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RESPONSES OF DIRECTIONAL GANGLION CELLS IN THE PIGEON RETINA

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SUMMARY

1. Extracellular single-unit records were taken from ganglion cells in the pigeon retina, and average response histograms were recorded, with base line spike counts.

2. Movements in the preferred direction in directional cells produce discharge peaks. Movements in the null direction produce spike deletion suggesting there is an inhibitory patch offset from the field centre, towards the start of the null sweep.

3. Bi-directional responses can be obtained from the preferred side of the field centre; bi-directional inhibition can be obtained at the null side. Scans orthogonal to the null-preferred direction passing through the inhibitory patch can produce deletions.

4. The latency of deletions from the inhibitory patch is slightly greater than of excitation from the field centre, judged by flashed or moving stimuli.

INTRODUCTION

Directional ganglion cells have been reported in the pigeon retina (Maturana, 1962; Maturana & Frenk, 1963; Holden, 1969; Pearlman & Hughes, 1976). The mechanism of directional selectivity has been examined in the rabbit (Barlow & Levick, 1965). Until the recent study of directional cells in the rabbit by Wyatt & Daw (1975) there has been no attempt to investigate the directional mechanism with averaging methods. Barlow & Levick (1965) suggested that directional selectivity results from local inhibitory connexions in the receptive field, which extend in the direction of null movement.

The present observations were made with averaging, using the modulation of the base line spike rate to show up the excitatory and inhibitory effects produced by moving stimuli.

The results confirm previous suggestions that an inhibitory system

produces directionality, and show that directional receptive fields are made up of two components, one excitatory and one inhibitory. These components partly overlap and can be studied in partial isolation.

METHODS

Intraretinal recordings were made *in situ* in the urethane anaesthetized artificially ventilated pigeon. Flashed or moving stimuli were projected on a tangent screen, which was illuminated either with background luminance of 0·85 cd/m^2 or 27 cd/m^2. The moving stimuli were produced by deflecting the projected beam by a front surface mirror mounted on pen-motors, driven by power amplifiers (Devices Ltd) and actuating the motion by wave forms obtained from function generators. Generally a single-cycle triangular wave form was used, triggered from the sweep of the averager (Hewlett–Packard 5480B Signal analyser). The amplitude of the movement could be adjusted by altering the amplitude of the driving wave form. The movement produced is at fixed velocity, neglecting tangent screen errors. In practice, the system showed fixed lag terms, of 3–5 % of the sweep amplitude when calibrated with a photocell placed in the path of a moving slit. If there were no such lag terms, the output when the leading edge crosses the photocell should line up in position with the trailing edge on the back sweep. These lag terms are presumably due to retarding couples due to the suspension, to air damping, or to eddy currents in the coil. The lag terms were only slightly improved by using small, light mirrors. Because of the lag terms the 'monitors of movement' shown in the Figures can only be taken as accurate to 3–5 %. For critical observations an independent measure of the position during the scan was provided either by mounting a photocell in the scan path, or by using a physiological response recorded from the retina, proximal negativity, to indicate position.

The data sample for this paper consists of average response histograms taken from 121 ganglion cells. The responses were recorded as well-isolated diphasic spike potentials, and were held from 0·5 to 6 hr. The chief interest was in searching for directional cells. One observation is included from a cell recorded in the experiments described in Holden (1977).

To be classed as directional, the cell was tested with stimuli moving through its receptive field in varied axes. The axis of movement was regulated by rotating a Dove prism in the projected beam. The same preference for direction held for white and dark targets moved through the receptive field. Most directional cells gave no response (a 'null' response) to a broad cone of directions of movements, with vigorous discharge in the opposite direction. The null-preferred axis was judged to be the axis which bisected this cone.

The experiments carried out were shaped by the account of rabbit directional cells given by Barlow & Levick (1965), who provided evidence that an inhibitory mechanism underlies directional selectivity, spreading laterally from the side of the receptive field nearest to the start of the null movement. In this paper I refer to this side of the receptive field as the null side, and to the side of the field closest to the start of the preferred movement as the preferred side.

Thus preferred motion is from the preferred side to the null side, and null motion passes from the null side to the preferred side.

In this paper the terms 'forward-sweep' and 'back-sweep' are used to describe the two phases of motion through the receptive field, as indicated by the monitor of movement. The forward sweep always precedes the back sweep on each histo-

gram. The terms are not used with particular reference to direction in visual space.

Since the majority of ganglion cells sampled in this preparation lack spontaneous firing, which might be used as a base line upon which inhibitory effects could be superimposed, driven activity of the cells was used to produce base line spike counts in the histograms. This was produced by moving a second stimulus, generally a small spot, in the receptive field, either through the field centre, or along a trajectory slightly displaced (by less than 1°) into the preferred side of the field. Occasionally base line counts were generated by flashing a $\frac{1}{2}$° spot in the field, or by the McIlwain periphery effect. Moving stimuli were more effective in producing smooth base line levels than flashed spots. These accessory stimuli were delivered unsynchronized with the sweep-timing of the averager, so that after a number of repetitions they filled the analyser bins more or less evenly. A test of cell excitability based on the modulation of a driven base line count has several inherent limitations. It is desirable to produce many rather than few base line counts, and so a potent stimulus has to be used. This means that the deletions occurring will reflect strong rather than weak effects. In principle it would be preferable to generate base line counts by a near threshold accessory stimulus, but this would greatly prolong the recording time needed to accumulate histograms.

