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SCOTOPIC ACUITY AND ABSOLUTE THRESHOLD IN BRIEF FLASHES

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Standard tests of acuity involve the resolution of the details of a test object. Pirenne's method (1946), the detection of the presence of a black disk against a briefly illuminated background, invites comparison with the absolute threshold task and a more direct interpretation.

The brighter the wide background the smaller the black target that can be resolved, within limits (Hecht, 1928; Shlaer, 1937; Pirenne, 1946, 1961; Mandelbaum & Sloan, 1947; Pirenne & Denton, 1952; Le Grand, 1956; Pirenne, Marriott & O'Doherty, 1957). Also at the absolute threshold the brighter the flash the smaller is the detectable luminous area (Le Grand, 1956; Pirenne & Marriott, 1959). What is the relation between luminance and target area for the *detection* of 'black' and 'white' test objects, all other variables being fixed?

METHODS

Circular diaphragms or opaque disks are placed before a system of large lenses which form a large image of the source in the plane of the 2 mm artificial pupil. Apparatus and calibrations have already been described (Hallett, Marriott & Rodger, 1962). It was necessary to remove the blue-green Ilford 604 filter and use white light for the highest intensities.

The dark-adapted subject fixates, releases the shutter, and receives at a known position on his left temporal retina either a circular light flash (absolute threshold task) or a 46° diameter flash in the centre of which is an opaque disk (simple acuity task). The flash duration is 2·6 msec. The fixation point is presumably much too dim to affect the sensitivity of the retinal region used (Pirenne & Denton, 1951). Fixation positions are scattered with a standard deviation of 5′ or less (Barlow, 1952; Cornsweet, 1956). Peripheral dioptrics are improved by the artificial pupil, and errors of refraction and fixation are negligible at low intensities because the image consists of only a few scattered quantum absorptions (Pirenne & Marriott, 1959).

The threshold criterion for black disks was fixed by training experiments using many blanks. At threshold the disk is seen as a dark blur near the middle of the field. All presentations were randomized. Frequency-of-seeing versus intensity curves corresponded in slope to Poisson sums of $n \geqslant 4$. Standard errors of the 55 % threshold are safe estimates, calculated according to the method of Hartline & McDonald (1957).

Retinal illumination is calculated by the method of Le Grand (1957) for a posterior nodal distance of 16·68 mm, 1′ of arc being equivalent to 4·85 μ of retina. Østerberg (1935) found $1{\cdot}49 \times 10^7$ rods/cm^2 at 20° eccentricity from the fovea in the horizontal temporal

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meridian of the retina. The rods absorb one tenth of the energy passing through the artificial pupil, using the transmission of the eye media, as estimated by Ludvigh & McCarthy (1938), and the absorption by the rods (Rushton, 1956).

Preservation of dark-adaptation: after-images. Direct tests were made for the possibility that bright test flashes may have affected subsequent measurements. $\frac{1}{2}$° and $\frac{1}{4}$° fields were set at such an intensity as to be just continuously visible at 20° eccentricity. 5 flashes of a 46° white field equivalent to $10^{8\cdot 87}$ quanta of $\lambda = 507$ mμ at the cornea/cm^2 (retina) per flash (5 quanta absorbed per rod per flash) were given in 15 sec. The small field was immediately seen when replaced 1–2 min later. Thus any effect of bright flashes must have been brief, in spite of the subjective brilliance and after-images which lasted perhaps half a minute. In experiments at the highest acuities only a small proportion of the flashes were so bright. The flash rate was then 1–2/min with intervals for rest.

Health. The common cold leads to disordered results. Back pain on 2 days caused a rise of nearly 1 log. unit in the thresholds of 1·2° and 1·7° disks.

RESULTS

In Figs. 1 and 2 sets of points determined on the same days lie on continuous lines (S.E. = 0·08 log. unit). In Fig. 1 the pairs of black and white circles with tails lying upon the same horizontal line are disk and field pairs respectively of the same size, each pair being determined on a single day with high accuracy (S.E. difference $<$ 0·12 log. unit). Day-to-day variations introduce an uncertainty (± 0·2 log. unit) into the absolute positions of the graphs. In Fig. 4 and Figs. 6–10 are illustrated accessory experiments of considerably lower accuracy than those of Figs. 1 and 2.

Absolute threshold

The area versus intensity curve (Fig. 1, open circles) has a gradient of -1 for flashes of less than 1° diameter, but at larger areas the gradient is steeper, i.e. for the smaller flashes the threshold energy is constant and minimal but for larger flashes the threshold energy rises. More extensive data for this subject are given in Hallett *et al.* 1962. Though at areas less than 10′ diameter constant threshold energy might be due to imperfections of the optical image or diffraction, the fact that 6–10 quanta will co-operate for a threshold light sensation, even when they are absorbed by separate rods within an area (the complete summation area) which is large in comparison with light scatter, is evidence (Pirenne, 1956) for convergence in the human visual system, cf. the convergence of the rods on to the retinal ganglion cells.

