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J. Physiol. (1973), **233**, *pp.* 143–156
With 7 text-figures
Printed in Great Britain

BACKGROUND CONFIGURATION AND ROD THRESHOLD

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(*Received 5 March 1973*)

SUMMARY

1. This paper investigates the variation in rod threshold when a small test flash is seen against backgrounds of different sizes. Over a substantial range of luminances above absolute threshold, the test flash is less easily seen against small backgrounds than large. This confirms earlier results.

2. If an annular surround is added to a small circular background, threshold is reduced when background and annulus are equiluminous (uniform field), but rises rapidly as the annulus is made brighter or dimmer than the background. This cannot be explained by the threshold-elevating effects of light scattered on to the background from the surround, for threshold rises with annulus luminance faster than it does on uniform fields of equal luminance.

3. If the surround is not a complete annulus but a windmill-shaped cross, threshold is higher than on a uniform field, no matter what the windmill luminance. Thus it is not the addition of light *per se* to the surround which reduces threshold.

4. This conclusion is reinforced by the results of another experiment. The test flash is seen on a large uniform field. When superimposed on this field, a thin ring, light or dark, which causes only a small change in mean luminance, produces an appreciable rise in threshold.

5. The addition of an equiluminous red surround to a small red background so as to create a uniform field causes a marked drop in test flash threshold, but a scotopically equal blue surround, that creates a uniform field for rods, does not alter the threshold. Since the test flash is seen only by rods it follows that signals from cones can alter rod threshold.

6. Known or probable behaviour of retinal mechanisms cannot account for our results. All the operations which elevate threshold above its level on a large uniform field produce contours in the vicinity of the test flash.

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This we take as evidence that signals from the test stimulus are suppressed or reduced by other signals present only when the background is locally non-uniform.

INTRODUCTION

In both scotopic and photopic vision the size of the background against which a test stimulus is seen is an important determinant of threshold. Parafoveal threshold is highest on backgrounds between 0·5 and 1° in diameter, falling steeply on smaller backgrounds and more slowly on larger (Crawford, 1940; Westheimer, 1965, 1967). The drop in threshold on smaller backgrounds is attributed to a reduction in the summation of adapting signals from the background – the fewer signals collected within the summing area, the less light-adapted will be retina under the test spot. It is known that retinal ganglion cells summate the effects of adapting light falling on receptive-field centres (Cleland & Enroth-Cugell, 1968) and that smaller adapting spots produce lower thresholds.

The fall in threshold on larger backgrounds is less easy to explain. Crawford supposed that enlarging the background removed from the region of the test stimulus a pattern which interfered with perception of the form of the test field. Fry & Bartley (1935) held a similar view. On the other hand, Westheimer (1965) regard the threshold drop ('sensitization') as a reflexion of the changing balance of excitation and inhibition in retinal receptive fields. Threshold rises until the background covers the receptive field centre because adaptation signals are pooled over an increasingly large region, but the encroachment of larger backgrounds on the receptive field surround reverses the trend. Adaptation signals from the surround antagonize those from the centre, thus increasing sensitivity.

Two quite different conceptions of the rise in threshold are represented in these views. In one, discontinuities of illumination in the vicinity of the test flash *reduce* sensitivity; in the other, light in the surround *increases* sensitivity of the enclosed region. Experimental techniques used in the earlier experiments make a choice between the hypotheses difficult, for enlarging the background confounds addition of light with removal of a contour. In the following experiments we have explored the implications of both hypotheses. Our results showing how rod thresholds are influenced by background configuration clearly support the perceptual interference hypothesis.

METHODS

The Maxwellian view optical system was slightly modified from that used by Alpern, Rushton & Torii (1970) and is fully described in their paper. It provides four channels (we used three) each of which forms a compact image of the tungsten filament source in the plane of a 2 mm artificial pupil. The pupil helped eliminate stray light which would have entered the eye from other directions; it did not interfere with the pencil of rays from the source. One channel (λ of Alpern *et al.*, Fig. 3) provided a test spot 7 min of arc in diameter, that was briefly exposed by a rotary shutter controlled by Tektronix pulse generators. Two other channels (μ and ϕ) provided background fields up to 10° in diameter. By interposing appropriately shaped masks (prepared on photographic slides) in one of the beams and using the background channels separately or in combination, all the backgrounds used in the experiments could be constructed. Neutral density wedges in all beams allowed their intensities to be varied independently.

