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Visual Receptive Fields in the Cat's Retina: Complications

Abstract. *Visual receptive fields have been mapped with moving patterns in the cat's retinal ganglion cells. A small, general-purpose computer was used to collect a matrix of 2500 data points covering a 25°-by-25° region of space. The analysis of 40 units reveals the existence of many nonconcentric receptive fields and also the presence of line and edge detectors.*

Various attempts have been made to classify unit responses recorded from retinal ganglion cells. Perhaps the most generally accepted classification deals with the "on-center" and "off-center" aspects of the recordings, the surround showing a response "opposite" to that of the center of the field.

The suggestion has been that the fields are more or less concentric and that the more complex responses obtained from higher stations in the visual system are composed or integrated from these elementary concentric units. There have been, however, a few indications that such a view of the structure of the receptive field recorded from ganglion cells may be oversimplified. For example, Rodieck and Stone (*1*) point out that all of the receptive fields they mapped were to some extent radially asymmetric, and that in some cases the surround region could be detected over only part of the receptive field or not at all. Kuffler (*2*) had also noted the "asymmetry" of some fields.

The present investigation was undertaken as part of a larger program delineating efferent control of input in the visual system. In these studies the control mechanisms of an *XY* plotter were used to move a white disc on a black background on any *X* or *Y* dimension. A Computer for Average Transients (CAT 400A) was used to compute averaged response histograms in a fashion similar to that described by Rodieck and Stone (*1*). While this method affords a great deal of precision, it is not very flexible, so that the shape of the receptive field, which is two-dimensional, has either to be inferred or reconstructed laboriously from a number of such scans, or to be attained by mapping point-by-point by hand.

To gain a better understanding of receptive-field organization we decided to take full advantage of the flexibility of the *X-Y* stimulus control system used and to use a small, general-purpose computer (PDP-8), to collect and display the data. A program was designed that could achieve the following:

1) Generate appropriate electrical functions for the *X* and *Y* servo ampli-

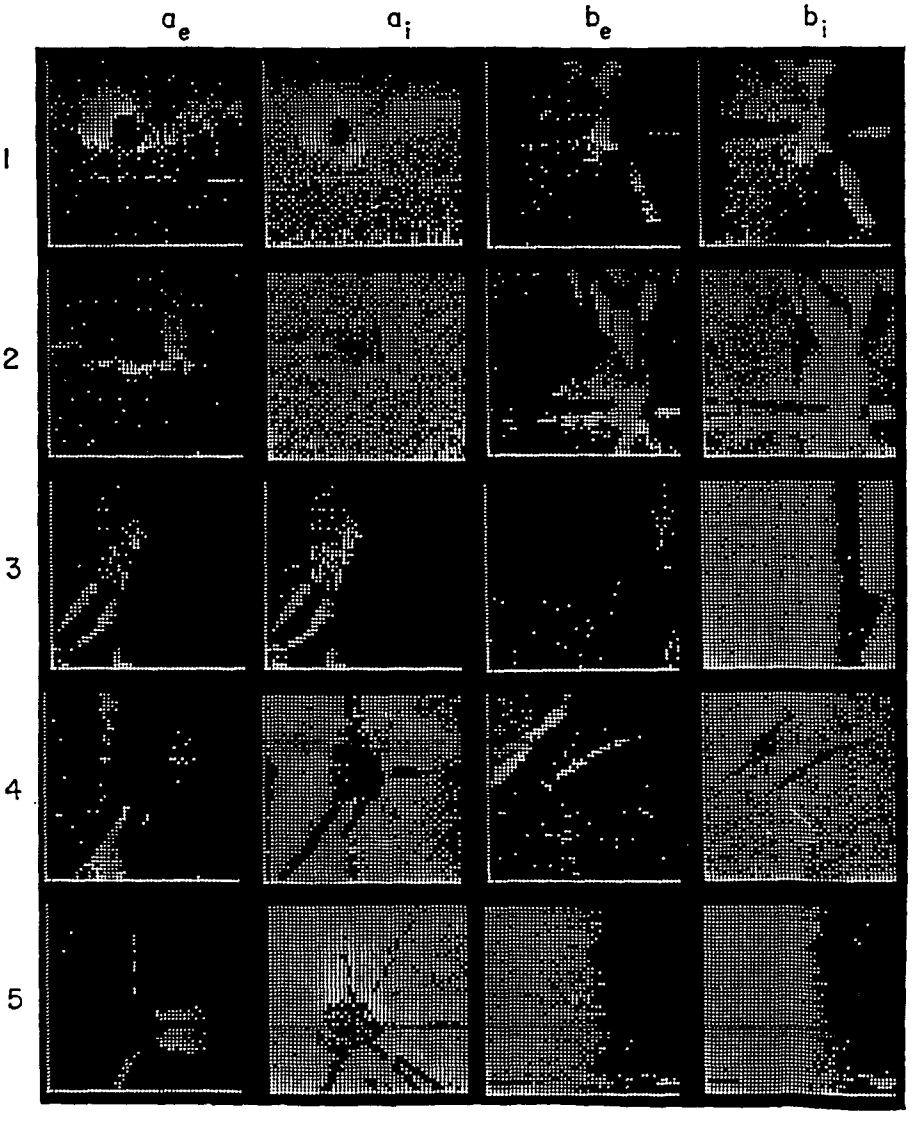

Fig. 1 (right). Columns a_e1 through b_i5 show, in order of "increasing complexity," ten of the receptive fields studied with this method. In column a_e, 1 through 5, the excitatory regions of five receptive fields are displayed by showing points where activity was greater than the mean background plus three standard deviations. In column a_i, 1 through 5, the inhibitory regions of the same five receptive fields are displayed as dark areas by showing all points with one or more counts. The same considerations apply to columns b_e and b_i, 1 through 5.

fiers so that the visual stimulus, consisting of a white disc (200 cd-m^2) 0.2° in diameter on a black background (0.02 cd-m^2) could be moved along a matrix of 50 by 50 points, starting with the bottom row and then returning the disc and moving it up row by row. The region of space scanned was 25° by 25°.

