Analyses of Bipolar Cell Responses Elicited by Polarization of Horizontal Cells

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ABSTRACT Simultaneous intracellular recordings were made from a bipolar cell and a horizontal cell in the carp retina. The properties of the bipolar cell were studied while injecting current into the horizontal cell. Hyperpolarization of horizontal cells, irrespective of their type, elicited a hyperpolarizing response in on-center bipolar cells and a depolarizing response in off-center bipolar cells. Analyses of the ionic mechanisms of bipolar cell responses revealed that depolarization of horizontal cells simulated and hyperpolarization opposed the effect of central illumination. The effect of polarization was exerted in such a manner that each type of horizontal cells modified the transmission from those photoreceptors from which they receive main inputs. In on-center bipolar cells, for example, the L-type horizontal cells receiving inputs mainly from red cones modified the cone-bipolar transmission accompanied by a conductance change of K⁺ and/or Cl⁻ channels, and the intermediate horizontal cells receiving inputs from rods modified the rod-bipolar transmission accompanied by a conductance change of Na⁺ channels. In off-center bipolar cells, the effect of polarization of any type of horizontal cells was mediated mainly by conductance changes of Na⁺ channels. Feedback mechanisms from horizontal cells to photoreceptors could explain these results reasonably well.

INTRODUCTION

Bipolar and horizontal cells are second-order neurons in the retina receiving direct inputs from photoreceptors. In the cyprinid fish, some bipolar cells called large bipolar cells receive inputs from both cones and rods, whereas other cells called small bipolar cells receive inputs from cones (Stell, 1967). Horizontal cells can also be classified according to the input they receive. The external horizontal cells of Cajal (1892) receive inputs from cones and the intermediate horizontal cells from rods (Stell, 1967; Kaneko, 1970; Kaneko and Yamada, 1972; Mitarai et al., 1974). The external horizontal cells are further classified into L, RG, and RGB types, according to their spectral response pattern. It is known that each type of cell forms a distinct sublayer (Mitarai et al., 1974; Hashimoto et al., 1976).

Horizontal cells have a large receptive field far beyond their dendritic field.
because of the extensive electrical coupling, as demonstrated physiologically in the smooth dogfish (Kaneko, 1971) and in the carp (Toyoda and Tonosaki, 1978 b). Morphologically, there are specialized junctional areas, the gap junctions, along the boundary of adjacent horizontal cells in the same sublayer (Yamada and Ishikawa, 1965; Witkovsky and Dowling, 1969; Raviola, 1976). Although the horizontal cells of the same type are electrically coupled, there is no electrical coupling between horizontal cells of different type (Toyoda and Tonosaki, 1978 b).

The receptive field of many bipolar cells consists of concentric central and surrounding regions. Some bipolar cells respond with depolarization to illumination of the center field that roughly corresponds to their dendritic fields and with hyperpolarization to illumination of the surround field. These cells are classified as on-center bipolar cells. Other bipolar cells respond with hyperpolarization to illumination of the center and with depolarization to illumination of the surround field. They are classified as off-center bipolar cells. Since the surround field far exceeds the dendritic field, it is generally assumed that the effect of illumination of the surround is mediated by horizontal cells (Werblin and Dowling, 1969; Kaneko, 1973). This hypothesis can be tested by studying the effect of polarization of horizontal cells on bipolar cells.

In the present experiments, the responses of a horizontal and a bipolar cell were recorded simultaneously and the effect of polarization of horizontal cells was tested by passing current through the intracellular electrode. The effect of polarization of different types of horizontal cells on each type of bipolar cells was studied and the ionic mechanisms underlying was analyzed from the reversal potential of the bipolar cell response thus elicited.

METHODS

Experimental methods were the same as those briefly described elsewhere (Toyoda and Tonosaki, 1978 a and b).

