THE RELATIONSHIP OF VISUAL THRESHOLD TO RETINAL POSITION AND AREA

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The absolute visual threshold of a field on zero background covering a given retinal area in the fully dark-adapted eye depends on at least three factors: the proportion of the incident light absorbed by the photosensitive pigment, the summation properties of the retinal area concerned, and the number of acting quanta necessary to evoke a visual response. This number may, of course, depend on the distribution, in space and time, of the quanta. The relationship between the areas and the thresholds of fields centred at a given retinal position has often been used as the basis for theories about the number of acting quanta required, but such deductions depend on assumptions—usually of uniformity of the retinal areas concerned—about the first two points. The present experiments were undertaken to test the validity of such assumptions, and to investigate the possibility of formulating a plausible theory of visual performance in threshold and simple acuity experiments on the basis of 'visual units', groups of receptors acting together. The experiments on acuity are described elsewhere (Hallett, 1961).

METHODS

Apparatus. Figure 1 is a diagram of the apparatus. The light source, *B*, is a 12 V, 48 W single-filament car headlamp bulb, under-run at 11·20 V from a 140 A-hr car battery. A wide-aperture condenser, *C*, forms a small image of the filament in the plane of a pendulum shutter, *S*, before illuminating an opal glass, *O* (diameter 25 mm). The shutter gives exposures of 2·6 msec. A green filter, *F*, Ilford 604 with maximum transmission at about 520 mμ, and neutral wedges, *W*, are mounted in front of the opal. A battery of large lenses, *L*, about 30 cm in diameter, collecting over a wide angle, forms an image of the opal glass in the plane of an artificial pupil, *P*, 2 mm in diameter, in front of the eye, *E*. The image of the opal source is considerably larger than the artificial pupil. The front lens of the battery is then seen in Maxwellian view as a uniform field 46° in diameter. Metal test objects, diaphragms of known size, can be placed in front of this large field (in the plane *XY*) to give smaller test fields of accurately known area and position. Near the centre of the field in the plane of the test objects, a length of 1 cm subtends 2° at the eye.

The subject's head is fixed by biting on his dental impression in dentist's wax. He controls the shutter himself and can release it at a chosen moment. An assistant records his response

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to each flash ('seen' or 'not seen'), varies the intensity with neutral wedges, and changes the test object.

A small red fixation point can be placed at any angle up to 25° with the axis of the apparatus; eccentricities up to 35° can be achieved by displacing the fields 10° from the axis of the apparatus.

Calibrations. The spectral transmission curve of the filter Ilford 604 was measured by the National Physical Laboratory. The transmission of the neutral wedges was measured, for the light transmitted by the filter, by comparison with sector disks. The light flux transmitted by the colour filter through the artificial pupil, with the wedges out, was measured by comparison with a standard source (calibrated by the National Physical Laboratory) both visually with a Macbeth type of illuminometer, and photo-electrically with a Spectra Spot Meter.
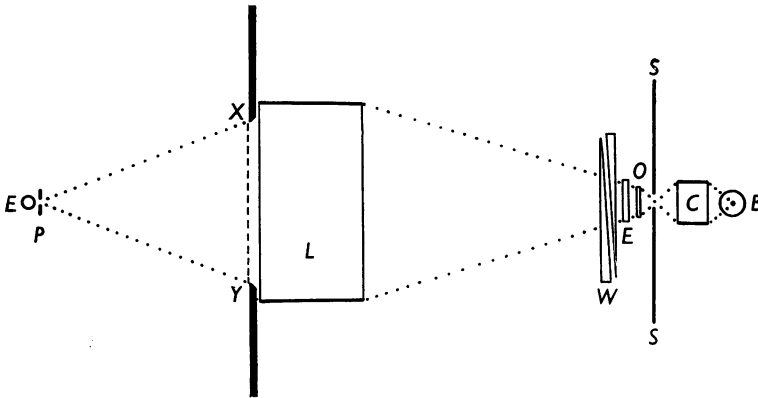

Fig. 1. Diagrammatic plan of the apparatus. An image of the single vertical filament of the electric bulb, *B*, is formed by the condenser, *C*, in the plane of the pendulum shutter, *SS*. The light then illuminates the opal glass disk, *O*. An (imperfect) image of the opal disk, *O*, is formed in the plane of the artificial pupil, *P*, by the large lenses, *L*. The spectral composition and intensity of the light are controlled by the colour filter, *F*, and the 'neutral' wedges, *W*. The eye, *E*, of the subject sees the lenses, *L*, in Maxwellian view. Test objects are placed in the plane *XY* in front of *L*. The fixation point is not shown on the diagram. Light screening is also not represented.