If u quanta are required for the excitation of a 'visual unit' and if the flash area is smaller than the unit, then we get the condition (i) or (ii) (Fig. 3) where the total energy is the same. If the flash is bigger than the unit we get (iii) where there are still u on the unit but an equal density (i.e. number per area) outside. This would lead, assuming that the quanta are uniformly distributed, to a slope of -1 for areas less than 1° and to a slope of ∞ for greater areas, since no intensity less than that placing u quanta on a unit could excite one. Quanta, however, are randomly spaced so that there is always a chance of u or more quanta clumping within a unit, even at very low intensities, and this chance is increased if the flash is sufficiently large. If threshold is reached when one unit responds, then

$$P = 1-(1-p)^N,$$

where P is the frequency-of-seeing, p the probability of stimulating each identical unit and N the number of units available. p is related to the unit quantum threshold (u) by a Poisson sum of value u. The frequency-of-seeing versus light-intensity curve being determined and the heterogeneity of the visual field being allowed for (Stiles & Crawford, 1937; Baumgardt, 1959; Hallett, Marriott & Rodger, 1962), the experimental

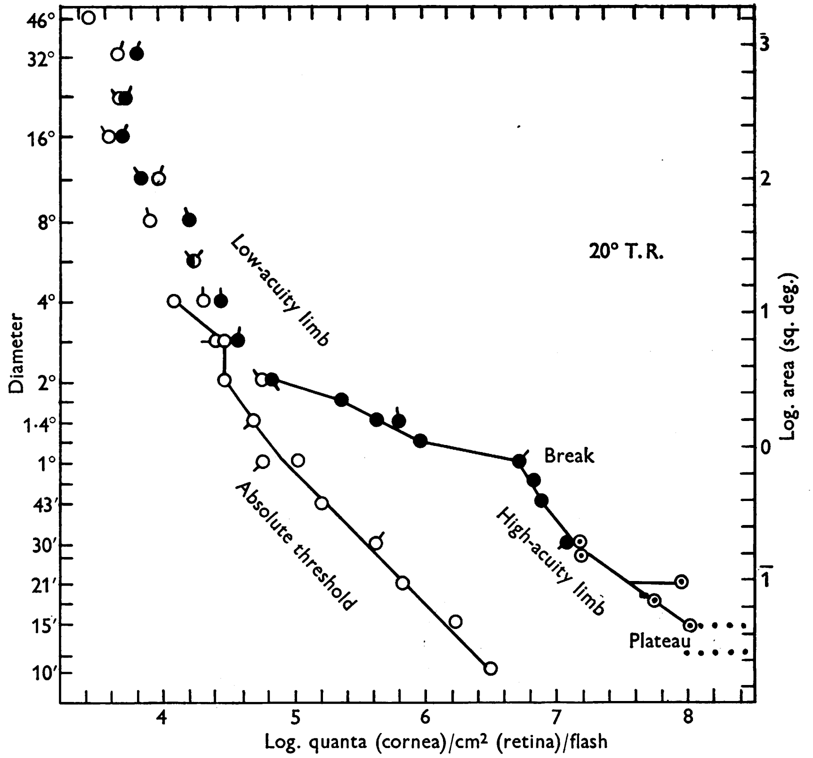

Fig. 1. Absolute threshold and simple scotopic acuity at 20° left temporal retina. 2·6 msec flash. Points determined on the same days are linked by lines. Points with tails represent a disk and field pair of the same size compared on the same day. ○, absolute threshold for fields; ●, simple acuity with black disks on a 46° diameter blue-green surround; ⊙, acuity results in white light only. Disks smaller than 11–14′ cannot be detected even at intensities as high as 10 log. quanta/cm².

area-intensity curve could no doubt be predicted if u and N were known.

Figure 2 (left) shows data for 7° eccentricity where complete summation holds to $\frac{1}{2}$° flash diameter (see also Hallett, Marriott & Rodger, 1962).

