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Receptive Field Mechanism in the Vertebrate Retina

Abstract. *In the catfish retina there are two types of ganglion cells: in one type (type A cell) a spot of light at the center of its receptive field gives rise to a sustained discharge whereas an annulus gives rise to a transient response, and in the other type (type B cell) the response pattern is reversed for a spot and an annulus. Current injected into the horizontal cell induces spike discharges of the ganglion cell very similar to that elicited by a spot of light or by an annulus. In both types of receptive fields, depolarization of the horizontal cell gives rise to a response of the ganglion cell similar to that elicited by a spot of light, whereas hyperpolarization of the cell gives rise to a response of the ganglion cell similar to that elicited by an annulus. Current through a single injecting electrode could drive two types of cells simultaneously. Interaction between a spot of light and an annulus can also be simulated by replacing one light stimulus by current of the proper polarization injected into the horizontal cells. Results suggest that interactions among three neuronal structures, the receptor, the horizontal cell, and the bipolar cell, produce the basic receptive field organization in the channel catfish.*

The organization of the receptive field of the vertebrate retinal ganglion cell has been a subject of intensive study (*1, 2*). Although the receptive field has been shown to consist of several subfields (*3*), the possible mechanisms underlying the organization have not often been explored. An exception could be found in the mudpuppy (*4*). In this report I present functional evidence which suggests that interaction among three neuronal structures, the receptor, the horizontal cell, and the bipolar cell, produces the basic structure of the receptive field.

The catfish retina possesses distinct advantages for the study of the organization of the receptive field because (i) the organization of the receptive field is simple (*5*), (ii) the horizontal cells are always hyperpolarized by light (*6*), and (iii) the spike discharge can be, as will be shown here, initiated by injecting current into the horizontal cells (*7*).

The excised eye of the channel catfish (*Ictalurus punctatus*) was used throughout the experiment, and the preparation was kept moderately dark-adapted. Under such conditions both the response from the horizontal cell and the spike discharges from the ganglion cell (*8*) were generated by signals from a single class of cones with a maximum sensitivity at 625 nm (*5, 6*). This provision excluded a possible complication by color-coded mechanisms such as that reported for the goldfish retina (*2, 3*). The response of the horizontal cell was recorded by means of a glass pipette filled with potassium citrate (resistance, 100 to 200 megohms) and the spike discharge was recorded by the use of one or two tungsten electrodes. The level of the intracellular potential of the horizontal cell was artificially altered by injecting current through the recording electrode, and the amount of current passed was monitored by a voltage created across a 1-kohm resistor placed between the preparation and the ground. As shown in Figs. 1 and 2, the rise and decay time of the current were adjusted so that they approximated the rise and decay time of the response of the horizontal cell. In the experiments for which results are shown in Figs. 1 and 2 the tips of both recording electrodes were placed within the retinal area illuminated by the central spot, and the two electrodes were approximately 0.2 mm apart. The magnitude of the current injected into the horizontal cell to initiate the spike discharge of the ganglion cell 0.2 mm away was less than 20 na. A two-channel photostimulator provided a central spot of 0.3 mm and an annulus with an inner diameter of 0.35 mm. The outer diameter of the annulus was 5.0 mm, which was roughly two-thirds of the diameter of the dissected eyecup preparation. The two stimuli were monochromatic lights of 525 nm, and they were placed concentrically on the retina. The intensity of flash used was 1.0 to 1.8 logarithmic units below $I_{1/2}$, the flash intensity required to give the horizontal cell response of half the maximal amplitude [see also equation 1 in (*6*)].

In the catfish, polarization of the horizontal cell potential by means of current passed through the recording electrode produced discharges of the ganglion cell very similar to that caused by the light stimulus. The possibility that this discharge might have been due to the direct effects of current on the ganglion cell was excluded because the injected current could initiate the ganglion cell discharge only when the electrode was at a position where it could record the response of the horizontal cell, and dislocation of the electrode resulted in the inability of the injected current to activate the spike discharge.