RESULTS

Two-hundred and sixty-six histograms were recorded from 121 ganglion cells. Thirty-four cells were directional, and were classed by centre type as: on-centre cells, four; on-off cells, twenty-six; off-centre cells, four. The main observations were carried out on on-centre and on-off directional cells. Off-centre cells have some anomalous properties, and are described separately.

Directional cells

General properties: movement of a target in the null-preferred axis produced spike responses only in the preferred direction (see Fig. 1*A*). During the null movement there was no spike discharge. The targets used to test directional cells were a square with sides subtending 0·75°, or a slit 4° by $\frac{1}{4}$°, which could be moved longways or broadside-on. With any of these configurations the cone of null responses extended for at least 45° on each side of the null-preferred axis.

When a target short in its sideways dimensions was moved through the field centre orthogonal to the null-preferred axis, the response was bi-directional, and symmetrical (see Fig. 3*C*). If the slit was moved broad-side-on orthogonal to the null-preferred axis, then responses were reduced or curtailed. Comparable properties have been observed in other studies of avian directional cells (Miles, 1972; Pearlman & Hughes, 1976).

Scans in the null-preferred axis

Fig. 1 illustrates three histograms recorded from a directional cell, responding to movement through its receptive field in the null-preferred axis. Histogram *A* is the response to sixteen repetitions of a 0·75° square, moving through 10° at 1·3°/sec. There is a leading edge and trailing edge response in the preferred direction (the forward sweep) and no discharge peak in the back sweep. When tested with flashed spots this cell had an on-off field centre, 1° in extent. The preferred movement was in an anterior direction in the visual field, the null movement was posterior in the visual field, along a horizontal axis. Histogram *B* is the result of accumulating sixty-four consecutive responses with the same synchronized stimulus as in histogram *A*, but in the presence of base line spike counts produced by moving a $\frac{1}{4}$° spot for 1° through the field centre at a frequency of 0·5 Hz. The histogram fills up with base line spike counts, and it can be seen that there are two principal modulations of the count rate. In the preferred sweep there is a marked leading edge response, possibly, though not clearly, followed by a trailing edge response. In the null sweep there is a period of spike deletion. Much of what follows is an attempt to infer properties of the mechanism leading to spike deletions in the null sweep, which may throw light on, or be the result of, the directional mechanism.

Histogram *C* is recorded from the same cell, responding to movement through its receptive field at 5·2°/sec. The chief features are vigorous discharge peaks in the preferred direction, and a period of deletions in the null sweep.

Fig. 1. Responses of a directional cell to a stimulus moving back and forth through the receptive field in the null-preferred axis. The stimulus was a 0·75° square, luminance 250 cd/m²; background luminance 27 cd/m². Calibrations for the histograms are given in spikes/sec; in each histogram the calibration is the equivalent of 25·6 counts/bin. Number of repetitions: *A*, 16; *B*, 64; *C*, 64; *D*, 32. Bin-width: *A* and *B* 80 msec: *C* 20 msec. Each histogram has 250 bins. *A*, response to moving square; there is a leading edge and trailing edge response in the preferred direction (forward sweep), and no response in the null direction (back sweep). *B* and *C*: accumulated in the presence of driven base line spikes, produced by a 0·25° spot, moving for 1° at the field centre, orthogonal to the null-preferred axis. There is a period of spike deletion in the null direction (back sweep). *D*, proximal negativity, recorded concurrently with histogram. *C*, the record is the average of thirty-two consecutive responses. In this and subsequent Figures movement is indicated by the wave form driving the pen-motor; the extent and velocity of the movement are indicated alongside. Below record *D* the inset shows diagrammatically the two components of the receptive field; the continuous circle shows the field centre, and the interrupted circle the deleting patch. The lettered arrows show the preferred (P) and null (N) directions of motion.

