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THE MECHANISM OF DIRECTIONALLY SELECTIVE UNITS IN RABBIT'S RETINA

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Directionally selective single units have recently been found in the cerebral cortex of cats (Hubel, 1959; Hubel & Wiesel, 1959, 1962), the optic tectum of frogs and pigeons (Lettvin, Maturana, McCulloch & Pitts, 1959; Maturana & Frenk, 1963), and the retinae of rabbits (Barlow & Hill, 1963; Barlow, Hill & Levick, 1964). The term 'directionally selective' means that a unit gives a vigorous discharge of impulses when a stimulus object is moved through its receptive field in one direction (called the preferred direction), whereas motion in the reverse direction (called null) evokes little or no response. The preferred direction differs in different units, and the activity of a set of such units signals the direction of movement of objects in the visual field.

In the rabbit the preferred and null directions cannot be predicted from a map of the receptive field showing the regions yielding on or off-responses to stationary spots. Furthermore, the preferred direction is unchanged by changing the stimulus; in particular, reversing the contrast of a spot or a black-white border does not reverse the preferred direction. Hubel & Wiesel (1962) thought that the directional selectivity of the cat's cortical neurons could be explained by the asymmetrical arrangement of on and off zones in the receptive field, and the simple interaction of effects summated over these zones, but the foregoing results rule out this explanation, at least in the rabbit's retina (Barlow & Hill, 1963).

In the present paper we go on from this point to describe experiments which show, first, that directional selectivity is not due to optical aberrations of some kind and, secondly, that it is not a simple matter of the latency of response varying systematically across the receptive field. After these negative results we describe experiments upon the organization of directional selectivity within the receptive field, and upon its mechanism. These lead us to the conclusion that the ganglion cells responding to a

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particular direction of motion are fed by a subset of bipolar cells that respond to the corresponding sequence of excitation of two neighbouring retinal regions with which they connect. Furthermore there is evidence that this sequence-discrimination is brought about by a laterally connecting inhibitory element from one of these regions, and this seems a likely function for the horizontal cells to perform. At this stage identification of the elements concerned is obviously tentative, but we were pleasantly surprised to find well known histological structures already at hand to fill the roles that the functional organization seemed to require.

All the experiments described here were performed upon on–off directionally selective units. We have reason to believe that the mechanism is different for the rare, on-type, directionally selective units and also for the centrifugal and centripetal motion sensitivity of the ordinary concentric type of units.

METHODS

Action potentials were recorded from the unopened eyes of rabbits. As described elsewhere (Barlow *et al.* 1964), it proved most effective to use fine tungsten electrodes, decerebrate or lightly anaesthetized (urethane and chloralose mixture) animals, and immobilization by continuous infusion of gallamine triethiodide (Flaxedil). Periodically the animal was allowed to recover from paralysis by using an infusion fluid without relaxant. One could thus ensure that the level of anaesthesia was neither too deep nor too light at the rate of anaesthetic infusion employed.

When a good on–off, directionally selective unit was isolated the first step was always to map out its receptive field on a plotting board 57 cm from the eye. A stationary spot was turned on and off; in most cases this was ¼° diameter at an intensity of 12 cd/m² and was superimposed on a background of 0·6 cd/m². Directional selectivity was tested for and null and preferred directions determined. Various techniques were used to provide the temporal and spatial patterns of light stimuli. For the two-spot experiment we initially used two glow modulator tubes controlled by pulse generators, but we later found that black and white cards moved behind apertures in grey paper provided a more flexible means of delivering the required stimuli. This method also has disadvantages (see p. 486) which we finally overcame by illuminating the apertures from behind with thin Perspex light pipes lit by low-current torch bulbs turned on and off manually. The changes of luminance occurring within the receptive field of the unit were monitored by a photocell whose output was recorded with the action potentials.

RESULTS

The results are presented in four sections. These are: (1) controls and negative results which rule out various preliminary hypotheses on the mechanism; (2) experiments which lead to the conclusion that the directional selectivity of the ganglion cell results from the sequence-discriminating activity of subunits—probably bipolar cells; (3) observations and experiments which show that sequence-discrimination is achieved by an inhibitory mechanism that prevents responses to sequences in the null direction; (4) observations showing that inhibition also occurs with stimulation of the surround of the receptive field.

Controls and negative results

Optical controls. It might be thought that the unequal responses to motion in the null and preferred directions were the result of a peculiarity of the light distribution in the retinal image caused by aberrations of the optical system. Although none of the schemes suggested to us, and none we could imagine, seemed at all promising, we considered this possibility, but were forced to abandon it at an early stage. The most direct disproof is given by the observation that two units recorded simultaneously, or within a short period of time, in the same retinal region can have their preferred axes opposite or at right angles to each other. An optical explanation of the phenomenon requires that there be some asymmetry in the light distribution to cause the asymmetry in the responses, and two different asymmetrical light distributions cannot co-exist in the same region.

A second disproof is provided by observing how little the phenomenon is affected by deliberately introduced optical aberrations. Figure 1 shows that clear-cut directional selectivity persists with spherical supplementary lenses causing more than 10 dioptres of refractive error in either direction. This was for the normal pupil diameter of our preparation—6 mm or more. Furthermore, reducing the aperture of the rabbit's optical system to 3 or 1·25 mm with an artificial pupil must greatly improve retinal image quality (since diffraction is most unlikely to be a limiting factor); yet we found that such stopping down merely extended the range of refractive error over which the directionally selective property was shown. It did not even improve acuity as judged by the finest grating giving any response to movement.

The best spherical correction was determined in each preparation, judging this opthalmoscopically and sometimes retinoscopically. In all the preparations the cornea and media were free from clouding, except occasionally at the very end of a 2-day experiment. Optical effects from the shank of the electrode can be excluded, for directional selectivity is often observed when recording from a nerve fibre. In such cases, no portion of the electrode intercepts light reaching the retina from the receptive field projection.

Finally, we should point out that for most of the tests used here the human eye's performance is superior by a factor of 10. The demands made of the rabbit's optical system are thus not at all severe, but of course the blur of the retinal image should be taken into account when interpreting quantitatively the results of our later experiments.

Latencies. The first idea about mechanism was that the latency of the response might be shorter at successive positions along a path through the receptive field traced in the preferred direction. It was thought that when

the image of an object moved in this direction the excitation from successive positions would arrive synchronously at the ganglion cell, and thus might be more effective than when movement was in the null direction and it was dispersed in time. An alternative scheme can be devised in which the temporally dispersed sequence is more effective because it avoids

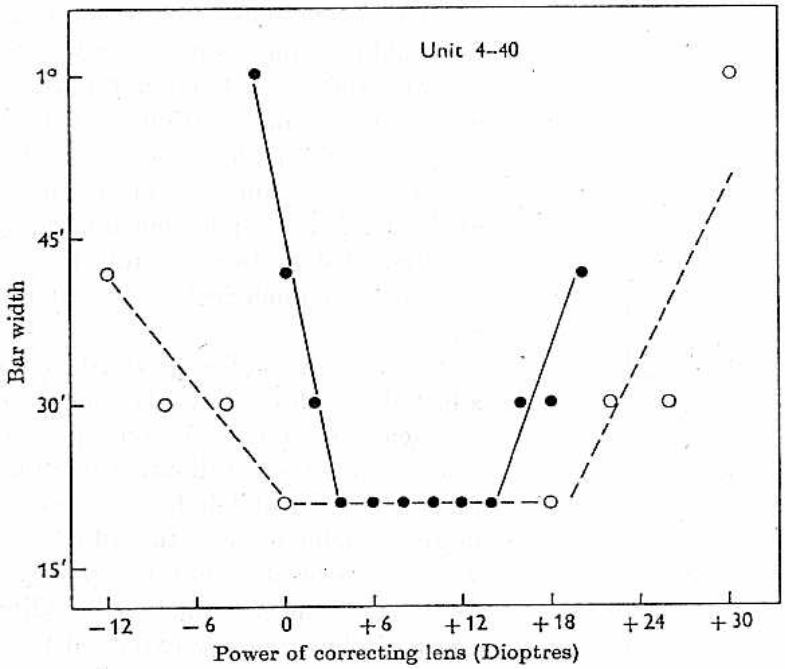

Fig. 1. The effect of refractive error and pupil diameter upon the acuity for a moving grating. Pupil dimensions were 6 × 8 mm (●) and 3 mm diameter (○); luminance of the white bars was 2·5 cd/m² for the large, 25 cd/m² for the small pupil. The points show the finest grating for which there was a distinctly greater response to movement in the preferred direction. Paradoxical responses, greater in the null direction, were not observed. A small discharge with movement was detectable in most cases for the next finer grating (71 % of the period), but this was not obviously different in the two directions. Notice that directional selectivity persists over a large range of refractive error, and that the finest resolvable grating is not affected by pupil diameter: optical aberration is not likely to be the cause of directional selectivity, and probably does not limit the optimum acuity of this preparation.

refractoriness. Thomson's (1953) work on the rabbit's retina, together with our own findings on the different latencies of centre and surround in concentric units (Barlow *et al.* 1964) lent some plausibility to the suggestion that the latencies might vary with position, but the result shown in Fig. 2 is entirely negative. In this and other experiments 'on' and 'off' latencies showed no sign of changing systematically with position in the receptive field.

