

INTENSITY DISCRIMINATION OF THE CENTRAL FOVEA MEASURED WITH SMALL FIELDS

By L. C. THOMSON

From the Vision Research Unit, Medical Research Council, London

(Received 15 January 1948)

By means of a small test field, subtending 15' at the eye, some information on the shape of the energy-response curve for the fovea has been obtained and reported in a previous paper (Thomson, 1947). This curve records the relationship between the retinal response and the amount of light energy applied to the receptors. It was found that the slope of the curve was not the same for all wave-lengths; in fact, red energy had to be increased by a larger factor than had blue-green energy in order to achieve the same increase in the response. Thus the slope of the blue-green was much steeper than that of the red curve (Thomson, 1947, Fig. 9). It would seem that the ability to discriminate between one intensity and another slightly higher one must rest to some extent upon the slope of these curves. Suppose a just noticeable increase in the response was the same for every wave-length, then, since the slope of the red curves is relatively less steep than that for other wave-lengths, one might expect that a larger increment of energy would be necessary to elicit a just noticeable difference of brightness at red wave-lengths.

Thus an investigation, with the small field method, of the energy increment necessary to evoke a just noticeable difference of brightness at various wave-lengths might provide corroboration for the shape of the energy-response curves and possibly other data of interest about the behaviour of the fovea to increasing amounts of light energy. Actually the results have been expressed as the logarithm of the fraction, $\Delta I/I$, and not as the energy increment itself, ΔI .

Some experiments were also made with the small field displaced by 40' from the fixation point into the left visual field.

METHOD

The measurements were made with the Wright colorimeter at Imperial College (Wright, 1946), and the field size was identical with that used in a previous investigation (Thomson & Wright, 1947). Briefly it consisted of a small circular aperture which was divided horizontally into an upper test and lower comparison field, each semicircular and of approximately equal area. The wave-length and intensity of the light illuminating each half was variable. The field was seen upon a dark surround.

For the observations at 40' a small red fixation spot was introduced in an appropriate position and maintained at a brightness similar to that of the main field. Some observations were also made with a divided field arrangement as shown in the insert to Fig. 5. In these measurements the lower comparison field remained at the fixation point, and the upper test field only was displaced by the required amount into the left visual field. Each figure in this paper contains an insert showing the type of field used.

Procedure. The wave-length of the light illuminating each half of the field was made equal and a series of between 10 and 15 (for most wave-lengths) arbitrary intensity values were chosen for the lower field which would cover evenly the whole brightness range at that wave-length from near the threshold of vision to the maximum attainable in the colorimeter; a range of intensity for most wave-lengths of about $\times 10^4$ when a small field is used at the foveal centre. Then, having set the lower field to the lowest of these chosen values, the observer (L.C.T., right eye) made a pair of brightness matches between the two fields. The readings of the neutral wedge controlling the intensity of the upper field were recorded, and the upper field intensity was then set so that a just noticeable increase in brightness could be detected. A further record was made and the just noticeable brightness step repeated, so that for each setting of the lower field intensity four readings of the neutral wedge were available: two 'matches', from which the intensity of the lower field, I , could be calculated and two 'steps', which would yield $I + \Delta I$, where ΔI is the increase in I required to produce a just noticeable difference of brightness. The next higher arbitrary intensity value was then set in the lower field and the four recordings repeated. Each wave-length setting was completed without a break, and five was the usual number of runs for any wave-length, each performed at a different observing session. Four wave-length settings were sufficient for one session, and these four were completed before doing any others. Thus a whole family of 22 wave-length curves was covered in groups of four, each member of the group being chosen from a different part of the spectrum.

Calculation. From the average wedge readings for I and $I + \Delta I$ at each intensity value of the lower field the amount of energy from each half of the field, which passed through the exit pupil of the colorimeter (diameter 2 mm.), was calculated. ΔI was then determined by subtraction and the result expressed as $\log \Delta I/I$, which values are the ordinates in the diagrams of this paper. The abscissae in the diagrams are usually the logarithms of the intensity I expressed in 'threshold' units, i.e. the amount of energy required to reach the threshold of vision at any wave-length was considered as unit energy for that wave-length. For this purpose a new and more complete determination of the threshold energy values for L.C.T. was undertaken in September 1947.

Conversion of the results. The values of $\log I$ in threshold units may be converted to the logarithms of the amount of energy from each semicircular field, which passed the exit pupil of the colorimeter, by adding the log threshold energy (log erg/sec.) given for each wave-length in Table 1. The resulting values may be converted into equivalent foot-candles (as seen through a pupil of diameter 2 mm.) by subtracting the further logarithm of 8.143. To convert the log erg/sec. values to millilamberts (pupil diameter 2 mm.) subtract log 8.111.