Experimental procedure. Each field was presented at a series of intensities, equally spaced on the logarithmic scale, ranging from levels at which the flash was never seen to levels at which it was always seen. The intensities were arranged in random order and usually covered a range of about 1 log.unit. In each series of about 10 exposures a 'blank' was included, in which, unknown to the subject, the light was completely cut off.

The threshold was determined by the method described by Hartline & McDonald (1957). The intensity step used was usually 0·1 log.unit. Standard errors were estimated from separate determinations of the frequency-of-seeing curve. Determinations in which the blank was reported seen were ignored. This occurred twice in about 1000 presentations of the blank. All experiments were carried out after the subject had been dark-adapted in total darkness for at least half an hour.

RESULTS

Thresholds for 10′ *field near* 20° *nasal*

Thresholds were measured for each of 117 positions (subject F.C.R.) in a square of side 6° centred at 20° nasal to the fixation point on the horizontal meridian, as shown in Fig. 2. In each experiment thresholds were measured in 13 positions along a horizontal line. The positions ranged from 17° to 23° eccentricity in the nasal field by $\frac{1}{2}$° steps. Nine different horizontal lines were used, namely the meridian through the fixation point and positions 1°, 2°, $2\frac{1}{2}$° and 3° above and below it. Two experiments, on different days, were done for each line. In one of these the thresholds were measured in order from 17° to 23°, in the other in the reverse order.
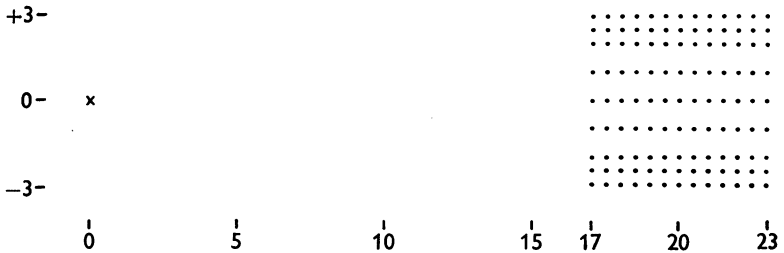
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        |           |           |         |   |     |     |
        0           5          10        15  17    20    23
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Fig. 2. Diagram of the 117 positions for which thresholds were measured around 20° nasal field for subject F.C.R. Thirteen positions at $\frac{1}{2}$° intervals from 17° to 23° eccentricity were used for each of 9 horizontal lines, the horizontal meridian and positions 1°, 2°, $2\frac{1}{2}$° and 3° above and below it. The fixation point is marked by ×.

Analysis of the results gives the following conclusions:

(1) The standard error of a single measurement was ± 0·12 log. units.

(2) No marked irregularities, such as small areas of very low sensitivity, were detected.

(3) Variations from day to day were highly significant.

(4) Differences between the horizontal lines were not significant. This comparison was not very accurate, since it involved differences between days; nevertheless, there was no indication of any systematic differences between lines.

(5) Differences between positions on the lines were highly significant, and indicated a roughly linear rise in log threshold as the position moved from 17° to 23° from the fixation point. The mean values are given in Table 1.

TABLE 1. Thresholds (means of 18 observations) for different eccentricities

Eccentricity in nasal field (degrees)	Wedge density	Threshold energy (quanta)
17	1·78	84
17½	1·77	86
18	1·70	102
18½	1·71	99
19	1·70	102
19½	1·71	99
20	1·71	99
20½	1·73	95
21	1·72	97
21½	1·68	106
22	1·64	117
22½	1·64	117
23	1·63	119
Standard error of each value	± 0·03	

Thresholds for 10' field on horizontal meridian

Thresholds for the 10' field (subject F.C.R.) were measured on the horizontal meridian at positions from 2° to 23° eccentricity in the nasal field, by ½° steps. Each threshold is the mean of two observations at least. The range from 2° to 23° was covered in five overlapping experiments, so that allowance could be made for any considerable day-to-day variations.

The results are shown in Fig. 3. The threshold falls steadily up to 9° eccentricity. From 9° to 15° it is fairly constant. From 15° to 23° there is a slow rise in threshold; this is somewhat masked by random variations, and does not show up so clearly as in the first experiment. The standard error of each value is about ± 0·09 log. units.