Unsuccessful two-spot experiments. One sees from the records of Fig. 2 that excitation of a point in the field causes a response at on and off: yet if a spot of light is moved through the field in the null direction no response occurs, even though each point crossed by the spot must have received an 'on' followed by an 'off' stimulus as the spot passed over it. The obvious next step in the analysis seemed to be to stimulate at two points and see how the response changed when the order and temporal interval between the stimuli was varied. We hoped to decide whether the response to

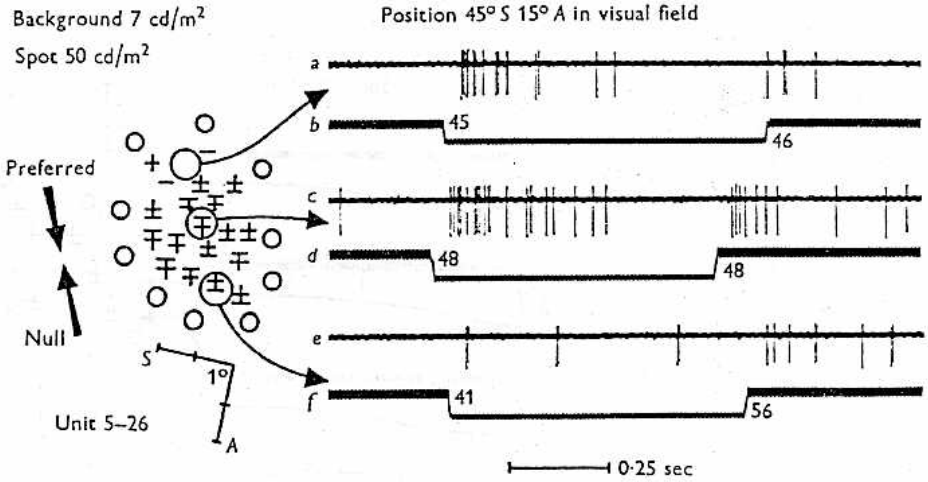

Fig. 2. Latencies of response at different positions. The receptive field map is shown at the left; positions yielding on and off responses to a stationary spot are marked + and −; positions yielding both are marked ∓ if off was greater, ± if on was greater; no responses were obtained on or outside the ring of ○'s. Records *a*, *c*, *e*, are the responses to a light turned first off, then on, at three successive positions along a line through the receptive field in the preferred-null axis, as shown to the left (negativity is upwards). Records *b*, *d*, *f*, are from a photomultiplier observing the receptive field (decreased light is downward), and the numbers show the latency of response in msec (one impulse was ignored in *a*). There is no significant trend in latency as one moves across the receptive field.

motion in the preferred direction was greater than the sum of responses to excitation of separate points along the path, or whether the unequal responses to motion in the two directions resulted from inhibition occurring when the motion was in the null direction.

The question seemed clear-cut, but the results were not. In the first place it was not nearly as easy to obtain unequal responses for the two sequences as it was to obtain unequal responses with real moving objects. Secondly, when we did get evidence of sequence-dependent responses, the result seemed highly variable and we were unable to decide whether summation or inhibition or both were occurring. This failure forced us to

realize that we did not know whereabouts in the receptive field we should put the spots, nor how far apart they should be. There was in fact a prior question to answer before the two-spot type of experiment could be performed and interpreted. The question, put in a form that avoids implications as to mechanism, is this: does the ganglion cell respond selectively to one direction of motion over all parts of its receptive field, or is there some critical zone or line which must be crossed? The following observations show that there is no such line and the directionally selective property is distributed over the receptive field.

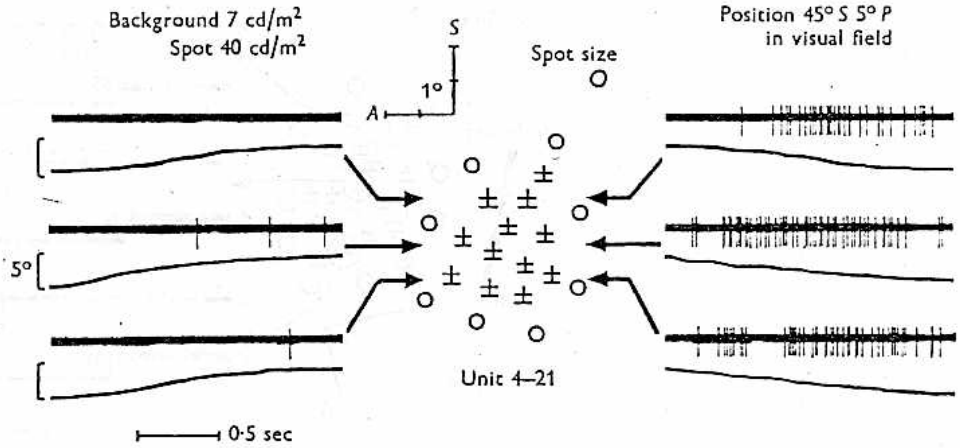

Fig. 3. Responses to motion along three different paths through the receptive field. The map in the centre shows the field and the paths through it; symbols as in Fig. 2. The records of the responses to traverses in the null direction are to the left, those for the preferred direction to the right. The lower trace of each pair is from a potentiometer and shows the position of the spot as it moved through the field (calibration at left). Top, middle and bottom parts of the receptive field all show the same directional selectivity.

Sequence-discrimination by subunits

Distribution of directional selectivity. Figure 3 shows the responses obtained when a spot of light was moved across the receptive field and back along three parallel lines. These were separated by more than the breadth of the spot, and therefore different receptors were covered by the geometric image of the moving spot in each case. It will be seen that the selectivity clearly exists along all these three pathways.

Figure 4 shows typical responses obtained when the spot was moved several times from one position to the next and back, as marked. It is clearly not necessary for the spot to cross any definite line in order to obtain different responses for the two directions of motion. If the experiment is repeated using a black spot the same result is obtained; direction

of motion, independent of contrast, can be picked out in a large number of widely separated regions of the receptive field. However, there is an interesting exception to the rule that all regions of the receptive field have the capacity to distinguish between null and preferred sequences of excitation of the receptors they contain. There is a zone adjacent to the edge of the field that is first crossed when motion is in the preferred

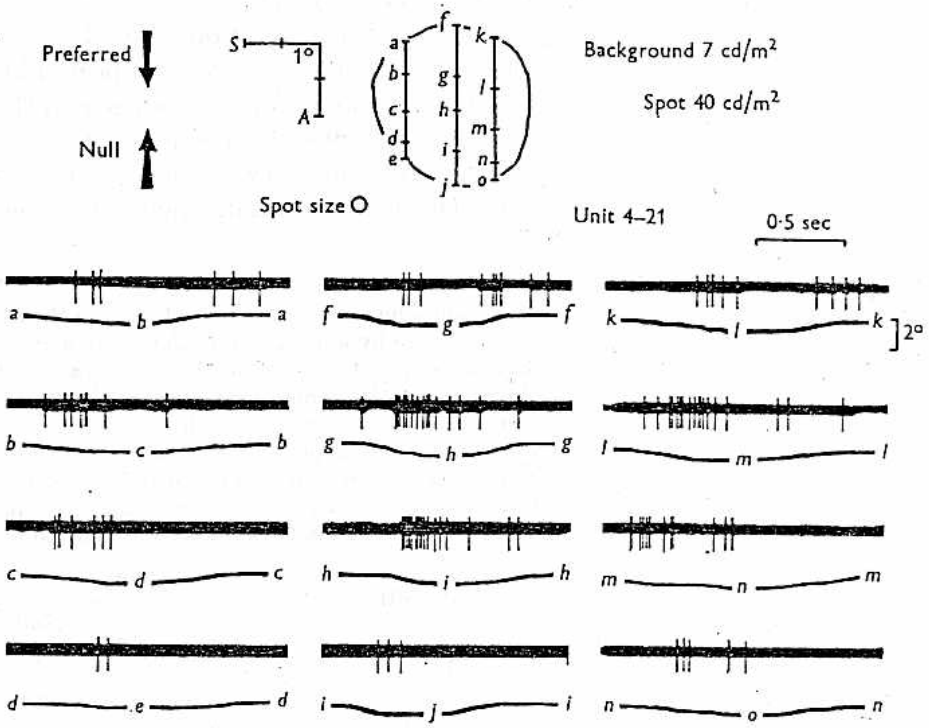

Fig. 4. Back and forth motion in different parts of the receptive field. The edge of the receptive field is mapped at the top, and the positions *a*, *b*, *c*, . . . , *o*, within it are indicated. The spot was moved back and forth several times between *a* and *b*, then between *b* and *c*, and so on. The records are samples of these back and forth motions. The lower trace of each pair shows the position of the spot in the field: downward movement of the trace corresponds to movement of the spot in the preferred direction. Marked asymmetry of response for the opposite directions holds in most positions in the field. Its absence in the top row of records is expected in the inhibitory scheme (see Fig. 7 and p. 490).