TABLE 1. Energy (erg/sec.) required at each wave-length and for the two field positions to reach the threshold of vision

μ .	Centre	40'	μ .	Centre	40'
0.44	8.058	7.640	0.56	8.219	8.097
0.45	7.898	7.502	0.57	8.208	8.129
0.46	7.678	7.356	0.58	8.228	8.154
0.47	7.443	7.101	0.59	8.345	8.238
0.48	7.364	8.971	0.60	8.384	8.235
0.49	7.273	8.931	0.61	8.459	8.284
0.50	8.992	8.630	0.62	8.567	8.384
0.51	8.753	8.517	0.63	8.730	8.553
0.52	8.636	8.438	0.64	8.892	8.721
0.53	8.370	8.221	0.65	7.043	8.873
0.54	8.249	8.149	0.66	7.203	7.036
0.55	8.220	8.088			

Precision. At each of several I values the standard error of the mean of five estimates of $\Delta I/I$ has been calculated according to the formula $\sqrt{\{\Sigma (x - \bar{x})^2\}/n(n-1)}$, where x is any value of $\Delta I/I$, \bar{x} the mean of the five estimates, and n the number of the estimates (five in most cases). To do this the colorimeter readings were not averaged at once, but each was expressed in energy units and each $\Delta I/I$ worked out separately. The mean so obtained did not differ very greatly from that calculated by the usual method, and although the calculation in this paragraph is strictly the more correct procedure, the labour involved prohibited its use for all readings. The points at which errors have been calculated are shown in the figures by a vertical line indicating a range of ordinate values of $\pm \sigma_{\text{mean}}$. The errors in the abscissae are very small in comparison and have been omitted. By estimating the standard deviation of the mean from a sample of five, the estimate itself is bound to have a moderately large error of its own, and it should be borne in mind when looking at the figures that on some occasions an error line might be one-third longer than shown.

Criterion. The criterion of discrimination used in this investigation is the just noticeable difference in brightness, and during the measurements the ΔI required to elicit a just noticeable difference of brightness did not always remain the same under similar conditions. It appeared that the criterion would remain moderately constant for many weeks during an unbroken series of sessions, but that if a rest was taken and a further series started, the criterion might be somewhat different. It was the usual practice to leave the results of any series unexamined until it was complete. This step seemed to lead to a stable just noticeable difference within that series. Further, stability was much increased as soon as the novelty of the experiment had worn off, and towards the end, when the experiment had become automatic, the colorimeter could be set whilst thinking of other things and the stability of the just noticeable difference was then at its best. Fluctuations of the criterion did not at any time influence the size of $\Delta I/I$ by more than 15%.

Calibration of the colorimeter. The absolute brightness calibration of the colorimeter rests upon a comparison (using a $1^\circ 20'$ field) between the spectral light of 0.520μ . and the white light from a standard lamp, standardized at the National Physical Laboratory, using a method similar to that described in a previous paper (Thomson, 1947).

The calibration of the relative amounts of energy at each wave-length depends upon new measurements made as follows. A ribbon filament lamp was calibrated for colour temperature against a lamp of known colour temperature (2848°K), which had been standardized at the National Physical Laboratory. The light from this lamp was then refracted into a spectrum with a simple auxiliary spectroscope, and the light passing through the exit slit allowed to fall on the cathode of a multiplier photocell. The output from the photocell was measured with a Cambridge Unipivot galvanometer and the deflexions were recorded for each $10 \text{ m}\mu$. of the spectrum. The light passing the exit pupil of the Wright colorimeter was then allowed to illuminate the cathode and the neutral wedge controlling the intensity so adjusted that, for any wave-length, the galvanometer deflexion was similar to that obtained at the same wave-length in the auxiliary spectroscope. The readings of the neutral wedge were recorded. Thus, after the relative energy values at each wave-length for the calibrated lamp had been weighted by a correction for the exit slit width of the auxiliary spectroscope, the amount of energy corresponding to a neutral wedge reading was known at each wave-length. Losses of light in the glass parts of the auxiliary spectroscope were neglected. Since the final calibration between wave-lengths 0.500 and 0.660μ . agreed to within 12% with the original calibration performed with a thermojunction, and since this agreement was obtained in spite of the fact that a different colorimeter lamp was in use, the calibration as a whole was considered satisfactory.

RESULTS

Central area. The results for the centre of the central fovea are shown in Fig. 1, and the field arrangement was as shown in the insert. Each set of points corresponds to a different wave-length setting, which is shown in μ . on the face of the figure, and since each, if plotted on the same ordinate scale, overlies the next, the scale of $\log \Delta I/I$ is correct for wave-length 0.660μ . only. Each scale