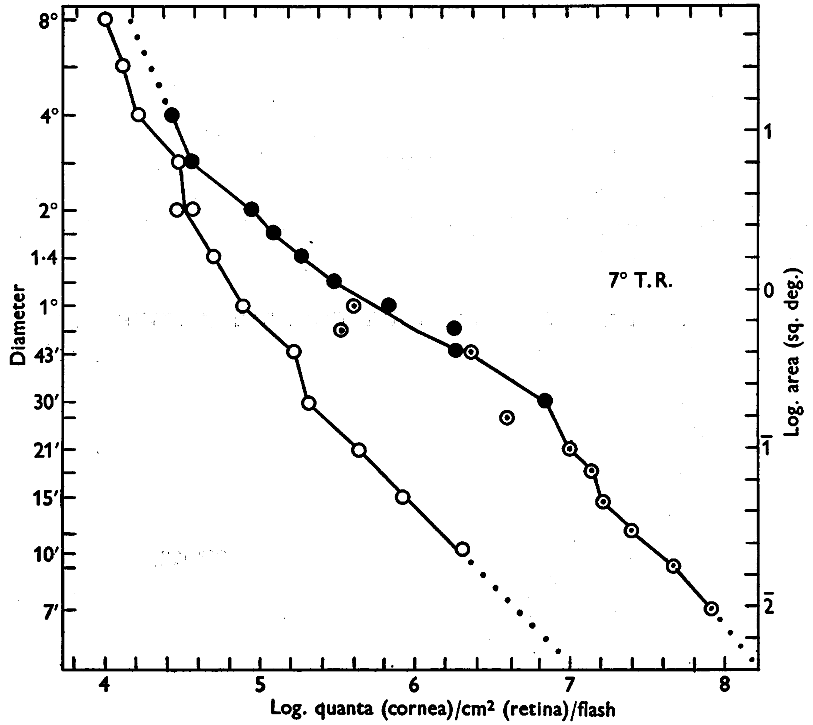

Fig. 2. Absolute threshold and simple scotopic acuity data at 7° left temporal retina. 2·6 msec flash. ○, absolute threshold for fields; ●, simple acuity with disks on 46° diameter blue-green surround; ⊙, acuity in white light only. The 6·6' diameter black disk does not represent the highest possible acuity at this eccentricity.

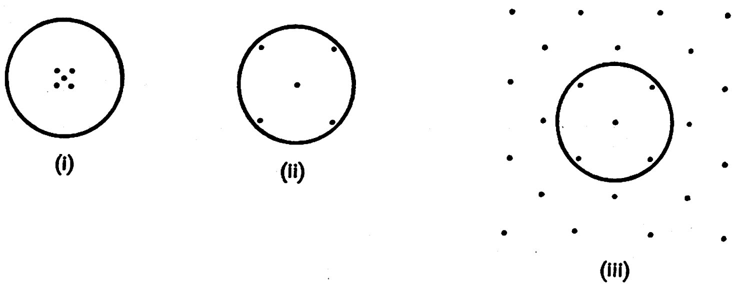

Fig. 3. A threshold number of uniformly distributed quanta fall within a unit in (i) and (ii). In (iii) a unit collects a threshold number of quanta from a flash larger than the unit.

Black disk detection

The low-acuity limb. The threshold of the full 46° surround is 1 quantum absorbed/47,000 rods and as the thresholds for the largest black disks are close to this it follows that there are 'dark gaps' between the effective clumps of u quanta and the black disk must be bigger than these gaps to be detected.

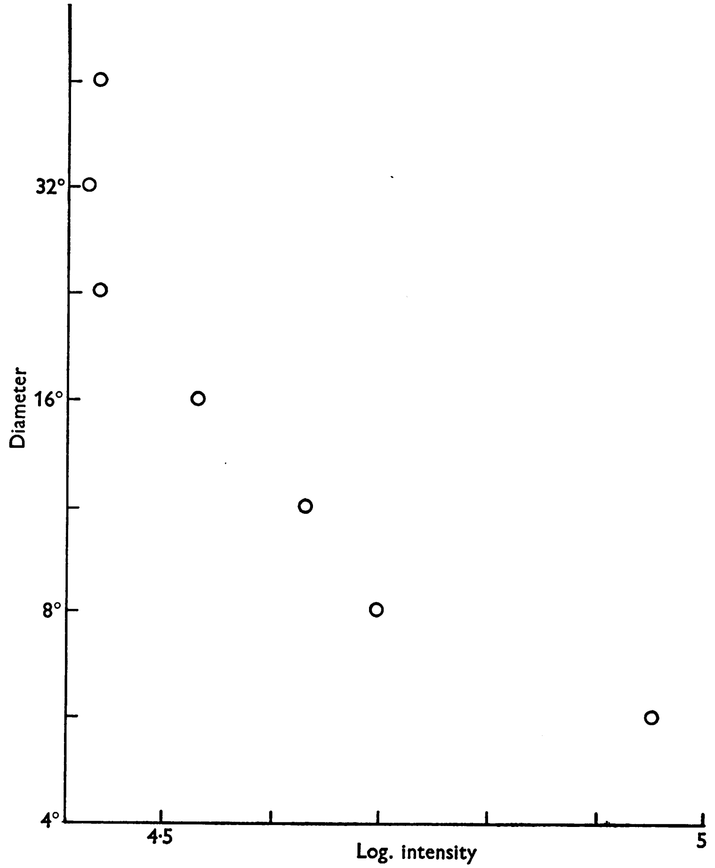

Fig. 4. The effect of variation of surround diameter on the intensity threshold of a 4° black disk seen at 20° left temporal retina. Some of the points were determined on different days. Log. intensity as the abscissa means log. quanta (cornea)/cm.^{2} (retina)/flash.

