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RECEPTIVE FIELDS AND TRIGGER FEATURES OF GANGLION CELLS IN THE VISUAL STREAK OF THE RABBIT'S RETINA

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SUMMARY

1. A survey of the properties of retinal ganglion cells in the central part of the rabbit retina has been carried out.

2. The five types of unit previously encountered in the peripheral retina were also found in the central region. Their receptive fields were smaller, and tended to be oval-shaped with the long axis horizontal.

3. In addition, three new types were discovered: orientation-selective cells, local-edge-detectors, uniformity-detectors.

4. Orientation-selective cells were sensitive to either vertically or horizontally extended targets. Analysis suggested they were modified concentric units with an incomplete antagonistic surround.

5. Local-edge-detectors responded to the appearance or movement of a contrasting border within the receptive field. They were inhibited by similar stimulation of the region surrounding the receptive field. Detailed attention was given to the demonstration of edge-detection.

6. Uniformity detectors had a relatively high level of ongoing activity in the absence of stimulation. All forms of stimulation (lights flashed on or off, movement of darker or lighter targets) produced a diminution or cessation of ongoing activity.

7. The results are compared with behaviour described in other species.

INTRODUCTION

A recent survey of the receptive fields of retinal ganglion cells in the rabbit (Barlow, Hill & Levick, 1964) brought out the fact that remarkable processing of visual information is carried out at the retinal level before the activity is passed on to higher centres. In addition to ganglion cells with concentrically organized receptive fields (on-centre and off-centre types)

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like the cat (Kuffler, 1953), the rabbit has others which are selective for the direction of movement of targets and for the velocity of targets moved across their receptive fields.

Some of the units encountered during the above investigation behaved in rather puzzling ways: the forms of stimulation customarily employed (moving large contrasting targets at moderate speeds of 10°/sec or so, flashing the background illumination, etc.) failed to evoke responses. It emerged that these units had small receptive fields (1–2° in diameter) with strong inhibitory surrounds. It was appreciated at the time that they did not form a homogeneous group; however, there were sufficient unifying features to justify calling them collectively 'small-field types'. These units were located in the region of densely packed ganglion cells. This part of the retina is called the visual streak and is an elongated strip occupying most of the horizontal meridian (Davis, 1929; Choudhury & Whitteridge, 1965).

A more detailed study of the units in the central region of the visual streak has now revealed that there are several classes of small-field units, each class signalling a different aspect of the retinal image. It is the purpose of this paper to present evidence for the differentiation of the various classes and the mechanisms whereby specificity for stimuli is achieved.

A preliminary classification of rabbit retinal ganglion cells has been published (Levick, 1965).

METHODS

The preparation has been described by Barlow *et al.* (1964). Briefly, pigmented rabbits were either lightly anaesthetized with urethane-chloralose mixture or decerebrated under thiopental or thiamylal anaesthesia. Muscular relaxation was produced by continuous infusion of gallamine triethiodide and the animal artificially ventilated with 97 % O_2 + 3 % CO_2. Anaesthesia was maintained in non-decerebrate preparations by adding urethane-chloralose to the continuous infusion. Periodically, anaesthetized preparations were allowed to recover from paralysis by using an infusion fluid without relaxant. One could thus ensure that the level of anaesthesia was neither too deep nor too light at the rate of anaesthetic infusion employed.

Recordings from ganglion cells or their axons in the retina were obtained with glass-insulated tungsten micro-electrodes introduced through a pressure-tight cannula penetrating the sclera just in front of the equator of the eyeball. Receptive fields were intercepted on an adjustable mirror placed before the eye and projected on to a horizontal screen of grey paper at a distance of 57 cm. Distortions caused by oblique viewing of the screen were always small. Fields were mapped with a spot of light projected on to the screen and turned on and off. In this paper, as in previous ones (Barlow *et al.* 1964; Barlow & Levick, 1965), 'receptive field' is to be understood as that part of the visual field stimulation of which by a small spot of light turned on or off yields a discharge from the cell. The properties of the units were investigated with mounted targets made from black and white card moved about on the screen by hand or by projecting stationary or moving patterns of light on the screen.

In view of the unusual behaviour of some of the units the possibility was considered that some of the recordings may have been from, say, amacrine cells or bipolar cells. This is highly unlikely. Deep penetrations of the retina were deliberately avoided. Moreover, the same types of unusual behaviour were identified with axon recordings from the nerve fibre layer.

The cornea was always protected by a plastic contact lens. Usually a 3 mm artificial pupil was used, either built in the lens or supplied by a diaphragm immediately in front of the lens. The natural pupil was dilated with atropine, but this was not needed with decerebrate preparations. Refractive errors were corrected with a spectacle lens selected by means of the relation between correcting lens power and the finest grating pattern still giving a response (Barlow & Levick, 1965). A spectacle lens was not always needed since the contact lens had been designed to provide additional refractive power.

Control experiments were performed on five excised eyes to assess retinal image size and quality by direct microscopic examination through the sclera. With contact lens and optimal correction, the posterior nodal distance varied from 11·3 to 11·7 mm and gratings with spatial frequencies at least as great as 8 c/deg of visual angle were distinguishable in the image.

RESULTS

General survey of visual streak units

On careful examination, about one third of the cells displayed properties which were essentially new. These will be described in later sections. The other two thirds were representatives of all of the classes encountered during the survey of the retina in general (Barlow *et al.* 1964); they included concentric (on- and off-centre), large-field and direction-selective (on–off and on) types; their relative abundance is indicated in Table 1. Although criteria already developed for distinguishing the classes were readily applicable, the properties differed in detail from those observed in units well away from the visual streak. The sizes of the receptive fields were, as expected, smaller, but the shapes of the fields were distinctly oval with the long axis horizontal. Moreover, many of the units, particularly the concentric types, had especially strong inhibitory surrounds, with the result that flashing the background illumination or moving large targets produced no effect, whereas local stimulation evoked powerful responses.

Table 1 indicates that a few so-called large-field units were found in the visual streak. Although their receptive fields were smaller than elsewhere in the retina and were oval, they had the typical sensitivity to fast target movement and faint dimming of background illumination. Their occurrence in the visual streak is further evidence that they are properly classified separately from off-centre concentric units. This question was left in some doubt in the previous survey (Barlow *et al.* 1964).

The units displaying essentially new properties could be subdivided into three types: orientation-selective units, local-edge-detectors and uniformity-detectors. The local-edge-detectors presented special problems during the search for units. Their receptive fields were small, they had no ongoing activity and they usually failed to respond to widespread brightening or dimming or to motion of targets at ordinary speeds (2–20°/sec). Further, their response to repetition of a stimulus often dwindled, and they responded feebly, if at all, to spatially extended (> 1°) targets. A useful aid to the search was a white piece of card upon which were pasted numerous pieces of black paper of irregular size and shape. If this was slowly shifted about across the projection of the visual streak, the local-edge-detectors could sometimes be provoked to fire before being inadvertently destroyed by electrode advance.

