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RECEPTIVE FIELDS OF GANGLION CELLS IN THE CAT'S RETINA

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In his analysis of retinal ganglion cells in different mammals, including the cat, Granit (1947, 1955) found that diffuse illumination of the retina gave rise to three types of responses: depending on the type of discharge the different ganglion cells were called 'on' units, 'off' units and 'on-off' units. The discharges were similar to those previously found by Hartline (1938) in the frog. Using small-spot stimulation, Kuffler (1953) has shown that on the basis of their receptive field organization there are only two types of ganglion cells in the cat retina. One gives 'on' discharges when the centre is stimulated and 'off' discharges to illumination of the periphery of the receptive field. The other type shows the reverse arrangement with 'off' responses in the centre and 'on' responses in the surrounding area. The 'on-off' response to diffuse illumination is the result of a combined contribution from the centre and periphery of receptive fields. Kuffler also showed that the central and peripheral portions within each receptive field are mutually antagonistic. These findings in the cat have subsequently been extended and confirmed (Barlow, FitzHugh & Kuffler, 1957*a*, *b*; Wiesel, 1958; Hubel, 1960).

The main object of the present study of retinal ganglion cells was to examine the size of field centres and the modification of discharges by inclusion of the surrounding area. The method of Barlow (1953) using light spots of different sizes and measuring thresholds for influencing the discharge from individual ganglion cells was found most useful. This area–threshold technique revealed striking differences between individual ganglion cells and between cells in the area centralis and the periphery of the retina. A preliminary account of some of this work has been published (Wiesel & Brown, 1958).

METHODS

A detailed description of the method used in these experiments has recently been given (Brown & Wiesel, 1959). Twenty-six cats were kept under light anaesthesia with intraperitoneal injections of sodium pentobarbital (initial dose 20–30 mg/kg) and Dial (allobarbitone; Ciba)

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with urethane (initial dose 0·25 ml./kg). The eyes were immobilized by continuous intravenous infusion of succinylcholine (about 10 mg/kg/hr), which made artificial respiration necessary. Atropine in 1 % solution was used to dilate the pupils and relax accommodation. The corneas were kept moist and clear with contact lenses and buffered lens solution.

The multibeam ophthalmoscope of Talbot & Kuffler (1952) was used for stimulation. This provided a steady background retinal illumination of 0·34 log lm/m² over an area 4 mm (16°) in diameter. Stimuli consisted of spots of light of various sizes with a maximum intensity of 1·85 log lm/m². Intensity of illumination was regulated by circular wedges. Spot sizes, centred in the area under background illumination, varied in steps from 0·125 mm (0·5°) to 3 mm (12°) in diameter. The spots and background could be positioned in different regions of the retina.

Electrical recordings from the retina of the intact eye were made with micro-electrodes, guided through the sclera by a hypodermic needle, approaching the retina from the vitreous side. A ball-joint arrangement made it possible to direct the electrode to different parts of the retina (Talbot & Kuffler, 1952). The electrode was advanced by a hydraulic system. Two types of electrode were employed. The most commonly used were 3 M-KCl-filled glass micropipettes with tip diameters less than 0·5 μ and d.c. resistances of 15–30 MΩ. The other type was a 10–15 μ glass-insulated platinum electrode similar to that developed by Granit & Svaetichin (1939). A negative-capacitance pre-amplifier with a grid current of 5×10^{-12} A was fed into a wide-band a.c.–d.c. amplifier which was connected to an oscilloscope.

The threshold of a stimulus spot was given by the lowest intensity of light which produced a clear and repeatable change in the maintained impulse activity. The change in discharge frequency was detected by observing the impulses on an oscilloscope and by listening to a loudspeaker. Each stimulus lasted 0·8 sec and was repeated every 10 sec. Several wedge readings were taken, first with increasing and then with decreasing spot sizes. Adaptive effects due to the recurrent stimulus were not observed, presumably because the background illumination was well within photopic range.

RESULTS

Receptive field size

Single-unit activity was recorded from a few hundred ganglion cells in various regions of the cat's retina. Micropipettes recorded this activity within the retina at depths up to 30–40 μ (Brown & Wiesel, 1959), whereas platinum electrodes only recorded from the surface of the retina. Cells were continuously active during steady background illumination; this maintained activity showed great variation from unit to unit (Kuffler, FitzHugh & Barlow, 1957). After a ganglion cell was located its receptive field was first mapped out by the smallest spot that gave clear on- or off-responses. Each receptive field had a centre more or less circular in shape, surrounded by a peripheral zone. The total receptive-field sizes including both centre and periphery were usually 2–3 mm in diameter. On- and off-centre units were recorded in about equal numbers both from the area centralis and from the periphery of the retina.