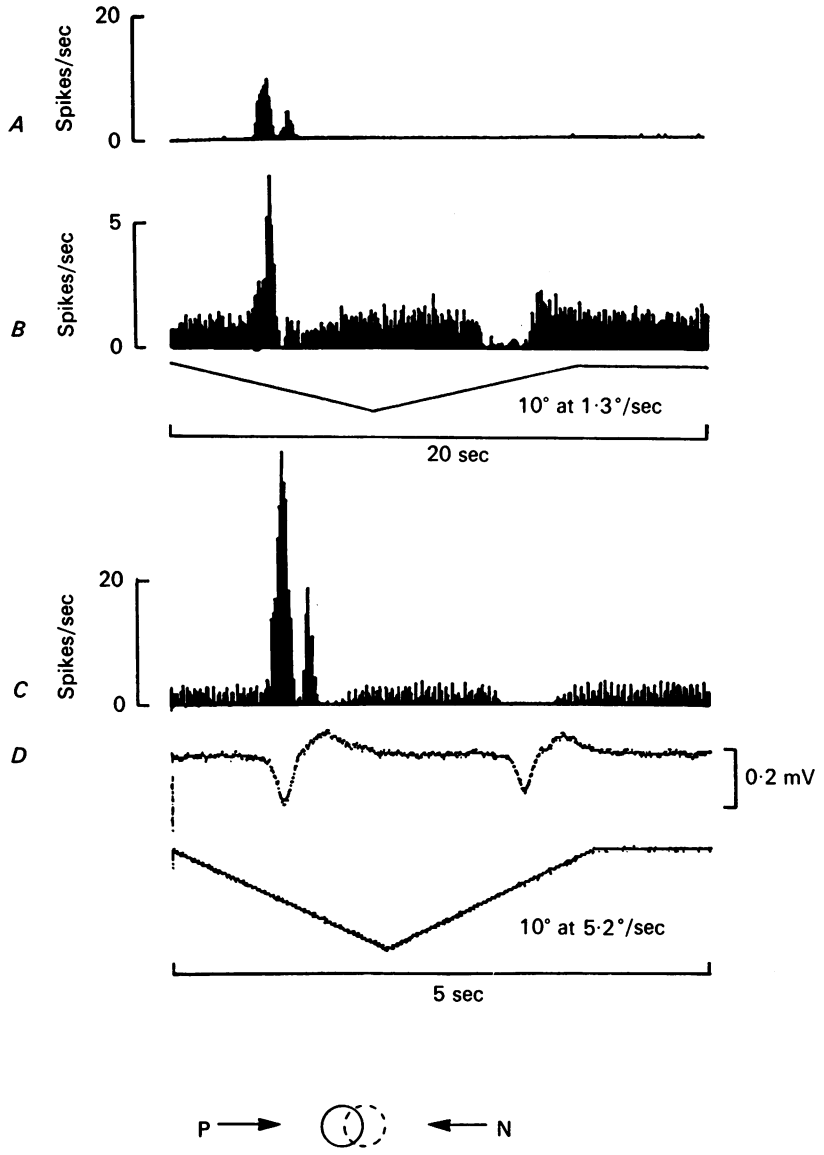

Fig. 1. For legend see opposite.

Proximal negativity and null-preferred scans

Proximal negativity, recorded concurrently with spike discharge, gives a measure of the time at which the stimulus edge is crossing the receptive field. The PNR was recorded concurrently with histogram *C*, and is shown in record *D*. Here the PNR consists of a leading edge transient, whose

origin lines up closely with the origin of the preferred discharge peak. But in the null sweep the PNR *lags* the onset of the deletions by 108 msec. For a velocity of movement of 5·2°/sec this lag has a spatial equivalent of 0·56°. Thus if the latency of the deletions is equal to, or greater than, the latency of the PNR, it follows that the deletions originate from a receptive field displaced spatially by at least 0·56° towards the start of the null sweep.

The time relations between spike discharge, proximal negativity, and the deletions, suggest a simple organization of directional fields, in which the field centre and the PNR share a receptive field, and the deleting disc or patch partly overlaps the field centre, extending as a rim towards the start of the null sweep. The arrangement is shown diagrammatically in the inset in Fig. 1. Given such an organization, it would be expected that deletions do not precede the discharge peak when the field is scanned in the preferred direction: during scans in the null direction it would be expected that deletions should precede proximal negativity. These aspects have been examined in the available histograms.

In total, thirty-two histograms were recorded in the presence of base line spike counts, with averager sweep times ranging from 0·5 sec to 20 sec, and velocities of movement ranging from 0·87 to 20°/sec. Base line counts were produced in all but three cases by a second moving stimulus, moving through 1° at the preferred side of the field. The direction of movement of the accessory target was usually orthogonal to the null-preferred axis, although in some cases a trajectory parallel to the null-preferred axis was used, offset from the path of the synchronized target and not overlapping it.

In these thirty-two histograms there are no deletions preceding the discharge peaks in the preferred direction. The histograms include cases examined with small spots, rectangles, and longways and broadside slits. Thus the absence of deletions preceding the discharge peak seems a general feature of scans of on-centre and on-off directional cells, and the records shown in Fig. 1 are typical examples.

Seventeen histograms were taken with a concurrent record of proximal negativity, and allow a comparison of the timing of the deletions and the onset of proximal negativity in the null scan. The deletions were not judged to follow the onset of proximal negativity in any histogram. In three histograms the deletions were judged to be simultaneous with the onset of proximal negativity. In fourteen comparisons the deletions were judged to precede proximal negativity, by periods ranging from 42 to 350 msec, with spatial equivalents of 0·3–1·5° (mean 0·71°).

Implications

The histograms show that the absence of deletions before the preferred response, and the precedence of deletions to the PNR in null scans are found consistently in directional cells in the pigeon. The inset in Fig. 1 suggests that directional fields are made up of two partly overlapped components, and that it should be possible to study these in partial isolation with flashed and with moving stimuli. The results which follow illustrate experiments which test whether the two patches are inherently directional, and test whether excitation and deletion have comparable latencies.

Bi-directional responses in the null-preferred axis

Entry and exit responses. It was possible to obtain responses to stimuli which entered and subsequently left the receptive field at the preferred side. The responses were bi-directional provided that the target did not travel into more than one-third of the receptive field. Responses could be obtained in back and forth movements down to $\frac{1}{4}°$. Fig. 2*A* illustrates such bi-directional responses, to a 0·75° square travelling towards the field for $2\frac{1}{2}°$, into it for $\frac{1}{2}°$, and then leaving. The velocity of movement was 4·7°/sec. There is a brisk discharge peak on entry, and a larger peak on exit. If the movement extends further into the receptive field, passing its midpoint, then the response on exit no longer occurs; it is 'vetoed' by the directional mechanism. The observation resembles the bi-directional 'rim' at the preferred side of directional fields in the rabbit retina, described by Barlow & Levick (1965). If the entry and exit were made from the null side of the field (entry being in the direction of the null movement) then the responses have a clear null-preferred nature.