Furthermore, current injected through an electrode placed 1.0 to 1.5 mm away from the spike recording site was still effective (at a current intensity of 30 to 50 na) in inducing the discharge of the ganglion cell. Current injected through a single electrode was also effective in inducing the spike discharge of two types of ganglion cells (types A and B) recorded simultaneously by two tungsten electrodes. These observations indicate that the current injected into a horizontal cell could spread laterally as in the case of the potential change induced by photic

Table 1. Discharge patterns of the ganglion cells of the catfish.

Stimulation	Response elicited by	Ganglion cell	
		Type A	Type B
Photic	Spot	Sustained	Transient
Photic	Annulus	Transient	Sustained
Electric	Depolarization	Sustained	Transient
Electric	Hyperpolarization	Transient	Sustained

stimulation. These observations also suggest that the current injected was able to influence the large number of ganglion cells.

On the basis of the difference in the discharge pattern in response to a spot of light and an annulus, the retinal ganglion cells of the catfish can be classified into two distinct types, type A and type B cells (9). In the type A cell a spot of light placed at the center of the receptive field produced a sustained discharge of the cell lasting the duration of illumination (Fig. 1a, traces 1 and 2), whereas an annulus gave rise to a transient response (Fig. 1b, traces 1 and 2). The transient response was either an "on" or an "off" discharge when the intensity of the stimulus was low, and it often turned into an "on-off" discharge when the intensity of the stimulus was 0.5 to 2 logarithmic units above the threshold intensity. In the type A cell, depolarization of the horizontal cells by means of current passed through the electrode placed in the cell produced a sustained discharge quite similar to that produced by a spot of light (Fig. 1a, traces 3 and 4). The number of spike potentials was roughly proportional to the magnitude of the current injected. On the other hand, hyperpolarization of the horizontal cells produced a transient discharge of the ganglion cell which was very similar to that produced by an annulus (Fig. 1b, traces 3 and 4). As in the case of annulus stimulation, a current of small magnitude, only a few nanoamperes, produced either "on" or "off" discharges, whereas a current of a greater magnitude (5 to 10 na) often produced "on-off" discharges.

In the type B cell the response pattern of the ganglion cell was the reverse of that seen in the type A cell. In this cell a spot of light placed at the center of the receptive field produced a transient discharge similar to that produced by an annulus in the type A cell, whereas an annulus produced a sustained discharge (Fig. 2a, traces 1 and 2) similar to that produced by a spot in the type A cell. In the type B cell, hyperpolarizing current produced a sustained discharge similar to that elicted by an annulus (Fig. 2b, traces 1 and 2), whereas depolarizing current produced a transient discharge similar to that elicited by a spot of light (Fig. 2c, traces 1 and 2).

In both types of cells the sustained discharge could be depressed in the presence of the stimulus that gave rise to the transient response. In the case of the type A cell, stimulus by a spot of light occurring during the period of illumination by an annulus failed to give rise to a sustained discharge. There was a similar interaction in the type B cell, in which the sustained discharge by an annulus (Fig. 2a, traces 1 and 2) was depressed when the annulus stimulation occurred during the illumination by a spot of light (Fig. 2a, traces 3 and 4). The spot alone gave rise to an "on-off" discharge. The depression of the sustained discharge by the stimulus which gave rise to the transient discharge could also be seen when the timing of the two stimuli was reversed. But the interaction was not so obvious as a result of the evoked "on-off" discharge added during the suppression of the sustained discharge.

Similar interaction between the sustained and the transient discharge could also be seen when either one of the photic stimuli was replaced by current of proper polarity. In the type B cell the sustained discharge by a hyperpolarizing current (Fig. 2b, traces 1 and 2) was depressed nearly completely when it was preceded by a spot of light (Fig. 2b, traces 3 and 4). Similarly, the sustained discharge by an annulus in the type B cell could be depressed by the depolarization of the horizontal cells by current injection which gave rise to an "on-off" discharge (Fig. 2c). However, the depression of the sustained discharge by the depolarizing current was not as complete as in the case of a spot of light (Fig. 2b). In the type A cell the sustained discharge produced by a spot of light could be depressed by hyperpolarizing current, and the sustained discharge by the depolarizing current could be depressed by an annulus.