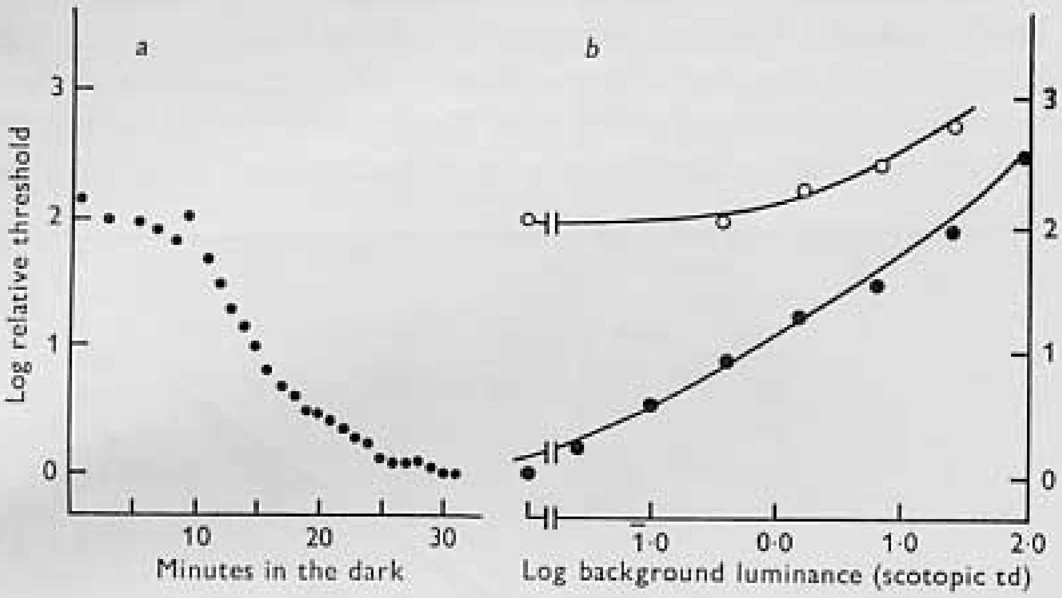

Fig. 1. *a*. Thresholds measured during recovery from a strong bleach in the dark, showing the cone plateau extending almost to 10 min. *b*. Threshold for the test flash superimposed on a uniform background, as a function of background luminance. Filled circles, thresholds measured after complete dark adaptation; open circles, thresholds during the cone plateau phase of dark adaptation.

The dark adapted observer (usually P.L.) looked with his right eye at an orange fixation point. The test spot appeared 8° to the right of this, and was presented for 10 msec every 3 sec. (Some observations we:e made with flashes every 1 sec, but although threshold was the same the task was subjectively more difficult.) Steady backgrounds when present were concentric with the test spot. The observer set threshold by adjusting the wedge in the test beam.

To ensure that we were measuring rod thresholds a blue interference filter (480 ± 7 nm) was kept in the test beam and, except where stated otherwise, both background beams passed through deep red filters that transmitted 0·1 % at 652 nm, 1 % at 656 nm, 10 % at 661 nm, 50 % at 670 nm and 89 % at longer wave-lengths. The red background keeps cone threshold above that of rods (Stiles, 1939). Two simple checks were made to confirm that the test flash was never seen by cones. In the first a strong bleach was given to the region where the test flash fell, and cone threshold was then found from the plateau of the dark adaptation curve; all less intense flashes must have been visible only to rods (Fig. 1*a*). The red backgrounds inhibited both rods and cones, in some cases raising threshold above the cone plateau. To show that on these backgrounds the flash was still seen by rods we measured threshold at different background luminances (Fig. 1*b*). Then a strong bleach was given, and when cones (but not rods) had fully recovered threshold was again measured

PRINTER'S ERRORS

IN FIGURE 1 THE VERTICAL AXIS SHOULD BE LABELLED "TEST PATCH AVERAGE INTENSITY" AND THE HORIZONTAL AXIS SHOULD BE LABELLED "BACKGROUND INTENSITY". THE OPEN TRIANGLES IN FIGURE 1 REPRESENT MEASUREMENTS AT A FLICKER FREQUENCY OF 4.5 HZ AND NOT 3.5 HZ AS STATED IN THE CAPTION.

on each of the red backgrounds. Had the thresholds been those of cones, the two sets of measurements should not have differed, but had the flash on the first occasion been seen by the now insensitive rods, the second set of measurements should have been higher. Fig. 1*b* shows a large difference between the two measurements, for all the background levels used in our experiments.

RESULTS

All the experiments described in this paper concern the change in threshold brought about by adding or removing light in the region surrounding backgrounds of 0·5° diameter or larger. In our first experiment we confirmed the observation of Crawford (1940) and Westheimer (1965) that rod threshold for the test flash is higher on a small background than on a large