It will be seen from Figs. 1 and 4 that the threshold intensity for a 4° flash is about 0·3 log. unit less than the threshold intensity for a 4° black disk on an approximately 12° diameter surround. This is what might be expected from the difference in the task of discrimination in the two cases. The former threshold represents the light energy of the flash such that there is a 50% chance that *u* or more quanta fall upon at least one 1° summation area. From the frequency-of-seeing curve in these circumstances we may read that an intensity 0·3 log. unit greater would be seen in 90% of the trials. Now the 4° disk at threshold is detected as darkness within a faintly luminous surround. If the surround is represented as in Fig. 5 by 6 open circles it is plain that *all* 6 must respond and be seen as 'bright' if the 'absence' in the centre is to be detected. But we have seen that at the intensity of the surround required for disk detection each open circle in Fig. 5 has a 90% chance of responding, and thus the chance of all 6 open circles responding simultaneously is

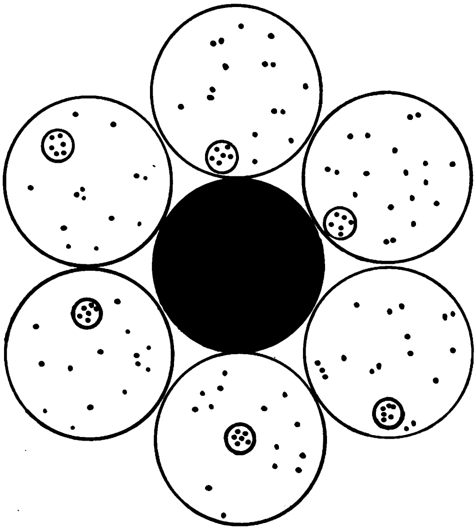

Fig. 5. A 4° black disk is seen against a 12° surround which consists, in effect, of six 4° comparison patches. Each patch has reached its absolute threshold because at least one unit in each comparison patch has by chance trapped a threshold number of quanta.

$$0{\cdot}9^6 = 0{\cdot}53,$$

which corresponds in fact to the frequency of disk detection.

For surrounds larger than the 12° surround just considered the threshold intensity for a 4° black disk decreases (Fig. 4). It is, however, difficult to apply the above analysis to the 46° surround used in the routine disk experiments because (i) so large an area is very heterogeneous, and (ii) the large surround may enable the subject to locate more easily the region where the black disk is expected.

The smaller disks and their comparison patches approach the size of the '*circa* 1° visual units'. The black disk curve actually levels out at about 1° diameter (Fig. 1), which is also the value of the complete summation area. An indication of a plateau at about ½° disk diameter can be seen in Figs. 2 and 7 for a retinal position closer to the fovea, where the summation area is ½°.

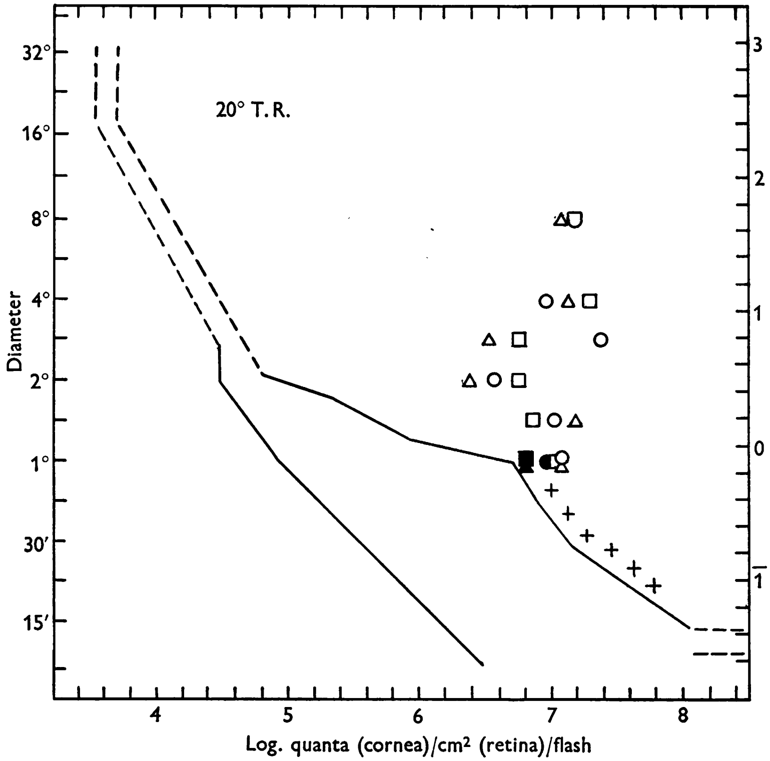

Fig. 6. Thresholds at 20° left temporal retina for the subjective change of disk appearance from black to white as the flash sensation dies away. 2·6 msec flash. The lines represent the data of Fig. 1, absolute threshold on left, scotopic acuity on right. White symbols, subjective change thresholds; +, region in which the subjective change was observed, not threshold measurements. Common symbols for points determined in the same experiment.