Thresholds for fields of different sizes

Thresholds were measured for fields of 10', 1° and $4\sqrt{2}°$ diameter (subject F.C.R.) at eccentricities 5°, 10°, 15°, 20°, 25°, and 30° in the nasal field on the horizontal meridian. Each field size was used in four experiments, two covering the range 5°–20° eccentricity and two 10°–30°. The results are shown in Fig. 4. The standard error of each value is ± 0·09 log. units.

For the 10' field the maximum sensitivity is at 15° eccentricity, thresholds at 10° and 20° both being higher. The difference is just significant ($P < 0.05$) for 10°–15°, but not quite significant for 15°–20°; the latter difference, however, is confirmed by the first experiment. For the 1° field thresholds at 15° and 20° are nearly equal. At 10° the threshold is just significantly higher ($P < 0.05$). For the $4\sqrt{2}°$ field the threshold at 20° is rather lower than that at 15° (not significant), while the threshold at 10° is definitely higher ($P < 0.01$).
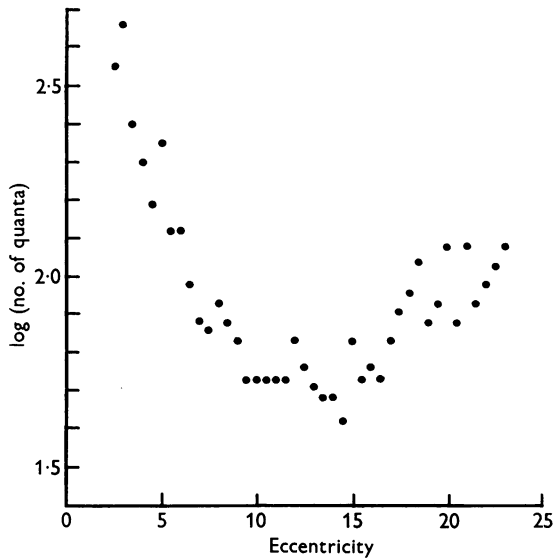
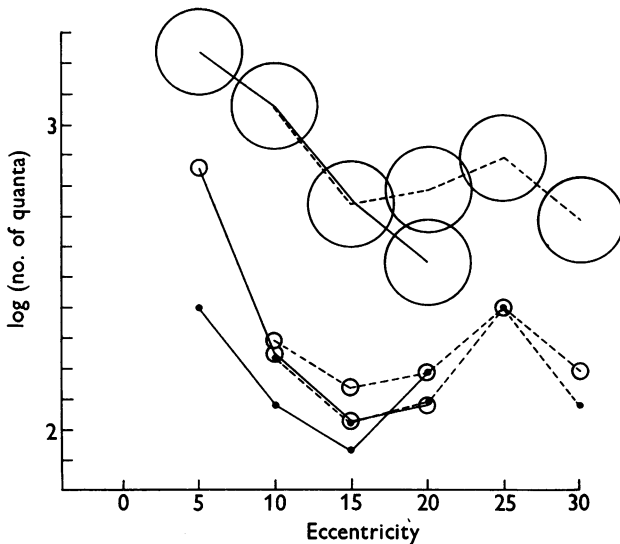Fig. 3. Thresholds for 10′ field (subject F.C.R.) at different eccentricities along the horizontal meridian in the nasal field.

Fig. 4. Thresholds for fields of diameters 10′, 1° and 4√2° at eccentricities between 5° and 30° on the horizontal meridian of the nasal field. The symbols show approximately the sizes of the 1° and 4√2° fields. Each point is the mean of determinations on 2 days, and has standard error ±0·09. The thresholds for 5°, 10°, 15° and 20° (continuous line) were measured on each of 2 days; those for 10°, 15°, 20°, 25° and 30° (dotted line) on each of 2 different days.

The relationship between threshold and area for five retinal positions

Thresholds were measured (subject P. E. H.) for concentric circular fields of different areas in five different retinal positions. The results are shown in Fig. 5. The standard error of each point is $\pm 0 \cdot 07$ log. units.