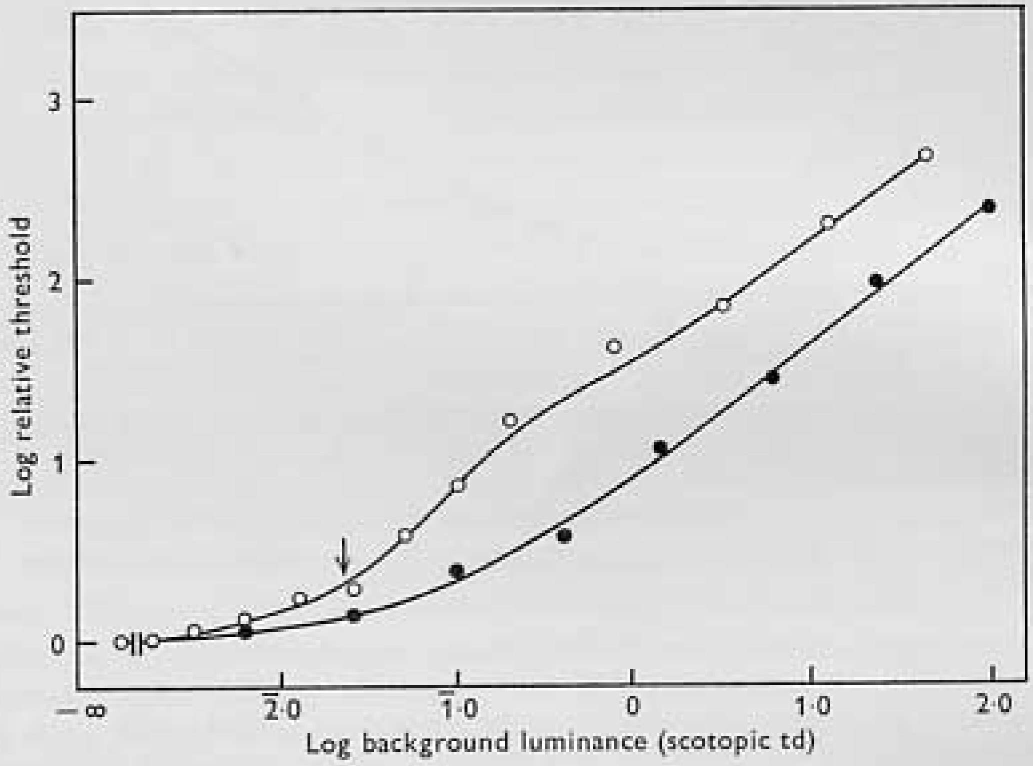

Fig. 2. Test flash thresholds as a function of background luminance. Filled circles, large (8°) uniform background; open circles, small (0·5°) background. Arrowhead shows the background intensity required for a clear perception of the background contour.

one. Fig. 2 shows increment threshold curves for red backgrounds of 0·5 and 8° diameter. Threshold on the small background rises initially like that on the larger one but climbs more steeply when background luminance reaches about $\bar{2}$·5 log scotopic trolands. The curves diverge just at the point where the small background itself appears clearly defined and this is important for some observations described below. Threshold was higher on 0·5° backgrounds than on any that were larger.

According to the centre-surround interaction hypothesis threshold is highest when the background against which the test spot is seen just fully covers the receptive field centre, and if we add to such a background annuli of different luminances, threshold ought to be progressively decreased as annulus luminance increases. Fig. 3 shows results from an experiment in which threshold was measured on backgrounds of 0·5–2° diameter, each enclosed by an annular surround (extending out to 8°)