Divergence of the acuity and absolute threshold curves as the test object approaches the size of the units, and the shapes of these curves, should be predictable consequences of the statistical recruitment of identical independent units by chance clumps of u quanta (cf. Pirenne, 1946). In fact the data of the low-acuity limb in Fig. 1 are subject to day-to-day variations, so that curves for $u = 2$ (Bouman, 1950) or $u = 4$–10 (Pirenne, 1946) cannot be fitted. Moreover, there is some doubt as to the maximum acuity of the low-acuity limb: area versus threshold-intensity curves only extend to the beginnings of plateaus and one may suppose that the plateau in Fig. 1 lies somewhere between 1·2° and rather less than 1°.

The break is not due to rod-cone transition. The eye was adapted to a large field of 15,800 cd/m^2 for 2 min, and a dark-adaptation curve made at 20° eccentricity for the detection of a 30′ black disk on a 46° diameter surround. If in Fig. 1 the 30′ black circle which lies upon the high-acuity line represents cone vision, then the dark-adaptation curve with this criterion should not show a kink and by 8 min it should have attained full cone adaptation, i.e. the value seen in Fig. 1. But the facts are that a kink occurred after 12 min, when only rods could be changing and the threshold was then about 1 log. unit above the final value (this experiment was conducted in collaboration with Dr C. Haig). Further, the dark-adapted eye does not perceive obvious colour until the final acuity plateau is reached,

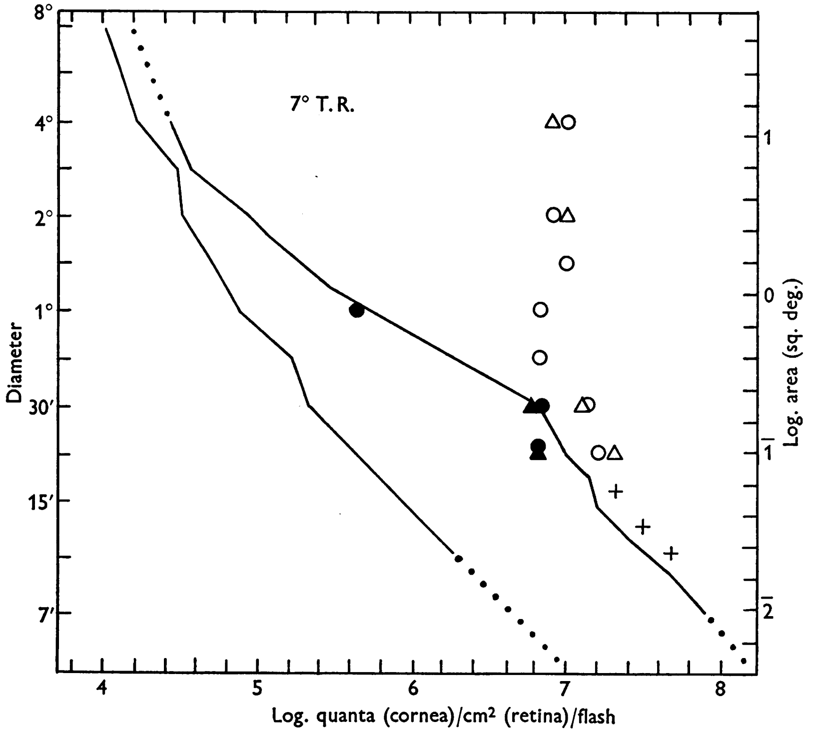

Fig. 7. Threshold at 7° left temporal retina for the subjective change of disk appearance from black to white as the flash sensation dies away. The lines represent the data of Fig. 2, absolute threshold on left, simple scotopic acuity on right. Black, new simple acuity data with black disk which confirm the suggestion of a break in the acuity curve at about 30′ disk diameter; white, subjective change thresholds; +, region in which the subjective change was observed, not threshold measurements. Common symbols for points determined in the same experiment.

i.e. 8·43 log. unit in Fig. 1, which is 1·28 log. unit above the final dark-adapted threshold for the 30′ disk and equivalent to 2 quanta absorbed per rod. Additional evidence is (*a*) that the intensity of the break in Fig. 1 is low (1 quantum absorbed per 27 rods), and (*b*) that the effective density of the green filter (1·46) corresponds to the calculated scotopic density of 1·59 (photopic would be 2·08).