The size of receptive field centres was determined by the area–threshold method. As the size of a centred spot increased, the threshold for the centre response usually decreased; similarly if the stimulus intensity

was kept constant the centre response itself increased. Thus, there was summation over this area. Increasing the spot beyond the size of the field centre did not cause a further lowering of threshold, but, on the contrary, the threshold actually rose as more of the periphery was included (Barlow *et al.* 1957*b*).

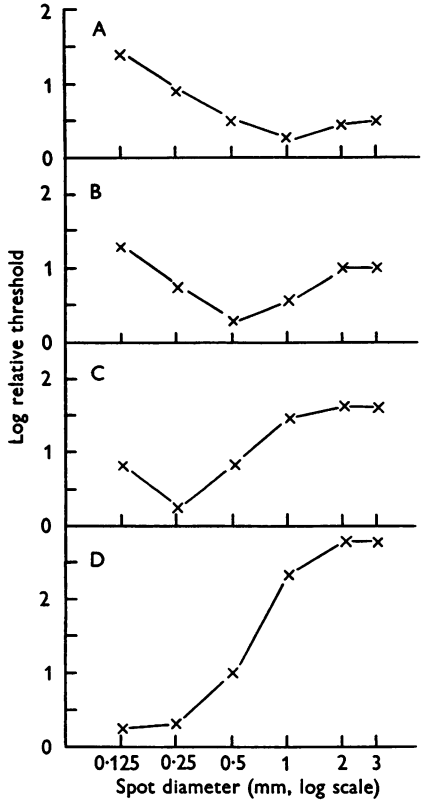
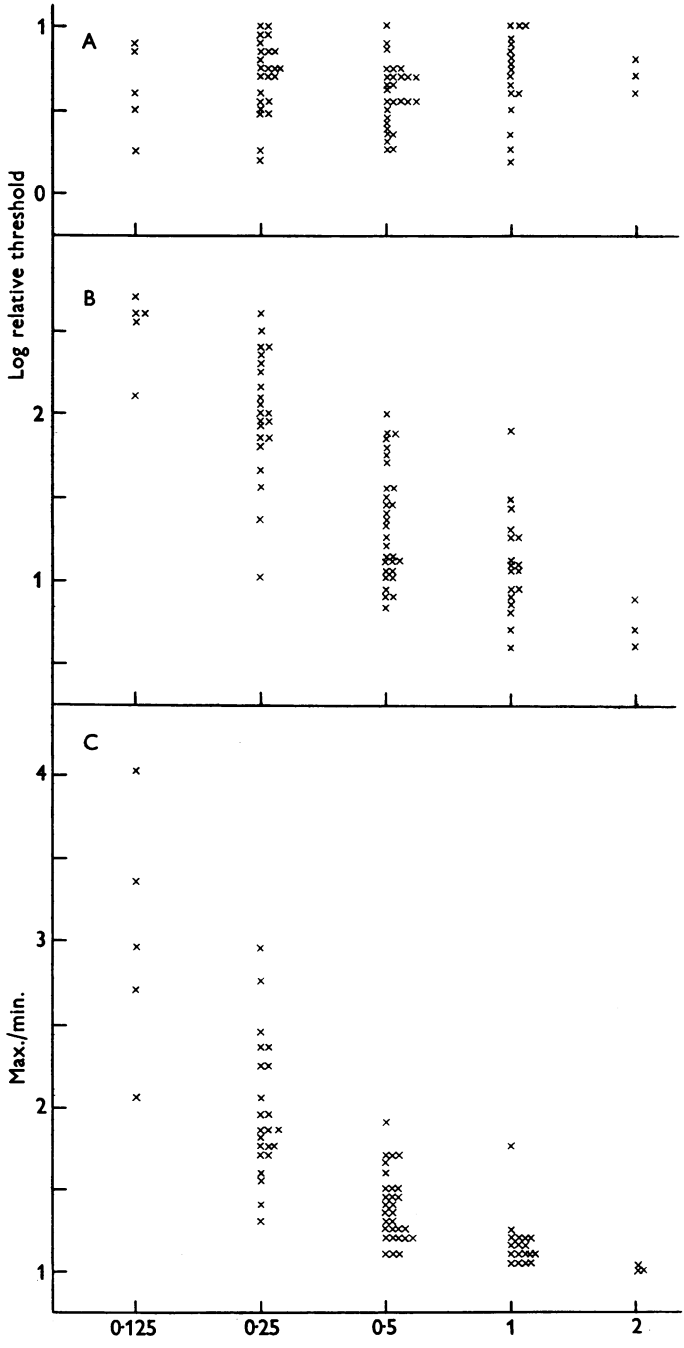