2) Control traveling time from one horizontal point to the next; in this experiment traveling time was held to 70 msec, so that one horizontal scan required 3.5 seconds; a 1.3-second interval was allowed after the return of the disc between one scan and the next.

3) Count and store the number of spikes produced by the unit while the stimulus moved along the matrix, so as to generate subsequently a matrix of 50 by 50 data points. Each data point thus contained the number of spikes produced by the unit while the stimulus moved with uniform speed from one point to the next, with the exception of the first point in each horizontal row, which contained the number of spikes generated during the 70 msec before movement started.

4) Print out all of the 2500 data points or any of the horizontal or vertical rows.

5) Display on an oscilloscope face any of the horizontal (H) or vertical (V) rows.

6) Show the whole matrix as an isometric display.

7) Display, two-dimensionally, only those points where activity exceeded a given value.

This last feature of the program is most useful because it allows direct appreciation of the receptive-field shape; this is obtained by displaying only those points where activity was more than three standard deviations away from the mean of the spontaneous activity of the unit.

Forty units were studied with this method in five cats. Unit activity was recorded from optic-nerve fibers with tungsten microelectrodes aimed stereotaxically at the intracranial and the optic foramen. Surgery was performed under thiopental sodium anesthesia, after which the animal was immobilized with Flaxedil (gallamine triethiodide) and artificially ventilated. All wounds and pressure points were infiltrated with a long-acting local anesthetic (Zyljectin).

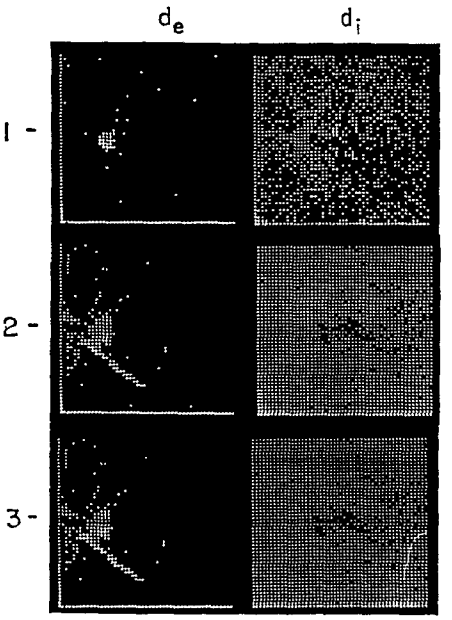

Fig. 2. These records show a dark-adaptation experiment. In d_e1 and d_i1 the excitatory areas and the inhibitory areas, respectively, of an optic-nerve fiber were mapped in the light-adapted eye. In d_e2 and d_i2 the receptive field was mapped after 30 minutes of complete darkness. Finally, in d_e3 and d_i3 the field was mapped again after 60 minutes of darkness. As already noted by Barlow *et al.* (*4*), the size of the center increases during dark adaptation. Also, d_e2 and d_e3 give an idea of the remarkable repeatability of these mappings.

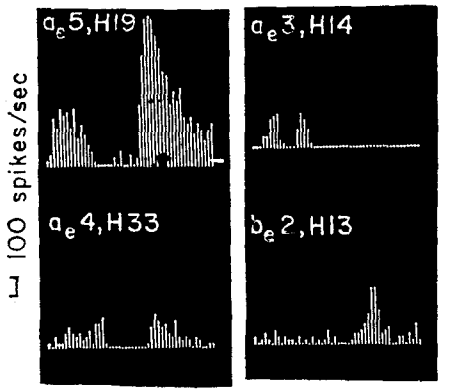

Fig. 3. Single horizontal scans at H19, H33, H14, and H13 are shown for units a_e5, a_e4, a_e3, and b_e2, respectively (see Fig. 1).

Figure 1, a_e1 through b_e5, shows, in order of increasing complexity, ten of the receptive fields studied with this method. In the $-_e$ columns are shown points where activity was more than three standard deviations from the mean background, thus displaying clear-cut excitatory regions; in the $-_i$ columns all points of the same fields with one count or more are shown: this displays inhibitory regions as dark areas. Figure 2 shows the effect of dark adaptation on an on-center receptive field; this figure also shows the remarkable repeatability of these mappings.

It is immediately apparent from the data that while there is no doubt about the circular organization of some receptive fields (a_e1 is one example), much greater complexity can also be found, and that more often than not, the analysis of a single axis taken at the appropriate level would have left one with the impression of dealing with a classically concentric receptive field (Fig. 3).

Rodiek and Stone (*1*) have demonstrated that the receptive field of a unit mapped with a moving light is directly correlated with the receptive field of the unit mapped with stationary spots, and, moreover, that the response of a unit to two stimuli presented simultaneously is the sum of the responses of the unit to two stimuli presented sequentially.

If this is the case it follows that the receptive field is a direct indication of the visual stimulus to which the unit is most responsive, namely, a black line for unit b_i3, an edge for b_i5, and so on (Fig. 1). Fields like b_i3 and b_i5 in Fig. 1 have been described in the cat's visual cortex and attributed to different ways of combining concentric receptive fields (*3*). However, it appears that the cat's retinal receptive fields are rather more complicated than had been supposed. Therefore, the hypothesis that more complex receptive fields have been combined from the activity of units with concentric ones in some simple fashion may need revision, at least for line and edge detectors.

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References and Notes

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