The discharge patterns of the ganglion cells of the catfish to stimulation by light or by injected current are summarized in Table 1. It can be seen that the properties of the receptive field of the two types of ganglion cells, types A and B, are complementary for both light and current stimulation. Table 1 also shows that, for both types of re-

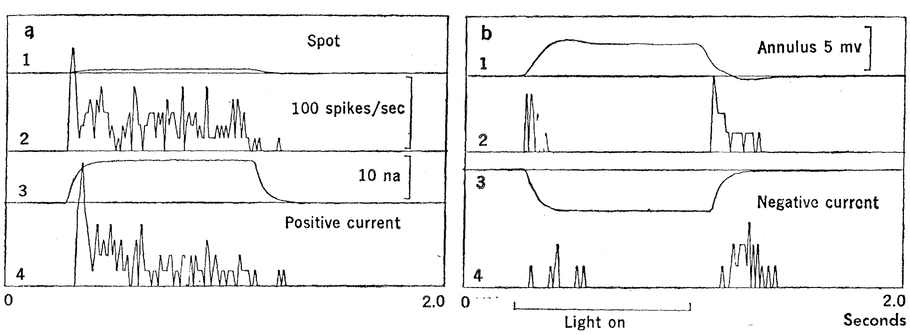
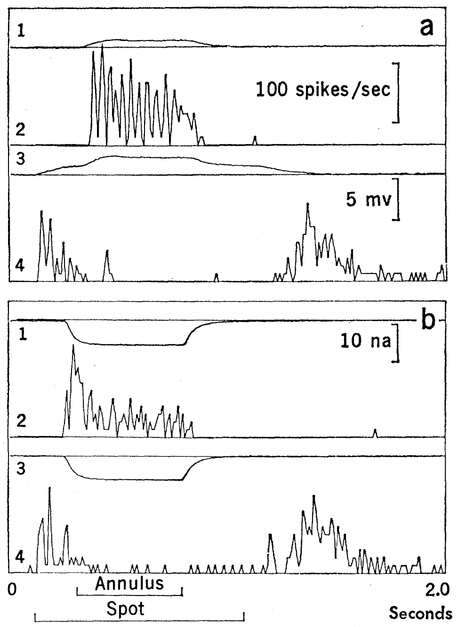


Fig. 1. Comparison of the spike discharge pattern elicited by light stimulus and by current injected into the horizontal cells in a type A ganglion cell. (a) A spot of light and depolarization of the horizontal cells by current injection give rise to sustained discharges. Trace 1 is the response of the horizontal cell to a spot of light; trace 2 is the spike discharge obtained in response to the same spot of light; trace 3 is the wave form of the current injected; and trace 4 is the spike discharge obtained in response to the current injected. The average number of spikes for each stimulus was 31.7 (S.D. = 5.0) for the spot of light and 26.6 (S.D. = 4.5) for the current injected (five runs on the average). (b) Four traces represent records similar to those in (a) obtained by an annulus (trace 1, the horizontal cell response; trace 2, the spike discharge), and by a negative current (trace 3, the current; trace 4, the spike discharge). Records in this figure were from the same horizontal and ganglion cell. In Figs. 1 and 2 records (for the response of the horizontal cell, spike discharge, and current) were an average of five successive measurements. For the horizontal cell response, hyperpolarization is shown as an upward displacement of the trace. The spike discharge was counted in a bin of 20 msec, and the calibration shows the firing rate as the number of spikes per second.