Fig. 1. Changes in threshold of centre responses with area of illumination measured for four different ganglion cells, all 'on'-centre units. Abscissa: spot diameter. Ordinate: threshold, relative logarithmic scale: 0 corresponds to a stimulus of $\bar{2}{\cdot}35$ log lm/m^2. Background retinal illumination 0·34 log lm/m^2. Stimulus duration 0·8 sec.

The relation between stimulus size and response was mainly studied with threshold stimulation. However, similar results were obtained by using supra-threshold stimuli of constant intensity and measuring latency and impulse frequency for different spot sizes (see also FitzHugh, 1957). Because of the effects of scattered light, measurements at more than about 2 log units above threshold intensities were considered unreliable.

Figure 1 gives a representative sample of area–threshold curves from



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which the sizes of receptive field centres can be determined. For cell A there was summation of centre responses up to 1 mm., i.e. its centre area was about 1 mm in diameter. In B the centre response summed over 0·5 mm, while in C the area was 0·25 mm in diameter. The ganglion cell of Fig. 1D had its lowest threshold for the smallest available spot, 0·125 mm in diameter. The optimum spot for ganglion cell A (Fig. 1) was thus sixty-four times that of cell D. Since the spot sizes were varied in fixed, rather coarse, steps, this ratio may not accurately reflect the ratio of the receptive field centre areas. However, it is clear that the centre areas must be strikingly different in size.

The antagonistic influence of the periphery of the receptive field on the centre can also be seen in Fig. 1. There was a rise in threshold of centre response as more of the surround was included in the area of illumination. The amount of this peripheral suppression of centre response varied from one cell to another. In the cell of Fig. 1D the difference in threshold for a spot 0·125 mm in diameter, illuminating only the centre, and a 2 mm spot covering the whole receptive field, was about 2·5 log units. The cells in B and C showed less peripheral suppression, and the cell in A with the largest centre showed only a small difference in threshold between centre and whole-field illumination.

For the units of Fig. 1, when the spots were increased beyond 2 mm in diameter there was no further change in threshold for the centre response. Presumably the spots were now larger than the receptive fields. Sizes of receptive fields measured by the area–threshold method agreed reasonably well with those obtained by mapping fields with small spots. Thus the total field diameter for each of these four ganglion cells was about 2 mm, despite the differences in centre size. Obviously, cells with smaller centres have relatively larger peripheral zones (as seen in Fig. 1) and ganglion cells with larger centres have narrower peripheral zones.

In comparing receptive fields striking differences were thus found in the size of centre portions. Cells were therefore divided into groups according to the size of centre areas and were studied by illumination of (1) only the centre portion and (2) both centre and periphery. In Fig. 2, eighty ganglion

Fig. 2. Eighty ganglion cells divided into five groups depending on sizes of the receptive-field centres. Abscissa: diameter of centre area (optimum spot). Stimulus parameters same as in Fig. 1. A. Distribution of threshold values of centre responses with illumination confined to the centre portion of the receptive field (optimum spot stimulation); ordinate: log. relative threshold. B. Distribution of threshold values of centre responses for the different groups on stimulation of both centre and periphery (whole-field illumination). Stimulus spot 3 mm in diameter. Ordinate: log. relative threshold. C. Ordinate: the ratio, taken for individual ganglion cells, of threshold values at whole-field illumination to threshold values at optimum spot stimulation.

cells are divided into five groups according to the size of the optimum spots; these groups are marked on the abscissa. Threshold intensities of optimum-size spots are shown in A. Threshold values were scattered over about 1 log unit for ganglion cells in the same group. All groups had this scattering and there seemed to be no systematic variations of threshold with size of optimum spot. This would indicate that if illumination is restricted to the centre region of receptive fields the sensitivity is not related to the size of the centre. These measurements were all made in the light-adapted state, well within the photopic range of background illumination: the situation may be quite different in the dark-adapted state.