The isolated retina of the carp, *Cyprinus carpio*, was used in the experiments. Electrodes were single- and double-barreled microelectrodes filled either with 2.5 M KCl or 4.0 M potassium acetate solution. Their resistance measured in Ringer's solution was ~100 MΩ. The coupling resistance of double-barreled electrodes was ~2 MΩ, but often their tip was bevelled so as to reduce their resistance to ~40 MΩ and their coupling resistance to <200 KΩ. Two electrodes were mounted each on one of the two separate blocks of a coaxial electrode holder (Narishige Co., Tokyo, Japan) with their tips within 50 μm of each other on a horizontal plane. The single electrode was first inserted into the retina until it recorded the response of a bipolar cell. Then the double-barreled electrode was advanced by means of an oil manipulator to record the response of a horizontal cell. Fig. 1 illustrates schematically the present experimental setup.

The test light was a diffuse white light of ~0.4 lm/m² after attenuation by neutral density filters and of 1.0 s duration. The stimulus pattern and the wavelength of light was changed when necessary by inserting a patterned diaphragm or an interference filter in the light path.

When a bipolar and a horizontal cell were recorded simultaneously, the effect of polarization of the horizontal cell was tested by passing an extrinsic current of 20–30
nA through one barrel of the double-barreled electrode. The reversal potential and the membrane resistance changes accompanying the bipolar cell response were studied by a bridge circuit built in a preamplifier (M701; WP Instrument, Hamden, Conn.) and by passing current of the order of 1 nA through the recording electrode. Responses were monitored on an oscilloscope and at the same time recorded on tape for later processing. The data were later reproduced and plotted on an X-Y recorder.

Experiments were carried out at a room temperature of 20–24°C.

RESULTS

Effect of Polarization of Horizontal Cells on On-Center Bipolar Cells

The effects on bipolar cells of polarization of three types of horizontal cells, L-type, RG-type, and intermediate (rod) horizontal cells, were studied in these experiments. Hyperpolarization of horizontal cells, irrespective of their type, elicited a hyperpolarizing response and their depolarization elicited a depolarizing response in on-center bipolar cells. Since the response of bipolar cells thus elicited is accompanied by a change in the membrane resistance (Toyoda and Tonosaki, 1978a) and shows, as will be described below, a certain reversal potential, the effect can be judged as mediated by chemical synapses.

Fig. 2 is an example of simultaneous recordings from an L-type horizontal cell (a) and an on-center bipolar cell (b). After testing their responses to a diffuse white light, the horizontal cell was artificially hyperpolarized and then depolarized by current. In this and all subsequent records, the voltage drop across the coupling resistance of the double-barreled electrode was not compensated for. To find the reversal potential, responses of the bipolar cell to these stimuli were recorded while its membrane was hyperpolarized by current through the recording electrode. An example of such records is shown in trace

![A schematic illustration of the experimental setup.](image-url)
Although there is considerable noise in this trace, it may be judged that the responses to polarization of the horizontal cell reverse their polarity by hyperpolarization of the membrane (see Fig. 3 of Toyoda and Tonosaki, 1978, for another example). The effect of polarization of L-type cells was detectable in 29 out of 30 pairs studied. In most of these pairs, the responses of the bipolar cells to polarization of the horizontal cells were suppressed or inverted by hyperpolarization of the bipolar cell membrane. In a few pairs, the effect of the membrane potential on responses was not tested. The response of these bipolar cells to white light was usually augmented by hyperpolarization of their membrane. It is probable that they receive dominant inputs from rods under the present experimental conditions because the rod signals are
mediated by ionic channels having a positive reversal potential, whereas those mediating cone signals have a negative reversal potential (Saito et al., 1979).

These results suggest that the effect of polarization of L-type horizontal cells on on-center bipolar cells is mediated by a conductance change of $K^+$ and/or $Cl^-$ channels. Hyperpolarization of L-type cells makes these channels more permeable and their depolarization makes them less permeable. This assumption is further supported by the observation that the hyperpolarizing response of these bipolar cells to polarization of L-type cells is accompanied by an increase and the depolarizing response by a decrease in the membrane conductance (Toyoda and Tonosaki, 1978a).