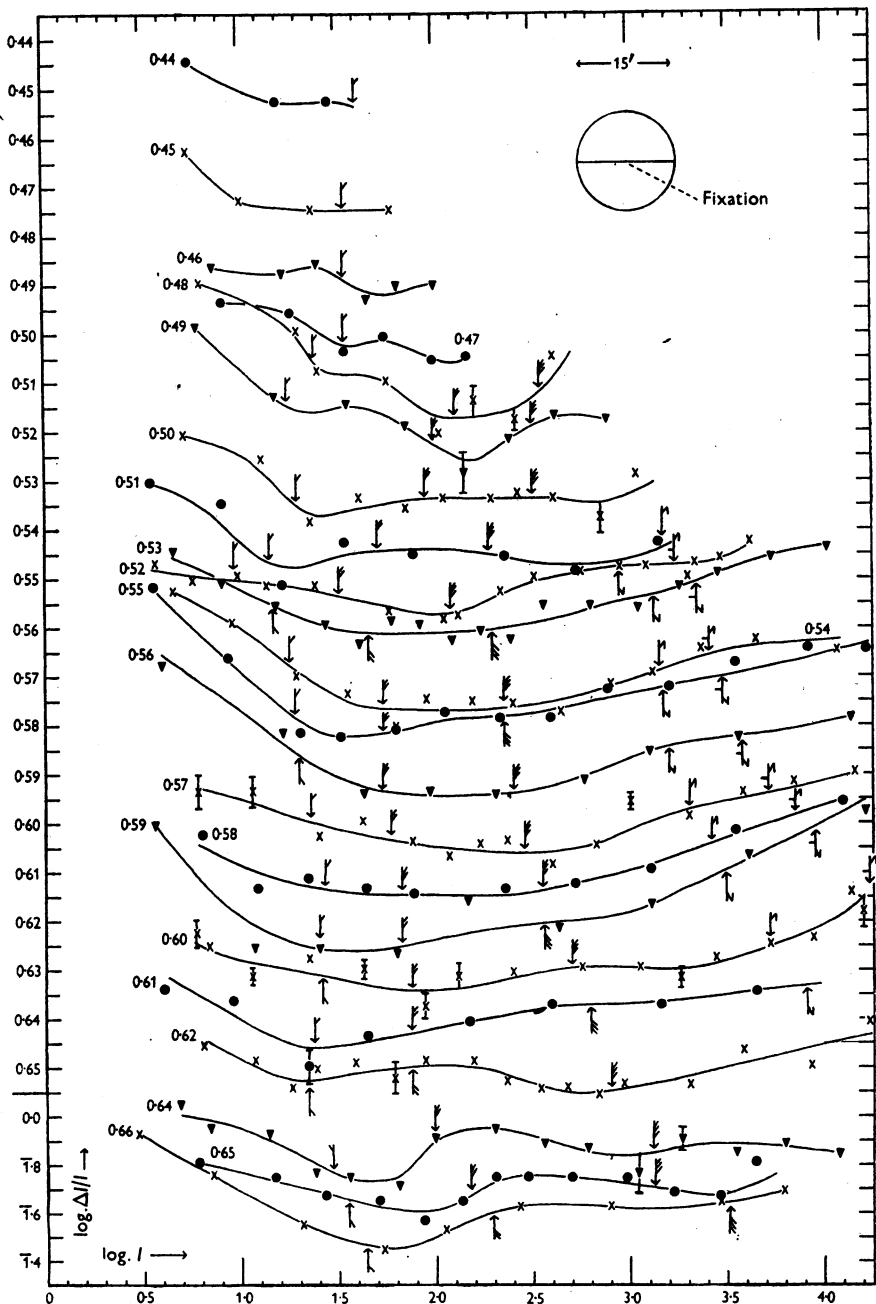


Fig. 1. Intensity discrimination of the centre of the central fovea for twenty-two wave-length settings. Insert shows the type of field used. Ordinate scale correct for wave-length 0.660μ . only; each other scale displaced upwards from the next by $0.2 \log$ unit, the value 0.0 for any scale being shown by the value of the wave-length in μ . on the ordinate. Curves are freehand. The arrows indicate equi-brightness levels. \downarrow level 1, \downarrow level 2, \downarrow level 3, \downarrow level 4, \downarrow level 5.

has been displaced upwards from its neighbour by 0.2 log unit and the value 0.0 for any wave-length is indicated by writing the value of that wave-length in μ . upon the ordinate. The curves drawn through the points are freehand to be a good fit to the data and do not represent any mathematical function.

Wave-lengths 0.450, 0.510, 0.560, 0.580, 0.590 and 0.610 μ . were all performed during the first few weeks of 1947, and, when first plotted on the same ordinate scale, showed a general increase in the size of $\Delta I/I$ upon that obtained at other wave-lengths, which were all completed before Christmas, 1946; an increase which was most probably due to an altered criterion. Hence the value of $I + \Delta I$ in these six curves has been lowered by 7.2% throughout in an attempt to allow for this change. A check on the validity of this adjustment will be mentioned below. From a previous investigation (Thomson, 1947) the amount of energy at each wave-length required to stimulate a sensation of equal brightness was known for this observer and for five brightness levels under similar observing conditions. The five levels have been marked on Fig. 1 with distinctive arrows. The curves divide into a low-intensity part, in which the discrimination is worsening as the intensity is lowered ($\Delta I/I$ increasing); a middle part in which $\Delta I/I$ is approximately constant; and an upper part, in which discrimination is again falling off as the intensity rises and the field becomes glaring in brightness. The degree to which discrimination falls off in the lower part varies with wave-length, and this is strikingly shown at wave-lengths 0.480, 0.470 μ . and in the region of 0.520 μ . At 0.480 μ . the decrease is so great that the curve for this wave-length has crossed that for 0.470 μ . even though they are as a whole displaced from each other by 0.2 log unit. A similar, but not so marked, effect is seen in the high-intensity region between wave-lengths 0.570 and 0.590 μ .