The new types of unit were encountered in unanaesthetized decerebrate preparations as well as in intact anaesthetized ones; the properties did not therefore depend upon centrifugal efferent activity, nor anaesthetic action.

The evidence for distinguishing these new units will be presented in the next sections.

TABLE 1. Receptive-field types in central visual streak

Type	No. of cells
Concentric (on-centre, 25; off-centre, 39)	64
Large-field	7
Direction-selective (on-off, 16; on 11)	27
Orientation-selective (horizontal, 10; vertical, 7)	17
Local-edge-detector	30
Uniformity-detector	4
Unclassified	5
Total	154

Orientation-selective units

There were some units which at first appeared to behave like the off-centre types when tested with small ($\sim \frac{1}{2}°$) circular discs or spots of light: it was possible to find some central region of the receptive field such that centrifugal motion of a spot lighter than the background, or centripetal motion of a darker spot would elicit a discharge. However, all radial motions did not give the same strength of response. Also, the receptive field map was different, in that regions giving on responses were rather difficult to find.

The divergence of behaviour became obvious when the receptive field was tested with long rectangular targets. In the example illustrated in Fig. 1, brisk responses were obtained for upward or downward motion of horizontally oriented rectangles lighter or darker than the grey background, whereas there was no response to a vertically oriented rectangle moved horizontally. The differences in timing and pattern of responses to black and white rectangles will be taken up later.

The orientation of the rectangle rather than its direction of movement was the critical feature. This was shown by moving a horizontally oriented rectangle in a horizontal direction across the receptive field. If this motion was carried out at the correct height, there was a brisk response. If the rectangle was oriented vertically and moved across the receptive field in a vertical direction, there was little or no response.

About half of the units (see Table 1) were selective for horizontally oriented targets, the other half for vertically oriented targets (example shown in Fig. 4). In every case the complete absence of response for either vertical or horizontal orientation respectively was found. Although the concentric type of unit in the visual streak often had a markedly oval-shaped receptive field, such a pronounced selectivity for the orientation of targets was never observed. There is no doubt that orientation-detectors form a distinct class.

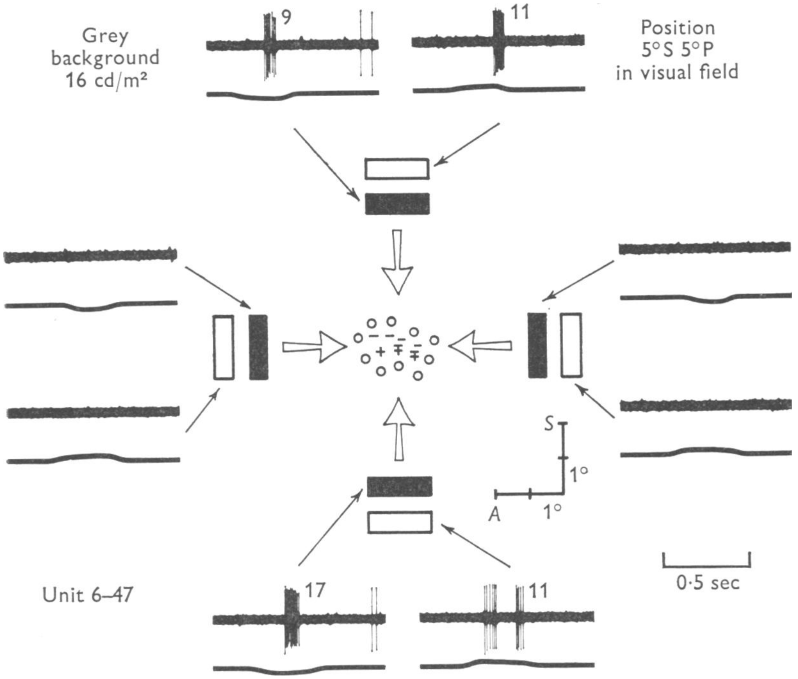


Fig. 1. Responses of an orientation-selective cell to movement of a rectangular target either darker or lighter than the background across the receptive field in different directions. Map of receptive field in centre; conventions: +, response to stationary spot at on; –, at off; ∓, at both on and off (at off stronger than at on); ○, no response; there were no responses outside the ring of ○'s. Anterior (*A*) and superior (*S*) meridians in the visual field are shown together with 1° calibration marks. All records read from left to right and each shows (upper trace) the response elicited (positivity down) and (lower trace) output of a photomultiplier focused on the receptive field (upward deflexion, increased light). The number of spikes is shown after each response. Only horizontally oriented targets yielded responses.

The selectivity for orientation could be demonstrated with stationary targets (Fig. 2). In this experiment a narrow rectangular strip of light was focused on the receptive field and oriented in different directions. When it was turned on and off, brisk responses at off were obtained only when the orientation was horizontal. As the orientation deviated more and more from horizontal so the response dwindled, and no response was obtainable for orientations at or near vertical.

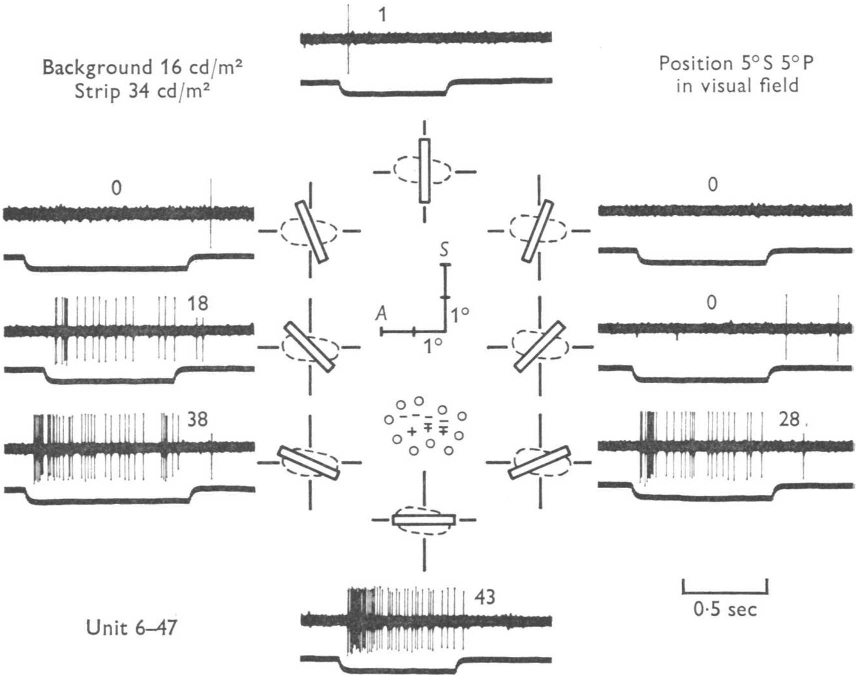


Fig. 2. Responses of orientation-selective unit to the turn-off of a rectangular strip of light oriented in various directions. The receptive field map is shown centrally and its outline is shown next to each record together with the rectangular stimulus. Same unit as Fig. 1, and conventions as explained there. The orientation of the flashed strip had to be near horizontal for strong responses.