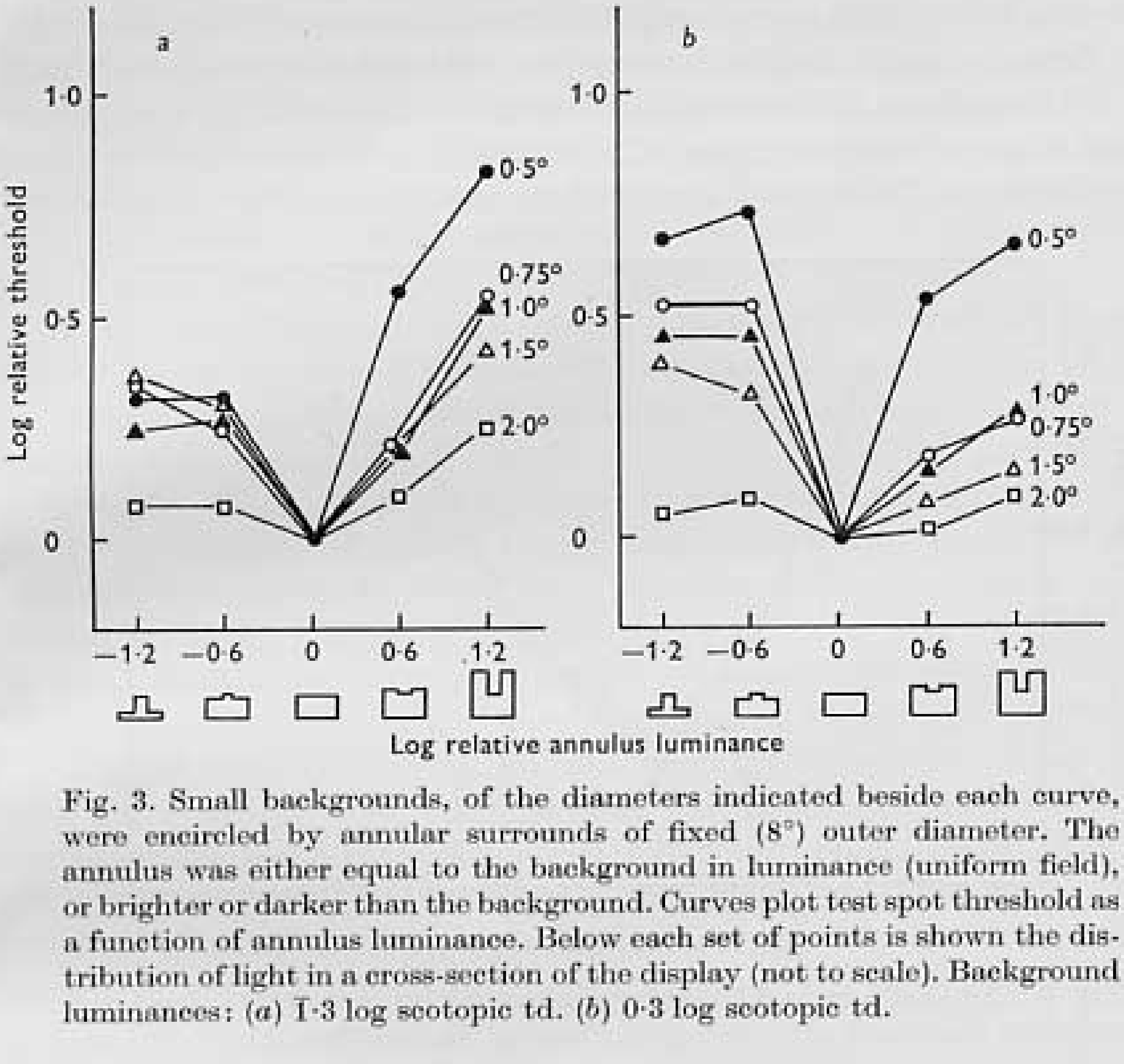

Fig. 3. Small backgrounds, of the diameters indicated beside each curve, were encircled by annular surrounds of fixed (8°) outer diameter. The annulus was either equal to the background in luminance (uniform field), or brighter or darker than the background. Curves plot test spot threshold as a function of annulus luminance. Below each set of points is shown the distribution of light in a cross-section of the display (not to scale). Background luminances: (*a*) $\bar{1}$·3 log scotopic td. (*b*) 0·3 log scotopic td.

whose luminance ranged in steps around that of the background. The graphs have several points of interest. First regardless of background diameter, threshold is always lowest when the annulus and background are equally bright (uniform field); annuli brighter or darker than the background can raise threshold more than fourfold. Second, large backgrounds are less susceptible than small ones to the influence of the annulus, and indeed threshold on a 2° background hardly differs from that on a uniform 8° field. Westheimer (1965) similarly observed that enlarging the background beyond 2° produced no further fall in threshold. Whatever spatial interaction is responsible for lowering threshold must exert its influence less than 1° away from the test flash.

Apparently a small difference in luminance (in either direction) between annulus and background can raise the threshold above its value on a uniform field. To obtain a more precise indication of the relation between annulus luminance and threshold we carried out a supplementary experiment in which annulus luminance varied in small steps around that of the background. These displays were built up by adding a dim 0·5° spot or annulus to a uniform field, so that small differences between annulus and spot could be precisely reproduced and precisely measured. When the added light formed a spot (annulus dimmer than central background) the intensity of the uniform field was reduced enough to maintain the central 0·5° region at a constant luminance. The results (Fig. 4) show that threshold rises sharply as the annulus departs from equality in either direction.

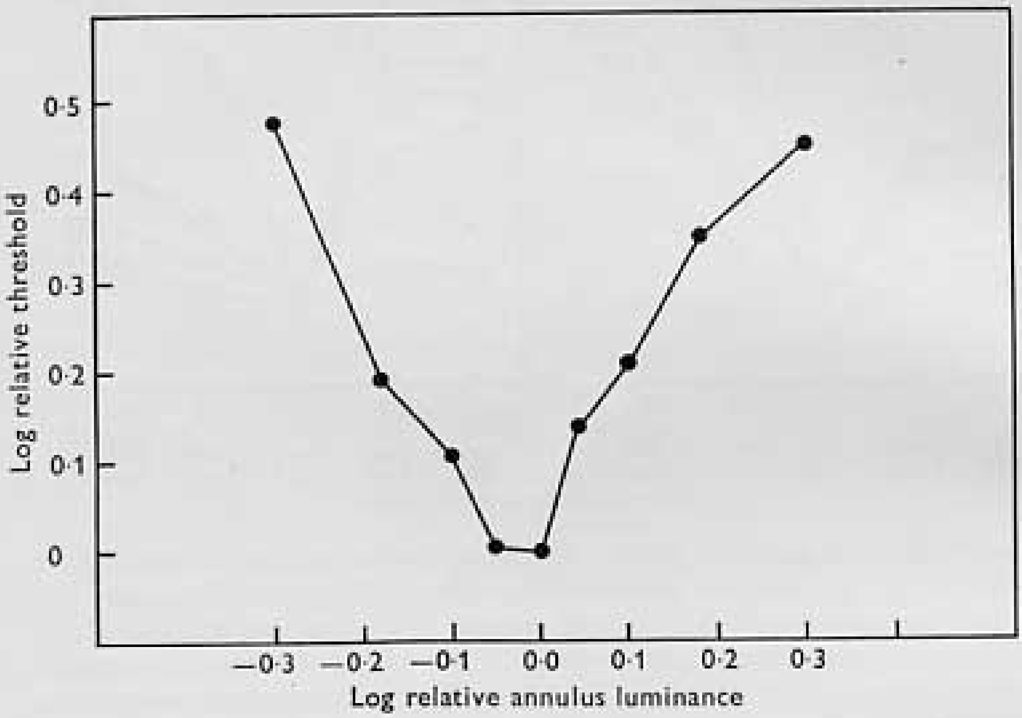

Fig. 4. Thresholds on a 0·5° background of 0·3 log scotopic td. when the encircling annulus is only slightly brighter or dimmer than the background.