Another feature is the large wave seen in the curves for red wave-lengths near brightness level 2. This wave is due to a disproportionate increase in the size of ΔI at this brightness level, and since it is at just this level that the red energy-response curves reported previously (Thomson, 1947, Fig. 9) diverge from their fellows for other wave-lengths, it seems that the energy-response curves do influence intensity discrimination to some extent. However, the disproportionate increase in ΔI is not maintained at higher brightnesses as one would expect from an examination of the energy-response curves. In addition, the red wave does not appear in any curve for wave-lengths shorter than 0.620 μ . even though the energy-response curves for several wave-lengths shorter than this show a decrease in slope, so that agreement between the two investigations is by no means perfect.

Several wave-lengths show a small depression near brightness level 1. This is well shown between wave-lengths 0.460 and 0.510 μ . and again between 0.610 and 0.660 μ . Experimental error accounts for neither this depression nor

the 'red wave', already mentioned. The high-intensity portion of the curve seems to begin either at or slightly above level 3.

Equi-brightness section. It is possible graphically to determine from the smooth freehand curves the value of $\log \Delta I/I$ for each wave-length at each of

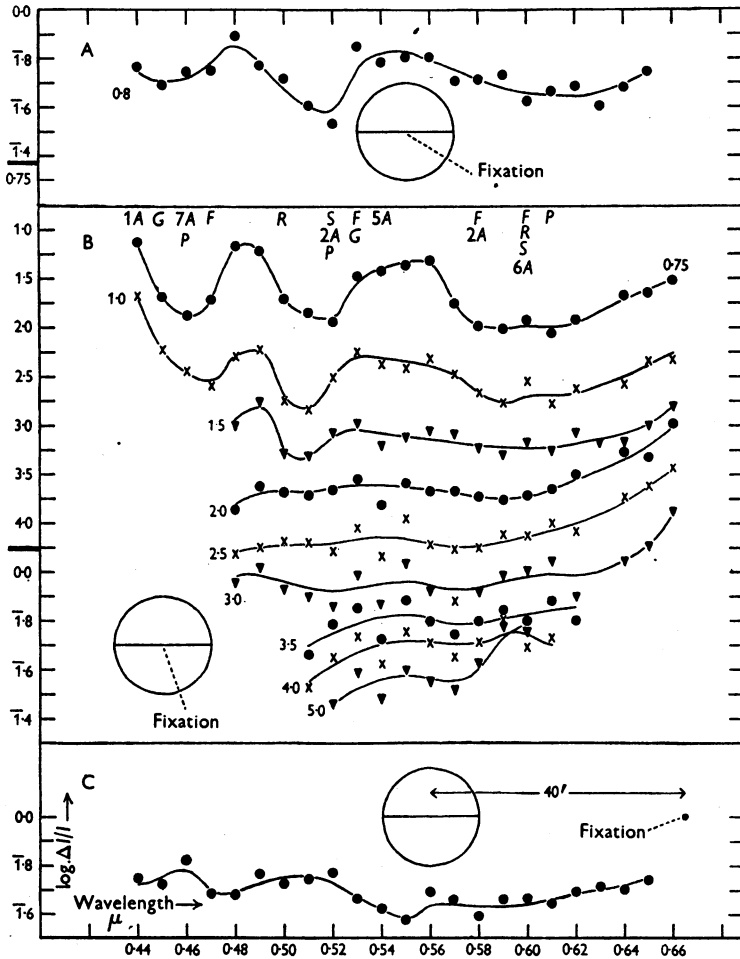


Fig. 2. Intensity discrimination of the fovea shown as a function of wave-length at equal brightness. Ordinate scale displaced as in Fig. 1. The letters in section B indicate the positions in the spectrum of maximum modulator activity as found by Granit. *F*, frog; *G*, guinea-pig; *R*, rat; *S*, snake; *2A*, two maxima found by adaptation; *P*, maximum found by polarization.

the five brightness levels, and in addition at other arbitrary levels: 0.75 between the threshold and level 1; half-way between levels 1 and 2, levels 2 and 3 and levels 3 and 4. The values of $\log \Delta I/I$ so obtained can then be plotted on the ordinate against wave-lengths as abscissae, and the result is shown in Fig. 2 B.

Here again the ordinate scale has been displaced and is correct for level 5 only. Each other curve is displaced upwards by 0.2 log unit.