Although most of the orientation-selective units had an off-core receptive field, two out of the seventeen had an on-core organization. Both were selective for horizontally oriented targets, the receptive fields were large and the responses rather sluggish.

The question arises: could optical imperfections, particularly astigmatism, be responsible for the behaviour? The arguments against an optical explanation are substantially the same as those given by Barlow & Levick (1965) for the direction-selective units. The strongest evidence is that units selective for horizontal and for vertical orientation can both be found in the same retinal region during the same experiment, as indeed can the ordinary concentric types. Furthermore, the focus of the eye can be altered with supplementary spherical lenses over a range of at least ± 6D without disturbing the selectivity for a particular orientation. Also, it is not possible to produce selectivity for orientation in the ordinary concentric type of unit by supplying cylindrical lenses up to ± 6D. Lastly there was no obvious shape distortion of a small circular disc of light projected on the retina and viewed ophthalmoscopically under the normal working conditions.

In addition to being insensitive to blurring of the retinal image, orientation-selectivity persists over a range of background intensities from 0·03 cd/m^2 to at least 500 cd/m^2 when the contrast of the target to the background is maintained at 1/5. It is clearly a secure property of the neurones that possess it.

Mechanism. The simplest hypothesis to account for the behaviour illustrated would call for a long thin region of off-responses to make up the receptive field. To some extent this has been borne out by the receptive field maps that have been plotted. To examine this idea a length-threshold experiment was performed. A narrow strip of light was focused on the receptive field and at each length the threshold intensity for an off-response was determined under two conditions: strip oriented horizontally and vertically.

Figure 3 is a plot of the results. The threshold for a horizontal strip fell rapidly as the length increased to about 1°; thereafter it remained approximately constant. For a vertical strip the threshold followed a similar course up to 0·6°. Beyond this, it rose progressively and became unmeasurable beyond 1·2°; although more light is being supplied by the greater lengths, the sensitivity is depressed. This result indicates that the ends of all but the shortest vertical strips activate portions of retina having a strong inhibitory influence on the response generated by the centre portion of the strip.

On the basis of the receptive field map, one might have expected that the threshold for the horizontally oriented strip would have continued to fall out to a length of 2–3°. The explanation for the discrepancy is probably that the horizontal orientation was not quite optimal for the unit (see Fig. 2, same unit); strips longer than 1° may have included small portions of the inhibitory flanks.

Detailed testing of other units showed that the inhibitory regions were paired and lay on opposite sides of the central core of off-responsiveness. The strengths of the two flanking regions were not always equal.

Inhibition was not the only effect obtainable from the flanking regions. Weak, inconstant on-responses could be obtained with small spot stimulation. Furthermore, the flanks could take advantage of areal summation and produce powerful on responses if stimulated *in toto* (Fig. 4). In two area-threshold experiments with the centre strip masked summation for the on-response occurred, out to about 2½° from the centre of the receptive field.

The experiment of Fig. 4 also demonstrates the mutual inhibitory interaction between the central core and the flanking regions: simultaneous illumination of both results in the suppression of both on- and off-responses.

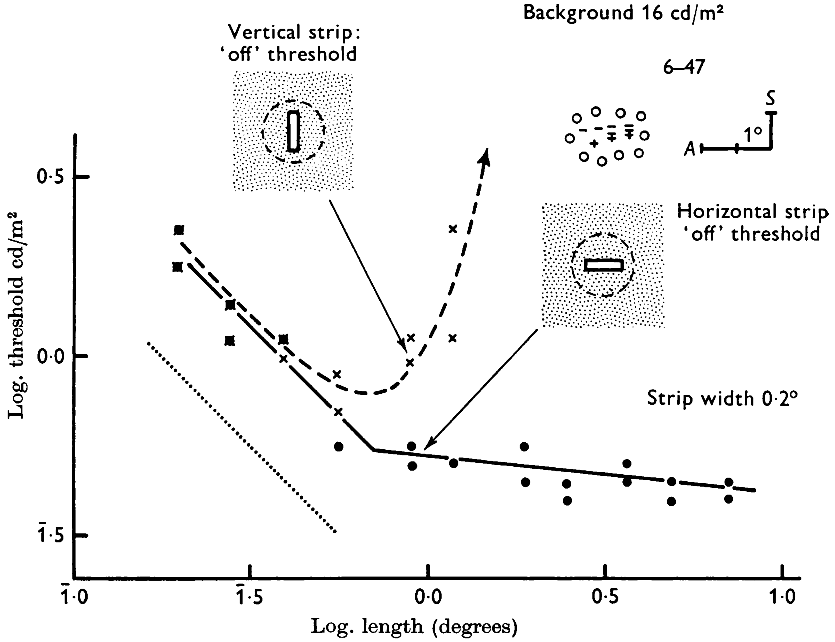


Fig. 3. Length–threshold relation of an orientation-selective unit for a narrow strip of light centred on the receptive field and oriented either vertically (×) or horizontally (●). Same unit as in Figs. 1, 2. The dotted straight line gives the expected slope of the relation if the threshold depended only on the total quantity of light delivered. Note the elevation of threshold for vertical strips longer than 0·6°.

The existence of at least one summating flank of on-responsiveness explains the pattern and timing of the responses to movement of horizontally oriented rectangles in the experiment of Fig. 1. With the black rectangle, a dense shower of spikes occurs as the figure moves up across the middle of the receptive field because the lower region of on-responsiveness is receiving an increase in illumination at the same time as the illumination of the off-core is decreasing. The response is weaker for downward movement because it is cut short by inhibition from the lower on-flank. The double response for upward movement of the white rectangle is caused by an early stimulation of the lower on-region, a period of inhibition as the white figure covers the off-core and a second stimulation as the figure moves off the off-core. The response for downward movement is single and late, most probably because the upper on-flank is feeble or absent (no upper on-responses in the receptive field map).