In several cells an attempt was made to produce bi-directional spike deletion by movements in the null-preferred axis which did not themselves produce a preferred discharge peak. The test was carried out by moving the trajectory of the stimulus to a position where, on qualitative testing, there was no preferred response, keeping the trajectory as close to the field as possible.

Fig. 2*B* shows such an experiment, on the same cell as produced the bi-directional responses above. The movement spanned 3°, and was placed so as to be at least $\frac{1}{2}°$ away from the perimeter of the receptive field as judged by hand plotting. It can be seen from the histogram that there are some spike deletions to base line for both phases of the movement. They are not well characterized, and constitute a 'thinning down' of the base line rate rather than a period of complete silence. The deletions in the forward sweep actually follow a small discharge peak, which could be

revealed in isolation by averaging the responses of the synchronized target in the absence of base line spike counts. Fig. 2 *B* shows the most convincing histogram obtained in these experiments.

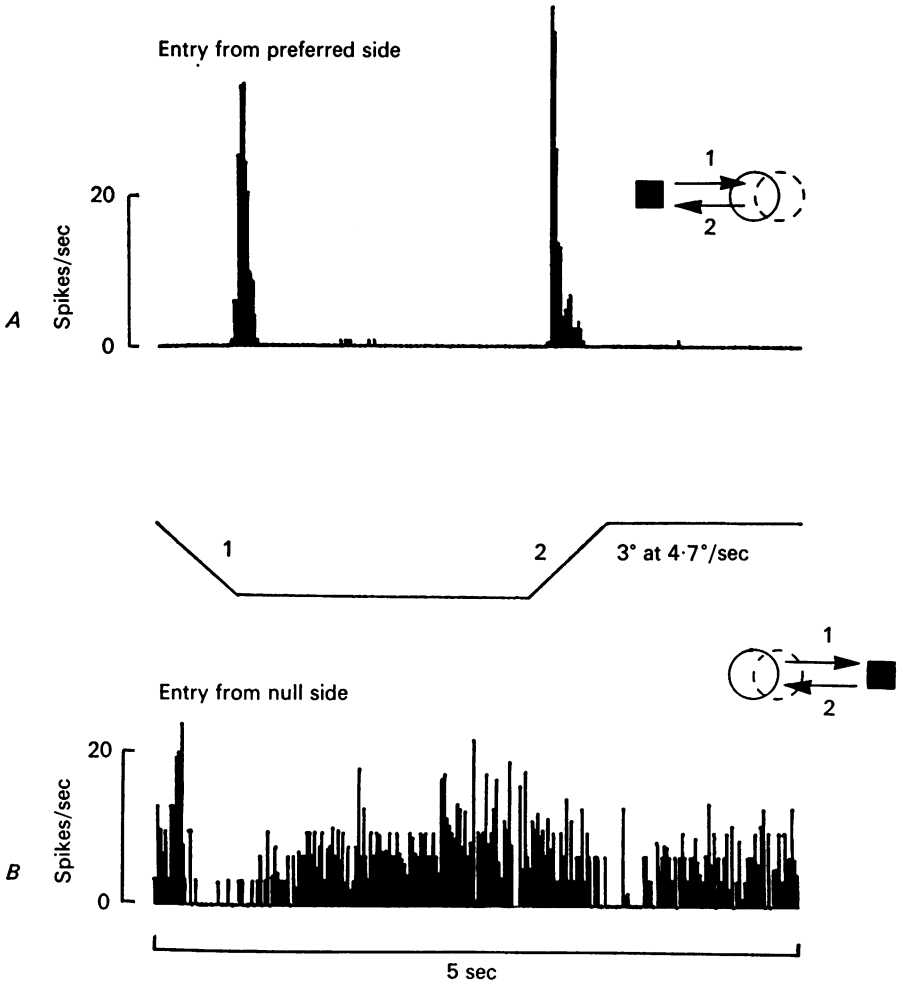

Fig. 2. Bi-directional responses produced by movement in the null-preferred axis. Spike calibrations show 20 spikes/sec; this is equivalent to 25·6 counts/bin. Each histogram is the result of sixty-four repetitions. Bin-width 20 msec; 250 bins. The insets by each histogram show diagrammatically the relation of the movement to the receptive field. The stimulus was a 0·75° square, as in Fig. 1, moving back and forth in the null-preferred axis for 3°. The driving voltage was a peak-limited triangular wave form. *A*, both phases of motion, in the preferred (1) and null (2) directions, are accompanied by a discharge peak. *B*, movement is at the null side of the field, base line spikes generated by a 0·25° spot moving at the field centre. Each direction of motion is accompanied by a period of spike deletion.

There is firm evidence for bi-directional deletion from scans in which a target passes entirely through the field centre, such as those illustrated in Fig. 1. The response in Fig. 1*C* is a typical one, in which the spike rate moves close to zero between the discharge peaks in the preferred direction, and stays at zero counts for 10 bins (200 msec) after the trailing edge discharge. In other histograms the deletions between the discharge peaks and following the trailing edge response were sometimes greater and sometimes less than those in Fig. 1: the longest period of deletions was *ca.* 1 sec in duration.

