



Directional Movement and Horizontal Edge Detectors in the Pigeon Retina

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visual or olfactory ones may be necessary to initiate feeding behavior.

Attraction to sounds involves some form of directional hearing. With the exception of Kritzler and Wood, most previous investigators of this phenomenon in fish have found it only at very close range or not at all (12). In our experiments, the possibility that the sharks simply followed a sound gradient seems remote because we frequently changed the intensity. True directionality is also suggested by the oriented attitude of the sharks upon entering the field of visibility.

An important factor is the maximum distance from which the sharks are attracted and whether it is acoustically near or far field (13). At present, however, we have no reliable method for measuring this distance. A comparison of the numbers of sharks seen during the periods of quiet and the periods of sound seems to indicate an attraction distance of well beyond the limit of visibility at 15 to 25 m. The near field of a dipole source such as our J9 transducer, extends to only about 15 m (14) at 20 cy/sec, the approximate low end of our transmitting system. Because the limit of visibility was usually beyond 15 m we can say that the sharks were hearing and orienting to the sounds in the far field.

The far field pressure wave of the low-frequency sound used in playback is theoretically detectable above ambient noise at about 2000 m in a calm sea. If sharks are capable of detecting pressure waves, then it is reasonable that they may respond at great distances from the source. Sharks, however, do not possess an obvious pressure detector such as a gas bladder, and it seems more likely that they would detect particle displacement. The maximum far field particle displacement of the sound used at 25 m is about 100 Å. The lowest measurement of sensitivity in the lateral-line of fish is 10 Å (15). The sound we used would have a displacement of 10 Å at about 250 m. Thus, although the sharks may be in the far field, the displacements are not small enough to rule out the possibility of utilization of the lateral-line, an organ regarded by some as a near field displacement detector (13; 16).

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Directional Movement and Horizontal Edge Detectors in the Pigeon Retina

Abstract. There are ganglion cells in the pigeon retina that respond selectively, some to any edge moving in a particular direction only, others to any vertically moving horizontal edge. This selective response to a specific stimulus arises from the selective sensitivity of each neuron to a particular spatiotemporal configuration in its afferent influences, and is independent of specific pathways.

In a recent paper Barlow and Hill (1) have shown that many ganglion cells of the rabbit retina respond selectively to movement in one direction and not in the reverse. Similar observations have been made in the frog retina (2) and in cortical cells of the cat (3). In general the works of Maturana *et al.* (2), Hubel and Wiesel (3), Mountcastle (4), and Barlow and Hill (1) show that in the central nervous system of vertebrates there are classes of highly specific cells that respond maximally or exclusively to a particular stimulus. Now we wish to present some of our observations on directional cells in the pigeon retina and to discuss some aspects of what seems to us is the fundamental insight that these findings give into the functional organization of the central nervous system.

We recorded the activity of single retinal cells from cut and intact optic nerves in curarized pigeons by means of metal-filled micropipettes. Thus we studied six classes of ganglion cells which differ in the visual configuration to which they respond. Of these we shall now mention only two. We shall not be concerned with the quantitative aspects of the responses which may vary markedly from cell to cell, but only with the mode of response. Nonetheless, we should mention that in general the size of the response (number of spikes and frequency) depends on the direction of contrast, the intensity of contrast, and the speed of movement.

Directional movement detectors form about 30 percent of the accessible cell population. They have five fundamental characteristics:

1) Small receptive fields (defined as the area from which a response can be elicited), which vary between $\frac{1}{2}^\circ$ and 1° in diameter (55 to 110 μ on the retina).

2) An optimal or exclusive response to the movement of an edge in one direction but not in the reverse (Fig. 1). The sharpness of the required edge depends on the size of the receptive field: the smaller the field, the sharper the edge needed.

3) An absence of response to phasic changes of the ambient light.

4) Directional mode of response independent of:

a) the intensity of the ambient light (we tried intensities up to four logarithmic units apart);

b) the direction of contrast across the moving edge: the mode of response is the same for moving objects lighter or darker than the background (Fig. 1, B, C);

c) color, at least to the extent that this can be judged by using different combinations of colored objects and backgrounds made with colored papers and lights (we used narrow band color filters);

d) the part of the receptive field in which the object moves (Fig. 1D).

5) A uniformly *on-off* receptive field. If there are exclusive *on* or *off* spots, these show no special relation to the direction of optimal response. The mode of response is not modified by a spot of light shone *on-off* on any part of the receptive field, nor by a ring surrounding the field or a crescent or any variegated background shone *on-off* in any part of the surroundings while the ob-

ject moves. These have some inhibitory effect on the size of the response but this effect is symmetric with respect to the receptive field. These properties and those that are noted under 4b and 4d indicate that the directional sensitivity of these cells does not depend on any asymmetry of the receptive field or its surroundings. Nevertheless, that inhibitory influences somehow play a role in the genesis of the mode of response of this class is shown by two observations:

a) if two objects enter the receptive field simultaneously, one moving in the direction of optimal and the other in the direction of minimal response, they interfere, and no response is obtained;

b) if one shines a spot of light *on-off* on the receptive field, displacing the spot a step each time during the *off* period (in complete darkness) in the direction of the optimal response, one obtains each time a response to the *on-off* of the spot. If one does the same