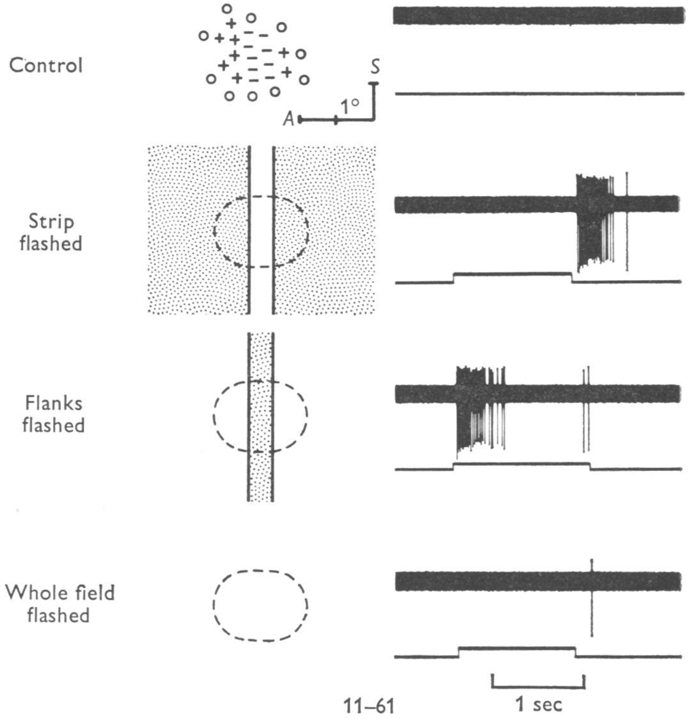


Fig. 4. Vertical orientation-selective unit. Receptive field map shown at top. Conventions as before. Control, absence of stimulation showing zero ongoing activity. Vertical strip stimulus yielded powerful discharge at off. Stimulus applied everywhere except for vertical strip yielded powerful discharge at on. Strip and flanks stimulated simultaneously yielded negligible response at both on and off.

The above analyses bring out many features of similarity between orientation-selective and off-centre concentric units: the pattern and timing of responses to moving targets (Barlow *et al.* 1964), the existence of summating regions of off- and on-responsiveness and mutually inhibitory effects from simultaneous stimulation of these regions. It is therefore natural to suggest that orientation-selective units are simply modified concentric units in which the antagonistic surround is effectively incomplete along the axis of their selectivity.

Local-edge-detectors

Amongst units previously reported by Barlow *et al.* (1964), those with on-off receptive fields were almost always direction-selective. However, this is not true of the visual streak units. About two thirds of those with on-off fields were non-selective for the direction of motion of targets. The receptive fields varied in size from 2° down to $\frac{1}{2}$° in diameter; some were circular, others were rather oval with the long axis horizontal. Responses at on and off were found at all points within the receptive fields. The relative sensitivities of on- and off-responses varied considerably from unit to unit.

The properties of a typical member of this class are illustrated in Fig. 5. The unit responded only to a small target ($<$ 1° in diameter), and then only if the target was moved slowly. If the motion carried the target across the receptive field at the usual speeds (2–5°/sec) the response was negligible (top record). Much stronger responses occurred if the target came to rest within the receptive field; when the target was moved away, a further strong response resulted. Much the same behaviour appeared whether the target was darker or lighter than the background. This pattern of activity is quite unlike that of on-centre or off-centre neurones because these new units respond to both centripetal and centrifugal motion of the same target.

The direction of motion was immaterial, as was the detailed shape of the target provided it was small. Much the same strengths of responses occurred when the background illumination was varied over the range from 0·08 cd/m^2 to 300 cd/m^2.

Stationary spots of light gave responses at on and off, but only if the spot was smaller than the receptive field (lowest 2 records, Fig. 5). This strongly suggests that stimulation of the region surrounding the mapped receptive field has an inhibitory effect on a response elicited from the centre. Yet stimuli confined to the surround region do not normally elicit impulses (example in Fig. 6, lowest record), a point which again distinguishes this class of unit from the concentric types.

The inhibitory surround. Some of the properties of the surround are illustrated in Fig. 6. Stimuli were applied to both centre (narrow strip) and surround (annulus with remote outer diameter) in different combinations. A summary of the results is as follows: inhibition was elicited from the surround when light was turned either on or off in the surround. The inhibition operated on both the on-response and the off-response elicited by centre stimulation, though not symmetrically, and was most effective when surround and centre events were simultaneous or nearly so. The results again distinguish this class of unit from on- and off-centre types.

Further observations on another unit are shown in Fig. 7. In this example, on- and off-responses to a small centred spot were brief. Simultaneous illumination of the surround ('whole field') cancelled the responses. However, when the stimulus pattern was modified by preventing stimulus light from reaching a circular patch within the receptive field ('unlimited annulus'), an on-response (delayed and weaker) reappeared.

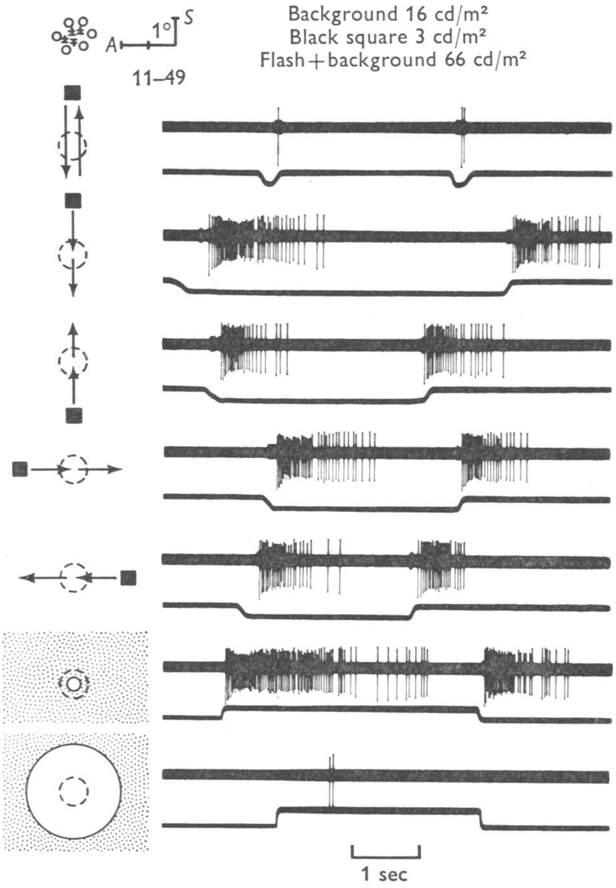


Fig. 5. Excitation of small on–off unit (local-edge-detector) by various stimuli. Receptive field at top left. Top record: small dark target (the shape is immaterial) carried across receptive field and back at about 3°/sec yielded little response. Next four records: same target moved into receptive field, stopped, moved out in four principal directions—vigorous response both on remaining in receptive field and on moving away after a pause. Note: the photomultiplier field was not accurately centred on the receptive field. Therefore, the timing relations of the response are not precisely deducible from the lower trace of each record. Last two records: small centred spot flashed yielded strong responses at on and off, but a larger spot gave negligible response. A second unidentified unit recorded at smaller amplitude appears in most of the traces.