Both scales are logarithmic. Log *diameter* is plotted at twice the magnification of the ordinate scale, so that log *area* (upper scale at the top of the figure), is the same as the ordinate scale. The initial horizontal part of each plot represents the area of complete summation. No summation (threshold *intensity* independent of area) would be represented
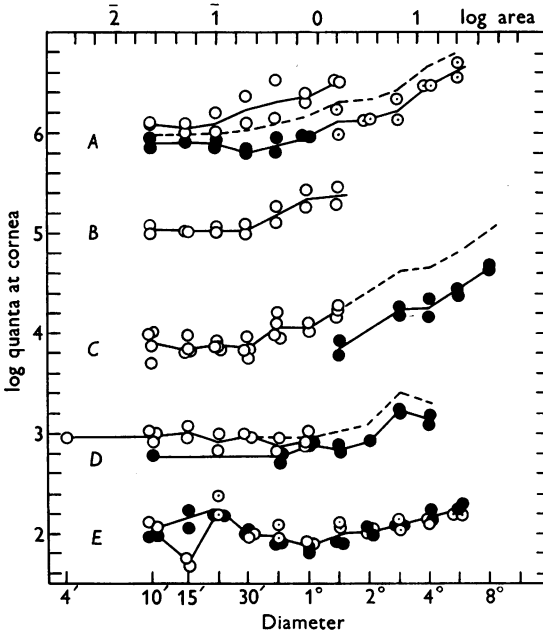

Fig. 5. Thresholds (subject P.E.H.) for concentric circular fields of different diameters in different retinal positions. The intensity and diameter scales are both logarithmic. The position of a curve depends on experimental accuracy (s.e. $\pm 0 \cdot 07$ for a single point) and on day-to-day variations (as much as $0 \cdot 3$ log. unit). The average position of a curve can be determined only by very many experiments. Continuous lines are drawn through the average of days, given the same symbol, which by chance reasonably coincide. The broken lines represent the *shapes* of the curves, not their mean positions, and are obtained by displacing one set of comparable points (continuous line) to agree with another set, or by averaging. The top four curves have been displaced from their true position by whole numbers of log. units. *A*, 5° nasal field displaced upwards by 4 log. energy units; 6 days. *B*, 7° temporal field displaced upwards by 3 log. units; 2 days. *C*, 7° nasal field displaced upwards by 2 log. energy units; 6 days. *D*, 20° nasal field displaced upwards by 1 log. unit; 4 days. *E*, 35° nasal field—correct locus; 8 days. Field diameters: 4′, 10′, 15′, 21′, 30′, 42′, 1°, 1·41°, 2°, 2·82°, 4°, 5·46°, 8°.

by a line of slope 1. Piper's law, energy proportional to the square root of area, corresponds to the line of slope $\frac{1}{2}$.

In curves, A, B, C (eccentricities 5°, 7° nasal, 7° temporal field), summation is complete up to about 30′ diameter. For D (eccentricity 20° nasal field) summation is complete to 1° diameter. For E (eccentricity 35° nasal field) some of the values are anomalous, but there appears to be complete summation up to 2° diameter.

<div align="center">DISCUSSION</div>

The area–threshold relationship has been used as evidence for the two-quanta theory of visual thresholds (Bouman & van der Velden, 1947; Baumgardt, 1948). The argument depends on two things: first, that the retinal area considered is uniform, or effectively uniform; secondly, that Piper's law (threshold energy proportional to the square root of area) holds over a considerable range of areas. The present results cast doubt on both these points.

Baumgardt (1959) has recently attempted to interpret the observed area–threshold relationship taking into account the non-uniformity of the retinal area concerned. The areas covered by the test field were corrected for retinal sensitivity, using the results for a 1° field obtained on different subjects by Pirenne & Marriott (1954). The author concluded that Piper's law was valid for the corrected, as well as the uncorrected, results. The calculation does not allow, however, for differences in size of summation area over the retinal area considered.

Non-uniformity of the retinal area can arise in several ways.

First, there may be local fluctuations in the sensitivity to small fields; for example, areas of high threshold possibly associated with blood vessels. These have been observed in other subjects (Stiles & Crawford, 1937). The experiments on F.C.R. gave no indication of any such effect. Fundus photographs of this subject showed that the temporal retinal field investigated had only small blood vessels, and the thresholds measured with a 10′ diameter field showed great dependence on distance from the fovea, but no marked local variations. The largest blood vessels in this region were estimated to be of the order of $30\,\mu$ diameter. This figure is based on a comparison with the largest vessels in the region of the blind spot and on the results of de Margerie (1960). Since the image of the 10′ field is at least $60\,\mu$ in diameter (allowing for diffraction at the 2 mm artificial pupil), it is perhaps not surprising that they had little influence.