The variable slope of the lower parts of the Fig. 1 curves noted earlier has produced at low brightness levels a markedly humped curve with three minima; one in the blue, one in the blue-green and another broader one covering yellow, orange and some red wave-lengths. Since the vertical position of a point on these curves depends upon ΔI , and since all the twenty-two curves were not obtained in the same series of experiments, it might be argued that these minima were due in some way to a variable criterion. In order to meet this criticism a value for I for each wave-length was calculated so that it would have a brightness approximately equal to 0.60 of level 1. Each value was then presented to the observer in random order (so that errors of criterion would be similar for all) and $\log \Delta I/I$ obtained in the usual way. The results of five runs are shown in Fig. 2A. At these low brightnesses the observer can only identify a wave-length by its colour in the broadest terms, i.e. reddish, greenish or bluish, and thus identification of a wave-length by its colour does not seriously interfere with the randomization. The points in Fig. 2A are, of course, subject to the full experimental error and were not obtained from smoothed curves. Bearing these facts in mind, the agreement between A and B in Fig. 2 is satisfactory, and thus alteration of the criterion is unlikely to have caused the minima in the data.

At high brightness levels a falling off in discrimination is seen in the region of wave-length 0.590 μ .

40' area. A few wave-length settings were repeated with the field displaced by 40' into the left visual field and the results are shown in Fig. 3. Here the worsening of discrimination at low brightness can again be seen, but unfortunately the lowest chosen arbitrary value was in most cases not as near the threshold as it might have been. The red wave in the 0.650 μ . curve is well shown, although it appears in these measurements to occur at a lower brightness level than in those for the centre. Wave-lengths 0.440, 0.480, 0.560 and 0.650 μ . are based upon three runs only, and this may partly account for the unusually large error given in the 0.560 μ . series. This error is quite unusual, and was, in fact, the largest of those calculated. For the middle spectral region a very marked decrease of discrimination occurred at high intensities. At the highest point on the 0.560 μ . curve, for instance, ΔI must be some 2.5 times the intensity I for a just noticeable difference to be seen. Brightness difference in its ordinary sense was impossible here, large movements of the intensity control appearing to have little or no effect upon the sensation of brightness.

To perform the measurements a different criterion was used. As the intensity control is operated, the apparent size of the small field changes, being larger for higher and smaller for lower intensities. Thus the two 'matches' were really size matches between the two halves of the field and the two 'steps', a just

noticeable difference of size. The apparent brightness of the upper field remained amazingly constant in spite of marked size fluctuation, which was, of course, associated with big intensity fluctuation. It seems that at these levels of brightness the receptors have reached a maximum in their brightness response. This effect was absent at blue, violet and red wave-lengths, but this may have been due to limitations in the energy delivery of the colorimeter.

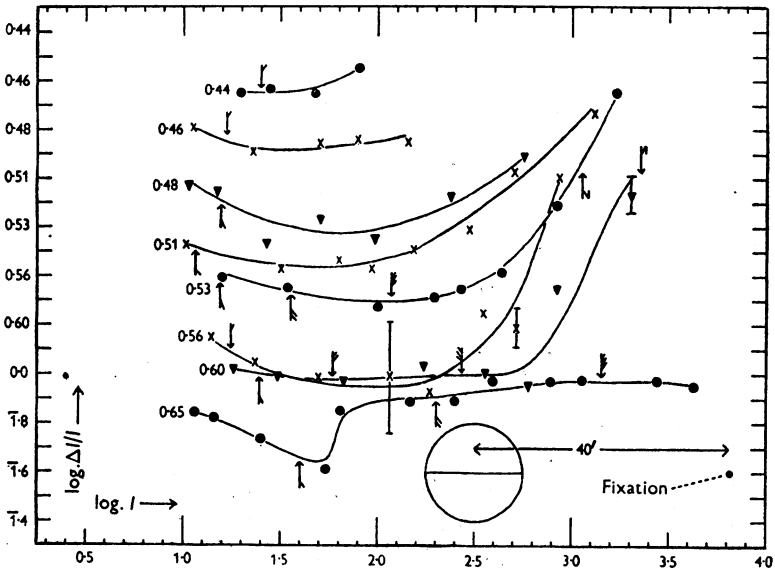


Fig. 3. Intensity discrimination of the fovea at a point displaced by 40' into the left visual field. Ordinate scale displaced as in Fig. 1.

Discrimination is as a whole poorer here than in the central position. The lower portions of the curves have been investigated more thoroughly and the results are shown in Fig. 4. In order to eliminate differences of criterion the wave-length settings were randomized throughout, and it is apparent that the errors are smaller than in previous series. The figure shows a decided wave in the curves for wave-lengths 0.520–0.560 μ ., but is otherwise uninteresting. The equi-brightness section at level 1, which is shown in Fig. 2C, is also disappointing.