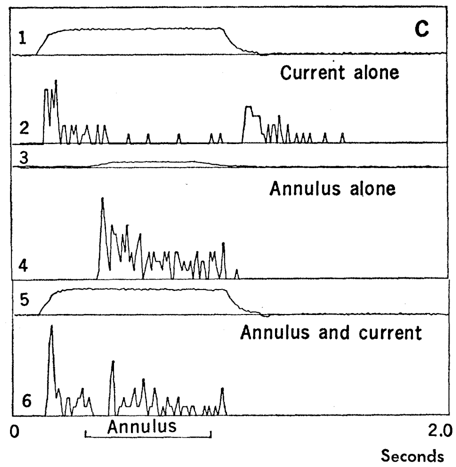


Fig. 2. (a) The interaction between a spot and an annulus in a type B ganglion cell. Traces 1 and 2 are the response of the horizontal cell and the spike discharge in response to an annulus (duration, 0.5 second). In traces 3 and 4 the same annulus stimulus was preceded by a spot of light. (b) The suppression of a current-induced sustained discharge by a spot of light. Traces 1 and 2 are the wave form of the injected current and the spike discharge by the current. The same current (trace 3) was preceded by a spot of light which suppressed the sustained discharge (trace 4). (c) Suppression of the sustained discharge evoked by an annulus caused by a current-induced depolarization of the horizontal cells. Traces 1 and 2 show the depolarizing current and spike discharge induced by the current. Traces 3 and 4 show the response of the horizontal cell and the spike discharge elicited by an annulus. In traces 5 and 6 the same annulus stimulation was given during the passage of the current. The average number of spikes elicited by the annulus was 22.7 (S.D. =1.9), and this value was reduced to 9.8 (S.D.=0.7) in the presence of the positive current (counted for the same period as in the case of the annulus alone). The annulus inhibited the "off" part of the transient discharge by the positive current. Records were from the same horizontal and ganglion cell.

ceptive fields, depolarization of the horizontal cells could produce the same response of the ganglion cell as that produced by a spot of light, whereas hyperpolarization of the cells gives rise to a response of the ganglion cell similar to that produced by an annulus. Since all light-induced responses of the horizontal cells in the channel catfish are hyperpolarizing, a spot of light cannot possibly mediate its influence on the ganglion cell through depolarization of the horizontal cells, as suggested by the current injection experiment.

The fact that not only could the two modes of ganglion cell discharge be reproduced by the artificial changes of the horizontal cell potential, but also that the spot-annulus interaction could be reproduced by replacing one photic stimulus by polarization of the horizontal cell, suggests that the basic organization of the receptive field results from the interaction taking place among the three neuronal structures in the outer plexiform layer, the receptors, the bipolar cells, and the horizontal cells.

It has been shown that the receptors hyperpolarize when stimulated by light, and that the size of the receptive field of a receptor is comparable to that of the cross section of a single cone (*10*). Thus it is highly improbable that potential change inside the horizontal cells, whether by light or by current injection, could influence the receptor potential. The experimental results described here can be explained if we assume that the bipolar cells receive and sense the difference between the inputs from both the receptors and the horizontal cells. The response of the horizontal cell, although its input is derived from the receptors, is the result of the integration of potentials arising in the rows of the horizontal cells (*11*). Thus for a small spot of light the input to the bipolar cell from the horizontal cell is less negative than the input from the receptors, which is sensed by the bipolar cell. The response of the bipolar cell and consequently that of the ganglion cell are determined in this case by the receptor input, which corresponds to a spot of light. The situation can be artificially reproduced by depolarizing the horizontal cells in the absence of photic stimulation. As seen from Table 1, the response of type A and type B cells to a spot of light is identical to the response to a depolarizing current. An annulus, on the other hand, can exert its influence only through the row of horizontal cells, and the effects of an annulus can be simply reproduced by hyperpolarizing the horizontal cell (Table 1). Furthermore, the possibility that each type of ganglion cell might have received a signal through different horizontal cells could be excluded by an experiment in which current injected into a horizontal cell could drive both types of ganglion cells simultaneously. Morphological study has thus far failed to identify the synaptic contact from the horizontal cells on the bipolar cell in the carp, although such synapses have been found in the retinas of other vertebrates (*12*).

Since its discovery, the role of the responses of the horizontal cell (S-potential) in the visual process has remained obscure. Maksimova has successfully shown that the current injected into the horizontal cell of the pike could evoke the spike discharge of the ganglion cells (*13*). She further noted that the response pattern is very similar to that produced by photic stimulation. The results presented here provide further evidence showing that in the catfish retina the horizontal cells with their spatial integrating properties participate in the organization of the receptive field.

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