The high-acuity limb. At 20° eccentricity the high-acuity limb was followed to the final acuity plateau, which is reached at an intensity when every rod has absorbed an average of 1 or more quanta. Disks smaller

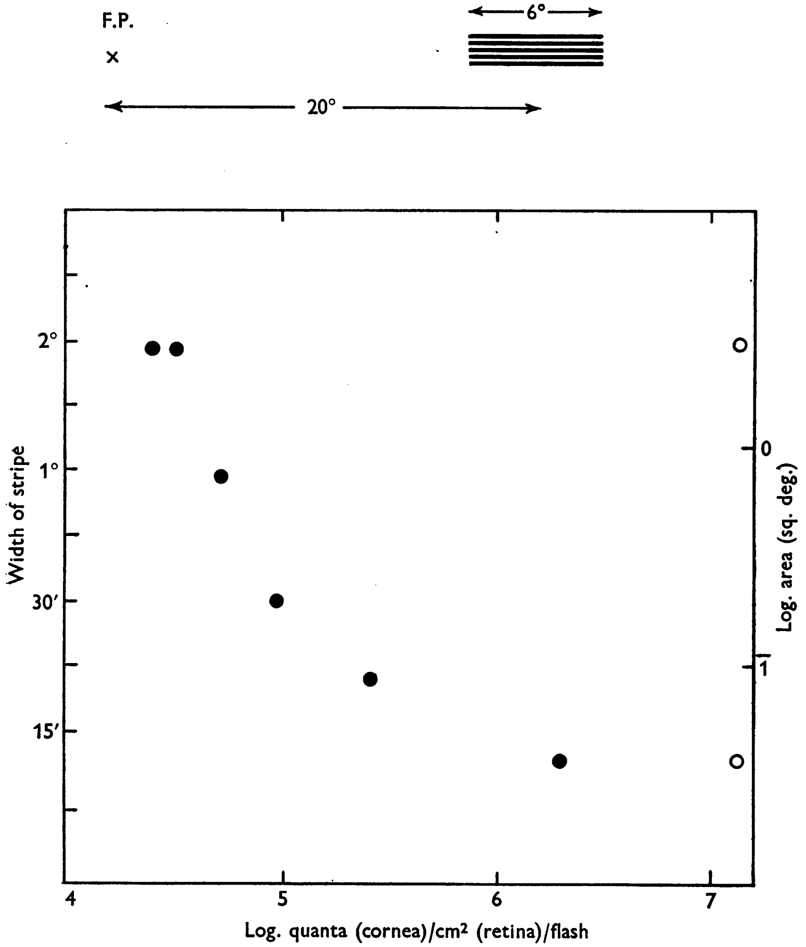

Fig. 8. Thresholds at 20° left temporal retina for the perception of a grating composed of five black bars, each 6° long, the spacing and width of the bars being equal. 2·6 msec flash. ●, resolution of the grating; ○, change of the black bars to white bars during the flash sensation.

than 14·4′ cannot be seen even at intensities as high as 10 log. unit (Fig. 1). Estimates of the final plateau at 10°, 20° and 25° eccentricity (6·6′–9·1′; 11·4–14·4′; 11·4′–14·4′) roughly agree with the smallest resolvable gap in a black Landolt C (Mandelbaum & Sloan, 1947; 9·1′, 17·5′ and 22·7′, respectively). The rod-cone break at 21′ gap described by these authors for 20° eccentricity is suggested by the high threshold of the 21′ black disk. Colour becomes obvious as the final acuity plateau is reached.

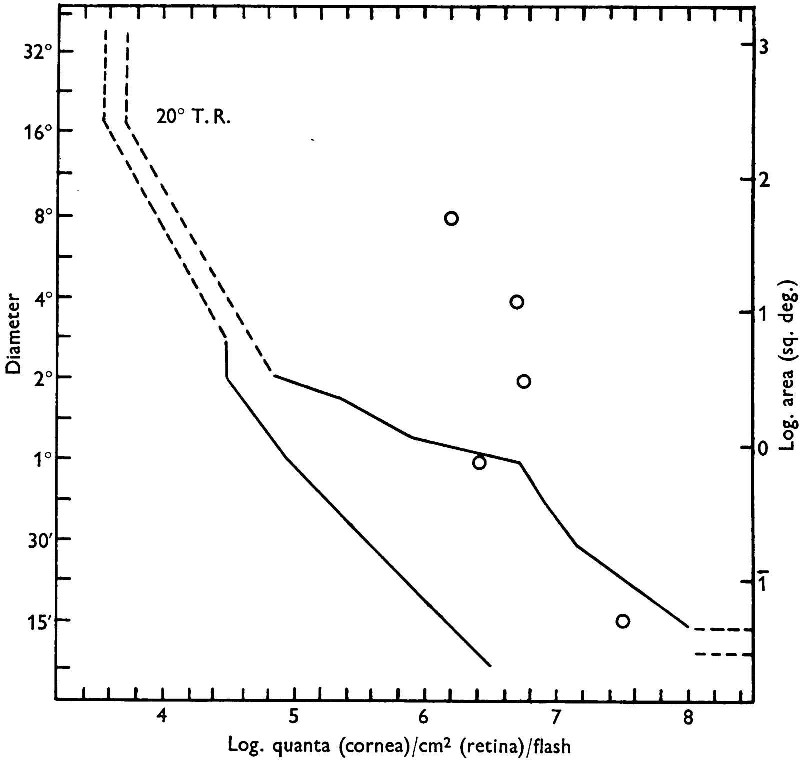

Fig. 9. Thresholds at 20° left temporal retina for the double perception of a single 2·6 msec light flash. The lines represent the data of Fig. 1, absolute threshold on left, scotopic acuity on right.

