RETINAL GANGLION CELLS RESPONDING SELECTIVELY TO DIRECTION AND SPEED OF IMAGE MOTION IN THE RABBIT

BY H. B. BARLOW, R. M. HILL AND W. R. LEVICK*

From the School of Optometry, University of California,
Berkeley 4, California, U.S.A.
and Physiological Laboratory, Cambridge

(Received 21 January 1964)

Since Hartline's (1938) account of single unit preparations of the frog's retina it has been clear that different ganglion cells respond to different features of the retinal image. He recognized three classes, those responding only when a light stimulus was turned 'on', those responding only at 'off', and those responding at both 'on' and 'off'. These classes differ from each other also in the rate of adaptation of the discharge, and in the presence or absence of inhibition from the surround (Barlow, 1953). Lettvin, Maturana, McCulloch & Pitts (1959) described additional types of unit that respond to 'convexity' of a dark object, and to 'net dimming' of the visual field. In the cat Kuffler (1953) described only two classes, those having an 'on' centre with an 'off' surround, and the converse type having 'off' centre and 'on' surround. Wiesel (1960), using smaller electrodes, found units with smaller receptive fields, and in the spider monkey Hubel & Wiesel (1960) found a few cells with colour specific responses. Wolbarsht, Wagner & MacNichol (1961) have found units in fish retinae with different spectral sensitivity for centre- and surround-type responses, and de Valois & Jones (1961) have evidence for similar 'colour-coding' in monkeys. In pigeons Maturana & Frenk (1963) have described two classes of units detecting direction of movement and horizontal edges respectively. Thus each animal has several classes of retinal unit, but the classes are different in different species.

Thomson (1953) made a preliminary study of retinal activity in the rabbit, but his work was not completed. Hamasaki & Marg (1962), Hill (1962), Hill & Marg (1963), Arden (1963a, b) and Schaeffer (1962) have recorded from higher levels in the rabbit's visual pathway, and knowledge of the receptive fields of the retinal ganglion cells is required to help in the interpretation of these results.

The survey of the rabbit's retina reported here was started without any

* C. J. Martin Travelling Fellow.
definite expectations as to the types of ganglion cell to be found. The first series of experiments was done in Berkeley using 15µ platinum-in-glass electrodes and Kuffler’s unopened-eye technique. The optical stimulating arrangements were simple, and, possibly because we were not using the somewhat inflexible multibeam ophthalmoscope, we quickly found two classes of cell in the rabbit that do not fit into the centre-surround pattern described by Kuffler in the cat. One type responds selectively to movements in particular directions, the other to rapid movements or changes of illumination. These findings were confirmed in a second series of experiments performed in Cambridge. Here the technique was improved in a number of ways, especially by the use of fine tungsten electrodes. These yield better records, and all those reproduced here are from this series. They also enable single units to be isolated in the central regions of the retina where the ganglion cells are densely packed. The notable new features of the cells so isolated are their small receptive fields and the fact that they respond most vigorously to very slow movements of objects in their receptive fields.

In this paper the evidence for the differentiation of these classes of ganglion cell is given, together with some new observations on the concentric type of unit. Observations and experiments bearing upon the mechanism whereby selectivity for direction and velocity are achieved will be reported later.

METHODS

First series

Preparation. Rabbits were lightly anaesthetized with urethane, 1·2g/kg body weight being given intravenously. This was supplemented when necessary with ether, pentobarbital sodium (15 mg/kg intravenous or intraperitoneal), or more urethane. Some rabbits were decerebrated under ether which was then allowed to blow off. Addition of anaesthetic to these preparations, and comparison with the fully anaesthetized ones, brought out the importance of keeping the animals as light as possible, and indicated that urethane has less influence on the retina than sodium pentobarbital. The general condition of the animal, and in particular the circulation to the eye, is also thought to be important, and in our experience the anaesthetized preparations were at least as good as the decerebrate ones, provided that the anaesthetic level was kept light.

The eye was prepared for recording by removing the lids, cutting the extra-ocular muscles, and removing the cartilage and bone at the top of the orbit. Four small holes were cauterized in the sclera just in front of the equator, and sutures placed to tie a metal ring (15 mm inside diam.) to the eye. The ring was held by a universal ball-joint through which a hypodermic needle passed and penetrated the sclera about at the equator. Through this in turn the electrode was passed and was advanced on to the retina by means of a three-speed drive assembly. This assembly was attached to the animal head-holder, and to change the recording position on the retina the universal ball-joint was loosened and the eye rotated. If necessary the attachment of the electrode drive unit to the head holder was readjusted to ensure loose positioning of the eye in the orbit, and free circulation.

Electrical. Electrodes were made of 15µ platinum-iridium wire sealed in glass, and had
a resistance of about 100 KΩ. The input went to a conventional capacity-coupled pre-amplifier, oscilloscope, and speaker. The amplitude of the spikes was of the order of 100–500 μV.

**Optical.** A contact lens was placed on the cornea to prevent drying. The corneal curvature varied from about 6.4 to 7.7 mm. To delay corneal mirsting it was found advisable to use a contact lens a little flatter than the cornea. Additional power was required to correct this the rabbit’s usual hyper-metropia (ca. 4 D), and the close viewing distance (58 cm). Some of this was provided by a +7 D addition on the contact lenses. The further correction required was determined by ophthalmoscopy, checked in many cases by retinoscopy, and was provided by a spectacle lens close to the eye. Residual refractive error was probably not more than 1 to 2 D; this gives a blur-circles diameter subtending less than 45 min with the normal pupil diameter of 6 mm. Occasionally the pupil was dilated with drops of 10% phenylephrin to allow better viewing when placing the electrode.

**Stimulation.** A white card was held 58 cm from the eye in the approximate position of the receptive field. This was illumminated at a constant background level (usually 0-6 cd/m²), and a projector shone various sized spots of light onto it. These lights could be turned on and off with a shutter, and their intensity could be varied by a neutral wedge. A geared pair of counter-rotating prisms just in front of the projector lens allowed the projected image to be moved in a straight line, and by rotating the whole assembly the orientation of the line of movement could be changed.

Intensities of the lights on the screen were measured with an S.E.I. photometer.

**Procedure.** After the preparation was complete it was left in the dark for about an hour. The sclera was then pierced and the electrode placed in position while observing the retina through a hand-held ophthalmoscope. To reduce the degree of light adaptation caused during the search for a usable unit, a red filter was placed in the beam in the later experiments. This filter was at a point in the optical path per focal with the retina, and its centre was pierced with a small pin hole, or in another case had an opaque dot. The image of white or black spot could be moved over the retina around the electrode tip to assist the search for a unit.