direction where this capacity is lacking: motion in either direction causes a response. This is shown in the top line of records in Fig. 4, and a possible explanation for the effect is given later (see p. 490).

Smallest region giving directional selectivity. Figure 4 shows clear directional selectivity when a spot of light is moved to and fro through 1° in a receptive field whose total diameter is about 3°. What then is the

smallest distance over which responses to motion in the two directions differ?

To answer this question we moved a strip of white card with a section painted black behind an aperture of variable width in a sheet of grey paper. The aperture breadth was 20 mm (subtending 2°) and the width measured in the direction in which the card moved varied from 1 mm (6′) to 11 mm (1° 06′). When the card was moved there was no change until the border of the black section entered the aperture, it then moved through a variable distance before it disappeared behind the other edge, after which there was again no further change and the aperture was wholly black. The sequence described above was called 'off' stimulation since with black trailing the receptors were successively exposed to a reduction of illumination. On the other hand, when the border of the white portion appeared in the aperture and moved along it they were successively exposed to 'on' stimulation. Clearly 'off' and 'on' stimulation could be applied in any direction and at any velocity, but we confined our attention to the preferred and null directions, and moved the cards by hand at velocities chosen to give optimum discrimination between the two directions—in most cases about 5°/sec. The variable studied was the width of the aperture, and the feature of the response attended to was the existence of a clear-cut difference between responses to stimulation in the preferred and null directions.

TABLE 1. Single slit experiment

A black–white border was moved through the receptive field, but the view of the motion was restricted by a fixed rectangular slit in a grey card placed immediately in front of the moving border. The width of this slit, measured in the direction of motion, was varied. Movement of the border causing the slit to change from white to black was called 'off' stimulation, movement causing it to fill with white was called 'on' stimulation. Each of these stimuli was applied with the edge moving in both null and preferred directions. We graded the unit's response from 0 to 6 after listening to several repetitions of these stimuli on the loudspeaker. This unit could distinguish the preferred from the null direction with slit widths down to about 17′ for both 'on' and 'off' stimuli.

Slit width	'Off' stimulus		'On' stimulus	
	Preferred	Null	Preferred	Null
1° 36′	6	1	4	0
1° 06′	6	2	4	1
48′	5	2	4	0
34′	4	2	3	1
24′	4	2	3	1
17′	3	2	3	2
12′	3	3	3	2
8′	2	2	2	2

The amplitude of the response was graded subjectively from 0 to 6, and Table 1 gives a typical result. The subjective grading was a crude but con-

venient way of quantification: records of typical responses are shown in Fig. 5. Altogether 10 units have been studied in this way, and the threshold aperture for directional discrimination varied from 6′ to 24′.

The straightforward interpretation of this result is that the complete mechanism for directional selectivity is contained within a subunit of the receptive field extending not much more than $\frac{1}{4}°$ in the preferred–null axis. Since the result does not depend critically upon the position of the slit within the receptive field, it looks, again taking the straightforward view, as

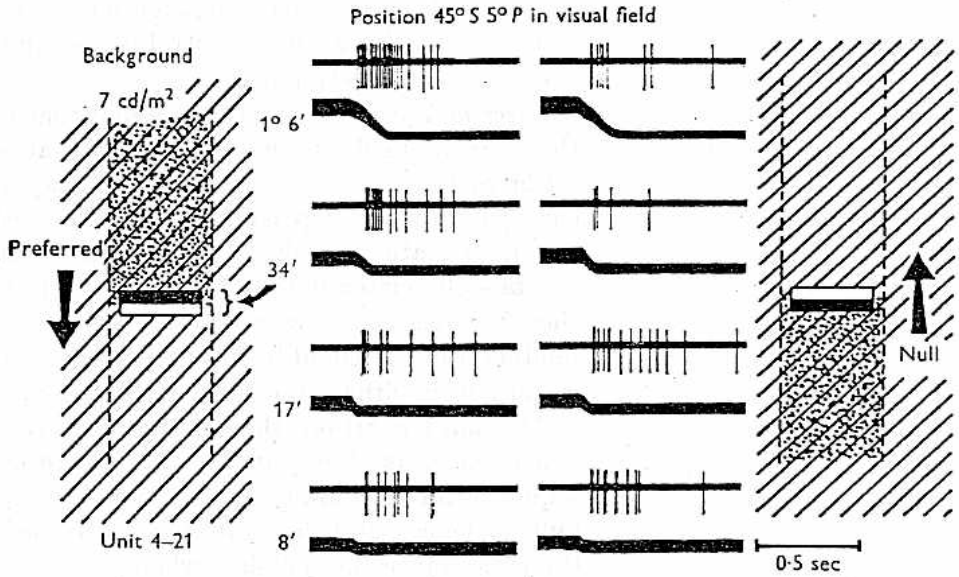

Fig. 5. Responses to motion of a black edge across slits of various widths (breadth was 2° in all cases). Results are shown for four slit widths, from 1° 06′ to 8′ measured in the preferred-null axis. The records to the left were obtained when the black border advanced across the slit in the preferred direction, those to the right when it moved in the null direction. The lower trace of each pair is the response of a photomultiplier aimed at the field. Notice that the differences between preferred and null motions are obvious in the top two records, when the distances through which the edge could be seen moving were 1° 06′ and 34′; the difference is only just detectable at 17′ and has vanished at 8′. The directionally selective mechanism appears to be contained within a retinal region subtending $\frac{1}{4}°$ to $\frac{1}{2}°$, whereas the whole receptive field subtended $4\frac{1}{2}°$.

if the sequence-discriminating mechanism must be reduplicated perhaps a dozen or more times to cover the whole receptive field. Would there be any escape from this conclusion if the image was of very poor quality so that, even for the small slits, it was diffused over a large part of the receptive field?

If the optics are poor, then the time course of light intensity changes at the two edges of the receptive field will be slightly different for the two

directions of motion, and one can set up somewhat elaborate schemes in which these differences form the basis of directional selectivity. The schemes have to be made even more complicated to account for the fact that black or white edges advancing through the slit show the same directional preference. Now it will be shown in the next section that the interaction responsible for directional selectivity occurs better at small separations of the stimuli than at large separations. We can think of no way in which neighbouring retinal regions would show more interaction than widely separated ones unless the subunit responsible for directional selectivity is itself a small compact one. In this way the experiment about to be described is a useful control confirming the conclusion reached from the single slit experiments.

Discrimination of sequence. The fact that movements within a region of the receptive field subtending less than $\frac{1}{4}°$ are sufficient to give directionally selective responses suggests a possible explanation for our failure to get clear-cut sequence-dependent results when we first attempted to excite with a pair of static stimuli at various temporal intervals. In these experiments spots closer together than about 1° had never been tried and we therefore designed new apparatus so that two strips of light each subtending $0{\cdot}1° \times 2°$ could be brought to within 0·1° of each other and turned on and off in either sequence (see Methods).

At small separations the experiment gave definite evidence of sequence-dependence, as shown in Fig. 6. The response is much greater in the sequence corresponding to movement in the preferred direction than for null sequences, and this is true for both 'on' and 'off' stimuli. However, these differences become less when the separation of the slits is increased to over 1° even though both slits remain inside the receptive field.