The intensity range of the high-acuity limb is characterized by several new phenomena. In Figs. 6 and 7 are represented the thresholds at which the black disk is perceived twice, i.e. the black disk changes into a white one as the flash sensation dies away, though the effect may be more complex when the subject is fatigued. For disks smaller than 1° the effect occurs close to the threshold for disk detection, but this is not true of disks larger than 1°. The minimum intensity required for the effect is very near the intensity of the break between the high- and low acuity limbs. Similarly the black bars of a grating change into white ones as the brightness sensation of the 46° surround dies away (Fig. 8). Fields on zero surround show an analogous effect: they are seen twice at intensities much above the absolute threshold (Fig. 9). All these threshold data are approximate only. Although the fully developed phenomena are striking, the threshold criterion is difficult and blanks cannot be used to check reliability of response. The lowest intensity at which 'double' perception occurs is only slightly different for the three test objects examined.

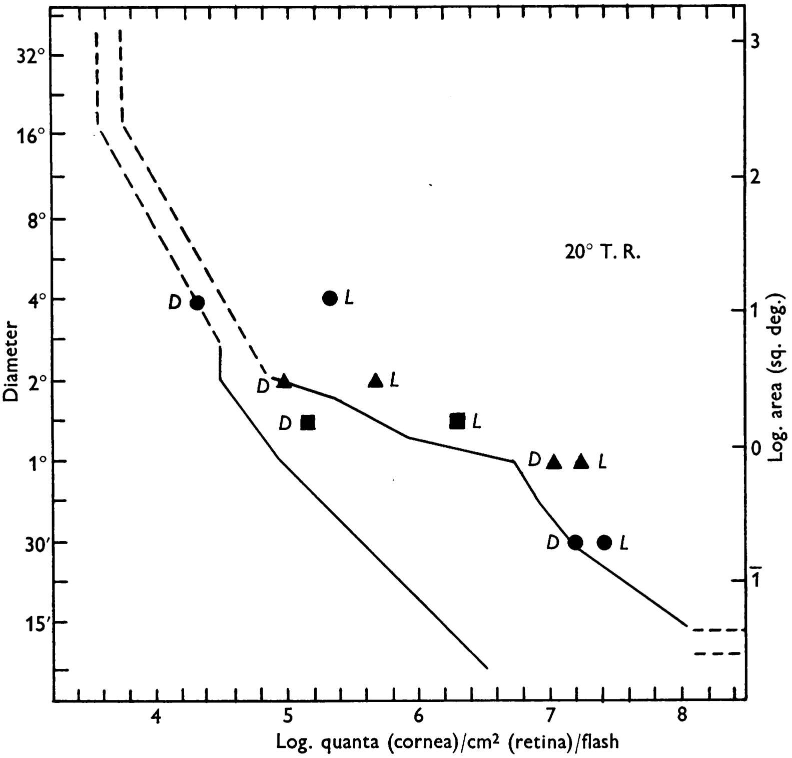

Fig. 10. Weak light-adaptation at 20° left temporal retina. The lines are the data of Fig. 1, absolute threshold on left, simple scotopic acuity on right. 2·6 msec flash. *D*, new dark-adapted simple acuity thresholds; *L*, simple acuity thresholds, each flash being presented 10–15 sec after a period of weak light-adaptation to a surface of luminance about 1 cd/m². Common symbols for points determined in the same experiment.

Figure 10 shows that the low- and high-acuity limbs do not equally recover from weak light-adaptation, the low-acuity limb being the more affected. The high-acuity limb for black disk detection can be explained either by recruitment of smaller visual units (cf. Pirenne, 1946) or by differences in the suprathreshold activity of the large 1° units (cf. Hartline, 1940*a*).

DISCUSSION

Previous work

Complete dark-adaptation and fixation. Pirenne (1946) examined several subjects with the black-disk method, using disks generally of 1° diameter or larger, 35 or 100 msec flashes, and natural or artificial pupil. He describes a break at about 2° disk diameter at 20° eccentricity from the fovea and at about 1·3° disk diameter at 10° eccentricity. This break is much less pronounced than that of Fig. 1 and tends to be less conspicuous on subsequent examination of a given subject. It should be noted that Fig. 1 does not exclude an additional break at about 2° disk diameter. Pirenne's acuity curves are possibly steeper than the low acuity limb of Fig. 1.