Fig. 3 is an example of simultaneous recordings from an intermediate horizontal cell (a) and an on-center bipolar cell (b). Intermediate horizontal cells can be easily distinguished from other horizontal cells by the sensitivity to light, the spectral sensitivity, and the time-course of their response. Trace c shows responses of the same bipolar cell while its membrane was hyperpolarized, and its responses while being depolarized by steady current are shown in trace d. As seen in these records, responses are augmented by hyperpolarization and are suppressed or inverted by depolarization of the membrane. Such an effect of the membrane potential on the response amplitude has been confirmed in all of the 18 pairs studied. The observation of the response reversal was difficult because of the electrode noise during depolarizing current. The reversal was actually confirmed in two pairs.

These results suggest that the effect of polarization of intermediate horizontal cells on on-center bipolar cells is mediated mainly by a conductance change of $Na^+$ channels. Hyperpolarization of the horizontal cells makes these channels less permeable and their depolarization makes them more permeable. This assumption is also supported by the observation that the hyperpolarizing response of these bipolar cells to polarization of intermediate horizontal cells is accompanied by a decrease, and the depolarizing response is accompanied by an increase in the membrane conductance (Toyoda and Tonosaki, 1978a).

Fig. 4 is an example of simultaneous recordings from an RG-type horizontal cell (a) and an on-center bipolar cell (b). To confirm their cell type, responses to diffuse white light and red light were tested before the polarization of the horizontal cell. Trace c shows the responses of the same bipolar cell while its membrane was hyperpolarized by current. The responses to red light was not tested under this condition. The effect of polarization of RG-type cells was detectable in 7 out of 13 pairs recorded. In these pairs the responses were augmented by hyperpolarization of the membrane. The measurement of the conductance change (not illustrated) showed that the hyperpolarizing response was accompanied by a decrease and the depolarizing response was accompanied by an increase in the membrane conductance. It is probable that the effect of polarization of RG-type horizontal cells, like that of intermediate horizontal cells, is mediated by a conductance change of $Na^+$ channels. However, since the effect was not detectable in a considerable number of pairs, these bipolar cells may receive a relatively small number of inputs from RG-type horizontal cells either directly or indirectly through a feedback pathway to photoreceptors.
Effect of Polarization of Horizontal Cells on Off-Center Bipolar Cells

Hyperpolarization of horizontal cells, irrespective of their type, elicited a depolarizing response and their depolarization elicited a hyperpolarizing response in off-center bipolar cells. The possibility of electrical interactions can be excluded by the polarity of the response. The responses thus elicited in off-center bipolar cells are also accompanied by a change in the membrane conductance and are affected by the membrane potential.

Fig. 5 is an example of simultaneous recordings from an L-type horizontal cell and an on-center bipolar cell. (a) Responses of an intermediate horizontal cell. (b) Responses of an on-center bipolar cell to diffuse white light and to polarization of the horizontal cell by a current of 20 nA. (c) Responses of the same bipolar cell during hyperpolarization of its membrane by a steady current of 2 nA. (d) Responses of the bipolar cell during depolarization of the membrane by a current of 3.7 nA. The response of the bipolar cell to light was not recorded during depolarization of the membrane.
cell (a) and an off-center bipolar cell (b). Trace c shows the responses of the same bipolar cell during hyperpolarization of its membrane by current. The effect of polarization of L-type cells was detectable in 16 out of 21 pairs recorded. In almost all of these pairs the responses were augmented by hyperpolarization of the membrane. The effect of depolarization of the membrane was not studied systematically. It was difficult to pass enough depolarizing current to elicit a response reversal without causing a tremendous electrode noise. In a few pairs, the responses were markedly suppressed by depolarization of the membrane. The reversal of light-evoked responses by depolarization of the membrane has been actually reported in the off-center
bipolar cells (Saito and Kondo, 1979). In the present experiments, there was a good proportionality in the effect of polarizing current on the bipolar cell responses to both light and polarization of horizontal cells. These observations indicated that the effect of the membrane polarization observed was not due solely to the rectification property of the bipolar cell membrane. It is suggested that the effect is mediated mainly by a conductance change of Na⁺ channels.