We have done similar two-slit experiments in which moving cards were used to provide 'on' or 'off' excitation at the two slits. These also indicated that sequence discrimination occurs at small separations but is reduced at large separations as shown in Table 2. It was not easy to judge the responses accurately but the difference between null and preferred sequences faded out for separations greater than $\frac{1}{2}°$ and other units showed a similar reduction for large separations. There is, however, a defect in these experiments which was not always fully controlled. In order to provide a vigorous stimulus with each slit it was made 0·1° wide. This is below the threshold for directional selectivity in most preparations, hence in these cases each slit by itself was equally effective for null and preferred sequences. However, this was not always true, and some of our results lack the necessary controls. In addition it might be held that there are effects of movement which are subthreshold for each slit by itself but become suprathreshold with the pair, and that it

is the summation of these subliminal effects that produces the asymmetry for the two sequences. A control observation (made on a unit in which directional selectivity occurred across the 0·1° slit) meets this criticism and is worth reporting because it reinforces the conclusion that sequence as such is effective.

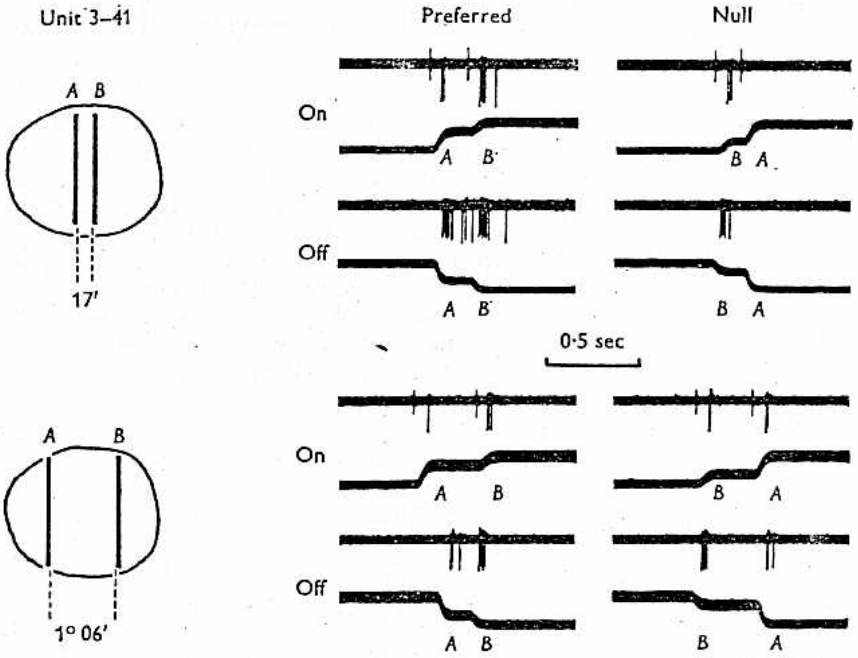

Fig. 6. Responses to different temporal sequences of two static stimuli. On the left the positions of the pair of stimuli are shown within the outline of the receptive field. Records for the small separation are shown above, those for the large separation below. Within each half, records for on are above those for off. The lower trace of each pair is the photomultiplier output: increasing light moves the trace upwards, and slit *A* was arranged to give the bigger step in every case, even though it was not brighter. Preferred sequences are on the left, null on the right. Notice that the preferred sequence yields more spikes than the null at the small spatial separation, but this difference ceases to be clearly visible when the separation of the slits is increased.

In this experiment the card behind the pair of slits had white and black regions arranged so that when the card was moved in one direction the sequence of lightening or darkening at the two slits corresponded to motion in the opposite direction. Under these conditions each slit by itself gave a greater response for movement of the card in the preferred direction. However, when both slits were used there was a greater response for movement of the card in the null direction: that is, the sequence of activation of the slits was overriding the effects of motion in the opposite direction within each slit.

It must be pointed out that the time interval between the two stimuli is an important variable that we have not yet studied systematically. In timing these stimuli manually we have varied the interval over as wide a range as possible, but in spite of this we never found as strong an interaction at large as at small spatial separations of the slits. Some further results with this type of experiment are given in Table 3 (see later) and it is hoped that a more systematic exploration will be presented in the future.

TABLE 2. Two-slit experiment

Same unit as in Table 1. The stimulus was again a black–white border moved through the receptive field in the null or the preferred direction, but the view of the motion was now restricted by a pair of narrow slits in a grey card placed immediately in front of the moving border. Each slit subtended only 6′, and responses to preferred and null directions were indistinguishable for each slit by itself. However, when the pair of slits was darkened or lightened in sequence, the strength of the response was found to depend upon the order in which the slits changed. The separation of the two slits, measured in the direction of motion, was varied and the unit's response graded as in Table 1. The effect of the order of stimulation was greatest at small separations, but null and preferred sequences were still distinguishable up to 24′ separation.

Slit separation	'Off' stimulus		'On' stimulus	
	Preferred	Null	Preferred	Null
1° 36′	2	2	2	2
1° 06′	3	3	3	3
48′	3	3	2	2
34′	3	3	2	2
24′	4	3	3	2
17′	3	2	3	1
12′	4	2	3	1
8′	3	1	3	1
6′	3	1	3	2

We think the results already given are sufficient to establish that directional selectivity may be based upon the discrimination of the sequence of excitation of only a pair of regions. Even though the image of a moving object falls on a long succession of receptors in a continuous succession of time intervals it is unnecessary to postulate the interaction of more than two regions to account for the directionally selective property.

Responses to gratings. The results so far reported suggest that sequence-discrimination is performed by subunits of the receptive field. Figure 1 shows that a directionally selective unit can discriminate the direction of motion of the bars of a grating subtending 15′ (period 30′). It is hard to see how this discrimination could be performed if the bars of the grating were small compared to the size over which each subunit integrates or averages the light, and in fact the resolvable grating size fits, to a first approximation, the size of subunit suggested by the preceding tests. Another result that may also fall into line is the shape of the curves found when determining threshold as a function of area (Fig. 5 of Barlow *et al.*

1964; see also Barlow, 1953). Complete summation (that is, threshold $\propto$ 1/area) does not hold out to the full diameter of the receptive field in the directionally selective units of the rabbit, and it is tempting to identify the limit to which it does hold (approx. 20′) as the integrating area of the subunits.

One negative result in the grating tests is worth comment. Hassenstein (1951) found paradoxical optokinetic movement responses in beetles: when a grating of period slightly greater than the angular separation of the axes of the ommatidia was moved in one direction, the beetles responded as for the opposite direction of movement. Nothing of this sort was seen in the present tests: when motion of a grating caused a response, this was never greater in the null direction than in the preferred direction. This is not too surprising, for the occurrence of paradoxical movement responses in the beetle must depend upon the regular spacing of its ommatidia.

Mechanism of sequence-discrimination

The foregoing experiments show that the directional selectivity of ganglion cells is based upon sequence-discrimination within subunits of their receptive fields, but they tell us nothing about the mechanism whereby a pair of stimuli causes a greater discharge in one sequence than in reverse. Figure 7 shows two schemes in which the preferred sequence, corresponding to motion in the preferred direction, elicits a greater response than the null sequence. These are intended to exemplify two broad alternatives, not to make exact specifications.

The left-hand scheme works by detecting a specific conjunction of excitations: activity aroused by increase or decrease of illumination in region *A* is delayed and arrives at the 'and' gate in the next layer synchronously with activity aroused when the image moves on to region *B*. Activity from *B* passes to the 'and' gate below it, and is also passed laterally to interact with activity from *C*. The sequence *ABC* is the preferred sequence, and the gates only respond when their respective conjunctions 'both *B* and delayed *A*', or 'both *C* and delayed *B*' occur.

Instead of selecting the preferred stimulus by a logical conjunction, the right hand scheme rejects the null stimulus by veto. Activity aroused at 'on' or 'off' in region *B* or *C* is again passed laterally and acts after a delay, but in this case it inhibits the next unit. As before, *CBA* is the null sequence, and when it occurs the inhibition from *C* prevents the response that would have resulted from *B* alone, and inhibition from *B* likewise vetoes *A*'s response. On the other hand if the sequence is the preferred one, *ABC*, then the inhibition from *B* does not arrive until the excitation from *A* has already got through, and likewise *C* is unsuccessful in vetoing *B*. It will be observed that this scheme only requires that inhibition persists

longer than excitation; a definite delay when it is passed laterally is not strictly necessary.