If the low threshold on a uniform field is a consequence of adaptive signals from a receptive field surround (the annulus) antagonizing those from the centre, we could expect that the brighter the annulus, the lower the threshold. Our experiment shows this expectation to be wrong and suggests that the hypothesis from which it is derived is wrong. But before we can be sure, we have to exclude the possibility that light scattered from the bright annulus on to the small background is acting to raise threshold, in opposition to any threshold-lowering adaptive signals from the surround. This can be done by comparing threshold on a bright annulus with threshold on a uniform field. In Fig. 4 the brightest annulus is twice the luminance of the dark centre, and threshold is 0·45 log units higher than on a uniform field that has the luminance of the centre. Referring to Fig. 2 we find that the uniform field that duplicates the annulus threshold must be four times the centre luminance, or twice the luminance of the annulus. Since scattered light at its worst could never make central background brighter than annulus, it cannot conceivably account for more than half the rise in log threshold. Moreover Gubisch's estimates (Gubisch, 1967, Fig. 12) of intraocular light scatter indicate that the bright annulus of Fig. 4 would have increased the luminance at the centre of the background in our display by only 1 %, a quite negligible change. To account for our results we are left with the hypothesis that edges near the test spot reduce sensitivity, a view consistent with results of Teller (1968) in experiments where rod threshold was measured on narrow black bars. The remainder of this paper examines this possibility in more detail.

The influence of edges. The alternative possibility that threshold depends merely on the amount of light in the surround can be tested in another experiment. Suppose we measure threshold on, say, a 0·5° background. We can add a fixed amount of light in the region around this and vary its distribution. If the effects of this added light summate linearly and it is simply the amount of light in the surround that is important, the effect of the light on threshold should be independent of its distribution. Teller, Matter & Phillips (1970) did just such an experiment, varying the distribution of light in the surround of a small background by using a windmill-shaped mask through which different numbers of vanes could be exposed. They found that the distribution was important, threshold being lower when the available light in the annulus was distributed evenly (annulus luminance then equalled background) than when it was concentrated into bright vanes separated by black areas. To explain this they suggest that threshold-reducing signals from the annulus increase in a negatively accelerated manner with increasing luminance. This threshold-reduction explanation is inconsistent with our high thresholds on bright annuli; but if edges raise the threshold, both results are accounted for. In the following experiment we tried to decide between these possibilities, using the configuration shown in the inset to Fig. 5. Each vane of the windmill has an area 1/32 that of the whole annulus, and the four vanes together were varied in luminance about that of the background. If light in the surround reduced threshold by releasing signals that are a compressive function of luminance, each windmill must be equivalent in its threshold-reducing effect to some annulus of lower luminance. But if edges raise the threshold, windmill threshold should be higher than annulus threshold and always rise with luminance. Fig. 5 confirms the second prediction: the brighter the windmill, the higher the threshold. No windmill threshold was as low as threshold on a uniform field, even though detection of light scattered between the vanes may have led to an underestimate of threshold at the lowest windmill luminances. This demonstrates that it is not the addition of light *per se* to the surround that alters threshold, for if luminance signals were important threshold should have fallen as windmill intensity increased from near darkness. The opposite happened.