Divided field arrangement. Some measurements have been made with a divided field arrangement as shown in the insert to Fig. 5. Two wave-length settings only are given. Comparing these results with those in Fig. 3, the presence of the gap between the matching fields at 40' seems to decrease the power of discrimination still further at most brightness levels, but it is usual to find an improvement towards the lowest intensities. This may be seen in the

20' curve for wave-length $0.530\mu.$, but was more striking at other green wavelengths. The red wave and the marked decrease in discrimination at high brightness are again well shown.

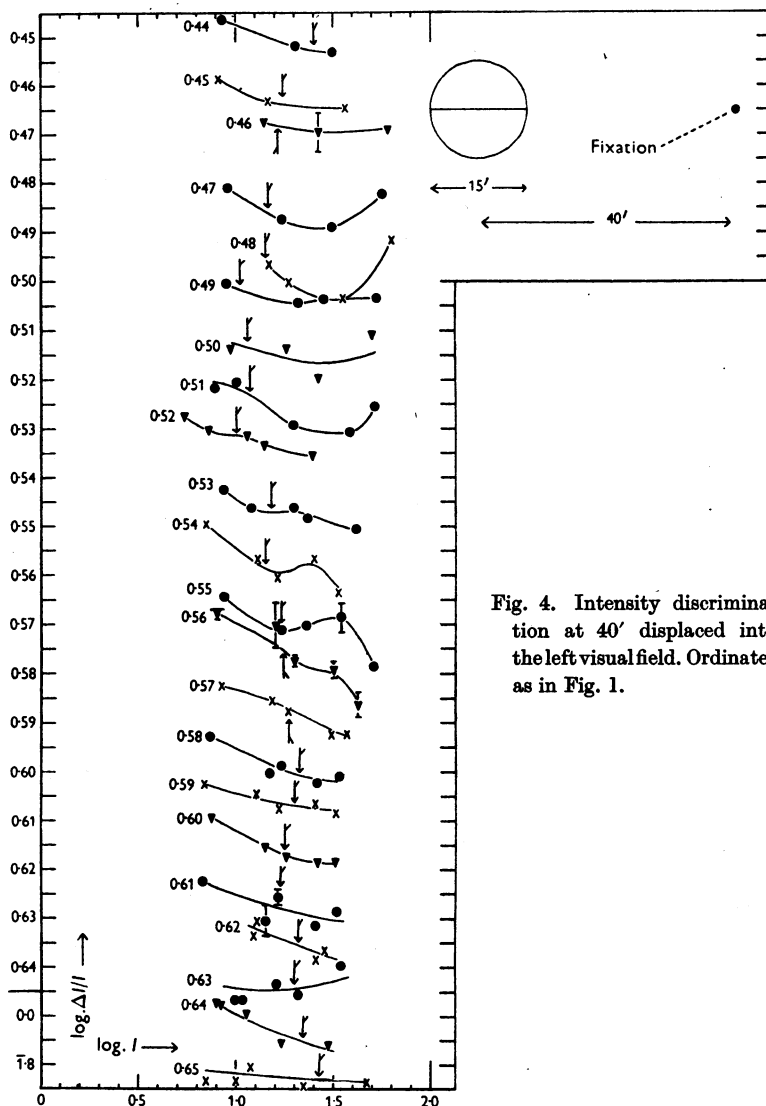


Fig. 4. Intensity discrimination at 40' displaced into the left visual field. Ordinates as in Fig. 1.

Further phenomena. A careful study of the data in Fig. 1 has led to the tentative suggestion that the curves may show certain other features. If the smoothed $0.600\mu.$ curve is examined, it is seen to pass outside the error range at three points and to be only just inside this range at three more. Since this range is the standard error of the mean, it is statistically somewhat unlikely

that the smooth curve really fits the points. In addition, one point at wavelength 0.570μ . between levels 3 and 4 is well off the smooth curve. The experimental error has also been much stretched to obtain a smooth 0.480μ . curve at high brightness, and there is some indication at several wave-lengths (0.500 , 0.510 , 0.540 , 0.550 , 0.570 , 0.600 , 0.620 and 0.650μ .) that there is a small dip between brightness levels 3 and 4.