Some evidence favouring the right-hand, inhibitory, scheme has already been given. (1) As shown in Fig. 2 a stationary spot turned on and off elicits a response. If the excitatory conjunction scheme was modified to account for this it would probably still predict a considerably lower threshold for a moving than for a stationary spot. As shown in Fig. 5 of Barlow *et al.* (1964), the thresholds for spots of various sizes moving in the preferred direction differ by small and inconstant amounts from those for the same spot turned on or off. (2) The most striking feature of these directional units is the absence of any impulses when movement is in the null direction. This prompts one to look for a mechanism that inhibits unwanted responses. (3) When testing for directional selectivity in

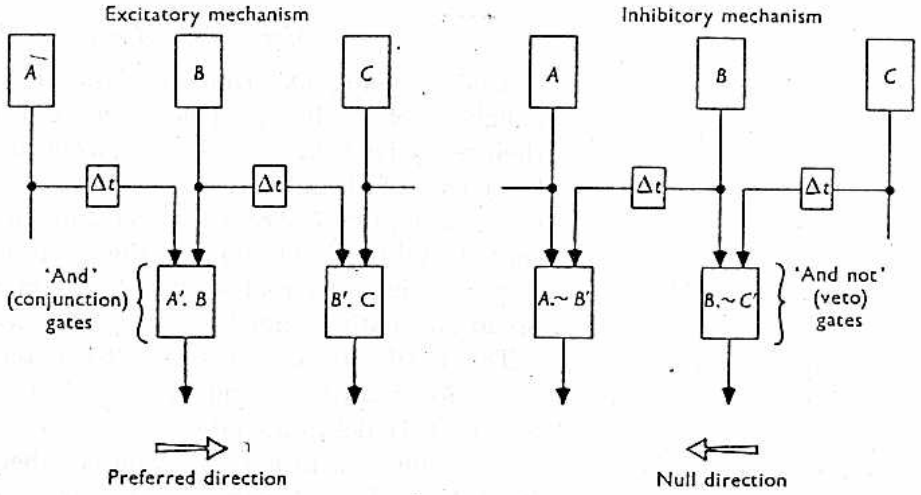

Fig. 7. Two hypothetical methods for discriminating sequence. For both, the preferred direction would be from left to right, null from right to left. In the excitatory scheme activity from the groups of receptors A and B is delayed before it is passed laterally in the preferred direction to the 'and' (conjunction) gates. If motion is in the preferred direction A' (delayed A) occurs synchronously with B, B' occurs synchronously with C, and these conjunctions cause the units in the next layer to fire. In the scheme on the right the activity spreads laterally, but in the null direction, from the groups of receptors B and C, and it has an inhibitory action at the units in the next layer; hence these act as 'and not' (veto) gates. The inhibition prevents activity from A and B passing through these gates if motion is in the null direction, but arrives too late to have an effect if motion is in the preferred direction. Notice that a special delay unit is not really necessary, for this scheme works if inhibition simply persists longer than excitation and can thus continue to be effective after a lapse of time. The excitatory scheme works by picking out those stimuli with the desired property, whereas the inhibitory scheme works by vetoing responses to unwanted stimuli; the latter is the one favoured by the experimental evidence.

different parts of the receptive field we found that the results obtained at one edge were anomalous in that movements in both null and preferred directions gave responses. Such responses are illustrated in the top row of records in Fig. 4. On the inhibitory scheme it may be possible to resolve this anomaly along the following lines. Responses from the last points crossed by a spot moving in the null direction are normally prevented by inhibition coming from the penultimate regions that have just been crossed. If the spot is moved to and fro solely in the rim, this penultimate region is avoided, and consequently it never inhibits the responses coming from the rim. Measurements of this 'inhibition-free' zone at the rim suggest that it may extend for as much as 1° inwards from the extreme edge of the receptive field.

These observations are not decisive, but they brought the inhibitory scheme to the front of our minds, and we now give some much stronger evidence favouring it.

Movements in null direction evoking responses. A spot of light moved continuously through the field in the null direction will evoke no impulses, but if such continuous motion is interrupted while the spot is in the receptive field, a burst of impulses occurs just when the movement starts up again. Evidently the inhibition that prevents the response when motion is continuous decays while the spot is stationary, so that when the spot moves on to new receptors the activity excited escapes inhibition and gets through to the ganglion cell. This response to intermittent motion is illustrated in Fig. 8.

If motion in the null direction is slow enough, a discharge can also be elicited, and this is illustrated in Fig. 9. Presumably the rate of rise and decay of the inhibitory process, together with the distance at which it operates, governs the range of speeds over which directional selectivity occurs.

Responses to slits singly and in sequence. What was thought to be a crucial test of the inhibition hypothesis was devised. Two slits were placed close to each other and the responses to each in isolation were recorded several times at on and off. The slits were then presented in null or preferred sequence, and several responses again recorded. The records were analysed by counting the impulses that occurred within $\frac{1}{2}$ sec of stimulation, and the averages of 4 to 7 responses are presented in Table 3.

First compare the figures in the last two columns, and notice that the result confirms what has already been said. Preferred sequences are more effective stimuli than null sequences at all separations studied, but the difference is most pronounced at small separations and decreases at the separations greater than 17′. Now compare the figures in the 'Null' column with those in the '$A+B$' column. In every case the 'Null' has the

lower figure, so that inhibition certainly occurs: when the sequence is in the null direction fewer impulses occur than when each region is excited separately. Finally, compare the figures in the 'Preferred' column with those in the '$A+B$' column. Here there is an excess in the 'Preferred' column at small separations, but not at large separations.

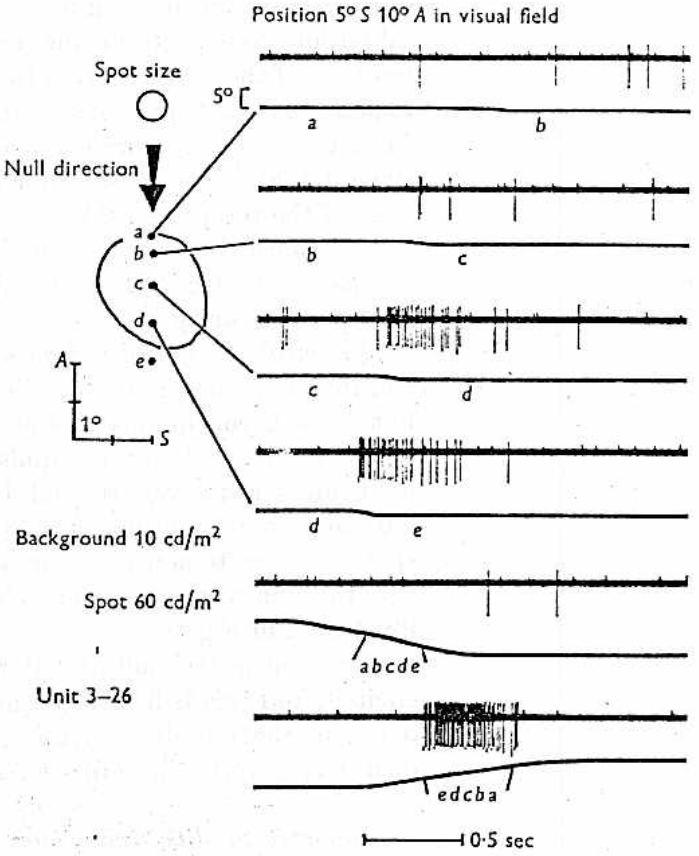

Fig. 8. Escape of impulses with intermittent movement in the null direction. Five positions are marked in relation to the outline of the receptive field shown on the left. The lowest two pairs of records show the effect of sweeping continuously through these positions in the null (*abcde*) and preferred (*edcba*) directions. In the upper four pairs the spot was moved discontinuously, first from *a* to *b*, then from *b* to *c*, then from *c* to *d*, then from *d* to *e* just outside the field. The lower trace of each pair shows the position of the spot in the field. As an example of the escape phenomenon notice that no impulses occur when movement from *c* to *d* is part of a continuous sweep (5th pair of records), but they do occur when this movement is made in isolation (3rd pair). The suggested interpretation is that 'on' or 'off' stimulation at any point inhibits 'on' or 'off' excitation of the next point in the null direction, but this inhibition decays with time. When the spot pauses at *c*, off excitation from *c*, and on excitation of the next point, occur after inhibition has decayed and impulses therefore escape.