It was usually only after several prods that the electrode yielded action potentials which were considered with reasonable certainty to come from a single neurone. The main criterion was uniformity of size and shape of the action potential, allowing for the usual changes that occur when the discharge is of high frequency. On rare occasions we were unable to decide whether one or two units were being detected: in such cases there were two distinctive shapes of action potential, but these were never seen superimposed, they did not have consistently separable receptive fields, and they got larger or smaller or disappeared together when the electrode was moved in and out. The receptive field always lay near the electrode tip, and it is conceivable that the two different shapes result from activation of a single cell through two different dendrites. Similar variable action potentials were recorded using fine tungsten electrodes. For obvious reasons we have avoided using such units when important issues were at stake.

Having isolated a good unit the first step was always to map out its receptive field by turning on and off an exploring spot. Later experiments of the first series were done with standardized conditions; these were a spot of light \( \frac{1}{2} \) in diameter at an intensity of 12 cd/m² on a background of 0-6 cd/m². The results at each position were lightly marked on the card, giving a map of the regions of the receptive field yielding on (+), off (−), on-off (±), or no discharge (0). The response to a moving spot was next tested, first, to see if the responses 'made sense' in terms of the on and off zones of the receptive fields, secondly, to see if the unit responded selectively to certain directions of motion, and thirdly, to find the velocity of motion that gave the maximum response. In many cases we also tried to determine whether the unit gave a greater response to movement than to the same spot turned on and off. The response to turning on and off the background light alone was usually noted,
together with the position of the unit in the visual field. If these investigations were completed, further observations and records were taken. Some units lasted several hours, but it was more usual to lose them after only a few minutes.

Second series

We found urethane-chloralose mixture (urethane 0.8 g/kg, chloralose 80 mg/kg) somewhat better than urethane alone in achieving the required anaesthetic level without depressing the retina. Some of these preparations were immobilized with gallamine triethiodide (Flaxedil), given by continuous intravenous infusion (5-10 mg/hr) after an initial loading dose (5-8 mg). In these cases 5% CO₂ in O₂ was given by artificial ventilation at 27 ml./breath, 32 breaths/min. Such preparations have often had active retinas 40 hr after the start of the experiment. Anaesthesia was maintained by supplementary injections of urethane and chloralose. We have also decerebrated rabbits anaesthetized with thiopentone sodium (45 mg/kg intravenously) which wears off completely in about 2 hr; these preparations were immobilized and ventilated as above. Twenty to forty millilitres of a solution containing 6 g dextran and 0.9 g NaCl per 100 ml. (Intradex, Glaxo Ltd.) were added to the continuous infusion of Flaxedil; here again the retina usually stays in very good condition for 30 hr or longer.

The preparation of the eye was modified to minimize trauma and avoid the loss of aqueous when the ring was saturated to the sclera. It was found that a much less extensive dissection without removal of any bone was adequate, and the eye ring was saturated to the conjunctiva. The preparation lay on a vibration-free mounting.

Fine, tungsten electrodes insulated with Synobel (xylonol-formaldehyde resin modified with Tung oil, I.C.I. Ltd.) were used. These had a high impedance, and it is thought that only the very tip was uninsulated. The impedance could be lowered in situ in the eye by passing brief pulses of current (0.5 μA, electrode negative) from a high impedance source until shunting the electrode with a 10 MΩ load to ground produced the change in wave form of a square wave input that was found by experience to correlate with the ability to isolate good units. These electrodes require a low capacity, low grid-current input stage.

The optical arrangements were different in detail; it was found convenient to plot the field on a horizontal surface, so an adjustable mirror was placed in front of the eye. Movement of the stimulus spot was achieved by rotating a mirror, and a signal representing displacement of the spot across the field was obtained from a potentiometer coupled to the axis of rotation. The luminances of the stimulating spot and the background were usually about 1 log unit greater than in the first series.

Difficulties arose in finding the receptive fields for two reasons. First, with tungsten electrodes we often made use of records from single fibres running over the retinal surface, and the electrode tip afforded only a poor guide to the positions of the receptive fields of such units. The second more serious source of difficulty lay in the peculiar properties of the central units that can be isolated with these fine electrodes. They are strongly inhibited from the surround, hence they only respond to localized stimulation; furthermore, rapid motion, even if well localized in the receptive field, fails to arouse them. Thorough search with a small object moving slowly is obviously liable to take a long time.

RESULTS

In the course of the first series of experiments it soon became clear that many of the retinal units in the rabbit are similar to those found by Kuffler (1953) in the cat. These have receptive fields with a concentric arrangement, the centre responding at on or off, and a surrounding annular
Fig. 1. Responses of a directionally selective unit (axon recording) to motion in different directions. Map of receptive field in centre. Each pair of records shows (lower trace) movement of a spot of light right through the receptive field in the direction of the adjacent arrow, and (upper trace) the response elicited. Conventions as follows. ±, Response to stationary spot at both on and off; 0, no response; there were no responses outside the ring of 0'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. In upper trace, electrode positivity is downward; the number of spikes is shown immediately after each response. For lower trace, vertical calibration bar shows 5° displacement of light spot; horizontal bar indicates approximately when the spot was within the receptive field.
zone responding at the opposite phase of stimulation (off or on), and inhibiting the centre. Certain additional observations made on this type of unit will be reported later.

Other units were found that did not have the concentric type of receptive field. These resembled the on–off units of the frog (Hartline, 1938) in that responses could commonly be obtained at ‘on’ and ‘off’ over the whole of the receptive field, not just from a zone separating centre and surround. However, the most striking property of these cells is their capacity to respond vigorously to stimuli moving across their fields in certain directions, and not to respond at all for motion in other directions. They thus provide a basis for discriminating the direction of motion of objects in the visual field. Results illustrating this property are given in the next section.

It was only at a later stage that we became aware that units were responding selectively to the speed as well as the direction of motion. Most of the units with concentric on- or off-centre fields responded to centripetal or centrifugal movements of a light spot carried out at the speed normally used for testing for directional responses (about 5–10°/sec). However, we found that certain units with large receptive fields failed to respond to these movements although they gave strong responses to the flashing of stationary light spots. Later we noticed quite accidentally that shadows flicking rapidly through their fields caused vigorous responses. The same turned out to be true for light spots provided the rate of motion was rapid enough. Finally, in the second series of experiments we isolated units with small receptive fields that responded only to very slow movements of the stimuli.

Units responding to fast and slow movements are described in the second and third sections of the results. In the fourth section some new observations on the concentric type of unit are reported. In the fifth section the numbers and positions of the units are given, and in the sixth section some unusual types of response are described.