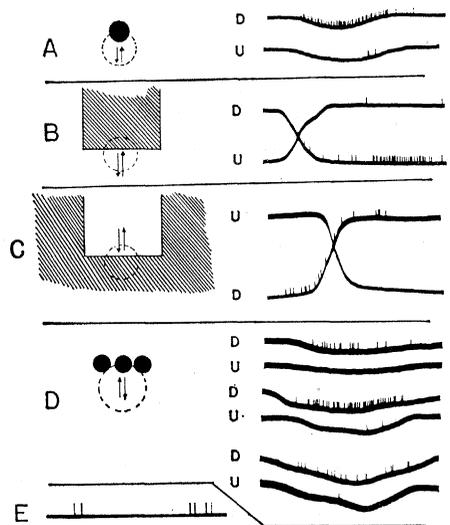


Fig. 1. Directional cell. Optimal response to an edge moving downward. For photographic purposes spikes were clipped at the lower end, just above the noise level, and brightened. The position of the base line was controlled by the output of a photocell focused on the receptive field. Darkening is given by a downward deflection of the base line. At left the drawings show the stimulus situation (the receptive field is indicated by a dotted circle and the arrows show the direction of movement). At right the oscilloscope traces show the responses to the downward (D) and upward (U) movements of the object. A, Small object; B, edge limiting a large field darker than the background; C, edge limiting a large field lighter than the background; D, small object moved across three different parts of the receptive field; E, response to the *on-off* of a spot of light.

in the reverse direction, the cell does not respond.

Horizontal edge detectors form about 5 percent of the accessible cell population. They have four fundamental characteristics:

1) If the head of the pigeon is in the orientation with respect to gravity that the animal maintains most of the time, the detectors respond maximally to a horizontal edge moved vertically up or down across the receptive field, or to the tip of a bar, or to the corner of a rectangle if the horizontal edge extends for some distance in the surroundings. They do not respond to a small object moved only inside the receptive field. The horizontal edge, to be effective, has to extend both into the field and the surroundings. Here the receptive field is defined as the area into which the tip of a horizontal bar has to enter to produce a response. Thus determined, the fields measure between 20 to 40 minutes of arc across (40 to 80 μ on the retina) (Fig. 2, A, E).

2) They do not respond to phasic changes of the ambient light, nor to the *on-off* of a spot of light.

3) They vary with respect to the deviation from the horizontal that they tolerate. Some will respond to the moving edge even when this is inclined 45° with respect to the horizontal, but most do not respond to edges inclined more than 20° to 30°. Within their range of tolerance they also respond to the inclined edge when this moves in a horizontal direction.

4) Similarly to the directional movement detectors, their mode of response is independent of the intensity of the ambient light, the direction of contrast across the edge, and the color of the objects and background.

In none of these classes of cells is it possible to explain their mode of response by the classic scheme of interactions of excitatory and inhibitory areas (3, 5). In this sense they resemble the cells described by Barlow and Hill (1), the complex receptive field cells of the cortex of the cat (3), and the first two classes described for the frog retina (2). That the interplay of inhibitory and excitatory processes plays a role of some kind in shaping the mode of response is apparent at least for directional movement detectors (see 5a and 5b). Therefore, it appears that in these cells the directionality depends on the actual displacement of the object across the receptive field in the optimal direction. We do not doubt that an ex-

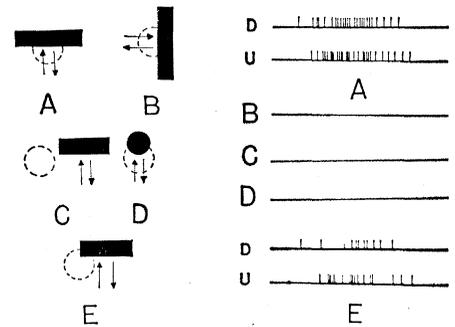


Fig. 2. Horizontality detectors; symbols as in Fig. 1; no photocell monitoring the presence of the object. A, Horizontal bar moving vertically; B, vertical bar moving horizontally; no response; C, horizontal bar moving vertically outside the receptive field, no response; D, small object moved inside the receptive field, no response; E, horizontal bar moving vertically with its tip in the receptive field.

planation will eventually be found as to how these various modes of response are generated, possibly related to the shape of the cells and the way they are connected to others. At present, however, we think two things of fundamental significance.

First, each ganglion cell, to respond to a particular kind of visual stimulus, needs to take into account what happens at any moment in its whole receptive field and surroundings, even if the mode of response is independent of position in the field. Since each ganglion cell is connected to hundreds of bipolars it has to receive afferent influences other than those due to the specific stimulus. That such is the case for whatever occurs in the visual field is apparent from the cell properties described above. It follows that some kind of integration of the afferent influences must occur at the level of the ganglion cells for them to respond only to a specific stimulus. That many cells in the central nervous system require temporal and spatial summation to respond is well known (6). However, our observations show that these cells are sensitive not just to any sum of afferent influences but only to a specific one defined by a particular spatiotemporal configuration of the afferent influences, such that any other spatiotemporal distribution is rejected.