In control observations on non-directional cells, where responses to movement were obtained in the presence of driven base line spike counts, it was observed that a large discharge peak did not entail a subsequent period of deletions. Thus there was no inherent constraint following a discharge peak (for example due to after-hyperpolarization) powerful enough to delete spikes. This suggests by analogy that the deletions produced during preferred scans through directional receptive fields are due to inhibition; the cell first produces a discharge peak, and there is subsequent activation of the deleting patch.

Scans orthogonal to the null-preferred axis

Fig. 3 illustrates histograms from a directional cell responding to stimuli moving orthogonal to the null-preferred axis. The synchronized stimulus was a square with sides 0·5° in length, and base line counts were generated by a small 0·25° spot moving through the field centre. Histograms *A*, *B* and *C* show the responses at two trajectories, placed so as to run either at the null or the preferred side of the field as illustrated diagrammatically in the inset. In histogram *A* the synchronized target was placed to move past the field close to the perimeter on the null side, but without generating spike discharge. The movement was paired with base line spike counts, and results in a well characterized period of deletion in each direction of movement. Thus the deleting mechanism is activated by movement orthogonal to the null-preferred axis.

In histograms *B* and *C* the start position of the synchronized target was moved sideways by 1½°, so that the trajectory passed through the preferred side of the receptive field. The target illuminated a sector of the field, corresponding to one-third of the area plotted with flashed spots. When moved alone this target produced a symmetrical response as judged qualitatively and by histogram *C*. The response in histogram *C* consists of a brisk discharge, occurring with a leading edge and trailing edge peak in each direction. The onset of the discharge peaks lines up closely with the onset of the deletions in histogram *A*. This implies that the patch

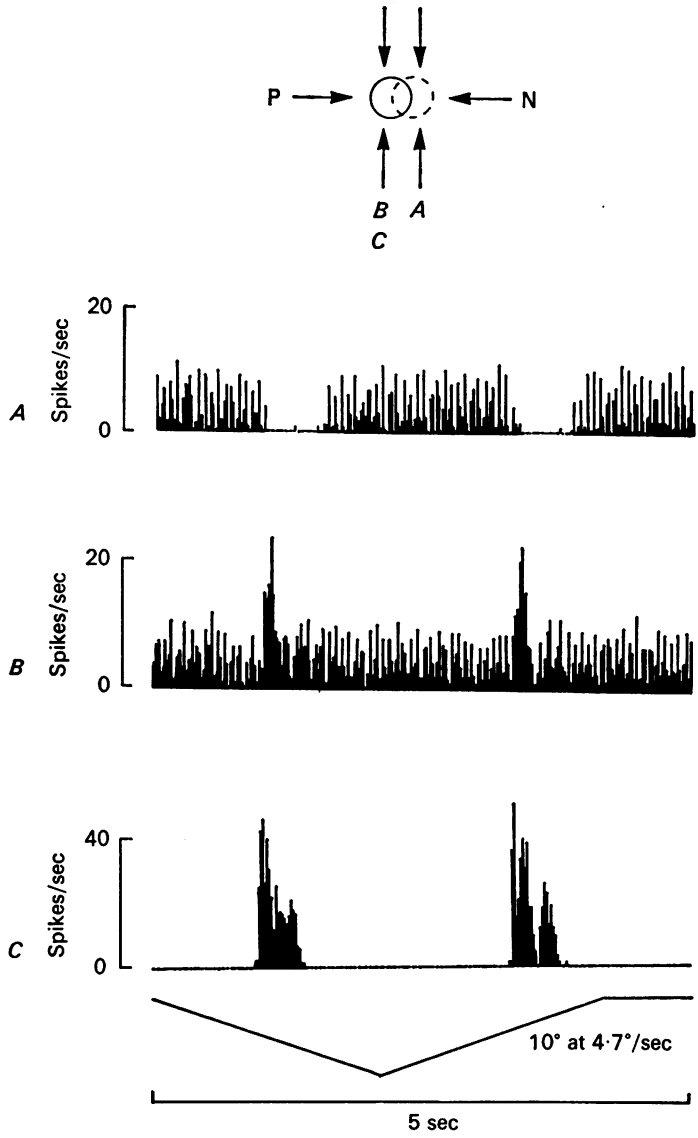

Fig. 3. Responses to movement orthogonal to the null-preferred axis. Calibrations of spike rate are shown by each histogram: *A* and *B* correspond to 25·6 counts/bin, *C* corresponds to 51·2 counts/bin. Bin-width 20 msec; 250 bins. *A*, effect of motion of 0·75° square moving back and forth through the deleting patch on base line spike counts produced by a 0·25° spot moving at the field centre. Sixty-four repetitions. *B*, the trajectory of the moving square is shifted to the preferred side of the field, otherwise as in *A*. *C*, the response to the synchronized target alone, moving as in *B*. Thirty-two repetitions. The inset shows the receptive field, the preferred (P) and null (N) directions, and the trajectories for histograms *A*, *B* and *C*.

generating the deletions has a width comparable to the width of the receptive field, assuming the two components have similar latencies. The duration of the deletions is longer than the duration of the discharge peaks. In histogram *B* which was taken in the presence of base line counts there is no evidence of deletions preceding or following the discharge peak. Thus the histograms provide further evidence that the receptive field consists of two components, a deleting patch at the null side of the field, and the excitatory centre.