**Directionally selective units**

*Responses to motion in different directions.* Figure 1 shows responses of a directionally selective unit to a spot of light moving through its receptive field in various directions. The receptive field was first mapped out with a 3° diameter spot at 60 cd/m² intensity on a background of 10 cd/m², and this field is shown in the centre of the figure. As with nearly all directionally selective units, the response occurs at ‘on’ and ‘off’ over most of the receptive field. A few responded only at ‘on’ under these conditions. At this intensity no responses were obtained either to turning on or off, or to movement, when the spot lay on or outside the ring of 0's.
Fig. 2. Movement responses of on-centre unit. Only 'on' responses (+) were obtained to a stationary spot, but 'off' responses could be elicited from the surround by special manoeuvres (see text). Symbols, calibrations, etc., as in Fig. 1. Cell body recording.
Fig. 3. Movement responses of an off-centre unit. Same conventions as in Fig. 1, except for the following: ± stands for responses at on and off when they are about equal or when response at on is greater; ⊥ when response at off is more prominent than at on. Axon recording.
The exploring spot was then left on and moved entirely across the receptive field in various directions at a rate of about $10^\circ/\text{sec}$. The discharges obtained for the various paths are shown next to the start of each path. It will be seen that the maximum discharge is obtained for movement towards the anterior quadrant of the visual field, the minimum discharge for movement towards the posterior quadrant, with intermediate levels of response for intermediate directions of movement.

Figure 2 shows the responses of a non-directionally selective, on-centre, unit for comparison with Fig. 1. The receptive field was mapped out and the spot moved through it as before. Discharges occur for all directions of movement and although the number of impulses is not the same in each case, there is no gross inequality as there is in Fig. 1. Similar results obtained in a non-directionally selective off-centre unit are shown in Fig. 3.

**Timing of the responses.** When records such as those of Figs. 1, 2 and 3 are being made one can observe whereabouts in the receptive field the spot of light lies when the discharge occurs. With directionally selective units it starts just after the spot has crossed the ring of 0’s and continues until the spot crosses the 0’s on the far side and moves out of the field. In on-centre units the response occurs as the spot approaches the centre and moves from the off to the on zone of the field. As soon as it crosses the centre and starts moving away the discharge abruptly slows or stops. In off-centre units the sequence is usually the exact reverse, the discharge occurring as the spot of light moves away from the centre, but it may be complicated by a preliminary, weaker discharge occurring when the spot first enters the annular on zone. These statements about the timing of the response are based on repeated observations of the same movement, but some of the features can be seen in the samples illustrated in Figs. 1, 2 and 3.

If the motion sensitivity of concentric-type units is tested with a black spot it is easy to show that the response occurs for movements away from the centre in on-centre units, towards the centre in off-centre units. These responses are exactly like those described by Bishop, Kozak, Levick & Vakkur (1962) in cells of the cat’s lateral geniculate nucleus: on-centre are centripetal white, centrifugal black; off-centre are centrifugal white, centripetal black. Furthermore, it will be seen that the timing of the responses in these concentric units is correctly predicted if one assumes that the ganglion cells respond to changes in the excitatory and inhibitory contributions summed over the whole field.

For the directionally selective units this notion that the response is simply controlled by summed contributions breaks down. If a black spot is used to explore their movement sensitivity it is found that they respond for the same direction of motion as when a bright spot is used
The same is true when a straight white–black border is moved through the field, whether white or black is leading. There is a rare type of directionally selective unit that gives only ‘on’ responses to a stationary spot at the intensity normally used. In some cases these have failed to respond to the sequence of off-excitations which occurs when a large black object is moved into their field.

Diversification of the preferred direction. It will be asked whether all directionally selective units in the same eye, or the same part of the retina, have the same axis of preferential response. This is certainly not so, for we have quite frequently recorded from two units simultaneously, and in such cases the preferred directions are often opposite; one unit responds for one direction of motion, the other for the reverse direction. The conclusion that the preferred axis is different in different units even in the same part of the retina is confirmed by the results to be shown in Fig. 9.

Misleading indications of directional selectivity. The difference in the response to back and forth motion of an exploring spot shown in Fig. 1 is typical of what is easily obtained in units here classified as directionally selective. It is not a marginal difference and stands out prominently once it is tested for, at least under the conditions of adaptation and illumination here employed. There are, however, two misleading results which should not be mistaken for true directional selectivity. First, one frequently obtains great differences in response to back and forth motion of a spot when one is doing no more than moving on and off the edge of the receptive field of a concentric type, non-directionally selective unit (Fig. 4). Even when one is well aware of this possibility it is easy to be misled into thinking a unit is directionally selective if one tests its responses to movement before mapping out the receptive field. Secondly, the differences in the responses shown in Fig. 2 should be borne in mind. Even a concentric unit is not quite symmetrical, and here the number of impulses varied from 39 for motion towards the posterior field to 56 for motion towards the inferior–posterior field. The difference might have been less if the paths of motion had been shifted laterally a little, but in any case there is no axis giving as great contrast for two opposing directions as is readily obtained on a unit like that of Fig. 1.

Speed of motion. In the experiments described the spot was moved by the rotating mirror device under manual control at a rate of about 10°/sec. It was clear that there is a broad range of speeds of motion for which the results are similar to those illustrated, but outside this range of speeds the directional selectivity is less apparent and unexpected results are sometimes obtained. If the motion is very rapid, the response in the preferred direction is very brief, and as usual there is little or no response in the null direction. If it is very slow, the increased frequency of response in
the preferred direction becomes hard to detect over the maintained activity.

In the opposite or ‘null’ direction the response to very slow motion is unexpected; units sometimes give a noticeable discharge, even though slightly faster motion in the same direction causes none. This is illustrated in a later paper (H. B. Barlow & W. R. Levick, to be published).

Fig. 4. Asymmetric responses to back and forth motion in a non-directionally selective, off-centre unit. Cell body recording. The edge of the receptive field is shown and arrows indicate how a spot of light was moved from a position just outside the receptive field into the centre and then back again to the initial position. The responses associated with four different radial movements are illustrated. In each case note the asymmetry of responses to movements in opposite directions.

Inhibition of maintained discharge. Many directionally selective units show a maintained discharge and it is an interesting question whether this can be suppressed by motion in the ‘null’ direction. This certainly does
occur, and is easily detectable in units which have high rates of maintained activity. In other units with little maintained activity, single observations give an uncertain answer, for the spot only remains within the receptive field for a fraction of a second, and pauses of comparable duration are not unusual without any stimulation. For the same reason single records are not very convincing, but inhibition is shown in Fig. 1 of Barlow & Hill (1963a). Another factor that makes inhibition hard to show is the unexpected excitation by very slow movements in the null direction. This causes the speeds yielding inhibition to lie within a narrow range.