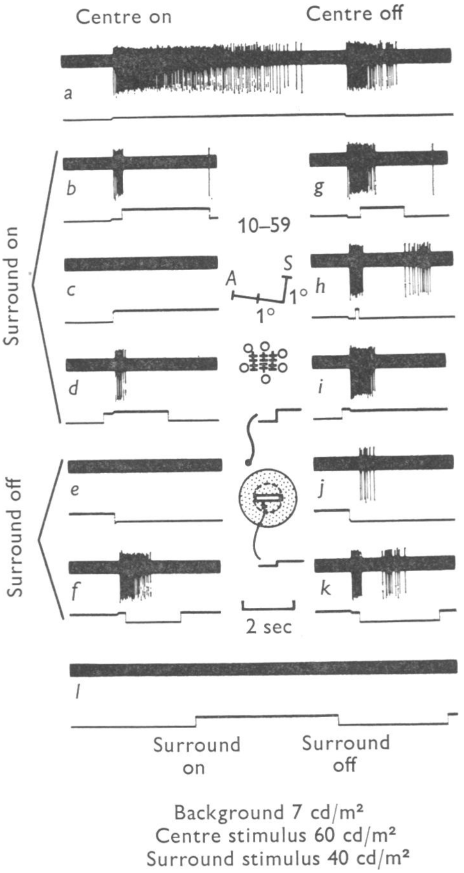


Fig. 6. Action of inhibitory surround of a local-edge-detector. Map of receptive field shown at the centre. Below it are diagrammed the stimuli in relation to the receptive field outline (dashed circle). Centre stimulus was a narrow strip of light shape is immaterial), surround stimulus was an annular patch, the inner perimeter of which is shown by the solid line surrounding the dotted region (unstimulated); the outer border of the surround stimulus was remotely located. The lower trace of each record is the output of a photomultiplier focused on the scene; larger step is caused by surround stimulus, smaller step by centre stimulus. Top (*a*) and bottom (*l*) are control records for centre and surround stimuli on their own. Left-hand column of records (*b*–*f*) shows the inhibitory effect on the on-response from the centre of turning the surround stimulus on (*b*, *c*, *d*) or off (*e*, *f*) with varying time relations including almost-simultaneous presentation (*c*, *e*). The right-hand column (*g*–*k*) shows the same information with respect to the off-response from the centre. Unfortunately, a record for simultaneous centre-off and surround-on presentation was not filmed, but the result was: complete suppression of response. Instead, record *h* shows that even a brief flash of the surround stimulus had a profound inhibitory effect.

This observation will be taken up in the next section. The point of interest for present purposes is the next record ('limited annulus'): the amount of light falling on the *surround* was also reduced by bringing the outer border of the annular stimulus closer to the receptive field. This abolished the response. Less light falling on the surround evoked greater inhibition. Could the stimulus for surround inhibition be the appearance of a contrasting border in the surround?

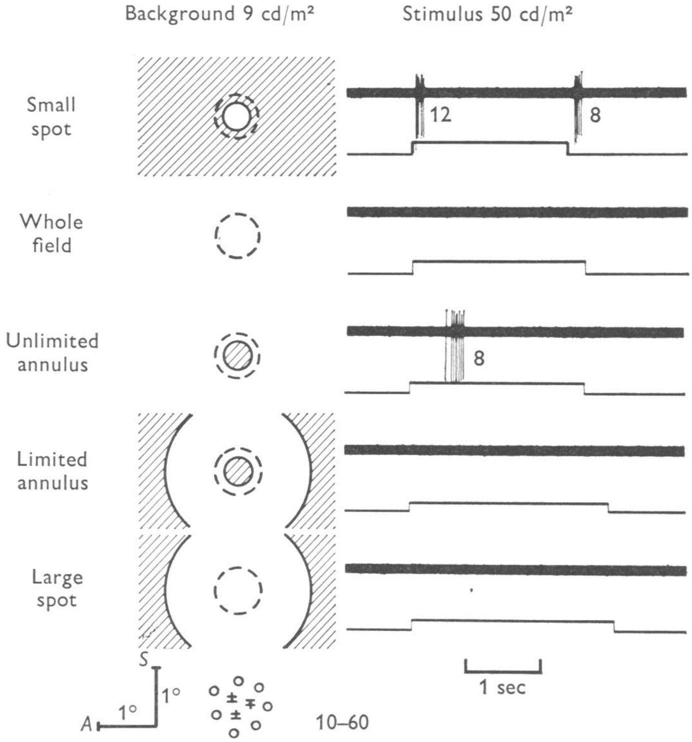


Fig. 7. Local-edge-detector. Receptive field map at lower left. Top record shows response to flashing a small centred spot. If the region around the receptive field is flashed as well ('whole field'), the response is abolished. If the light is prevented from reaching part of the receptive field 'unlimited annulus'), the response comes back. If light is also prevented from reaching part of the surround ('limited annulus') the response is abolished again. The simplest interpretation is that the requirement for a response is the appearance of a contrasting border in the receptive field and the non-appearance of a border in the surround. The bottom record ('large spot') shows that there is no response to the appearance of a border in the surround alone.

Three further types of observations on other units supported this idea. First, in the case of the 'limited annulus' stimulus, the response weakened as the outer diameter of the annulus decreased below 5°, disappeared for diameters below about 2½°, but returned when the outer perimeter fell within the receptive field. Secondly, to test explanations in terms of disinhibition (Ratliff, 1965, p. 113), the 'limited annulus' stimulus was modified by substituting a pattern of diverging radial stripes of light in the surround interrupting the simple circular outer boundary. This arrangement actually intensified the inhibitory effect. The reverse was expected on the basis of disinhibition from more distant retinal regions. Thirdly, fine grating patterns moved through the surround suppressed the responses elicited by the part of the grating moving across the receptive field (see Fig. 9, top 2 records). Although these tests point to the importance of contrasting borders in evoking surround inhibition, they do not exclude the possibility that changes in the diffuse illumination of the surround may also evoke inhibition.

Analysis of the centre response. While the experiment of Fig. 7 provided some evidence for edge-detection in the inhibitory surround, it also raised the question of edge-detection in the receptive field centre. To investigate this point, the threshold was measured for a centred spot of light turned on and off as a function of spot diameter; the threshold in the complementary situation, namely, light turned on and off everywhere except in a centred circular region was also measured. The results are shown in Fig. 8. On- and off-thresholds were very close in all situations. For the spot stimulus, the thresholds fell rapidly as diameter increased to about 0·3°; between 0·3° and 1·0°, it fell more slowly; beyond 1·3° it abruptly became unmeasurably high. For small spots the slope of the relationship suggests that the product of spot area and intensity is constant (Ricco's law of complete summation). However, for larger spots the slope suggests that the threshold now varies approximately inversely with the spot diameter or spot perimeter. This observation is consistent with the idea of edge detection but is hardly sufficient evidence on its own. The very abrupt rise in threshold as the spot perimeter goes beyond the receptive field edge is also suggestive but again not conclusive; if the rise in threshold were caused by illumination of the inhibitory surround one would have expected a more gradual rise.