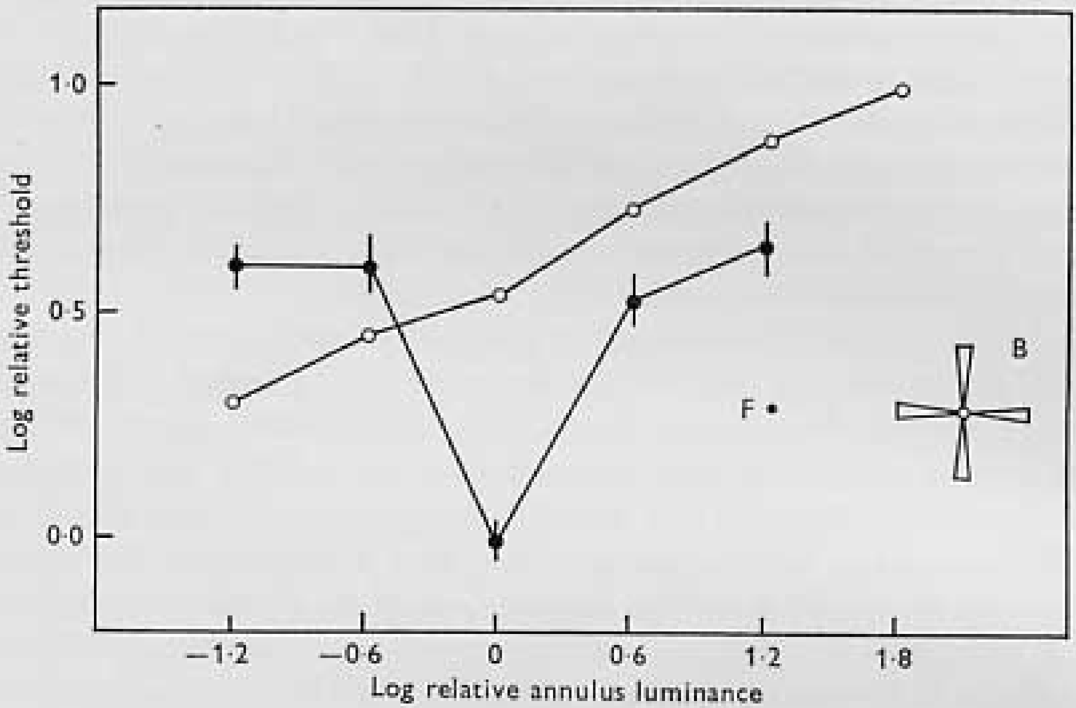

Fig. 5. Thresholds on a 0·5° background of 0·3 log scotopic td. Filled circles, annular surround complete as for Fig. 3. Open circles, annulus masked to form windmill surround. Inset: windmill display. F, fixation spot. B, background. Vertical lines show ±1 s.e.

Yet another procedure which brings a contour into the vicinity of the test flash is to superimpose on a large uniform field a thin ring concentric with the test flash. The ring may be too thin to substantially affect overall illumination of the surround, but still sufficient to define a clearly visible border. Fry & Bartley (1935) and Westheimer (1967) observed the effect of contour on cone threshold in this way, with conflicting results. The former found a dark ring to have the same effect on threshold as a luminance difference between background and surround, while Westheimer found no effect. Possibly differences in ring width account for the discrepancy: exceedingly thin rings may have no effect on threshold while slightly broader ones may. It is of interest to know what ring width is sufficient to alter sensitivity. In making measurements on rods we used an 8° uniform background on which could be superimposed light or dark rings of variable width. All had an internal diameter of 0·5°. In Fig. 6 are shown the effects on threshold of the various rings. Plainly even thin rings markedly alter sensitivity, although the thinnest dark ring is much less potent than the others. This agrees with recently published observations of Wyatt (1972). These results therefore reconcile the observations of Fry & Bartley (1935) whose ring width was 0·5°, with those of Westheimer (1967) who used a ring 2 min of arc wide. They also show that the reduced sensitivity observed with rings is not a consequence of slight changes in illumination near the test spot: threshold was raised by light and dark rings alike.

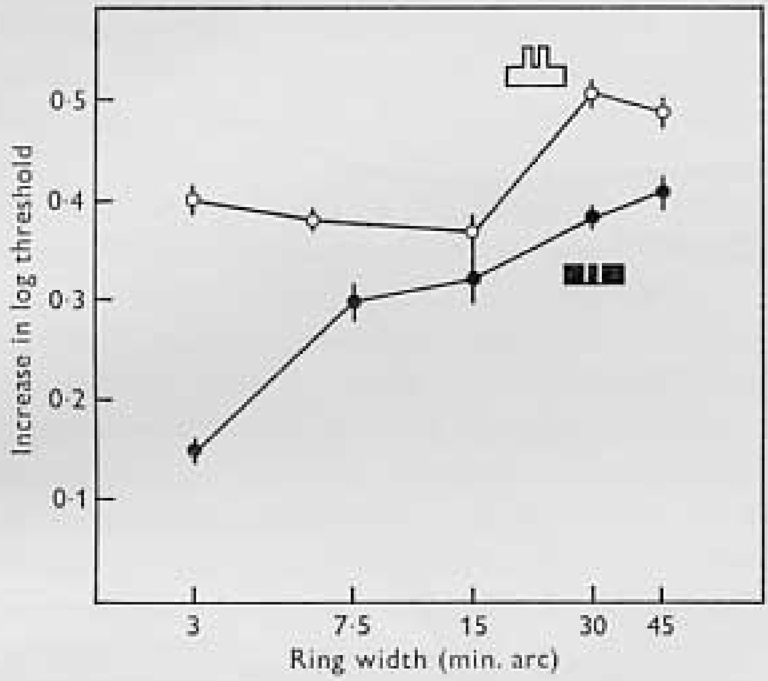

Fig. 6. The 8° background of 0·3 log scotopic td was modified by incorporating bright or dark rings of various widths, all having an internal diameter of 0·5°. The ordinate is the increase in log threshold from its value on a uniform field. Filled circles, dark rings (luminance: 3·8 log scotopic td). Open circles, bright rings (luminance: 1·1 log scotopic td). Cross-sections of the displays (not to scale) are shown beside each curve. Vertical lines show ± 1 S.E.

Rod-cone interaction. The increment threshold on steady backgrounds is usually studied using uniform fields with edges far away from the test spot. Under these conditions rod threshold depends only upon the background's effect on rods, cone threshold upon its effect on cones (Stiles, 1939). The rods and the cones are evidently equipped with quite separate sensitivity regulating mechanisms ('gain boxes' of Rushton, 1965) so that adaptation signals originating from a uniform background seen by cones do not act upon the rod gain box. Do background edges also raise the threshold in this way? If they do, an edge seen only by cones should not affect rod threshold.