![Graph](image)

Fig. 5. Area-threshold relation for a directionally selective on-off unit. The threshold was determined for spots of varying diameter turned on (+), off (−), or moved through the field in the preferred direction (○). Responses to leading (⊕) and trailing (⊖) edges could be distinguished at large spot diameters. Diameter of receptive field 3°, background 0.8 cd/m². The points for moving spot (○, ⊕, ⊖) have been displaced 0.5 log. units downwards for clarity.

**Lateral inhibition.** Directionally selective units often give little or no response to turning on and off the background light. When threshold is determined as a function of area (see Fig. 5), it is found that the threshold intensity rises when the spot spreads onto the surrounding retina. This
confirms that there is lateral inhibition which in this case was more pronounced for 'on' than for 'off'. This area–threshold curve also shows that summation within the receptive field is incomplete, Piper's square root law (threshold $\propto 1/\sqrt{\text{area}}$) holding approximately in the range 20 min to $3^\circ$ diameter. This area–threshold curve is very similar to those obtained on on–off units of the frog (Barlow, 1953).

In this experiment the threshold intensity for motion in the preferred direction was also measured. The points are shown in Fig. 5 displaced downwards by 0·5 log. unit. In all cases it was a little lower than the 'off' threshold, which in turn was lower than 'on'. The threshold fell up to $3^\circ$ diameter, which was the receptive field diameter. For bigger spots thresholds for the leading and trailing edges could be determined separately. Notice that the thresholds for the leading edge (on-stimulus) rises as the spot extends over the edge of the receptive field. Thus lateral inhibition appears to be the factor causing the greater response to small 'convex' objects than to straight edges (Lettvin et al. 1959; Gaze & Jacobson, 1963).

After-effects of stimulation. In the rabbit these directionally selective units are presumably the basis for the visual perception of the direction of movement. It is natural to ask if they show after-effects of stimulation of a type which might account for subjective after-effects in man (the 'waterfall phenomenon'; Wohlgemuth, 1911). Observations reported elsewhere (Barlow & Hill, 1963b) indicate that during the $\frac{1}{2}$ min following exposure to movement the maintained discharge is reduced in those units that were excited during the movement. The converse phenomenon, enhancement of maintained discharge following exposure to motion, has not been observed, possibly because complete inhibition by motion in the non-preferred direction is difficult to achieve, and in any case the change in the number of impulses fired, even with complete inhibition, is relatively small.

A reduction in the maintained discharge of directionally selective units may explain the waterfall phenomenon in man, but there is evidence that in this case the effect does not occur at a retinal level (Barlow & Brindley, 1963).

Large-field type of unit

During the first series of experiments we came across certain units which gave 'off' responses over a rather large area, and contained a smaller region giving 'on' responses somewhere towards the edge of the field. At first these were regarded as off-centre units with an unusually asymmetric or incomplete 'on' annulus. However, other characteristics seemed to be associated with these large fields. First, we noticed that movements of the
$\frac{1}{3}$ exploring spot like those used to elicit the discharges shown in Figs. 1–3 evoked a feeble response or no response at all in these units. On the other hand shadows accidentally falling on the plotting screen often gave very vigorous bursts, and by following up this observation it was found that rate of movement was the critical factor. Both bright and dark spots gave

Fig. 6. Responses to rapid movement from a large-field unit. The records are the responses to back and forth movement of a black disk (a–f) and a white disk (g–j) across the receptive field (shown at left) in the direction of the arrows. The upper trace of each record pair (a, c, e, g, i, k) is the response of the axon recorded in the nerve-fibre layer. The lower trace of each pair is a signal derived from a photomultiplier focused on the centre of the receptive field (increased light upward). The 100 c/s ripple on the trace is from the mains-driven lamp. The speeds used are shown at the right of each record. The figures (on records a–i) are the numbers of spikes in the immediately preceding responses. The lowest record pair (k, l) shows rhythmic bursts of spikes in response to 'off' and 'on' excitation. To bring out the 'on' response from the surround a black disk was left in the central 'off' zone while the lamp was turned off, then on. 'Off' latency 20 msec; 'on' latency 70 msec.
very vigorous discharges if the movement was fast enough (Fig. 6). Furthermore, shadows of thin threads or wires gave good responses when moved rapidly through the receptive fields, even though these seemed feeble stimuli to human vision. In many units of the first series with large fields and the ability to respond to fast movements, the action potentials were unusually large and well isolated, and they often had a vigorous maintained discharge that increased or decreased when the general level of illumination was changed. The nature of the volleys of impulses seemed also to differ in that they were of short duration, but reached very high frequencies. A powerful response usually broke up into a rhythmic succession of high-frequency bursts (lowest record, Fig. 6).

Although the combination of unusually large receptive field, feeble response to slow movement, and brief high-frequency volleys to rapid movement made it easy to place some units in this category, there have been others possessing only some of these characteristics that we have had difficulty in classifying, and we do not feel that it is as clearly differentiated a group as the directionally selective units. These doubts were reinforced by the second series of experiments. We were able to confirm that units differ markedly in the range of speeds to which they respond, units with large fields responding to rapid movements, and those with small fields to slow movements. There is no doubt that units are selective for velocity as well as direction of motion, but we are unable to say whether there are distinctive groups responding to fast, medium, and slow speeds, or whether, for instance, the concentric units respond to faster movement and have larger receptive fields in the more peripheral regions of retina.

Small-field type of unit

The special features of this class of units are: (i) the response occurs only to slow movements of the stimulus spot; (ii) vigorous responses are obtained only with small stimulus spots; (iii) the receptive fields are small and are usually located in the region of densely packed ganglion cells; (iv) the receptive fields possess a powerful inhibitory surround; (v) responses readily diminish when stimuli are repeated at short intervals.