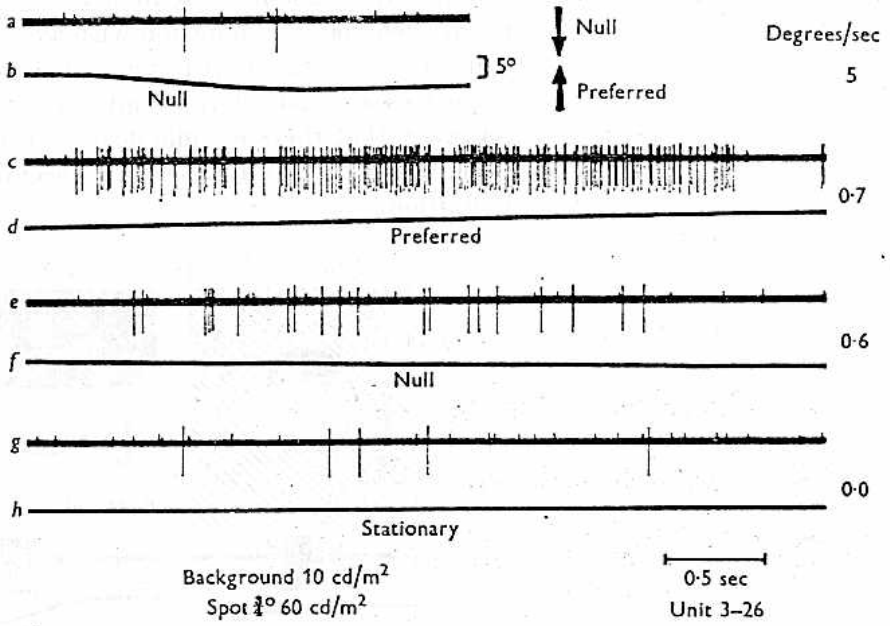

Fig. 9. Paradoxical response to very slow motion in the null direction. As before the lower trace of each pair shows the position of the spot of light. For movements at about 5°/sec a vigorous response was obtainable in the preferred direction, but the top pair of records shows that in the null direction there is no increase over the maintained firing rate with no stimulation (lowest pair of records). When motion was at about 0·7°/sec there was still a vigorous response in the preferred direction (2nd pair), but in the null direction (3rd pair) there was also a distinct increase compared with the maintained discharge (4th pair). If movement is slow enough, the inhibition at a point in front of the advancing spot must have declined by the time the spot reaches it to a level where extra impulses are allowed to pass.

TABLE 3. Inhibition and sequence-discrimination

Two narrow rectangular slits *A* and *B* were lit from behind, and were spaced various distances apart along the preferred-null axis of the receptive field. Responses were recorded when each slit was turned on and off, first, in isolation, and then in sequences corresponding to the null (*BA*) and preferred (*AB*) directions. The figures are the average numbers of spikes that occurred within ½ sec of stimulation (4–7 responses averaged). For the null sequence there was always a deficit of spikes compared with the sum of the spikes produced by the two slits separately.

Slit separation	Stimulus	*A*	*B*	*A* + *B*	Null *BA*	Preferred *AB*
1° 06′	On	2·6	1·7	4·3	2·0	1·8
	Off	9·3	4·7	14·0	5·9	8·0
34′	On	5·2	3·2	8·4	3·4	6·3
	Off	10·2	6·2	16·4	4·6	14·9
17′	On	5·1	3·2	8·3	1·6	13·9
	Off	9·1	4·1	13·2	3·2	19·8
8′	On	5·0	4·0	9·0	2·0	13·0
	Off	8·5	5·5	14·0	1·8	17·7

Individual responses are highly variable and the experimental situation needs systematic exploration with averaging techniques. At this stage we can say that the experiment obviously supports the idea that null sequences are ineffective stimuli because of inhibition. It also indicates, however, that there is some degree of facilitation for preferred sequences, though it is fair to add that this seems a less important effect than the inhibition.

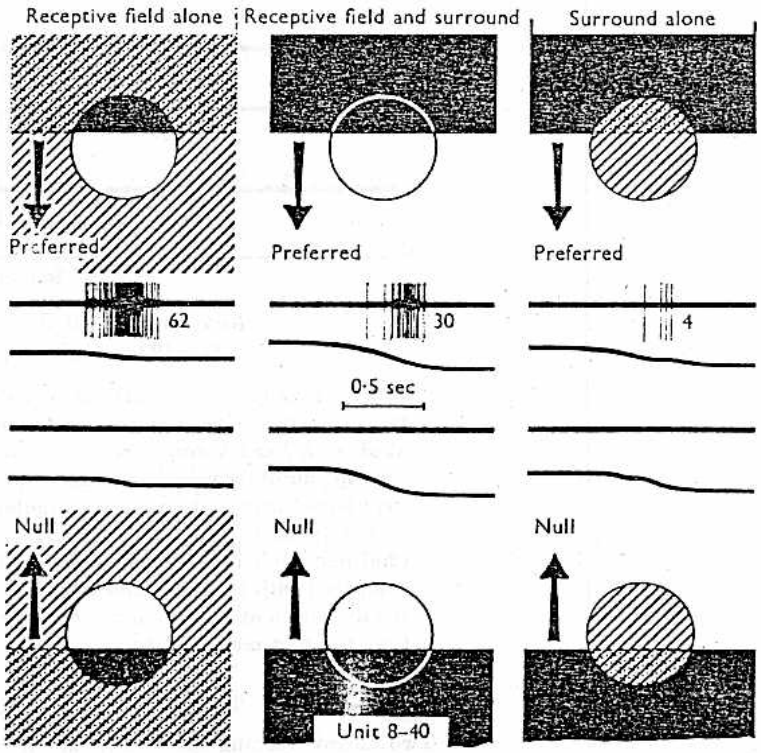

Fig. 10. Lateral inhibition and responses to movement. A black edge was moved behind a mask of grey paper (cross-hatched) so that the advancing border crossed a 4° hole exposing the receptive field alone with the surround masked off (left), the surround alone with the receptive field masked off (right), or it crossed both together, with no mask (centre). The records show the responses; the lower trace of each pair came from a photocell aimed at the receptive field. No impulses were obtained when motion was in the null direction (lower pair of records). In the preferred direction some were obtained in each case, but the response was much greater with the surround masked off than when it crossed surround and centre together (62 instead of 30 impulses). Motion in the surround inhibits the response to motion in the centre, just as light going on or off in the surround inhibits on or off responses from the centre.

Inhibition from outside the receptive field

The type of inhibition postulated to account for directional selectivity, and shown up in the experiment of Table 3, comes from within the receptive field—that is, from within the region where light can evoke impulses. There is also an inhibitory mechanism acting from outside the receptive field—that is, from the surrounding region where light stimuli evoke little or no response. Figure 10 shows an example of the effect of this inhibitory mechanism on the discharge evoked by a moving object. Figure 5 of Barlow *et al.* (1964) shows the effect of this inhibitory mechanism on the threshold.

DISCUSSION

Physiological function and anatomical structure

We think that the experiments described establish without need of further discussion these four points about directional selectivity. First, it is not caused by optical aberrations, nor by simple differences of latency for discharges evoked from different parts of the receptive field. Secondly, it is not necessary to cross any critical region or line in the receptive field: the mechanism responsible for the property resides in small subdivisions of the field and must be extensively replicated. Thirdly, these replicated subunits distinguish between null and preferred sequences of excitation of a pair of regions with which they connect; thus the directional selectivity of the ganglion cell is built up from sequence-discriminating subunits. Fourthly, inhibition plays an important part in this discrimination by preventing responses to sequences corresponding to motion in the null direction.

By themselves these results probably do not justify any further conclusions, but the complexity of function that they have revealed is beginning to match up to the long-known complexity of neural structure in the retina. It is a challenging problem to fit together the jig-saw puzzle of anatomical elements in the hope of revealing the picture of physiological function, and a tentative solution is shown in Fig. 11. It is certainly incomplete, for it does not specify the connexions of the concentric type of ganglion cell, nor of those selectively responsive to fast and slow movement (Barlow *et al.* 1964). Furthermore, we assume that there is a duplicate set of bipolar and horizontal cells that are activated at 'off'. We have some evidence, to be presented elsewhere, that 'on' and 'off' systems do not interact with each other at this level, and therefore for simplicity we have omitted the 'off' system. Because of the diversity of types of bipolar and horizontal cells (on and off for at least four different directions) one can see why a very large number of bipolar cells are required to handle the input from a group of receptors.