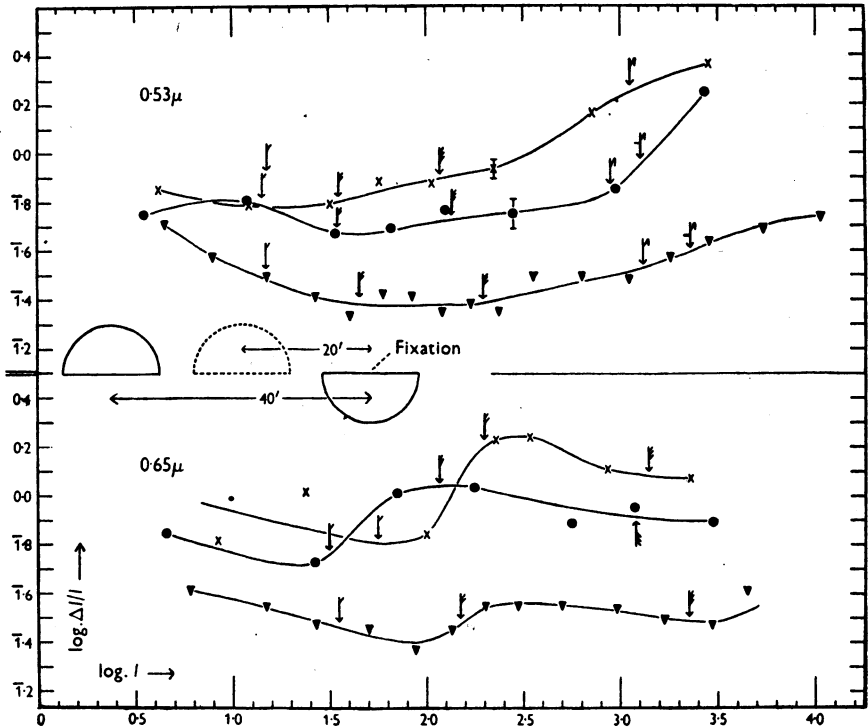


Fig. 5. Intensity discrimination with a divided field arrangement at wave-lengths 0.650 and 0.530μ . ▼—▼ central; ●—● $20'$; x—x $40'$.

In an attempt to elucidate these features a very thorough investigation of wave-length 0.600μ . was undertaken in December 1947. The whole range of brightness was covered by four runs of 15 points each, so that no two chosen values of the lower field were alike. Each run of 15 points was then performed in the usual way, so that there was no change in the observing conditions. Runs were taken in random order, and the results of the whole series, comprising upwards of 1200 settings of the colorimeter, are plotted with distinctive symbols in Fig. 6 A. A smooth curve is shown as a full line and a more complicated function as a dotted one. The question at once arises as to whether this curved function is the result of experimental error or not. The points composing one only of the four runs can scarcely provide an answer, because

the arbitrary choice of the position of the points will sometimes prevent a run from showing all the features. When Fig. 6 A is examined as a whole, however, it does appear to support the curved function better than the smooth. It is the arbitrary choice of points which may account for the somewhat sporadic appearance of the small dip between levels 3 and 4 in Fig. 1. Although the effect is not striking, Fig. 6 A goes some way to showing that the intensity discrimination function in small fields is not a smooth one.

Some corroboration for the curved function has been found in earlier readings. Two series, each of five runs, which were obtained more than a year and a quarter previously are shown in Fig. 6 B. Whilst the two functions have been reproduced without alteration in shape, they have been displaced downwards

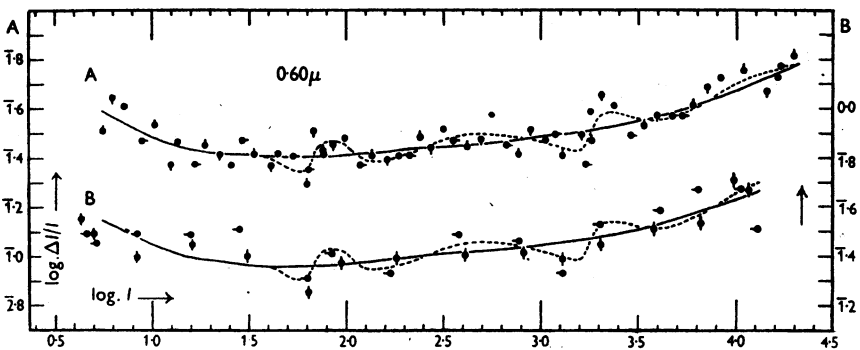


Fig. 6. A thorough investigation of the intensity discrimination of a single wave-length, 0.600μ .
 •, ▲, ■, ♦ December 1947; - July 1946; † October 1946.

by about 12%. In view of a probable overall change in criterion this is a very small shift. In addition, the points of Fig. 6 B appear to have been uniformly lowered in I value, when they are compared with those in Fig. 1. This is due to the use of a different threshold value in Fig. 6 B. The early threshold values as already published (Thomson, 1947) were incomplete, and new values, obtained in September 1947, were used throughout Fig. 1 in the interests of consistency, but in Fig. 6 B the old value is used because it is strictly the more appropriate to these two series given. The agreement over the centre section between these two series and the function obtained from the more recent four runs seems to the author to be too close to be merely due to experimental error. However, agreement is not so good at low intensities, and the curved function is therefore reported as tentative only.