In the case of P. E. H. the high threshold for a 21′ field at 35° nasal might possibly be attributed to such variations, and there is also a suggestion that at 20° nasal the threshold for a 1° field is *lower*, in terms of

total energy, than those for 4′ and 10′. The reasons for these findings are not clear.

Other authors have studied retinal heterogeneity; for a discussion of the literature see Pirenne (1956). The possible reasons for variation in threshold with retinal position are discussed in Cabello & Stiles (1950); see also personal communication from Stiles cited in Pirenne (1956).

Secondly, sensitivity to a small field varies widely with retinal position, and in particular with distance from the fovea. The great range of this variation is shown in Fig. 3. Obviously no valid conclusions can be drawn if uniformity is assumed for parts of the retina which extend into regions near the fovea. Further, Table 1 shows that even for a restricted range of eccentricities in a region generally regarded as comparatively homogeneous there may be marked variations. Between 17° and 23°, for subject F.C.R., the threshold for a 10′ field rose by 40 %.

Finally, even if an area of the retina is found which, for the subject used, shows little or no variation in threshold for a small field, the assumption of uniformity may be invalidated by variations in the summation properties. The experiments with P.E.H. show clearly that the area within which total summation holds is different in different parts of the retina. The simple hypothesis of a retinal mosaic of identical visual units cannot be maintained. If such units exist they must vary in effective area according to retinal position, and further evidence (Pirenne, 1946; Hallett, 1961) shows that units of very different sizes must be active at different intensities in the same retinal area.

The status of Piper's law has been the subject of considerable discussion. For very small areas threshold *energy* is independent of field size (Ricco's law). For very large areas threshold *intensity* is effectively independent of field size. There is an intermediate range, and for some experimental conditions a square-root relationship gives a good fit over a considerable range of areas (Baumgardt, 1959). Baumgardt (1959), and Bouman & van der Velden (1947) regard this as a fundamental law; Barlow (1958), on the other hand, concludes from a long series of experiments that 'temporal and spatial summation in human vision are complex, interrelated phenomena which are not adequately described by the simple empirical laws (Bunsen-Roscoe, Ricco, and Piper) except within certain rather narrow ranges.'

The results of P.E.H. do not suggest that Piper's law has any general or fundamental validity. At 7° there is a fair approximation to the law between about 1° and 8° diameter (Fig. 2C), but at 5°, 20°, and 35° the slope of the curve is considerably less than 0·5.

On the assumptions of uniformity and identical units the two-quanta hypothesis predicts a slope of 0·5 and a unit threshold higher than two

quanta would lead to steeper slopes. Any break-down of the simple assumptions would reduce the slope of the curve. The present results, therefore, do not clearly contradict either hypothesis, although the slope of 0·5 for 7° eccentricity, for fields covering an area far from homogeneous, suggests that if a fundamental area–threshold relationship does exist for a hypothetical uniform retina the slope must be greater than 0·5.

Upon the whole the results suggest that, in practice, the effect of area upon threshold depends on the extension of the field to more sensitive areas or units with greater collecting power, rather than on theoretical statistical considerations.

The method of threshold measurement used in these experiments is that described by Hartline & McDonald (1957) and fully discussed in Pirenne, Marriott & O'Doherty (1957); it was independently developed by Stiles & Crawford (1934). It has the advantage that the subject is uninfluenced by any knowledge of the nominal intensity of the flash (cf. Piéron, 1960) and at the same time it is quick and simple to use.

The relevance of these results to experiments on acuity, and their interpretation in terms of visual units, is discussed elsewhere (Hallett, 1961).

SUMMARY

1. The absolute threshold in energy units of blue–green light for detection of a brief (2·6 msec) light flash was measured for different field sizes and for different positions in the extrafoveal retina.

2. For a small test field, 10′ in diameter, marked differences in threshold were found at different eccentricities.

3. For larger test fields there were also differences in threshold at different eccentricities. These did not, however, follow the same course as those for small fields; in particular, the position of the field for minimum threshold depended on the size of field.

4. The relationship between area and threshold was examined at different retinal positions. The form of the relationship, and in particular the area of complete spatial summation, varied according to the retinal position.

5. It was concluded that different retinal areas differ, not only in their sensitivity as measured with a small test field, but also in their properties as regards spatial summation. The relevance of this finding to theories concerning the visual threshold is discussed.

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