to Stiles's data (apart from

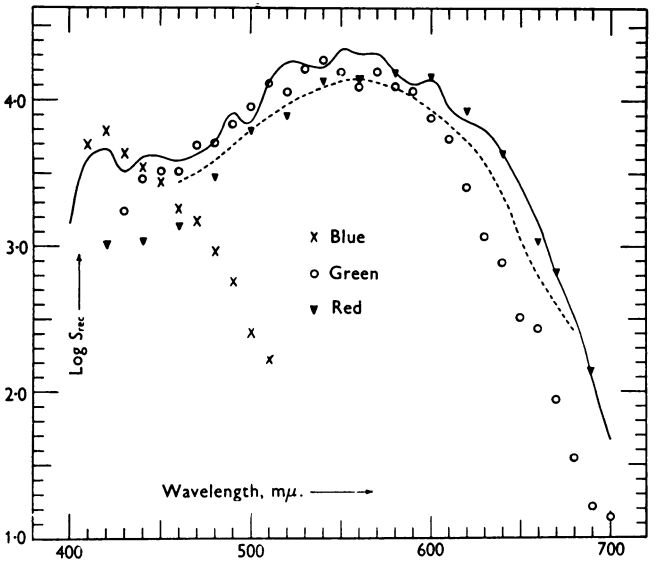

Fig. 11. Full line: the mean values for observer W.D.W. of log $S_{rec.}$ with a leaf xanthophyll correction of 30% of Wald's estimate. Points: the values of the fundamental 'response' curves derived by Stiles (1939). Dotted curve: the values of the sensitivity of the frog's dominator measured by Granit (1947).

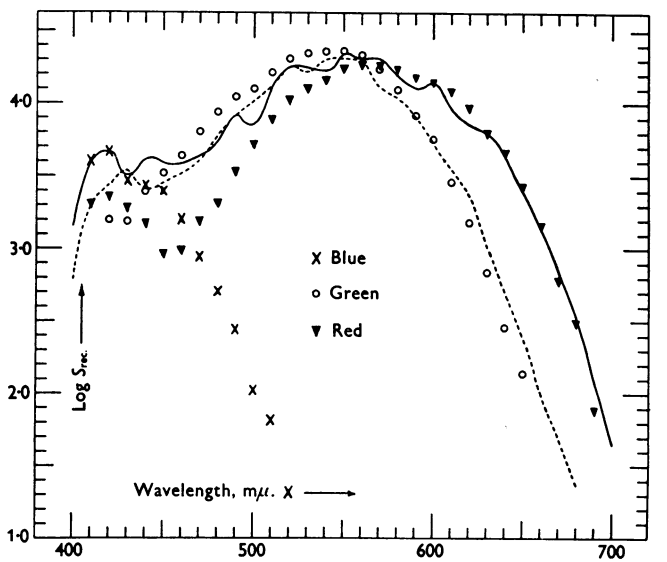

Fig. 12. Full line: the mean values for observer W.D.W. of log $S_{rec.}$ with a leaf xanthophyll correction of 30% of Wald's estimate. Points: the values of the fundamental 'response' curves calculated from Pitt's data (1944). Dotted curve: the mean values of log $S_{rec.}$ for the protanopic observer G.D.P.

the correction due to a_λ) have been to lower the red curve relative to the others by 0·2 log units and fit the curves as a whole to the data for observer W.D.W. by equating the values at wave-length 580 mμ.

Stiles's results, which are based on the assumption that the threshold energy value is entirely determined at any wave-length by the mechanism which is the most sensitive, show that three broad sensitivity curves, corresponding to three colour mechanisms, are alone sufficient to account for the threshold values, there being no need for a mechanism such as the photopic dominator. This view is in accordance with the Young-Helmholtz trichromatic theory of colour vision.

Stiles's curves cannot explain the protanopic spectral sensitivity curve which descends more steeply on the red side of the maximum than either his red or green curve. However, a further set of fundamental 'response' curves derived from those given by Pitt (1944) and compared with the values of log $S_{rec.}$ for observer W.D.W. in Fig. 12, might explain protanopic vision.

Pitt's original curves (1944), which are based upon his determination of the positions in the colour diagram of the fundamental stimuli, refer to the spectral sensitivity curve of the standard C.I.E. observer. Since the standard curve is probably too low in the blue and violet region of the spectrum (Wald, 1945), Pitt's results have been recalculated to refer to observer W.D.W.'s own spectral sensitivity curve recently measured by a flicker method (Thomson, 1949*b*), and it is these curves (corrected for absorption of light in the ocular media and macular pigment (30%)), which are shown in Fig. 12.

If we accept Stiles's assumption (vide supra) these curves account well for the present data, and, in addition, the classical idea that the protanope merely lacks the sensitivity curve due to the red mechanism is also substantiated, since the curve describing the sensitivity of the green mechanism agrees well with the values obtained for the protanopic observer G.D.P. (Fig. 12, dotted curve).