Second, as was shown by Maturana *et al.* (2), owing to the overlapping of dendritic arbors many ganglion cells that perform different and/or similar functions are connected to the same bipolars, and through these look at the

world through the same receptors. From this it follows that in the retina any cell that responds selectively to a particular configuration of the afferent influences must do so independently of specific pathways. By specific pathway we mean a pathway that would be used only for the detection of a particular pattern, to the exclusion of other patterns. We do not refer to the specific excitatory or inhibitory properties of the cells.

These arguments also apply to other retinal and cortical cells that perform specific functions, regardless of whether one can or cannot at present explain analytically their mode of operation. Excitatory and inhibitory processes certainly play a role as components of the input to the cells, but it is to the spatio-temporal configuration of these processes in the input that the cells appear to be specifically sensitive, and thus it is this configuration of the input which we have to consider as the actual stimulus to the cell. Some cells like those which we have discussed may require a very complex configuration, while others may respond to a more simple one, as do ganglion cells in the cat retina (3).

In general we think that the cells of a particular kind will respond to all events that occur in the outside world, in the organism, or in the nervous system capable of producing such a configuration in the input, treating them as equivalent. In other words, we think that a cell will treat these events as members of the same class, the class being defined by the specific configuration to which the cell is sensitive, and hence by some element common to the organization of all the events that produce it. The meaning of the class will arise from the context (functional, behavioral, and so forth) in which the cell activity occurs and the activity developed by a cell when responding will thus represent this class. We believe that neurons behave in this way regardless of their position in the central nervous system. For cells anatomically located further in the central nervous system, the configuration of afferent influences which stimulates them will of necessity depend on the activity of cells in other centers and they are thus able to detect classes made up of other classes. We believe that this mode of operation, in which nerve cells (or part of them) behave as unitary elements capable of class (pattern) recognition independently of spe-

cific pathways, is a fundamental feature of the functional organization of nerve cells in the central nervous system. It seems to us that an adequate understanding of this point leads to a new approach to the problem of the functional organization of the nervous system and the questions of pattern recognition and learning (7).

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Contour Interaction and Visual Resolution: Contralateral Effects

Abstract. Detection of the gap in a four-position Landolt C presented to one eye is impaired by critically spaced surrounding bars seen only by the other eye. The intensity and spatial extent of this contralateral contour interaction match those obtained ipsilaterally. These results indicate that the neural site for this loss of visual information is suprarretinal.

Human visual resolution is known to depend upon the physical characteristics of the test object, the optical properties of the eye, and the physiological state of the system. Thus, with a given eye and a known or at least constant state of the system, the resolution of a certain kind of target is determined by its size, contrast, brightness, and duration of presentation. Less well known, but none the less important, is the influence of nearby borders or surrounding contours on the visual resolution of a target of interest (1). Such *contour interaction* can be sufficiently powerful to obliterate resolution of an above-threshold test letter (2). This effect has recently been quantified by using a

four-position Landolt C and introducing to the same eye four surrounding bars symmetrically placed at various eccentricities from the test C (3) (Fig. 1).

Visual detection of the gap in the C was maximally impaired when the bars were located about two gap widths from the C. Resolution impairment was generally less for separations smaller than this and was essentially absent when the bars were more than five gap widths away from the C. This was true even though the eyes studied covered a wide range of resolving capacities; the spatial extent of interaction was proportional to the resolving capacity of the eye. Thus, resolution impairment occurred with contours separated by only 2 minutes of arc from the C for eyes having high acuity, but as far out as 24 minutes of arc for low-acuity (amblyopic) eyes. Optical spread in an in-focus image is too small to account for the extensive range of this effect; it has therefore been argued (3) that this contour interaction has a neural basis. The question is whether such neural interaction occurs at a retinal level or somewhere higher in the visual system. The previous monocular studies fail to answer this question; our study was designed to do so by looking for possible impairment of resolution of a target seen by one eye when peripheral contours are presented to the *opposite* eye.

Contralateral presentation of a Landolt C to one eye and peripheral bars to the other was accomplished in the present experiment by means of suitably arranged polarizing filters. For comparison, ipsilateral presentation of the C and bars to one eye, with a matching (56 ft-lam) blank white field for the other eye, was made possible by rotating the filters at the target. Contralateral and ipsilateral presentations of the bars were randomly intermixed; the subjects were unaware of the arrangement. Prior to exposure of the C and bars, the subject binocularly fixated a small spot on a matching white field seen in a mirror. Elevation of the mirror exposed the C and bars for 0.5 second; no eye movements were required for foveal imagery during this interval. Each subject's ametropia was corrected with spectacle lenses. The Landolt C was placed at a viewing distance which permitted about 80 percent correct identifications of gap orientation. At this viewing distance, the frequency of seeing was also determined for each of a series of targets differing only in the