Turn now to the complementary stimulus results. For the smallest diameters, the threshold was unmeasurably high; it became measurable at a diameter of 0·3° and for the next few sizes the thresholds were almost identical to those for the corresponding spot stimuli. Again there is an abrupt rise of threshold for diameters greater than 1°. All this is totally unlike the behaviour to be expected if the receptive field was simply responding to the change in total quantity of light falling on it. Less stimulus light was being supplied to the receptive field, yet the threshold fell. On the other hand, it does resemble the behaviour expected on the hypothesis that the excitation of the unit depends upon the length of an edge appearing within its receptive field. Note, for instance, the remarkable similarity of the threshold for a spot and for the complementary stimulus in the range 0·5–1° diameter. The only feature common to the pairs of stimuli is the perimeter along which they meet. The ineffectiveness of annular stimuli with inner diameters less than 0·3° could be attributed to the inhibition evoked by strong stimulus light falling on the surround.

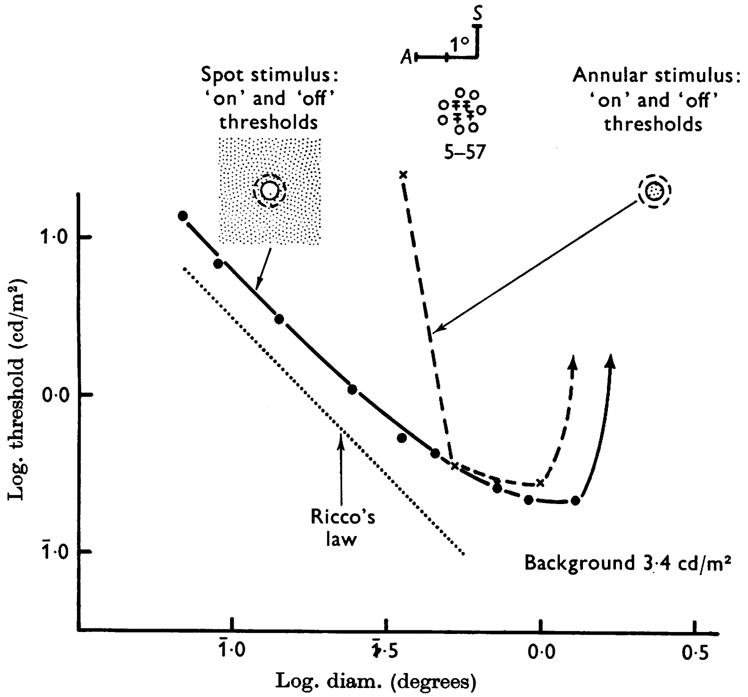
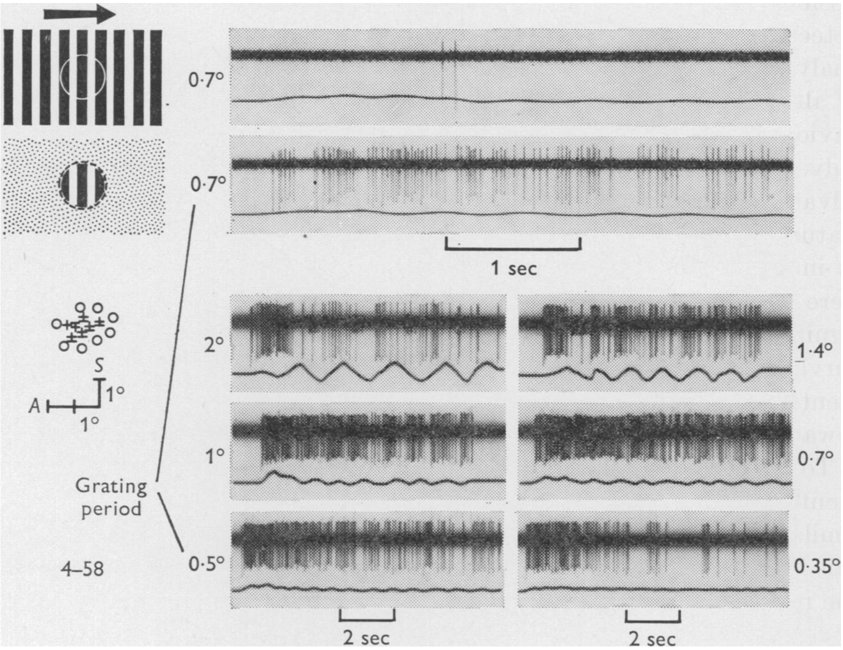


Fig. 8. Diameter–threshold relation for a local-edge-detector. The threshold of on- and off-responses was determined for centred spots of light (●) of varying diameter, and for centred annular stimuli (×) having varying inner diameter but fixed, very large outer diameter. The dotted straight line gives the expected slope of the relation for the spot stimulus if the threshold depended only on the total quantity of light delivered. Note the similarity of thresholds in the range of 0·4–1° diameter and the very sudden rise of threshold when the edge of the stimulus lies beyond the receptive field in the surround.

The experiment of Fig. 9 offers further support for the hypothesis of edge-detection. A pattern of equal-spaced black and white bars (square wave grating) of any period moved across the receptive field at about 1°/sec produced no response (top record). Masking off the inhibitory surround immediately released a vigorous discharge to movement (second record). The point of interest was that as the period of the grating was decreased from 2° to 0·7° the strength of the response obviously increased (all gratings were moved with approximately the same speed). At 0·5° period, the response was almost as strong as at 0·7°; at 0·35° period, the response was weaker and no response occurred for finer gratings. If the receptive field centre was simply responding to the amplitude of the change in flux reflected from the receptive field, the response should have dwindled progressively with grating period. On the other hand, the length of edge exposed to the field centre increased as finer gratings were used.



Square wave gratings, 90% contrast, mean luminance 17 cd/m²

Fig. 9. Response of local-edge-detector to moving gratings. Receptive field shown at left, middle. Grating pattern moved across receptive field and surround failed to evoke a response (top record) but if the surround was masked off, a vigorous discharge accompanied grating motion (second record). For the remaining records, the surround was masked off and progressively finer gratings (periods 2–0·35°) were moved, each at approximately the same linear speed. Though the amplitude of the change in flux reflected from the receptive field decreases (lower trace, output of photomultiplier focused on the field) the response increased with finer gratings down to 0·7–0·5° period. A second unidentified unit recorded at much smaller amplitude appears in the responses to the 2°, 1·4° and 1° gratings.

It is true that concentric units respond to unmasked gratings in a somewhat similar fashion: gratings of an intermediate period produce a greater discharge than those of greater or smaller period. However, it is found that the bar width of the optimum grating corresponds approximately to the diameter of the receptive field *centre*; the behaviour is readily explained in terms of optimal matching of the excitatory and inhibitory regions of the receptive field with black and white regions of the grating. Such an explanation will not work for the local-edge-detectors: on- and off-responses are found uniformly throughout the receptive field; there are no discernible subdivisions of the receptive field map which could be matched with the grating pattern.