Taken together with the observations in Fig. 2, it would appear that the deleting patch can be activated by movement in the null and preferred directions, and by orthogonal movements. The patch thus appears to be non-directional. The same conclusion follows for the excitatory field, if considered at its preferred side, where bi-directional responses can be obtained, and where equal responses can be obtained to movements orthogonal to the null-preferred axis. Movements in the null-preferred axis which encroach upon the bulk of the field centre, or enter from the null side, are of course completely directional.

Observations with flashed stimuli

Experiments were carried out with flashed stimuli intended to illustrate further differences between the null and the preferred sides of the receptive field centre; fine-grain 'sequence' experiments like those of Barlow & Levick (1965) remain to be done. Fig. 4 illustrates the response of a directional cell to flashed spots, delivered either singly or in combination. Histogram *A* is the control response to a single $\frac{1}{2}^\circ$ spot flashed at the field centre. It results in phasic discharge peaks at onset and offset, as is typical of on-off cells. In histogram *B* two spots are flashed; the spot flashed in histogram *A* is repeated, but is preceded by a side spot delivered to the null side of the field. The on-off discharge produced by the central spot is almost entirely removed. In histogram *C* the conditioning spot is flashed at a symmetrical position at the preferred side of the field. Here the response to the central spot is still present, though considerably reduced in amplitude. Taken together the histograms suggest that a spot flashed on the null side of the field can largely delete the response to a centred spot, whereas a spot flashed at the preferred side cannot.

Fig. 5 illustrates further responses of the same cell. For histogram *B* a slit 4° by $\frac{1}{4}^\circ$ was positioned parallel to the null-preferred axis, extending out of the field across the preferred side as indicated diagrammatically in the inset. The end of the slit nearest the null side was positioned at the mid-point of the field as determined by hand plotting. When the slit is flashed there is brisk on-off firing. For histogram *C* the same slit was

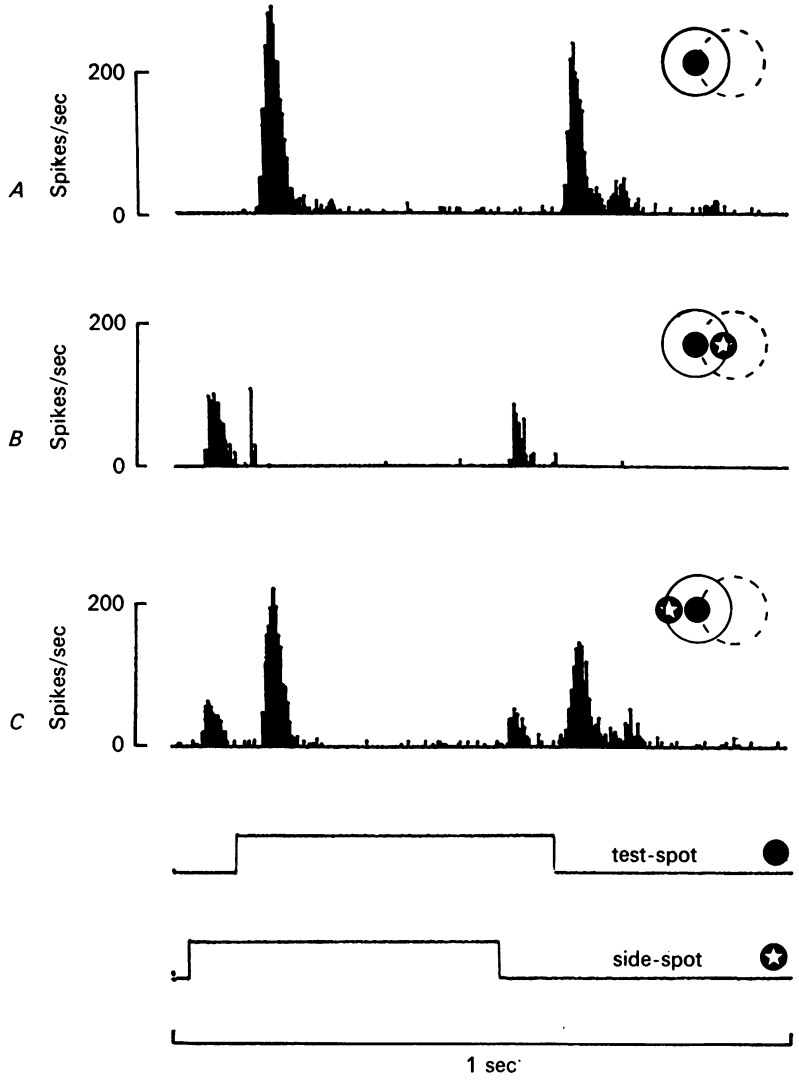

Fig. 4. Response to single and paired spots. Spike calibrations of 200 spikes/sec correspond to 25·6 counts/bin. Bid-width 4 msec; 250 bins. Test spot and side spot 0·5° in diameter, and luminance 109 cd/m^2; background luminance 27 cd/m^2. The insets by each histogram show the receptive field, and the location of the test spot and side spot. The timing of the spots is indicated below (*C*). *A*, response to test spot alone, flashed at the centre of the receptive field. *B*, response to side spot and test spot, flashed in a 'null' sequence. *C*, response to side spot and test spot, flashed in a 'preferred' sequence. The histograms show that the null and preferred sides of the field have differing properties; a spot flashed at the null side can largely delete the test discharge, while a spot flashed at the preferred side cannot.

moved so that its other end was positioned at the centre of the field, the body of the slit extending across the null side of the field. When the slit is flashed, the on-off firing is considerably reduced; the early bins contain counts, and the later counts are deleted.