Usually the speed of movement eliciting the most vigorous response was as slow as 0.3 or 0.1°/sec, and there was frequently little or no response at all for movements faster than 4°/sec (Fig. 7). The 1° testing spot used routinely to plot receptive fields in the second series usually produced only feeble responses from this class of unit; larger spots mostly produced no response at all; however, 0.5° and even 0.1° spots were much more effective, enabling the receptive fields to be mapped. Fields were usually 1–2° in diameter and not as regular in shape as those of the other classes of units. The response type was usually uniform over the receptive field
Fig. 7. Responses to slow but not fast movement in a small-field unit. Map of receptive field is shown at left, middle. Records are responses to movement of a small light spot to and fro at various speeds across the receptive field in the direction shown by the arrows. Upper trace of each record pair (a, e, i, j) is the response of the ganglion-cell body; lower trace, signal representing displacement of spot across visual field. The approximate periods when the spot was within the receptive field are indicated by horizontal bars. Figures following each response represent numbers of spikes. Approximate spot-velocities shown to right of each record. There is little or no response when the velocity exceeds about 4°/sec.
and units with on, off and on–off responses have all been observed. Some of the on and on–off types were directionally selective. Responses from the surround at the opposite phase to those from the centre were not present and could only rarely be revealed by the special manoeuvres described below for concentric units. Nevertheless, the surround could readily suppress the response from the central region if stimuli involved both centre and surround simultaneously. Thus, turning on and off the illumination of the whole field usually failed to evoke any response at all.

The tendency of responses to dwindle with rapid repetition of stimuli raises the suspicion of poor condition of the retina; however, observation of the retinal circulation and palpation of the heart yielded no evidence of disturbance. Other units recorded immediately before and immediately afterwards were typical representatives of the other classes, in some cases having receptive fields enclosing those of the small-field types.

In view of the special properties of this class of units, it was not surprising that the receptive fields were difficult to locate and plot. It was even difficult to know at first whether or not such a unit was being recorded by the electrode, since there was usually very little or no maintained activity.

**Concentric units**

These are broadly similar to those described in the cat by Kuffler (1953) and also found in the monkey by Hubel & Wiesel (1960), but the following supplementary observations are worth reporting.

*Bringing out responses from the surround.* The opposite phase response from the surround was usually not present in on-centre units explored under our standard conditions, and off-centre units had only an on–off zone, and no pure on zone. However, the following manoeuvres enabled the off surround of on-centre units and the on surround of off-centre units to be seen clearly. The first was light adaptation of the whole field with white light from a hand-held ophthalmoscope. The effect is rather strange, for as a result of light-adaptation responses can be obtained that were previously below threshold. It is thus an example of light adaptation lowering the threshold, or raising the sensitivity the opposite effect to that found by Lipetz (1961). This phenomenon is clearly related to the disappearance of lateral inhibition during dark adaptation and its reappearance during light adaptation (Barlow, FitzHugh & Kuffler, 1957).

A second way to reveal the contribution of the surround is to damp down the responses from the centre by flooding this zone with constant light. If the exploring spot was aligned on the central zone and left on, then turning on and off the background would often bring out a response from the surround which had previously been undetected, or make it pre-
dominate over the centre-type response if both had been present. Here is an example of a maintained light producing an effect the opposite from that expected according to signal/noise considerations; the flooding light adds noise, but this enables a response to be obtained that was not obtainable before.

**Responses to diffuse illumination.** Units have been found which yield off responses when the background is turned on and off, but give no off

responses when explored with the $30^\circ$ exploring spot at an intensity $20 \times$ higher than the background. Apparently contributions to the surround-type response can be summated over a great area, and it is certainly incorrect to assume that the centre-type response necessarily dominates when the whole retina is evenly illuminated.

**Latencies.** A preliminary survey of the latencies of responses showed that, when a given intensity of spot elicits responses both from the centre and from the surround, that from the surround has a considerably longer latency (cf. Thomson, 1953). Under such conditions the response from the surround was usually weaker, and it might be thought that the longer latency was simply the consequence of this fact: this is not so, for the difference of latency was maintained if the spot was moved away from the centre of the field so that centre and surround responses were approxi-
mately equal as shown in Fig. 8, or alternatively if the spot was weakened when in the centre of the field to give a discharge equal to or less than that elicited in the surround.

It was observed that the latency of the surround-type response was greater even in those units which gave a more vigorous discharge of surround-type with whole-field illumination. Hill & Marg (1963) found a bimodal distribution of latencies when recording from the nucleus of the trans-peduncular tract in the rabbit, and suspected a peripheral origin. The present result supports this, and adds the information that the long latency responses probably result from excitation of the surround, rather than the centre, of the receptive fields.

In directionally selective units on and off latencies are nearly equal (Fig. 8). This shows that the latency difference is associated with concentric centre-surround organization.

Inspection of records from cortical cells in the cat (Hubel & Wiesel, 1962) suggests that here again the ‘core’ of the receptive field yields responses of shorter latency than the ‘flanks’, irrespective of which is ‘on’ and which ‘off’.

Size of action potentials. Though the amplitude of the action potentials was not routinely measured we have the strong impression that those recorded from concentric-type units were of medium size, whilst those recorded from directionally selective units were smaller than usual and those recorded from the large-field units were larger than usual. These differences did not show up in the second series when fine tungsten electrodes were used instead of the 15μ platinum type.

Numbers and positions of units

First series. Receptive fields were plotted on 100 units; 93 fitted into the categories described above, but we were uncertain how to classify 7 of them, and these are discussed in the next section. Fifty-six units were explored under standard conditions of illumination (0·6 cd/m² background, 3° exploring spot 12 cd/m²), without strong pre-adaptation by the unfiltered ophthalmoscope, and with residual refractive error that could only spread the image of the exploring spot a small amount compared to the receptive field diameter. The properties of these units are shown in Table 1. It will be seen that the directionally selective units have small fields and the large-field type have large fields, compared with the off-concentric type. The on-concentric are slightly smaller than the off-concentric, but this may be associated with another difference between them. The diameters shown in the table are the over-all diameters, and therefore include the antagonistic surround in those units which showed one with this intensity of exploring spot and this degree of light adaptation.
Table 1. Main characteristics of the five classes of unit. Standard deviations are for the populations of diameters and eccentricities. Standard errors are for the estimates of the slopes of the regression lines. The figures were analysed statistically and the following selection of t-test results shows which differences between classes are significant. The figure given after each pair is the probability of obtaining as big a difference in means by random sampling from a single population. (1) For diameters, on-off directionally selective were smaller than off-centre concentric (< 0.001); 'on' directionally selective were smaller than off-centre concentric (0.007): on-centre concentric were smaller than off-centre concentric (0.003): off-centre concentric were smaller than large field type (< 0.001). (2) For eccentricities the most significant difference was between the 'on' directionally selective group and the large field type (0.04): other differences were not significant. (3) For regression of diameter on eccentricity t tests showed that the probability of obtaining as steep a slope if diameter did not depend upon eccentricity was 0.013 for the whole directionally selective group: the probability was 0.08 for the large field type, even higher for other classes.