Rod threshold was measured on a 0·5° red background to which could be added either the usual red annulus or a blue one produced by an interference filter peaking at 460 nm. The difference in scotopic density between red and blue filters was determined by measuring the luminances of red and blue uniform backgrounds required to bring a fixed scotopic flash to threshold. The blue had a photopic density 0·72 greater than the red, and a scotopic density 1·90 less. Using this information we could find for any luminance of red the luminance of blue that was equivalent for rods. If

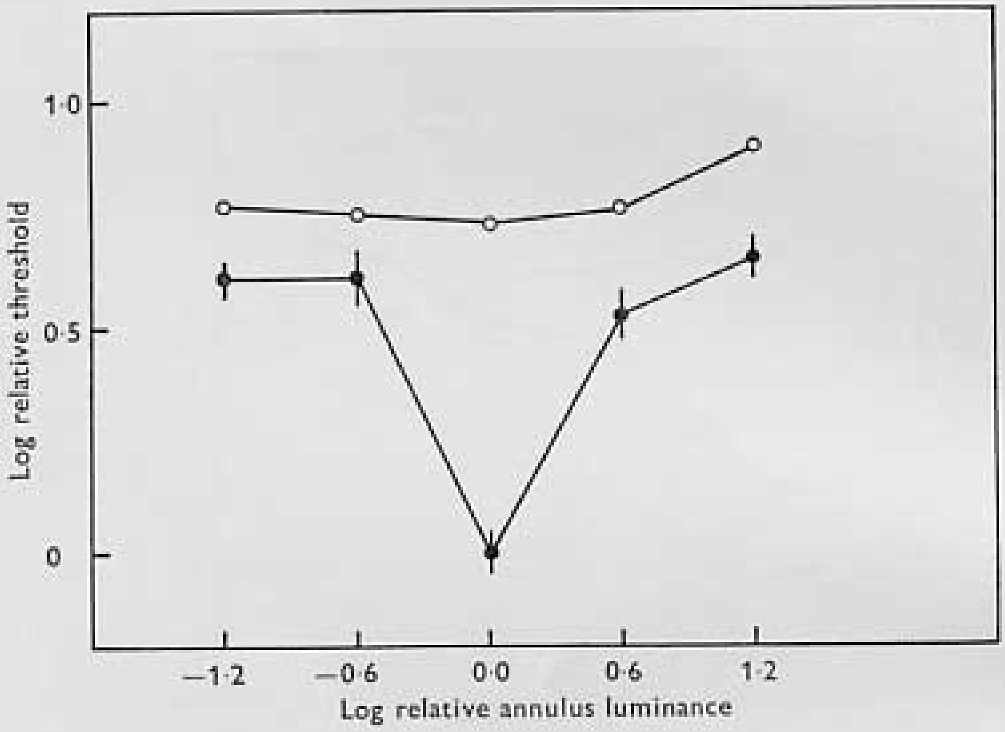

Fig. 7. Thresholds on a 0·5° background of 0·3 log scotopic td. Filled circles, red annular surrounds as in Fig. 3. Open circles, blue annular surrounds equated in scotopic luminance to the red ones. Vertical lines show ± 1 S.E.

only rods can alter rod threshold, red and blue annuli equivalent for rods must give the same threshold. Fig. 7 shows that they did not: blue annuli never reduced threshold, red ones did. With blue or red surrounds equal in scotopic luminance to the red background, threshold on the blue/red display is much higher than on the uniform field. This must be the work of cones, for there was no contour for the rods to see!

DISCUSSION

Previous work. Our results disagree with previous observations on two important points. First, we never found any annulus which, when superimposed upon a uniform field, reduced threshold for a test spot in its centre. Secondly, we found that on a blue and red field uniform for rods but not for cones, rod threshold was higher than on a truly uniform field.

Westheimer (1965, Fig. 7) reported that the addition of a large surrounding annulus to a small background of approximately 1 scotopic troland progressively lowered threshold as annulus intensity was raised to 0·5 log units above the background. In a further paper (Westheimer, 1970) an experiment was described in which the addition to a uniform field of a thin red annulus 0·7 log units brighter reduced threshold 'by about 1/4 log unit' and the size of the effect depended on the scotopic luminance of the annulus. In a number of experiments we have varied the inner and outer diameters of blue and red annuli added to a uniform field, but have never been able to decrease the threshold. The results of Fry & Bartley (1935) and Heinemann (1961, Fig. 2) agree with ours in showing high thresholds in the presence of bright surrounds. We have no explanation for the conflict of evidence.