Fig. 5*A* illustrates an attempt to obtain a measure of the latency of the deletions. A $\frac{1}{2}°$ spot was positioned adjacent to the receptive field perimeter, at the null side. Base line spikes were generated by moving a $\frac{1}{4}°$ spot across the field centre orthogonal to the null-preferred axis. When the spot was flashed there were two periods of deletions. At spot onset the deletions reach zero counts at a latency of 30 msec; at offset the deletions follow a brief discharge peak which itself occupies 3 bins, or 12 msec; zero counts are reached at 35 msec after spot offset. When this cell was flashed with a central spot, as has been shown in Fig. 4*A*, the on-discharge has a latency of 28 msec, and the off-discharge has a latency of 21 msec. Thus the process responsible for deleting spikes has a latency which is only 10 msec or so longer than the excitatory responses of the field centre. This estimate has been made with a conservative criterion of the latency of deletions (the bin at which zero counts occur), and probably represents an over-estimate of the latency of the inhibitory effect.

The histogram in Fig. 5*C* can also be used to estimate the extra latency of the deletions. Since the discharge peak is reduced to a duration of 3 bins (12 msec), this is a measure of the extra time needed for the inhibitory process to silence the spike discharge.

Latencies inferred from responses to moving stimuli

A simplified method was used, based on that described by Bishop, Coombs & Henry (1971): if the velocity of movement is varied inversely with the sweep-time of the averager, and the amplitude of movement is kept fixed, then each averager bin has a fixed spatial equivalent. A histogram for motion in the null-preferred axis is taken at a suitable sweep-time, for example 2 sec; the sweep-time is then increased tenfold to 20 sec, and the frequency of the driving wave form is reduced by ten times. A photocell in the scan-path checks that output is produced at a fixed position on both scans. The bin widths for the two histograms are, respectively, 8 and 80 msec. It can be assumed that the latency of response falls into one or two bin durations at the slower sweep. The differences in bin number at which a response occurs on the two sweeps is related to its latency. If all of the latency is indeed contained within one bin for the longer sweep-time, then the difference in bin number gives the latency to an accuracy of one bin (8 msec).