<table>
<thead>
<tr>
<th>Receptive field</th>
<th>Most effective stimulus</th>
<th>%</th>
<th>No.</th>
<th>Av. diameter (deg. ± s.d.)</th>
<th>Av. eccentricity (deg. ± s.d.)</th>
<th>Regression of diameter on eccentricity. Slope: deg./deg. ± s.e. of slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>On-off, directionally selective</td>
<td>Movement of a small object in a particular direction</td>
<td>30</td>
<td>17</td>
<td>3.1 ± 1.1</td>
<td>23 ± 13.4</td>
<td>+0.043 ± 0.016</td>
</tr>
<tr>
<td>On, directionally selective</td>
<td>within a localized region of the retina</td>
<td>11</td>
<td>6</td>
<td>3.3 ± 1.0</td>
<td>15 ± 6.6</td>
<td></td>
</tr>
<tr>
<td>On-centre concentric</td>
<td>Local brightening</td>
<td>25</td>
<td>14</td>
<td>3.6 ± 1.0</td>
<td>27 ± 16.3</td>
<td>+0.0054 ± 0.018</td>
</tr>
<tr>
<td>Off-centre concentric</td>
<td>Local dimming</td>
<td>23</td>
<td>13</td>
<td>5.0 ± 1.1</td>
<td>22 ± 12.1</td>
<td>+0.021 ± 0.029</td>
</tr>
<tr>
<td>Large-field</td>
<td>Fast movement in any direction within a larger region of retina</td>
<td>11</td>
<td>6</td>
<td>8.7 ± 1.7</td>
<td>29 ± 13</td>
<td>-0.10 ± 0.045</td>
</tr>
</tbody>
</table>
This happened in the majority of the off-centre units (10/13), but a minority of the on-centre (2/14). Thus most of the on units showed a homogeneous field under these conditions, whereas in most of the off units the diameter given includes part of the on zone as well as the central off zone.

![Diagram](image)

Fig. 9. Location in the visual field of 56 units of various types. Type of unit, and preferred axis of directionally selective units, do not appear to be correlated with position. +, On-centre; −, off-centre; ••, on-off directionally selective; \(\backslash\), on directionally selective; \(\bigcirc\), large-field.

**Table 2.** Preferred direction of movement in the visual field of 22 directionally selective units, grouped by quadrants

<table>
<thead>
<tr>
<th>Preferred direction in visual field</th>
<th>On</th>
<th>On-off</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior to anterior</td>
<td>2</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Anterior to posterior</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Inferior to superior</td>
<td>3</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Superior to inferior</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>
Unfortunately few fields were plotted in sufficient detail to enable us to estimate the diameter of this central zone.

Figure 9 shows the location in the visual field of the 56 fields analysed above. Possibly the large-field type of unit lies more peripherally than the directionally selective 'on' group, but there are no other notable features in the distribution of the units within the region explored. In Table 2 the direction of preferential response for the 23 units showing directional selectivity is shown. There are more responding to movement towards the anterior visual field than any other direction, but the $\chi^2$ test indicates that this may be due to the small sample, not an uneven distribu-
tion of preferred axes. Returning to Fig. 9, one can detect no relation between the axis of preferential response and the position of the unit in the visual field.

Figure 10 shows size of receptive field plotted vertically against distance from the optic axis horizontally, for each class of unit. There appears to be no definite trend of field size with position, except in the case of the directionally selective units, where the calculated regression line (not drawn) indicates an increase of field diameter by 1° for every 23° eccentricity. It should be noted that this rather unsuccessful attempt to correlate size with position was made without the more detailed knowledge of retinal ganglion cell distribution that is becoming available (Whitteridge, personal communication), before small units were isolated with fine micro-electrodes, and using the over-all field diameter instead of the core diameter (cf. Wiesel's (1960) results).

Statistical tests. The results obtained on the 56 units under standard conditions have been analysed statistically to elucidate the relations between type of unit, eccentricity in the visual field, and diameter of receptive field. In Table 1 the types of unit are arranged in order of increasing average receptive field diameter. To determine the significance of the results, t tests were performed for all pairs of diameters and a selection of the results is given in the heading of Table 1. The figure given for a pair is the probability that two random samples from a single population would have differed as greatly in their means. The results are not given for obviously significant or obviously insignificant pairs. Eccentricities were treated in the same way, but in this case the most significant difference was only marginal. It will be seen that there is ample evidence against the view that all types of unit have the same size of receptive field, but very little evidence against the view that they are evenly distributed over the retina.

There remains the possibility that, within each group, field size is related to eccentricity. To test this, regression lines were fitted to the data shown in Fig. 10, and a test applied to see if the slope of the line differed significantly from zero. The figures in the heading of Table 1 are the probabilities of obtaining the experimental result if the field size was unrelated to eccentricity. Only for the directionally selective group was there an indication ($P = 0.014$) that field size increased with eccentricity.

Second series. Receptive fields of 177 units were examined under stimulus conditions similar to those of the first series. There was a small number (11) which did not readily fit into one of the six categories. Of the remaining 166, 33 (20%) were on–off directionally selective, 4 (2%) were on directionally selective, 49 (30%) were on-centre concentric, 55 (33%) were off-centre concentric, 11 (7%) were large-field types, and 14 (8%)
were small-field types. The proportion of small-field types was low because no deliberate attempt was made to explore the area centralis. Although relatively more concentric types were found, the general similarity of the proportions from the two series is remarkable considering the different types of electrode employed.

Other classes of unit

Among the 100 units whose receptive fields were plotted in the first series there were seven that we were unable to place in the classes described above. Six of these were among the first 50 units isolated, and further analysis might have enabled us to place them in one or another category, but two unusual fields should be mentioned. One was an off unit with directional selectivity, the other an on–off unit without directional selectivity.

One difference between units has been observed, but has not been used to classify the cells. This is the extent to which the discharge is maintained when the eliciting stimulus is maintained. Certainly the rapid movement type adapts more rapidly than the concentric type, but amongst the latter there is also considerable variation. The main reason for discounting such differences is the great sensitivity of the maintained component of the discharge to anaesthetics, particularly barbiturates.

Occasionally units have been found that behave in an irregular fashion. An unusually powerful stimulus may be required to excite such a cell, but thereafter it responds freely a few times to a weaker stimulus. However, upon repetition the discharge declines and becomes irregular, and it may be necessary to pause several seconds before re-stimulating in order to re-excite. Similarities can be found between this type of behaviour and that of the ‘newness’ or ‘sameness’ neurones described by Lettvín, Maturana, Pitts & McCulloch (1961) in the frog’s tectum, and also by Arden (1963b) in the rabbit’s geniculate. However, we have little doubt that such irregular behaviour occurs in the rabbit’s retina only when its condition is poor. The main evidence for this view is that if one unit is found behaving irregularly, other irregular units are often found in the immediate vicinity, but normal ones are not. Also, a cause for the poor condition was sometimes found—for example, a poor heart beat, restricted circulation to the eye, or a mechanically injured retina. Obviously this explanation for unusual behaviour may not apply to the units described by others, but it is certainly important to be aware that a failing or abnormal preparation can give this kind of result. The ‘spreading depression’ of the retina described by Gouras (1958) should be recalled in this connexion.