Olgilvie, Ryan, Cowan & Querrengesser (1955) have used white Landolt C test objects on zero surround and black Cs on luminous surrounds, the exposure being 1 sec. The resolution of a black Landolt C has at least a practical resemblance to the detection of a black disk, even though the relative importance of the C (black target) and the gap in the C (white target) as stimuli is unknown: both black C and black disk require a higher intensity for their recognition than the corresponding white target on zero surround.

Light-adaptation and fixation. The present experiments have already been compared (p. 183) with those of Mandelbaum & Sloan (1947, black Landolt C exposed for 1 sec) in which the subject adapted to the prevailing intensity.

Light-adaptation, the eyes moving freely. When black and white disks are viewed against a grey screen to which the observer adapts, black disks are more easily detected than the white ones in the rod range of luminance (in contrast to *complete dark-adaptation and fixation* above) but there is scarcely any difference between the targets at cone luminances (National Physical Laboratory, unpublished). In these experiments the reflexion factors of the black, grey and white surfaces were 1, 44 and 88 %, respectively.

The acuity versus intensity curves for grating (Shlaer, 1937) and black Landolt C test objects (Pirenne *et al.* 1957) show discontinuities which apparently represent the transition from rod to cone function. Pirenne (1957) has shown that the black C itself and not the gap is the effective stimulus under these conditions.

In brief, previous work demonstrates that the area–intensity relations for black and white targets can be very different for conditions closer to ordinary night vision than the simplified experimental situation used here. Breaks similar to that of Fig. 1 may not be noted experimentally if the test object is viewed at various distances from the fovea during each exposure. Fixation and flash must prevent the black target from causing off-responses by moving over previously illuminated retina (Pirenne, 1957). If the observer were to adapt to the prevailing intensity, then Fig. 10 suggests that the break of Fig. 1 would become less apparent. The use of brief flashes, however, allows even brilliant illumination without much lasting change of dark-adaptation (see Methods).

Unit size

We know that convergence or spatial summation must occur in human vision, because a few quanta co-operate for a light sensation even when absorbed in separate rods. Definition, however, of 'unit size' from the complete summation area for circular flashes alone is quite arbitrary. It is therefore of interest that black-disk thresholds are described by two curves, the change from the low- to the high-acuity limb occurring when the black disk is no longer large enough to keep light out of the 'big unit' definable by the complete summation area for circular fields. Complete summation and acuity plateaus do not necessarily reveal the true size of a 'unit' and may give an under-estimate. In the frog or cat retinal ganglion-cell complete summation is confined to only a part of the receptive field and is then only approximate (Hartline, 1940*b*; Barlow, Fitzhugh & Kuffler, 1957).

Now Bouman (1950) and Bouman & van den Brink (1952) have presented evidence for small units, i.e. smaller than those indicated by the complete summation area in the present subject (Hallett *et al.* 1962). At 18° eccentricity Bouman & van den Brink find that complete summation between two light spots extends to about 8′, but that there is some physiological summation at about 18′ separation. Such small units may be concerned in the high-acuity limb for the detection of black disks and in the 'double perception' phenomena.

In conclusion, the present experiments show that human dark-adapted vision is mediated by two rod mechanisms. These mechanisms are possibly two types of receptive field which are of different sizes.

SUMMARY

1. The area–threshold intensity relations are compared at 7° and 20° eccentricity from the fovea (*a*) for the 50 % detection of 2·6 msec light flashes and (*b*) for the 50 % detection of black disks seen against a 46° surround lit for 2·6 msec. The subject was completely dark-adapted.

2. The absolute-threshold curve (*a*) shows that complete spatial summation extends to 1° at 20° eccentricity.

3. At 20° eccentricity the acuity curve (*b*) shows *two* distinct limbs. Each limb consists of a steep section during which acuity rises rapidly as intensity increases, and a plateau section during which acuity increases slowly or not at all.

4. The steep section of the *low-acuity limb* is close to the absolute threshold. The disks of the plateau section are close to the size of the complete spatial summation area. The change from the *low-* to the *high-acuity limb* is not due to rod-cone transition. The steep section of the

high-acuity limb is considerably above absolute-threshold intensities. The final plateau is at 11′–14′ disk diameter and colour vision is then subjectively apparent.

5. Accessory experiments include light-adaptation, variation of surround size, grating test objects and thresholds for the 'double perception' of flashes and black disks.

6. The absolute threshold and low-acuity limb may represent the recruitment of large units of 1° or more. Higher acuities for black disks require some other mechanism.

Dr M. H. Pirenne kindly made apparatus and facilities available to me but I especially thank him for interesting me in visual research. My thanks are due to Professor E. G. T. Liddell for a grant from this laboratory. Drs W. S. Stiles, W. A. H. Rushton, and F. H. C. Marriott have made valuable criticisms. This investigation was supported in part by a research grant B-1810 from the National Institute of Neurological Diseases and Blindness, United States Public Health Service. The apparatus was built with the help of a grant from the Nuffield Foundation.

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