At whole-field illumination, or diffuse light stimulation, when centre and periphery were stimulated simultaneously, differences in thresholds for centre responses ('on' or 'off', depending on the cell) varied with the size of the centres. In Fig. 2B a spot 3 mm in diameter was used, and threshold values were plotted for the same groups of ganglion cells as in Fig. 2A. It is clear that to obtain a response with such a large spot a strong stimulus was necessary if the centre of the receptive field was small. Ganglion cells with large receptive field centres, on the other hand, were influenced at much weaker intensities; threshold values for whole-field illumination could be as much as 2 log. units lower for large centre compared with small-centre ganglion cells.

The differences in sensitivity between centre-field and whole-field illumination were usually not great for large-centre ganglion cells, indicating weak antagonism from the periphery of the receptive field. The small-centre ganglion cells, however, showed strong peripheral suppression of centre responses. This suppression of centre responses from the periphery of the field is also expressed in Fig. 2C. Here the ratio between threshold values for the spot covering the entire field (B) and for the optimum spot (A) is taken for the ganglion cells in the different groups. The ratio is large when the antagonism from the periphery is large, and approaches unity as the peripheral influence on the centre response becomes insignificant. In other words, ganglion cells with small centre areas have a high ratio and this ratio tends towards unity with increasing centre areas.

Peripheral-type responses

So far only centre responses from ganglion cells have been considered. That is, in determining thresholds attention was focused on the 'on' response for 'on' centre units, and on the 'on'-suppression and 'off' discharge for 'off' centre units. If, for instance, in an 'on' centre unit, an 'off' discharge developed as the periphery was invaded, this part of the response was ignored in determining thresholds. For each ganglion cell, however, responses from the periphery of the receptive field can be tested

in the same manner as for the centre. The periphery was stimulated by annular stimuli, i.e. rings of light which did not illuminate the centre. The outside diameter was kept at 3 mm, centred on the field, and the inside diameter was constricted so as to include more and more of the receptive field. In Fig. 3 threshold values are shown for a ganglion cell stimulated by spots and annuli. The solid line represents the area–threshold curve for the centre response as already described in Fig. 1. The broken line shows the threshold values of the peripheral response for different sized annuli. The inside diameters of the annuli are plotted on the abscissa together with spot diameters, so that for the annulus the area of stimulation increases when reading the curve from right to left. Both types of responses showed summation within their respective regions: the centre response summed within an area of 0·5 mm in diameter, whereas the summation of the peripheral response was over an area given by an annulus of 0·5 mm inside and 3 mm outside diameter. The presence of mutual antagonism can also be deduced from the two curves: the threshold of the centre response increased when the stimulus spot invaded the periphery of the receptive field and similarly the peripheral response had higher threshold when the annulus included part of the centre in the area of illumination.

For annuli of optimum size the threshold values for peripheral responses were always higher than thresholds obtained with optimum spots for centre responses (see Fig. 3); sometimes this difference between centre and peripheral thresholds was very small. Some ganglion cells gave 'on-off' responses to whole field illumination at threshold intensities. This was true for both 'on' centre and 'off' centre units but was somewhat more common for 'off' centre units. Since the thresholds of centre and periphery may be equal or almost so, it is not surprising that 'on-off' responses are often encountered at whole-field illumination (Granit, 1947).

Comparison of ganglion cells in the area centralis and in the periphery of the retina

The area centralis in the cat is homologous with the foveal region of certain other species. It can be recognized by the relative absence of vessels, by the radial arrangement of surrounding vessels and by differences in pigmentation. There are also electrical criteria for finding the area centralis. Thus a platinum electrode touching the peripheral retinal surface records mass discharges from non-myelinated axons, which are just under the inner limiting membrane. These axons are from more peripherally located ganglion cells on their way towards the optic disk. The area centralis is practically free from such 'passing' fibres and consequently no mass discharges of axons are recorded from this region. These different criteria made it possible to position an electrode either within the region

for central vision or else in clearly peripheral parts of the retina. No comparison was made between different parts of the periphery, and only that region of the retina which has a tapetum was studied.