Since units of this class bear some resemblance to the 'convex edge detectors' of the frog (Maturana, Lettvin, McCulloch & Pitts, 1960), the analysis was taken a little further. The question was: is it the small size, or alternatively curvature of the boundary which is involved in the behaviour of the units? Certainly the inhibitory surround will ensure that only small-sized targets are effective. But in the frog, evidence was advanced that convexity *within* the receptive filde was the effective feature. To check this possibility, the inhibitory surround was masked off as in Fig. 9 and targets presenting concave, straight and convex edges were advanced across the isolated receptive field (Fig. 10). There was no significant difference in the responses; moving edge independently of its curvature was the effective stimulus. It could also be shown in experiments of this kind that it did not matter whether the edge was moving toward or away from the centre of the receptive field.

To summarize: this class of unit is excited by the appearance or movement of contrasting borders within the receptive field and is inhibited by similar stimulation of the region surrounding the receptive field. To reflect this behaviour as 'local' is a more appropriate adjective than 'convex' in the name given to these units: local-edge-detectors.

Uniformity detectors

A small proportion (Table 1, p. 288) of the visual streak units had very peculiar properties. Unlike most of the others, these units had strong maintained discharges of about 10–20/sec in steady light. To begin with, the receptive fields were difficult to find because no stimulus could be devised which would accelerate the discharge. As soon as it was appreciated that slowing or cessation of discharge was correlated with presentation of targets, the fields could be mapped. The key features of one example are shown in Fig. 11. A spot of light flashed on the field abruptly stopped the discharge; turning the spot off immediately restored the discharge. It was not possible to accelerate the discharge by applying light mainly to the region surrounding the receptive field ('annulus flashed'); the suppression observed was probably caused by light falling on the extreme periphery of the mapped receptive field. Flashing of the whole background illumination produced the same effect as the centred spot, namely a suppression while the light remained on. The suppression was well sustained but did not last indefinitely: after some minutes, the discharge slowly started up and gradually returned to its former level. If the light was now turned off, the discharge stopped again for some minutes before returning to its former level.

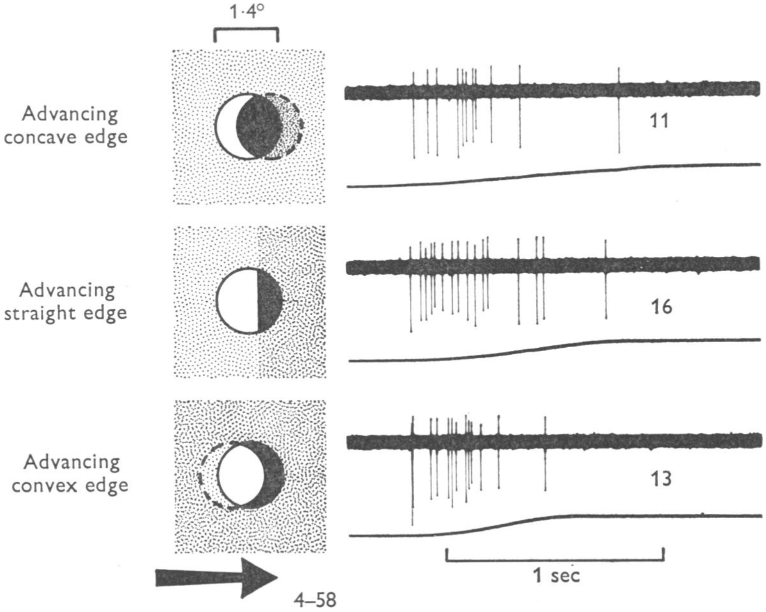


Fig. 10. Local-edge-detector: test for 'convexity-detection' by receptive field centre. Same unit as in Fig. 9. The surround was masked off by a grey card with a circular aperture 1·4° in diameter just fitting within the receptive field. A piece of card bearing black and white regions was moved from left to right so that the exposed portion changed from black to white. The advancing boundary was concave, straight or convex to the right in the three passes illustrated. The radii of curvatures were $-0{\cdot}7^\circ$, ∞, $+0{\cdot}7^\circ$ respectively. The number of impulses elicited is shown on the right of each record. The responses did not differ significantly.

Moving targets also produced sustained suppression (Fig. 11). The size, shape, orientation or direction of movement were not of special consequence. Targets either lighter or darker than the background elicited sustained suppression when moved into the receptive field. Grating patterns having periods down to 0·35° also effectively stopped the discharge.

Not all units in this class manifested such well sustained suppression. Others were only transiently ($\sim$ 0·5 sec) stopped by the stimuli described. In such cases, removal of the stimulus was also accompanied by transient stoppage and persistent suppression could be obtained only by moving or flickering the stimulus.

Although opportunities to study units of this class have been too rare to permit a detailed analysis of their mechanism, the following summary of their behaviour is warranted. The evidence shows that they differ radically from all types previously described: no stimulus could be found to increase the ongoing discharge; nor could an inhibitory or antagonistic surround be found. The suppression produced by fine gratings (Fig. 11) strongly suggests that they are inhibited by contrasting borders as well as by general increase or decrease of illumination.

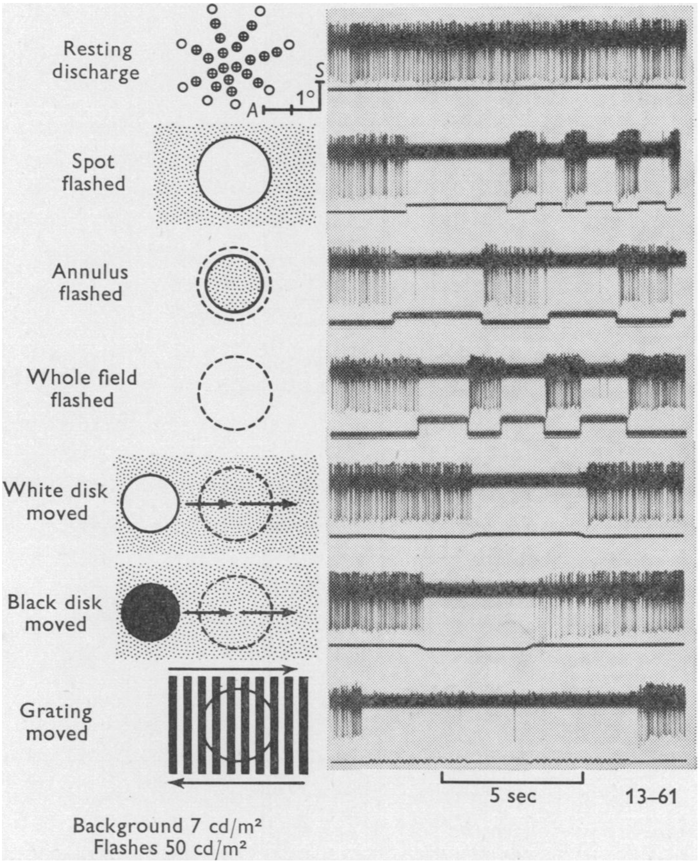


Fig. 11. Properties of uniformity detector. Receptive field map at top left. New symbol ⊕ indicates position where flashing a small light spot on stops or slows maintained discharge. At no position could an increase in firing be obtained. Top record: maintained discharge. Remaining records illustrate the variety of stimuli which suppress the discharge.