It may be suspected that there are other types of cell, or that the classes
given here are subdivisible, and it is therefore worth mentioning the ways in which this survey is incomplete. First, exploration has been confined to the inferior retina (superior field); secondly, colours have not been used; thirdly, the state of adaptation has not been widely varied; fourthly, the electrodes used may be selective; and fifthly, we have used a large exploring spot and have not tried to map out fine detail. Obviously all possible spatio-temporal patterns of stimulation cannot be employed, but it is worth noting that two of the distinguishing characteristics—directional selectivity and sensitivity to rapid movement—were discovered more or less accidentally rather than by deliberate search.

**DISCUSSION**

This survey of ganglion cells in the rabbit’s retina confirms the fact that complex analysis of sensory information occurs in the periphery, before the neural activity is projected to the higher nervous centres. Each class of cell has its own ‘trigger feature’ to which it is most sensitive, in the same way that different classes of cutaneous neurones are selectively sensitive to mechanical deformation, temperature change, tissue damage, and so on. Evidently in the rabbit the speed and direction of motion of the image are particularly important in determining which ganglion cells are stimulated in a particular part of the retina.

**Optical controls.** The question must be raised whether optical defects are responsible for any of our results. It is difficult to see how regular or irregular aberrations could give rise to directional selectivity, or to selectivity for rate of movement, and it is worth noticing the following facts. (1) The preparations were refracted, by retinoscopy in many cases, and the retina was always inspected ophthalmoscopically. Definition of vessels, the strands of myelinated fibres and the micro-electrode tip appeared sharp, though we were of course using a restricted aperture. (2) Fields have been plotted before and after refracting. The main features appear to be unchanged even by large refractive errors. (3) We have occasionally used 1·2 mm or 3 mm artificial pupils. Evidence of improved definition was obtained in tests to be described in another paper, but the main features of the fields were unchanged.

The essential properties of the receptive fields of the different classes of units were also seen in unanaesthetized decerebrate preparations; we therefore do not think the behaviour is related to centrifugal efferent activity or to the effects of anaesthesia.

In the next section the results on the rabbit will be compared with those reported in other species, and in the final section the problem of the coding of sensory information will be discussed.
Comparison with the frog

Lettvin et al. (1959, 1961) and Maturana, Lettvin, McCulloch & Pitts (1960) have described five classes of retinal unit in the frog which must be compared with those reported here in the rabbit.

At first the comparison merely confirms the expected species differences. Our large-field types are unlike their ‘dimming’ or ‘darkness’ detectors in several respects. They possess ‘on’ regions in their receptive fields, they give an exceptionally brief response to dimming, and they respond with a characteristic high frequency volley to rapid movements, none of which are recognized properties of the frog’s units. Our concentric ‘on’ and ‘off’ centre units also fail to fit in with the classification of frog cells given by Lettvin et al. but they do appear to be similar to the units described by Kuffler (1953) in the cat. There may, however, be greater similarities between rabbit and frog among the units we have classified as directionally selective. Those yielding both ‘on’ and ‘off’ responses to stationary spots are superficially similar to those in the frog, not only in this respect, but also in the rapid adaptation of the response and in the presence of inhibition from the surround. Neither Hartline (1938, 1940a, b), Barlow (1953), nor Lettvin et al. (1959, 1961) have described directional selectivity in these cells, but in the light of the present results it would certainly be worth re-investigating the point. For the two classes with smaller receptive fields Maturana et al. (1960) describe behaviour which probably does indicate directional selectivity. They say these units respond to motion in one direction and not in the reverse direction, but it is not entirely clear whether they moved their stimulating spot right through the receptive field, or only on and off one edge. Nor do they show whether the direction of motion yielding the greatest response is dependent upon the object being darker or lighter than the background. However, if these units in the frog are like those in the rabbit in responding to a particular direction of motion throughout their receptive field, and without regard to the contrast of the stimulus, then this is certainly their most important feature.

Lettvin et al. (1959, 1961) describe other characteristics of these small field units that we have also found, but they are not as prominent as they describe and are explicable by known properties of retinal ganglion cells. Thus they say that their ‘convex edge detectors’ respond strongly to a black spot moving into their receptive field, but not at all to a straight black–white border crossing it. In most of our units, straight borders give the response if moved in the right direction, and do so whether the black or white part is leading, though the two responses may not be equal in magnitude. It is true that a spot, or a black strip moved in end first,
RETINAL UNITS OF RABBIT

usually gives a bigger response than a straight border, but this is probably accounted for adequately by lateral inhibition. A straight border, or any large object, will move through the surround of the receptive field, and thereby inhibit the excitation aroused by the part that moves through the centre. This would account for the rise in threshold with large spots in Fig. 5; the experiment of Gaze & Jacobson (1963) seems to establish this as the correct explanation.

Letvin et al. (1959, 1961) describe the phenomenon of ‘erasibility’ in their ‘movement gated convex boundary detectors’: a dark object brought into the field evokes a maintained response which is ‘erased’ by turning off the illuminating light and fails to reappear on re-illumination. In contrast to this they describe the continued ‘muttering’ of a ‘sustained edge detector’ when an object is brought into its receptive field and the light is then completely extinguished. The ‘muttering’ is said not to occur if no object is in the receptive field when the light is extinguished. Units in the rabbit typically have a slow maintained discharge that can be changed, transiently or for longer periods, by changing the general level of illumination. We have not observed ‘erasibility’ and ‘muttering’ but these interesting phenomena should be examined further in an anaesthetic-free preparation, for the level of anaesthesia certainly has a big effect on the maintained discharge.

Other species. Maurana & Frenk (1963) have reported units with directional selectivity in the pigeon, and it seems probable that they occur in many species. However, it should not be assumed that they are universal; the failure to find them in the cat is quite likely significant, especially in view of the fact that Hubel & Wiesel (1959, 1962) noticed directional selectivity in higher level units, whereas they did not notice it when recording from fibres of the optic radiation. The account of the receptive fields of geniculate neurones given by Bishop et al. (1962) strengthens this conclusion. They observed the responses of these units to movements of black and white spots, and their description tallies exactly with what we found in on and off concentric units: had there been directionally selective units, they would quite possibly have spotted them.