Importance of contours. Many of our observations implicate a contour-sensitive mechanism in the change of threshold found as background configuration is altered: (1) in the t.v.i. curves of Fig. 2, threshold on the small background began to diverge from that on the larger one when background contours became visible; (2) small differences in luminance between a small background and an annular surround are sufficient to produce a large rise in threshold (Fig. 4), and phenomenally this rise is associated with increasing distinctness of the border separating the background and annulus; (3) in the windmill experiment, threshold always rose with luminance of the vanes, while threshold with a uniform annulus first fell then rose again (Fig. 6). The threshold here is correlated with visibility of contour in the neighbourhood of the test flash, for with a uniform annulus contrast of the contour first decreases as luminance is increased, and then increases, but windmill contours in the region of the test flash only become more conspicuous; (4) a blue annulus equal in scotopic intensity to the small red background always raised threshold, while the corresponding red one did not (Fig. 7). Again, the blue annulus produced a conspicuous contour while the red one did not; (5) finally, there is a striking difference in the appearance of the test spot seen on small and large backgrounds. On a uniform field it appears crisp and well defined, but on any contoured field it produces a diffuse, uncertain sensation at threshold. This has been noticed before on small backgrounds by Westheimer (1965) and Teller, Andrews & Barlow (1966) and has been attributed to light scattered from the test spot. However, its invariable occurrence where high thresholds were observed in our experiments, even those where an annulus brighter than background should have effectively masked stray light, suggests that it may be intimately involved with the threshold rise.

Evidence from single units. It is worth while to examine whether retinal mechanisms could be responsible for our findings. Observations on ganglion cells are the most crucial, for any more distal processes will be reflected in their behaviour. Physiological evidence seems to rule out an explanation in terms of centre-surround interaction: experiments in which small stimuli to the centre of the receptive field have been used in threshold measurements on cat retinal ganglion cells have shown that steady light falling on the receptive field surround does not alter sensitivity in the centre. Cleland & Enroth-Cugell (1968) did experiments modelled on those of Westheimer (1965); threshold for a small test spot presented in the receptive field centre was measured on concentric backgrounds of different sizes. Threshold rose as background size increased, reflecting the pooling of adaptation signals within the receptive field centre, but it never fell as the background encroached on the surround, instead reaching a constant level when background size exceeded that of the receptive field centre.

Channel selection hypothesis. But different ganglion cells have different properties, and a change in background may well alter the composition of the *population* of ganglion cells which signals the presence of the test flash, the most effective cells on one background giving way to others as background changes. Two ways are known in which this might happen, *selection by illumination*, and *selection by pattern.*

Selection by illumination is reported by Enroth-Cugell & Shapley (1973). At absolute threshold ganglion cells having different receptive field sizes show no consistent difference in sensitivity to small spots. As the luminance of a background on which the stimulus is presented increases, cells with larger receptive-fields are the first to become light-adapted, for it is the flux (luminance × area) falling on the receptive field centre which determines sensitivity, not luminance alone. Thus on bright backgrounds, a small test flash will always be detected best by those ganglion cells with the smallest field centres. This could account for the observation that at absolute threshold a test flash appears diffuse, while on brighter uniform backgrounds it appears crisp: in darkness the flash may be detected by any ganglion cell, but on lighter backgrounds the most sensitive are those with small receptive fields.

Selection by pattern was described by Pantle & Sekuler (1968) and Blakemore & Campbell (1969*b*) in experiments in which the viewing of a high-contrast grating depressed sensitivity to gratings over a range of greater or lesser bar widths. These investigators infer the existence of visual 'channels' each sensitive to a specific range of stimulus sizes, and each capable of being made insensitive by exposure to its adequate stimulus.

Perhaps selection by illumination, operating alone on a uniform field, is counteracted by selection by size when the small test spot appears on a small concentric background. On any bright background, selection by illumination isolates the smallest channels by rendering the larger ones insensitive. But if the background is a small one, or is locally non-uniform, signals from the background also reduce the sensitivity of the small channels, in the manner described by Blakemore & Campbell, so that in this case vision must rely mainly on the less sensitive larger channels. Hence the high threshold and diffuse appearance of the test spot. Results from the windmill experiment are readily accommodated by this scheme: windmill contours stimulate a greater range of size-selective channels than do those of a circular background, so more of the mechanisms potentially available for detection of the test spot have their sensitivity reduced. The hypothesis accounts for all the results described here, though not for the observation of Westheimer (1965) that a large surrounding annulus, brighter than the background it encloses, can under some circumstances reduce threshold to below its level on a uniform field.

Selection between size-selective mechanisms probably occurs in cortex: size-selective processes are orientation-dependent (Blakemore & Campbell, 1969*a*) and orientation selectivity in higher mammals is unknown before cortex. This makes it easy to understand how a cone stimulus can influence rod threshold: cortical units can be stimulated by rods and cones alike. Further, if it is assumed that stabilized images when invisible fail to stimulate the cortical size-selective channels, the channel selection hypothesis can account for the otherwise puzzling observation of Barlow & Sakitt (1973) that in stabilized vision background size has little, if any, effect on threshold. The observations of Westheimer (1968) and Teller & Gestrin (1969) that threshold on a bleached ('dark light') background is independent of the size of the bleached area may be explained in the same way.

This work was supported by AEC Contract No. AT-(40-1)-2690, NSF grant GU-2612, and by a grant from NIH (1R01-EY00-684-01-VIS) to Professor W. A. H. Rushton. P. L. held a Harkness Fellowship.

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