Using this method, the latency of the discharge peaks and of the

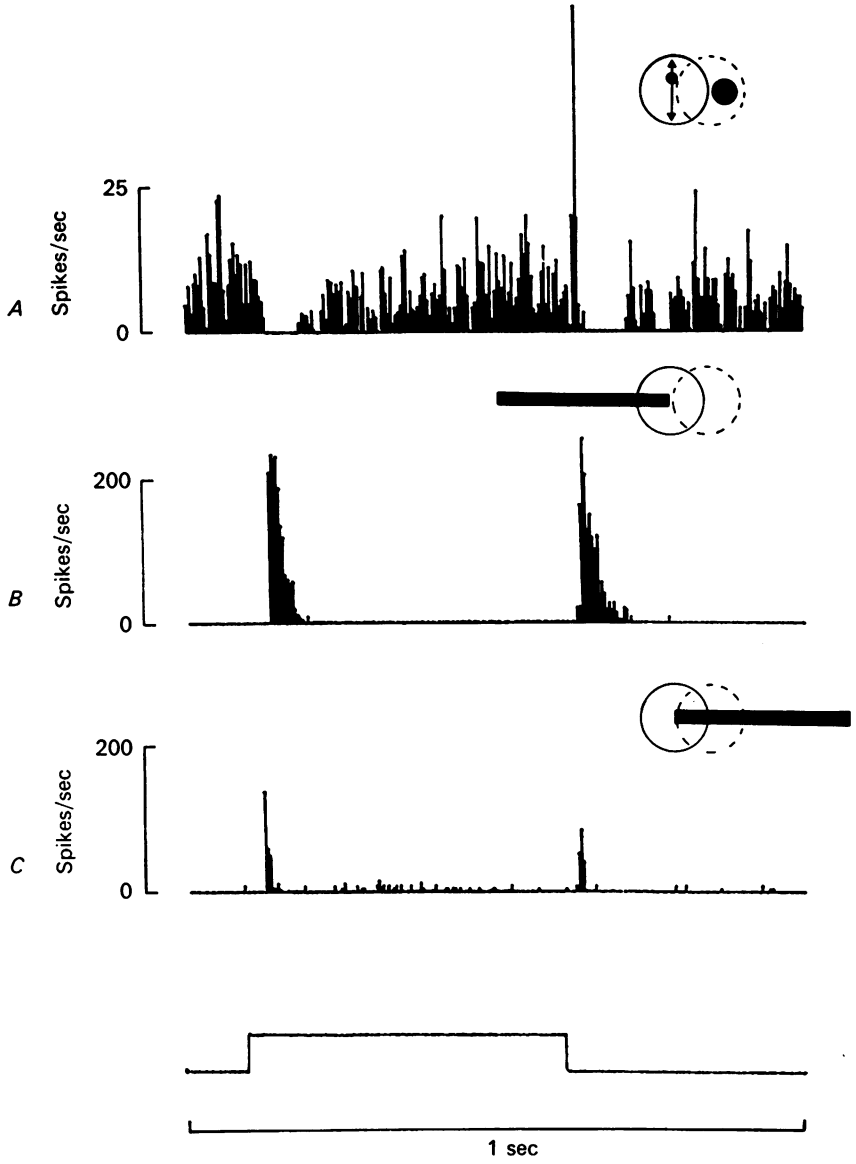

Fig. 5. *A*, effect of spot flashed at deleting patch on base line counts. *B* and *C*, response to flashed slit extending across preferred or null side of field. *A*, spike calibration of 25 spikes/sec corresponds to 12·8 counts/bin. 128 repetitions, 4 msec bins; 250 bins. A 0·5° spot is flashed at the deleting patch, timing shown below *C*. Base line counts generated by a 0·25° spot moving at the field centre. Positions of stimuli shown in inset. *B*, spike calibration of 200/sec corresponds to 25·6 counts/bin. 250 bins, bin-width 4 msec. A slit, $\frac{1}{4}$° by 4° is flashed as shown in the inset, extending from the field centre across the preferred side of the field. Thirty-two repetitions. *C*, conditions as in *B* but slit is positioned to extend from field centre across the deleting patch. Timing for flashed slit shown below.

deletions was measured from pairs of histograms taken with a tenfold change in sweep-time. The leading edge discharge peaks would shift by 40 msec where the deletions shifted by 40–56 msec. Given the difficulty in measuring the onset of deletions from an uneven level of base line counts, this estimate is in fair agreement with the difference in latency of excitation and inhibition measured with flashed targets (Figs. 4, 5). For the response illustrated in Fig. 1 the offset between the deletions and the PNR was calculated as 0·56°. Correcting this for an extra latency of 15 msec associated with the deletions gives a value of 0·64°.

DISCUSSION

The experiments show that an inhibitory or deleting patch is a component of the receptive fields of on-centre and on-off directional cells. The patch is spatially offset from the field centre, in a direction towards the start of the null movement, and considerably overlaps the field centre. The extent of the offset, assuming that central responses and spike deletions have equal latencies, has a mean value of about 0·7°. Since the latency of the deletions resulting from flashed or moving stimuli is longer than responses of the field centre (by 10–15 msec), the actual spatial offset is slightly more than 0·7°. The deleting patch can be activated by the onset and offset of flashed spots, and at its null side is non-directional, since it can be activated by preferred, null, or orthogonal movements.

If the field centre is examined at its preferred side, then it too is non-directional. Responses to moving stimuli can be obtained to entry and exit in the null-preferred axis, and to movements orthogonal to the null-preferred axis. Movements which encroach upon the region where the field centre and the inhibitory patch overlap, are directional.

Wyatt & Daw (1975) have presented results which point to a similar organization of rabbit directional ganglion cells, based on the deleting action of null movements. They suggest that the inhibitory area may be continuous with the receptive field surround. In the present results it would appear that the width of the patch measured orthogonal to the null-preferred axis is only slightly greater than that of the field centre.

In the present experiments it was found that stimuli moving in the null direction could delete driven spikes, whether produced by flashed spots, or moving stimuli. Spikes were deleted whether the accessory target moved in the null-preferred axis, or orthogonal to it. Deletions could also be obtained when base line spikes were produced by the McIlwain periphery effect. Thus the deleting action is produced uniformly on several types of driven activity.

The results confirm with averaging methods the observation of Barlow

& Levick (1965) that there is a bi-directional rim at the preferred side of the receptive field. They extend the characterization of directional fields by showing that there is a deleting rim at the null side of the field. In the rim zones the excitatory and inhibitory components can be studied in partial isolation, and they are non-directional. The existence of an inhibitory rim is implicit in the model of Barlow & Levick (1965), where it would represent the lateral spread of inhibition underlying directionality: the present results show that the rim can extend for 0·5–1·5°.

Directionality and sequence detection

The findings suggest a simple explanation for the null-preferred nature of directional responses and for their polar properties, as a result of the interaction of the two partly overlapped patches. The cell would respond in the preferred direction as an edge crosses the excitatory patch; in the null direction the offset inhibitory patch ensures that the field is inhibited before the edge crosses.

But the present results do not exclude the possibility that there is local sequence detection within the area of overlap of the two patches, of the sort suggested by Barlow & Levick (1965). Further experiments are needed to examine whether the receptive field contains local *and independent* directional sub-units.

The contrast between these two alternatives may be more apparent than real, for one would expect a spatially distributed structure such as a receptive field or a branching cable to show both local and global properties, depending on the geometry and temporal pattern of its inputs (see chap. 7 of Jack, Noble & Tsien, 1975).

Nature of the 'patches'

The present results suggest that the directional receptive fields are made up of two patches, one excitatory and one inhibitory to the ganglion cell. Each patch would correspond to the receptive field of a prior on-off element which responds to moving stimuli on a non-directional basis (resembling the non-directional ganglion cells or the PNR in this respect). It seems likely that each patch is made up by convergence upon a particular class of amacrine cell. It would be of interest to establish whether both patches are equivalent to receptive field centres, by examing the contrast sensitivity of directional responses, and by examining the radial selectivity of each component. These tests might also show up aspects of organization common to directional and non-directional cells.

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