At various points there are alternatives to our scheme that are not excluded by the evidence at present available. On the other hand the roles of the anatomical elements and their postulated connexions are not as arbitrarily assigned as a naive reader is liable to suppose. For discussion, take what is perhaps the most controversial and interesting feature of the scheme—the assignment to horizontal cells of the role of inhibitory elements that prevent bipolar cells responding to null sequences. There are two main questions to be answered: why place the inhibitory element in the inner nuclear layer? And why postulate that the horizontal cell

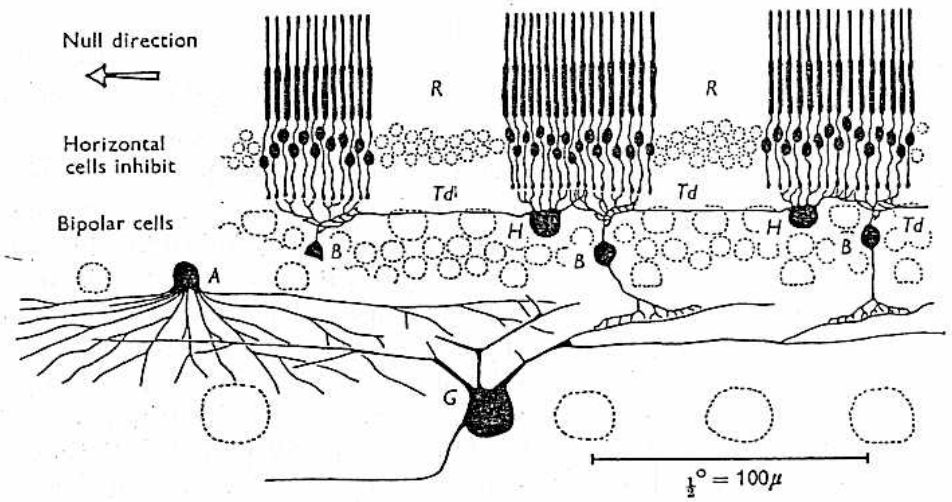

Fig. 11. Suggested functional connexions of the retinal elements concerned with directional selectivity. The elements are freely adapted from Cajal (1893), and are assembled in accordance with the functional organization suggested in this paper. The scale of the diagram is approximate and a posterior nodal distance of 11·5 mm has been assumed. The pathway of excitation is from receptors (*R*), through bipolars (*B*), to the ganglion cell (*G*), but activity in this direct pathway is modified by the associational cells. The horizontal cells (*H*) pick up from receptors, conduct laterally in the null direction through a teledendron (*Td*), and inhibit bipolars in the neighbouring region. This prevents responses when an image moves in the null direction, but has no effect when motion is in the preferred direction. Horizontal cells have the function of the laterally conducting elements in the inhibitory scheme shown in Fig. 7. The amacrine cells (*A*) are thought to pick up from bipolar endings in the inner plexiform layer and to conduct activity throughout their axo-dendritic ramifications; they are assumed to make synaptic connexion with the ganglion cells and inhibit them, thus mediating lateral inhibition of the type illustrated in Fig. 5 of Barlow *et al.* (1964) and Fig. 10 of this paper. The off-responding mechanism is not illustrated, but seems to require duplicate horizontal cells and bipolar cells. Notice that the ganglion cell must connect selectively to those particular bipolars which respond selectively to the sequences for one particular direction. Its response is specific for this pattern of stimulation but is invariant with respect to contrast and position in the receptive field. It may be said to achieve some degree of 'stimulus generalization'.

connects from receptors to bipolar cells, rather than, for instance, from bipolars to bipolars?

The strength of the proposed scheme arises from the fact that a function can naturally be assigned to the neural elements that are known to exist, without making esoteric or revolutionary assumptions about how they work. Sequence-discrimination is assigned to bipolar cells because the ganglion cell appears to pick up from subunits that are replicated in different parts of the receptive field, and bipolar cells are the replicated anatomical elements that feed ganglion cells. There is physiological evidence of inhibitory interaction acting from one side on these subunits. This is not like the classical lateral inhibitory interaction which counteracts the pooled excitatory influences reaching the ganglion cell: the evidence points to inhibition that acts locally. Excitation aroused from a particular region of the receptive field is inhibited by preceding excitation of the region that a light image has just crossed when motion is in the null direction. This same inhibitory region has no influence on excitation aroused from the neighbouring region on the opposite side, for it fails to block the excitation when motion is in the preferred direction. The physiological evidence thus indicates that each excitatory region has its own private inhibitory region on one side, and one can construct a number of schemes to account for this. Inhibition might act on the ganglion cells, but in such a way that it only blocks one particular branch of the dendritic tree: or it might act presynaptically on the bipolar cell endings. Another possibility one might consider is that the inhibition is mediated by the receptor-to-receptor connexions described by Sjöstrand (1958) in the guinea-pig. The distance over which the inhibitory effects have to be passed may be a difficulty here, and this notion shares the difficulty described below for other forms of inhibition which act on the receptors. Since the horizontal cells are known to have processes conducting laterally the natural starting hypothesis is that they are the cells carrying this inhibition from one region to another.

If this is granted there is still scope for argument as to where this inhibition is picked up from, and where it feeds to. Might it not inhibit receptors rather than bipolar cells? Might it not even pick up from bipolar cells and feed back to receptors? The key observation here is that a region which has itself been inhibited from its own private inhibitory zone on one side can none the less inhibit activity aroused in the neighbouring zone on the other side. Motion through the receptive field in the null direction may elicit no impulses whatever. Consider what is happening half way through such a traverse: one sees that excitation of the receptors at the mid-point prevents the discharge from the next group of receptors the spot is going to cross, even though no activity is transmitted centrally from the receptors

at the mid-point. This indicates that the inhibitory connexion runs from an early point on the path from the inhibition-arousing zone to a later point on the path from the zone that is inhibited. Presumably then it runs from receptors to bipolar cells, and in that case the inhibition can act in the ordinary way by stabilizing the membrane potential of the bipolar cells. However there is clearly a point here open to histological investigation. Do the horizontal cells make this pattern of connexion in the rabbit? Polyak (1941) describes the horizontal cells of the monkey as making receptor-to-receptor connexions.

No further information has come to light on the pathway mediating ordinary lateral inhibition of the type shown in Fig. 10. This probably acts on the ganglion cells, and amacrine cells remain the most plausible guess.

It is clear that our allocation of functions to particular structures must be regarded as provisional, but we were pleased to find how well the physiological organization seems to fit in with the anatomical structure.

Other proposed anatomical correlates in other species. Maturana, Lettvin, McCulloch & Pitts (1960) and Lettvin, Maturana, Pitts & McCulloch (1961) have also attempted to relate structure and function in the retina, in their case in the frog. Their discussion has something in common with ours, but they place greater emphasis on the concept that the ganglion cell's properties are determined by the shape and size of its dendritic tree. They believe that the different strata of the inner plexiform layer carry information as to different properties of the pattern of light falling on the receptors; the ganglion cell is then thought to pick up the appropriate combination of these properties by ramifying in the various layers. This may explain how a ganglion cell is able to make connexion with a specific subset of bipolar cells, and their notion does not contradict ours. Where we feel that our scheme goes further is in showing how the complex task of signalling direction of movement can be broken down into simpler tasks that can be performed by elements making simple excitatory and inhibitory connexions.

Maturana & Frenk (1963) have described directionally selective units in the pigeon's retina. These obviously have much in common with the units in the rabbit, for they show the same directional selectivity independent of the path through the field and the contrast of the moving object. Furthermore, they made an interesting observation which led them to the conclusion that an inhibitory mechanism is involved in directional selectivity. They turned a spot of light on and off in one place in the receptive field, eliciting responses in the usual way. While the light was off they moved it to another position in the field displaced in the null direction from the first position, and turned it on and off again. No responses were obtained, whereas, if the spot had been displaced in the preferred direction, responses

were obtained as usual. Clearly this is similar to the two-spot experiment described here, but it seems from their brief description that inhibition must persist for a long time in the pigeon. They do not attempt to make detailed suggestions about which anatomical structures are responsible for the specificity of the stimuli that generate responses in a particular unit, but they give the impression that they believe it is achieved by the ganglion cell. In our view the specificity originates with the bipolars, and the ganglion cell generalizes for position and contrast by picking up only from those bipolars that respond to sequences of on or off stimuli corresponding to one particular direction of motion.

Grüsser-Cornehls, Grüsser & Bullock (1964) tested movement-sensitive units in the frog with various stimuli, and came to the conclusion that movement detection was really 'change-of-position' detection. Their experiment suggests that they are distinguishing between continuous and discontinuous change of position, and in that case our conclusions are not too far apart: discontinuous change of position, as in the two-spot experiment, can activate the directionally selective mechanism. However, they were not dealing with units responding selectively to the direction of motion, for unlike Maturana *et al.* (1960) they failed to find such units in the frog, although they confirmed many of these authors' other findings.