The present results do not, unfortunately, assist in harmonizing Granit's ideas with the classical trichromatic theory of vision.

SUMMARY

1. The spectral sensitivity curves have been measured with a test field subtending 15′ at the eye, and viewed with the central fovea, in five observers, two with normal colour vision, two with protanopic vision, and one with protanomalous vision.

2. The *retinal sensitivity* and the *receptor sensitivity* have been defined and an attempt has been made to evaluate the corrections needed for their calculations.

3. The allowance suggested by Wald (1949) for light absorbed by the yellow macular pigment, which is probably leaf xanthophyll, is too large. This

overestimate may be due to differences of receptor sensitivity which were neglected in his investigation.

4. Any allowance for the light absorbed by haemoglobin may be neglected except in the violet region of the spectrum.

5. Several irregularities of the results remain when all the corrections have been applied. The relationship between these and the colour vision of the observers is discussed.

Once again I should like to thank Dr W. D. Wright for his kindness in allowing me the unrestricted use of the colorimeter at Imperial College, and also for acting as one of the observers. My thanks are also due to Miss P. W. Trezona and Messrs A. V. Evans and G. D. Pennycook, for allowing me the use of their abnormal colour vision, and to Dr W. S. Stiles for several sets of original figures and much useful discussion, and to Dr I. G. Wootton for the results of his determination of the absorption coefficient of haemoglobin, and to Dr Norman Ashton for allowing me access to injected specimens of the retinal blood capillaries, and to Dr H. J. A. Dartnall for much useful criticism and discussion. I am also grateful to the Medical Research Council for their continued support for visual research at Imperial College.

REFERENCES

Dartnall, H. J. A. & Goodeve, C. F. (1937). *Nature, Lond.*, **139**, 409.
Dartnall, H. J. A. & Thomson, L. C. (1949). *Nature, Lond.*, **164**, 876.
Donner, K. O. & Granit, R. (1949). *Acta Physiol. Scand.* **17**, 161.
Elderton, W. P. (1927). *Frequency-curves and Correlation*, 2nd ed. London: C. and E. Layton.
Fisher, R. A. & Yates, F. (1943). *Statistical Tables*, 2nd ed., p. 20. London: Oliver and Boyd Ltd.
Gibson, K. S. & Tyndall, E. P. T. (1923–4). *Sci. Pap. U.S. Bur. Stand.* **19**, 131.
Granit, R. (1947). *Sensory Mechanisms of the Retina.* London: Oxford University Press.
Hartridge, H. (1946). *Nature, Lond.*, **156**, 482.
Hartridge, H. (1947). *Philos. Trans.* B **232**, 644.
Hecht, S. (1937). *Physiol. Rev.* **17**, 239.
Hecht, S. (1949). *Doc. Ophthal.* **3**, 289.
Houstoun, R. A. (1932). *Colour Vision.* London: Longmans, Green and Co.
Karrer, P. and Jucker, E. (1948). *Carotinoide*, Band 3. Basel: Verlag Birkhäuser.
Ludvigh, E. & McCarthy, E. F. (1938). *Arch. Ophthal., N.Y.* **20**, 37.
Pitt, F. H. G. (1944). *Proc. Roy. Soc.* B, **132**, 101.
Pitt, F. H. G. & Wright, W. D. (1934). *Proc. Phys. Soc.* **46**, 459.
Stiles, W. S. (1939). *Proc. Roy. Soc.* B, **127**, 64.
Stiles, W. S. (1948). *Trans. Opt. Conv. Spectacle Makers Co.* p. 98.
Stiles, W. S. & Crawford, B. H. (1933). *Proc. Roy. Soc.* B, **113**, 496.
Thomson, L. C. (1946). *Nature, Lond.*, **157**, 805.
Thomson, L. C. (1949*a*). *J. Physiol.* **108**, 78.
Thomson, L. C. (1949*b*). *Proc. Phys. Soc.* B, **62**, 787.
Thomson, L. C. & Trezona, P. W. (1951). *J. Physiol.* In the Press.
Thomson, L. C. & Wright, W. D. (1947). *J. Physiol.* **105**, 316.
Wald, G. (1945). *Science*, **101**, 653.
Wald, G. (1949). *Doc. Ophthal.* **3**, 94.
Wolff, E. (1948). *The Anatomy of the Eye and Orbit*, 3rd ed, p. 112. London: H. K. Lewis.
Wright, W. D. (1946). *Researches on Normal and Defective Colour Vision.* London: Henry Kimpton.
Zscheile, F. P., White, J. W., Beadle, B. W. & Roach, J. R. (1942). *Plant Physiol.* **17**, 331.