The over-all receptive field diameters measured with the area–threshold method were between 1·5 and 3 mm, but no striking differences in total field size were found between cells in the area centralis and the periphery

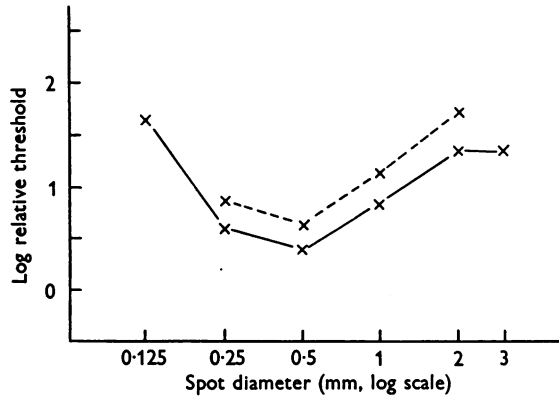

Fig. 3. Area–threshold curves for both centre- and peripheral-type responses of a ganglion cell recorded in the middle periphery about 15° from the area centralis. Abscissa: diameters of spots evoking centre-type responses or inside diameters of annuli producing peripheral-type responses. Outside diameter 3 mm for all annuli. Ordinate: thresholds, relative log. scale. Stimulus conditions as in Fig. 1. ——, area–threshold curve for centre-type response; – – –, area–threshold curve for peripheral-type response.

of the retina. In contrast, the sizes of centre portions of receptive fields showed a difference in distribution between the two retinal regions. In Fig. 4A ganglion cells are again grouped according to the area over which the centre response summed. In each group the white columns represent units from the area centralis and the black columns units with receptive fields in the periphery of the retina. Eighty-two units are included in the histogram: forty-nine of these are from the area centralis, and thirty-three from the periphery. The majority of ganglion cells from the area centralis summed only over an area up to 0·25 mm in diameter, whereas most cells from the periphery showed summation over a larger area.

In the lower histogram (Fig. 4B) are included eighteen cells from the area centralis (white columns) and seventeen cells from the periphery (black columns) all of which were recorded with platinum electrodes. With this electrode, as with the pipette, the centres of cells from the area centralis tended to be smaller than those of cells recorded in the periphery. However, the much larger platinum electrode did not record ganglion cells

with centres smaller than 0·5 mm in diameter; these were quite frequently found with micropipettes.

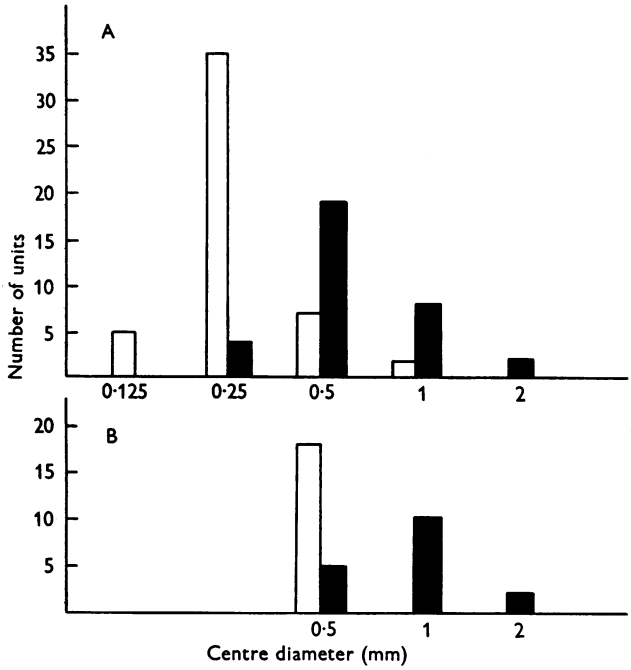

Fig. 4. Distribution of receptive field centres with respect to diameter. White columns indicate cells recorded in the area centralis, black columns, cells from the periphery of the retina. Abscissa: diameter of centre of receptive field. Ordinate: number of cells. A. Eighty-two ganglion cells recorded with micropipette electrodes; forty-nine are from the area centralis and thirty-three from the periphery. B. Thirty-five cells recorded with platinum electrodes; eighteen from the area centralis and seventeen from the periphery of the retina.