Directional system in insects. Reichardt (1957, 1961*a*, *b*) has proposed a mechanism capable of explaining the responses of insects to movement in their visual field. This seems at first sight very different from the one we have arrived at, for his scheme depends upon evaluating the cross-correlation between the signal from an ommatidium and that from its neighbour modified by passage through a low-pass filter. This is closer to the excitatory-conjunction scheme that we rejected than it is to the inhibitory scheme. However, one should probably regard Reichardt's proposal as the simplest physical system with a performance specification similar to the beetle's eye, and one should not be too surprised if the realization of a system in 'biological hardware' is different from what it would be in physical hardware, even if the operation performed is very similar.

Pattern recognition, trigger features, and stimulus generalization

Maturana & Frenk (1963) suggest that an understanding of the type of behaviour they describe in the ganglion cells of the pigeon retina clarifies certain problems of pattern recognition. We think there are two aspects of recent work on the visual pathway that are interesting in this respect. The first is the specificity of the features that are effective in triggering the activity of sensory neurones. Examples of this are provided by the 'fly detectors' (Barlow, 1953) and 'convexity detectors' (Lettvin *et al.* 1959) of the frog's retina, the linear elements of the cat's cortex (Hubel & Wiesel,

1959, 1962), the 'horizontal edge detectors' of the pigeon retina (Maturana & Frenk, 1963), and the directionally selective elements found in all these preparations as well as in the rabbit's retina. Now in pattern recognition by machines, Grimsdale, Sumner, Tunis & Kilburn (1959) broke the task into two stages by first detecting the presence of certain key features of the patterns to be discriminated and then looking for the characteristic combinations of these features. Most of the successful systems for recognizing printed or handwritten characters make use of a similar scheme (Selfridge & Neisser, 1960; Uhr & Vossler, 1961; Frishkopf & Harmon, 1961; Kamentsky & Liu, 1963), and it is interesting to see why it is necessary for the computer to view its text through these 'feature filters'. It is because even the largest computor cannot recognize letter A by comparing the input with a complete list of all members of the class of A's. Such an approach would require the separate representation of each of the 2^n possible states of the n binary inputs and this becomes unmanageable for values of n that are very small by biological standards. Presumably the trigger features of the visual system likewise enable the input states to be classified in an effective way without requiring a googolian number of separate representations.

The second aspect we want to draw attention to is the detailed manner in which the specific and general properties of these trigger features are picked out. This discussion will be based upon our suggested mechanism for directional selectivity, and we shall introduce certain simplifications which, though not entirely justifiable, make it easier to compare the neural process with artificial pattern recognition.

According to our analysis the operation of abstracting direction of movement is done in two stages, each with the same two steps. The first step in each case is the summation or pooling of selected excitatory influences, and the second step is the inhibitory interaction of another element that has, as it were, the power of veto. The first step loses information, for the bipolar cell which pools inputs from a number of receptors does not reflect in its output which particular ones were active. As pointed out by Reichardt (1961*a*, *b*) the inhibitory step could in principle regain this lost information, but in the case of bipolar cells it does not do this; instead it makes the response more selective by bringing in new information. Without this inhibitory interaction a bipolar cell would simply say, when it became active, 'Light fell in this region'; with the inhibition it says 'Light fell in this region and was not preceded by light falling in that region'. Compared with the receptors in the preceding layer, the bipolars have lost some information about the exact position of the stimulus, but they have extracted some information about the presence of a particular sequential pattern in the stimulus.

The same two steps are taken in the next stage, occurring in the next layer. Here a ganglion cell does not pool from all the bipolars in the receptive field, but it picks up selectively from all those which respond when a stimulus moves in a particular direction, irrespective of the location of the bipolar cell or whether it belongs to the 'on' class or the 'off' class. It thus discards the information as to the contrast of the stimulus object and whereabouts in the receptive field it was; it 'generalizes' by grouping together activity resulting from movement in a particular direction, regardless of contrast and exact position. This is followed by inhibitory interaction which again makes the response more specific. Light going on or off in the surround (Fig. 5 of Barlow *et al.* 1964), or movement in the surround (Fig. 10, this paper) reduces or prevents the response, so that when activity occurs it implies that changes were not occurring in the surrounding retina at the time they occurred within the receptive field.

Let us now express the logical pattern of these repeated operations symbolically. The pooling or generalizing operation is equivalent in some ways to the formation of a logical union (inclusive 'or', symbolized by v), and the inhibitory or veto operation is equivalent to 'and not...' (symbolized by $.\sim$). If B is the class of inputs to which a bipolar cell responds, and R_a, R_b, etc., are the inputs causing activity in the receptors a, b, etc., then

$$B = (R_a \vee R_b \vee R_c \ldots) . \sim (R_r \vee R_s \vee R_t \ldots).$$

Likewise the class G of inputs causing activity in a ganglion cell is expressed in terms of B_a, B_b, etc., the inputs which activate the selection of bipolars it connects with; thus

$$G = (B_a \vee B_b \vee B_c \ldots) . \sim (B_r \vee B_s \vee B_t \ldots).$$

If we symbolize by E^{ψ} the class of inputs which is effective in exciting a particular element after ψ synapses, and by $E^{\psi+1}$ the class effective for an element after one more synapse, then $E^{\psi+1}$ is given by

$$E^{\psi+1} = (E_a^{\psi} \vee E_b^{\psi} \vee E_c^{\psi} \ldots) . \sim (E_r^{\psi} \vee E_s^{\psi} \vee E_t^{\psi} \ldots).$$

Notice that only a small proportion of the possible logical functions of the E^{ψ} can be expressed in this form, and it is therefore not at all a trivial restriction.

We are suggesting that the classification system at one level in the nervous system is built out of the classification at the preceding level by a combination of pooling or union, and inhibition or veto (and not...). Can we regard the proposed mechanism for directionally selective units as a paradigm of the neural mechanisms responsible for the classification system imposed on our sensory input? Is pooling analogous to 'stimulus

generalization', and is greater specificity of response always achieved by the veto of an associational neurone, an interposed inhibitory element? These are intriguing questions.

SUMMARY

1. The mechanism of directional selectivity has been investigated in retinal ganglion cells of decerebrate or lightly anaesthetized rabbits.

2. The property of responding to one direction of motion (preferred) but not to the opposite (null) direction occurs in on–off units, but the responses to movement cannot be predicted from the map of the receptive field obtained with static stimuli; the property cannot be explained by optical aberrations (see Fig. 1), nor by progressive changes of latency across the field (see Fig. 2).

3. There is no critical line or region that must be crossed to produce unequal responses to preferred and null motion (Fig. 4): small subsections of the receptive field possess the property (Fig. 5).

4. The response to successive stimulation of two small regions depends upon whether the order corresponds to motion in the preferred or null direction (Fig. 8). This effect is strong when the two regions are within about $\frac{1}{2}^\circ$ of each other, but declines at greater separations.

5. This is thought to indicate that directional selectivity results from the discrimination of sequence. Normal movement excites many points in a long succession, but the mechanism works by discriminating the sequence of individual pairs of regions.

6. When two stimuli are presented in the null sequence the number of impulses elicited is much less than the sum of the numbers elicited from each stimulus in isolation (Table 3). There is a small excess of impulses over this sum when the stimuli are presented in the preferred sequence.

7. From this and other findings it is concluded that sequence-discrimination results primarily from an inhibitory mechanism that vetoes the response to null sequences, rather than from the detection of the conjunction of excitation from two regions with an appropriate delay (see Fig. 7).

8. If the image of a moving object spreads outside the receptive field on to its surround there are fewer impulses than when it is confined to the receptive field alone (Fig. 10). This must be the inhibitory mechanism that elevates the threshold for large compared with small spots, and it is presumably different from the inhibition responsible for sequence-discrimination.

9. The functional organization is discussed in relation to the anatomical organization (Fig. 11). It is suggested that horizontal cells conduct

laterally and inhibit the bipolars on one side, thus preventing them from responding to null sequences; the ganglion cells then pick up from the bipolars responsive to like sequences and it is thought that the inhibition from the surround may be mediated by amacrine cells.

10. The ability to abstract direction of motion irrespective of the position in the receptive field and the contrast of the moving object has elements in common with much more complex feats of pattern recognition. The two steps—inhibition by associational neurones and selective pooling—may also play a part in these more complex feats.

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