It is difficult to find a simple but accurate descriptive name for the behaviour. Since change (spatial or temporal) is what stops the impulses, then lack of change is the condition for obtaining the discharge; this is the argument for the label 'uniformity detector'.

DISCUSSION

The results presented are a further step towards specifying what the rabbit's eye tells the rabbit's brain. Detailed study of the central portion of the retina has added three new classes of ganglion cells, each having a distinctive trigger feature, to the five classes found in the inferior part of the retina (Barlow *et al.* 1964; Levick, 1965). In the diversity of function represented by the optic nerve output, the rabbit exceeds the extravagance described for the frog (Maturana *et al.* 1960) and pigeon (Maturana & Frenk, 1963). Even so, the specification is not complete: the superior retina and anterior and posterior ends of the visual streak remain to be checked and some puzzling observations on the earlier classes have to be resolved. It is little wonder that Arden (19~~6~~53 *a*, *b*) encountered some problems in the rabbit lateral geniculate nucleus.

Experience with each of the three new classes of unit again bears out a point made earlier by Maturana *et al.* (1960) and more recently by Barlow *et al.* (1964): in the initial stages, both one's attitude and one's equipment must be completely flexible even at the expense of some precision of measurement. For instance, the orientation-selective units were thought to be off-centre concentric types until they were tested with elongated targets; careful measurement of area-threshold relationships with centred spots and annuli failed to make the distinction.

Orientation-selectivity

Units selective for the orientation of targets have now been found in the visual cortex of cat and monkey (Hubel & Wiesel, 1962), and in the pigeon retina (Maturana & Frenk, 1963) as well as in the rabbit retina. Different units prefer different axes of orientation, and the activity of a set of such units is capable of being used to determine the orientation of targets in the visual field. However, the rabbit's retinal system is rather crude: there are relatively few units and only two preferred orientations are represented, horizontal and vertical.

The question arises; how useful would this system be to the rabbit? One deficiency is immediately recognized: the output of the set of units would be ambiguous with respect to targets inclined at 45° and 135° to the horizontal. Van Hof (1966) has recently examined the rabbit's ability to discriminate between striped patterns of different orientation and found that there was no difficulty for targets inclined at 45° and 135°. The animals learned the discrimination just as readily as with horizontal versus vertical targets. Barring the unlikely possibility of special eye and head movements, there seems little doubt that the rabbit uses information other than that provided by the retinal orientation-selective system in the 45–135° discrimination task.

Edge-detection

By using the term 'edge-detector', one is implying no more than that the relevant observations of unit behaviour are thereby most economically described and most meaningfully interpreted. One of the main tasks of this paper was to present the observations and make the case for edge-detection by a particular class of unit. It is not claimed that edge-detection is the only good description or even the best. There is always some doubt that a sophisticated stimulus revealing subtle behaviour has been missed. It is also possible that the breadth of even human language may not enable one to capture the essence of a rabbit-unit's behaviour in a single, simple phrase.

Edge-detectors in the frog. Three of the five classes of ganglion cell in the frog retina are specifically concerned with the detection of contrasting borders in the visual field (Maturana *et al.* 1960; Lettvin, Maturana, McCulloch & Pitts, 1959; Lettvin, Maturana, Pitts & McCulloch, 1961). Perhaps the type most closely resembling the rabbit edge-detectors is the 'moving or changing contrast detector'. These are probably the on-off units first described by Hartline (1938, 1940*a*, *b*) and subsequently analysed in more detail by Barlow (1953) who supplied observations and arguments for regarding them as movement-detectors and showed that they possessed inhibitory surrounds.

Lettvin and colleagues described an interesting property named 'erasibility' in which the sustained response to a small target moved into a receptive field was abolished by transient darkening of the background illumination. Some of the effects of the inhibitory surround of the rabbit edge-detectors (Fig. 6) could be described in terms of erasibility. The property might serve a useful function for the animal: blinking the eye would not only wash the cornea; it would also wipe clean the map of the visual world provided by units of this class. The place in this map where activity occurs after a blink would then signal the most recent or most urgent development in the visual scene; the value of erasure would be in simplifying this detection.

Comparison with direction-selective units. There are some interesting similarities between the edge-detectors and on-off direction-selective units: (*a*) both have receptive fields with more or less transient responses at on and off to a small stationary testing spot; (*b*) both respond about equally to targets lighter or darker than the background; (*c*) both give strong responses to movement of gratings (edge-detectors require masking of the inhibitory surround); (*d*) both resolve gratings with periods going down to about 0·7–0·5°; (*e*) they have similar diameter-threshold relations for spot stimuli, at least up to the receptive field size of the edge-detector; (*f*) they have similar diameter-threshold relations for annular stimuli (unpublished observations on direction-selective units); (*g*) both have surround regions which deliver inhibition when light is turned on or off or when contrasting borders are moved, but ordinarily release no excitation (cf. on- and off-centre units) to the cell.

Now it has been shown (Barlow & Levick, 1965) that direction-selective ganglion cells are very likely picking up from a subset of bipolar cells sensitive to a particular sequence of stimuli in their locality. On this view there must be at least four subsets of bipolar cells sensitive to different spatial sequences because there are ganglion cells selective for at least four different directions of motion. Could it be that the edge-detectors pick up non-selectively from bipolar cells of all four subsets? This would explain how the two classes of units share so many common properties, though only one of the classes preserves a selectivity for direction.

If the suggestion is correct, an immediate consequence is that the structural arrangement underlying the selectivity for sequence for the direction-selective cells (Fig. 11, Barlow & Levick, 1965), is also what is required for edge-detection.

Functional significance. When a rabbit suddenly stops sniffing around in the foliage and lifts head and eyes above the long grass to study the distant environment, its brain will continue to be bombarded by an irregular roar of activity from the on- and off-centre ganglion cells in the retina signalling the contrasts of the new view, but at least one class of unit will at first be completely silent—the local-edge-detectors. Gross movement of the visual field associated with the change of attitude blocks them via the inhibitory surrounds. Soon, something in the distance moves against the now steady background; its retinal image will be small and will move slowly; one of the edge-detectors therefore starts signalling. It is providing the position information of the most significant event in the environment for the rabbit; it tells where in the tumult of information from concentric units special attention is required.

Such speculation can easily be continued, but it is already beyond the safe ground of fact. Nevertheless, it does give the flavour of this type of work, and it will help guide the pursuit of the coded messages centrally.

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