DISCUSSION

Adaptation level of the eye. There are several references in the literature to the need for the eye to be adapted to the intensity I before the discrimination measurements are made. It is contended that if this is done,

the discrimination will then continue to improve up to the highest brightness attainable, and that the worsening of discrimination shown in this paper at high brightness is fallacious and is due to inadequate adaptation to the brightness level. However, an investigation in which the adaptation of the eye does not correspond to the brightness of the test patch is not without interest, and in the present experiments the general adaptation of the fovea is probably not far removed from the dark-adapted state even when the highest test field brightnesses are being measured. The reason for this is that a glance technique was used, so that the adapting power of the small test field itself was minimized. The part of the total observing time during which the observer was actually looking at the field was only about 20% of the whole, and this 20% was not all consecutive. Of course the high brightness test fields must have some adaptation effect, but it was felt that the departure from the dark-adapted state was not large. Thus the breakdown of brightness discrimination, noted for green wave-lengths in the 40' position, indicates a maximum receptor response, when, with the foveal mechanisms nearly dark adapted, a high intensity of stimulation is suddenly presented over a small area.

In practice the onset of a profound state of dark adaptation made the observations difficult. Let us suppose a completely dark visual field was maintained between observations. The retinal lights gradually increased in spite of making further measurements until the clarity of the field was impaired. If, on the other hand, the eyes were directed between observations towards the black wall of the room which was illuminated by stray light from the colorimeter, retinal lights were controlled and observing was much easier. Thus dark adaptation was not complete, but nearly so in these experiments.

Equi-brightness section 0.75. By an electrophysiological method Granit (1947) divides the responses of single-fibre optic nerve preparations into dominator and modulator elements. The dominators have wide spectral sensitivity curves and respond to some extent to most visible wave-lengths. The modulators, on the other hand, are more selective in their response and confine their maximum activity to three main spectral regions.

It is interesting to try to correlate the spectral positions of the minima in the 0.75 equi-brightness section with the maxima of modulator activity found by Granit. The maxima obtained by direct isolation with the micro-electrode technique in the frog were 0.470, 0.530, 0.580 and 0.600 μ .; from the guinea-pig, 0.450 and 0.530 μ .; from the rat, 0.500 and 0.600 μ .; and from the snake, a double-peaked curve with one maximum at 0.600 μ . and the other at 0.520 μ . The spectral positions of these maxima are indicated in Fig. 2 by distinctive letters. More recently, Granit has developed a method in which the micro-electrode technique was combined with selective adaptation of the receptors to coloured light. Modulator maxima were again found when this method was applied to the cat. Of eight curves deduced by this method, two had maxima

at 0.580μ . and the rest at 0.600μ . Of seven further curves, five had maxima at 0.540μ . and two at 0.520μ . In the blue, seven out of eight curves had maxima at 0.460μ . and only one at 0.440μ .

In a recent paper Granit (1948) has used a further new method of investigation. The micro-electrode technique was combined with polarization of the eye by the passing of a current across the optic cup from side to side. Cats were again the experimental animals, and by means of a statistical method, modulator activity has again been demonstrated. The maxima are at wave-lengths 0.460 , 0.520 and 0.610μ . From Fig. 2 it can be seen that the correlation between these maxima and the minima found in the present experiments is, apart from wave-lengths 0.540 and 0.530μ ., remarkably close, and it suggests that the minima are in some way the result of modulator activity.

Why are the discrimination minima not present at higher brightness levels? Granit regards the dominator activity, which, owing to its broad spectral sensitivity response, could be of little use as a means of hue discrimination, as a brightness response, and he reminds us that colour, which may be signalled to the brain by red, green and blue modulators, is to some extent independent of brightness. Both modulators and dominators would, however, contribute to the brightness sensation, but at normal levels this sensation would mainly depend upon dominator activity. Thus intensity discrimination should also depend at these levels upon the dominator response and the value of $\log \Delta I/I$ be much the same throughout the spectrum. As the intensity is lowered and the dominator becomes less active, the modulator response would contribute more to the total brightness sensation, and intensity discrimination should therefore tend to become a function of modulator activity and might be expected to show minima at those wave-lengths at which the modulators are most active.

Thus the fact that the discrimination minima do not persist as the brightness is raised can be made to fit into the dominator-modulator idea.

SUMMARY

1. The intensity discrimination of two areas of the foveal retina at twenty-two different wave-lengths has been investigated with a small field ($15'$).

2. The worsening of discrimination seen at low intensity varies with wave-length, discrimination remaining moderately good at spectral regions in which Granit has found modulator activity.

3. When the field is displaced $40'$ into the left visual field, the receptors reach a maximum response for the observing conditions at high brightness, and the relationship between this and the adaptation of the eye is discussed.

Once again my thanks are due to Dr W. D. Wright for his hospitality at Imperial College and also to Miss Gillian Frowde, who has recorded the observations. My thanks are also due to the Medical Research Council for their continued support for visual research at Imperial College and also to Dr H. O. Hartley for his statistical opinion.

REFERENCES

- Granit, R. (1947). *Sensory Mechanisms of the Retina*. London: Oxford University Press.
Granit, R. (1948). *J. Neurophysiol.* (in the Press).
Thomson, L. C. (1947). *J. Physiol.* **106**, 368.
Thomson, L. C. & Wright, W. D. (1947). *J. Physiol.* **105**, 316.
Wright, W. D. (1946). *Researches on Normal and Defective Colour Vision*. London: Kimpton.