DISCUSSION

A comparison of single unit responses in the visual system of the cat indicates that the balance between excitatory and inhibitory influences becomes more critical at successively higher levels (Hubel & Wiesel, 1959). A similar trend was observed in this study for ganglion cells if central and peripheral regions were compared. It was, for example, found that in order to be influenced by diffuse light ganglion cells in the area centralis required much more intense light than peripheral cells. This does not necessarily mean that ganglion cell responses in the area centralis are genuinely less sensitive to any light stimulation, since if only the centre portions of cells in the two regions were illuminated they had similar sensitivity. This is probably related to the fact that ganglion cells in the

area centralis tend to have small but concentrated centre portions and relatively large, strongly antagonistic peripheral zones. Ganglion cells in the periphery, on the other hand, tend to have larger centres and relatively narrow and less influential surrounds. It should be noted that these findings apply to the light-adapted retina only. In darkness the relative influence of the surround is diminished or may disappear (Barlow *et al.* 1957*b*; Wiesel & Brown, 1958).

The relatively large receptive fields, 6° to 12° in diameter, found for ganglion cells in this and previous studies (Kuffler, 1953; Barlow *et al.* 1957*b*) would seem at first sight difficult to reconcile with the high visual acuity of the cat (Smith, 1936). However, the important dimension of receptive fields from the standpoint of acuity is probably the size of the centre portion. In these experiments the smallest available spot had a diameter of 30 min; ganglion cells with smaller centre regions, which may be abundant, could not be studied. Receptive fields with small centres have been found in retinal ganglion cells in the spider monkey by a projection method of retinal stimulation (Hubel & Wiesel, 1960). No recordings were made from foveal ganglion cells but units with receptive fields close to the fovea had centre diameters down to 4 min of arc. Further away from the macula the centre diameters became progressively larger. Thus the receptive field centres of foveal ganglion cells in the monkey may approach in size the minimum separable acuity of about 1 min of arc, determined for primates with a well developed fovea (Grether, 1941). In a discussion of possible mechanisms in high-acuity vision not only the centre size should be considered; the antagonistic peripheral portion of receptive fields is probably equally important. Peripheral suppression of the centre response renders big spots relatively ineffective; centre-size spots thus become the most powerful stimuli. Furthermore, a sharp border between centre and periphery of receptive fields is very likely significant for good visual performance, particularly in respect to moving images, where movement from an 'off' to an 'on' region is doubtless a powerful stimulus (Hubel & Wiesel, 1959).

In recordings from retinal ganglion cells in the cat Rushton (1949) concluded that a 25 μ platinum electrode recorded mainly from very large, 'giant' ganglion cells. He felt that ganglion cells recorded by this method may not be representative for the population of ganglion cells, in which small cells predominate. Kuffler (1953) also found that platinum electrodes (10–15 μ) selected larger ganglion cells, which, however, could be smaller than the 'giant' type. In the present experiments platinum electrodes recorded only cells with receptive-field centre diameters of 0·5 mm (2°) or more, in agreement with the notion that electrode size, cell size and measured receptive field sizes are related. Such a relation is suggested by

the predominance of small cell bodies and small receptive-field centres in the area centralis. Micropipettes with very fine tips showed less selectivity and accordingly recorded cells with a range of centre sizes from 0·125 mm (0·5°) to 2 mm (8°). The selectivity of different electrodes is also reflected by the finding that among fifty-six ganglion cells recorded in the area centralis with platinum electrodes there were three times more 'on' centre than 'off' centre units, whereas micropipettes, in the same area, recorded ganglion cells of the two types in about equal numbers.

SUMMARY

1. Ganglion-cell discharges were recorded in the intact eye with micropipettes and platinum electrodes. Receptive fields of ganglion cells were studied in the light-adapted state mainly by measuring the relation of threshold to area of illumination.

2. For different ganglion cells receptive-field centres varied in diameter from 0·125 mm (0·5°) to 2 mm (8°). With the light stimulus restricted to the centre of receptive fields the sensitivity of ganglion cell responses was not dependent on the size of the centre region.

3. Ganglion cells with small receptive-field centres showed an increase in threshold of up to 2·5 log. units when the peripheral portion of receptive fields was included in the area of illumination. This peripheral suppression of centre responses was less pronounced for large-centre ganglion cells. Thus at whole-field illumination (diffuse light stimulation) there was a clear difference in sensitivity of ganglion-cell responses depending on the size of field centres.

4. Ganglion cells with small field centres were most often recorded in the area centralis, the region for high acuity vision; larger field centres were more common for ganglion cells recorded in the periphery of the retina.

5. Micropipettes recorded activity from ganglion cells with a wide range of field-centre sizes, whereas ganglion cells with large receptive-field centres were favoured by platinum electrodes, which presumably recorded from larger diameter cells.

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