Trigger features and the coding of sensory information

At first one is baffled by the complexity of the relation between the optic nerve discharge and the changing pattern of retinal light that causes it. The mechanism responsible for the relation may be the major problem, but we must also consider what reason or method lies behind the selection of the relations that we find. We are puzzled partly because we do not understand the principles upon which sensory information is coded, and clearly the first step towards clarifying these principles is to break the code
in as many instances as possible. There is, however, an important factor that may delay this step.

When doing these experiments one’s first problem is to establish experimental grounds for differentiating one class of unit from another. One may easily fail to take the next step, which is the important one for the coding problem, namely, the attempt to discover what part of the information provided by the animal’s normal environment each class of unit transmits: what normally triggers its response? What feature does it abstract from the spatio-temporal pattern of quantal absorptions in the receptors? Tests which are adequate to differentiate different classes of unit may fail to give one useful clues about this, as our own experience shows. The response to static spots of light turned on and off enables one to differentiate ‘on–off’ units from the others, but one has to test with moving spots to understand that these units signal the direction of motion of objects in the visual field. If one’s apparatus is inflexible, or if one’s attention is too narrowly confined to the problem of differentiating classes of units, one may easily omit the relatively crude observations and experiments that tell one most clearly what are the trigger features, and hence reveal most about the code.

Under laboratory conditions one’s guide to the trigger feature is the type of stimulus which is most effective in eliciting a response. If one is to be precise, the only valid basis for comparing the sensitivity to different stimuli is the quantum efficiency (Barlow, 1962). However, the differences between the different classes of unit are so great that qualitative tests appear to be sufficient if one bears in mind that, for obvious reasons, bright lights are easier to detect than dim, large objects easier than small, and so on. In practice, the quantitative aspect of determining which is the ‘most effective stimulus’ is probably less important than the difficulty of devising appropriate types of stimuli. It is worth observing that two of the important properties of these ganglion cells (directional selectivity, and the sensitivity to speed of movement) were discovered almost accidentally; the barrier to progress may lie in the limited variety of test situations employed rather than in the inaccuracy of qualitative judgements.

Much of this discussion is in close agreement with the ideas of Lettvín and his co-workers but we do not feel happy with the names they give their units. Thus they name one class of unit in the frog ‘movement gated convexity detectors’. If these are truly directionally selective we would list their most effective stimulus or trigger feature as ‘motion of a small dark object in a particular direction in restricted retinal region’. This is lengthier, but it more aptly describes both the relevant observations that have been made on the units, and their probable importance in the visual life of the animal. The greater response of these units to small objects is
simply the consequence of inhibition from the surround caused by large objects that extend beyond the borders of the receptive field. The response has nothing to do with 'convexity' as such: frogs are interested in flies, not the mathematical abstractions that pre-occupied the investigators. However, this should not obscure our fundamental agreement with Lettvin and his co-workers that the coding of sensory information is the important problem that this type of experiment brings up, and the one that needs to be attacked first. The scissors, string, and shadows on the wall required to answer the questions that arise at this stage may resemble the equipment for a children's party more than scientific apparatus, but the answers are necessary before more quantitative analysis becomes worth while. It would be ridiculous to analyse the sound output of a motor car without being aware that cars are useful as means of transport. Would it be any less absurd to investigate the spectral sensitivity of a retinal unit without realizing that it signalled direction of motion? Different classes of unit convey information about different features of the environment, and this fact must be taken into account when planning the observations that are to be made on them.

**SUMMARY**

1. Single retinal units have been isolated in the rabbit's retina, using 15 μ platinum-in-glass or fine tungsten electrodes, and lightly anaesthetized or decerebrate preparations.

2. A series of 56 units was studied under standardized conditions with 15 μ electrodes; 27 (48%) had concentrically arranged receptive fields, 14 (25%) with a central 'on' zone, 13 (23%) with a central 'off' zone. These concentric units are similar to those described in the cat, but special manoeuvres were required to bring out the response from the surround in most of the on-centre and some of the off-centre units.

3. The latency of the response from the centre is shorter than that from the surround, even when the frequency of the discharge from the surround is as great or greater than that from the centre.

4. Among the 56 units 23 (41%) showed 'directional selectivity', i.e. when the exploring spot was moved all the way across the receptive field, they gave a much greater discharge of impulses for motion in one direction (called preferred) than they did for motion in the reverse direction (null) whatever the nature of the moving stimulus. Seventeen of these units gave on and off responses all over their receptive fields, and 6 gave only on responses.

5. The preferred direction differs in different units.

6. Motion in the null direction can inhibit a maintained discharge. Very slow motion in the null direction may evoke a response.
7. Directionally selective units are strongly inhibited by stimulation of
the region surrounding their receptive fields, and this accounts for
the greater effectiveness of small, 'convex', moving objects.

8. Some units have large receptive fields. They tend to be less sensitive
to slow movements, but more sensitive to fast movements, than are the
usual concentric type of unit.

9. In a second series of experiments, 177 units were isolated with fine
tungsten electrodes, of these 166 could be classified: 104 (63%) were
concentric, 49 (30%) with on-centre, 55 (33%) with off-centre; 37 (22%)
were directionally selective types; a further 11 (7%) responded to fast
movement, and 14 (8%) were of a new type described below.

10. The new type was isolated in the densely packed central region of
the retina. Some of these units have small receptive fields, are strongly
inhibited by stimulation of the surround, and are excited by very slow but
not by fast movements. Some are directionally selective.

11. It is concluded that direction and speed of motion, as well as
localized dimming and brightening, are abstracted from the retinal image
by separate classes of ganglion cells in the rabbit's retina. Hence the
analysis of sensory information is carried much further in two synaptic
layers than is commonly supposed.

This work was supported by U.S.P.H.S. grants B-3834 and NB-03154.

REFERENCES

Arden, G. B. (1963a). Types of response and organization of simple receptive fields in cells

Arden, G. B. (1963b). Complex receptive fields and responses to moving objects in cells
of the rabbit's lateral geniculate body. *J. Physiol.* 166, 468–488.

69–88.


Barlow, H. B. & Brindley, G. S. (1963). Inter-ocular transfer of movement after-effects

Barlow, H. B., FitzHugh, R. & Kuffler, S. W. (1957). Change of organization in the


Bishop, P. O., Kozak, W., Levick, W. R. & Varkur, G. J. (1962). The determination of
the projection of the visual field on to the lateral geniculate nucleus of the cat. *J. Physiol.*
165, 508–539.

primate colour-vision system. In *The Visual System: Neurophysiology and Psychophysics*,

*J. Physiol.* 169, 1–33.

195, 28–32.
RETINAL UNITS OF RABBIT