Fig. 5 is an example of simultaneous recordings from an L-type horizontal cell and an off-center bipolar cell. Recording conditions were the same as in Fig. 2 except that a steady current of 2 nA was used to hyperpolarize the bipolar cell membrane.

Fig. 6 is an example of simultaneous recordings from an intermediate horizontal cell (a) and an off-center bipolar cell (b). Trace c shows the responses of the same bipolar cell during hyperpolarization of its membrane by current. The effect was observed in 10 out of 11 pairs studied. The measurement of conductance changes in a few units showed that the hyperpolarizing responses were accompanied by a decrease and the depolarizing responses were accompanied by an increase in the membrane conductance. The ionic channels mediating this effect must be the same as those mediating the effect of L-type cells.
The effect of polarization of RG-type horizontal cells on off-center bipolar cells was also studied by simultaneous recordings of the two. However, in most pairs recorded, the polarization of the horizontal cell did not elicit a detectable response in the bipolar cell. Only in 2 out of 15 pairs recorded was the effect detectable. Fig. 7 is one of the two rare examples. As in Fig. 5, the responses to diffuse white light and red light were tested before polarization of the horizontal cell by current. Trace c shows the responses of the same bipolar cell during hyperpolarization of its membrane by current. The hyperpolarizing current augmented the depolarizing response, but its effect on the hyperpolarizing response was not prominent. It is not clear whether such an asymmetrical effect is characteristic of these pairs, since a slight asymmetry has been observed in many other pairs. The ionic mechanisms may not be different from those mediating the effect of other horizontal cells; namely, the Na⁺ channels become more permeable by hyperpolarization and less permeable by depolarization of horizontal cells.

The difficulty in observing the interaction between RG-type cells and off-
center bipolar cells in a number of pairs recorded may be due to sparse connections between them either directly or indirectly through a feedback to photoreceptors.

DISCUSSION

In both on-center and off-center bipolar cells, hyperpolarization of horizontal cells elicits a response similar in polarity to that elicited by surround illumination. The essentially same results have been reported for bipolar cells of the turtle retina (Marchiafava, 1978) and for off-center bipolar cells of the carp retina (Trifonov and Byzov, 1977), although these authors did not pay any attention to the type of horizontal cells. Since the surround illumination with white light hyperpolarizes horizontal cells, these results are consistent with the assumption that the surround response of bipolar cells is mediated by horizontal cells.

There are two possible pathways by which the effect is mediated. One is the direct synaptic pathway from horizontal cells to bipolar cells. The other
is the indirect one involving a feedback pathway from horizontal cells to photoreceptors. A possible synaptic connection between dendrites of horizontal and bipolar cells has been reported in some amphibians (Dowling and Werblin, 1969; Lasansky, 1973) and in the catfish (Naka, 1976). Conventional synaptic structures between horizontal and bipolar cells have not been reported in the cyprinid fish. However, there are occasional close contacts between dendrites of horizontal and bipolar cells with specialized submembrane densities or with specialized membrane particles, which Stell (1978) suggests might be the site of unconventional synaptic contacts. Thus the direct synaptic interaction cannot be excluded, although it is difficult to prove it physiologically.

Feedback synapses from horizontal cells to photoreceptors, on the other hand, have been suggested mainly from physiological studies. The first evidence obtained in the turtle retina is the fact that hyperpolarization of horizontal cells by current elicits a depolarizing response in cones (Baylor et al., 1971). In the cyprinid fish, the feedback mechanisms involving a potential change in cones have long been questioned because of the difficulty in detecting the response of cones to polarization of horizontal cells or to surround illumination. The feedback is suggested in the perch retina, in which the hyperpolarizing cone response is reduced when the size of a light spot is increased (Burckhardt, 1977).

Recent histochemical studies suggest that the L-type horizontal cells in the cyprinid fish retina contain γ-amino-butyric acid (GABA). They actively take up GABA and this uptake is affected by light (Marc et al., 1978). The presence of GABA in the L-type cells and the effect of bicuculline, a specific GABA antagonist, on the frequency characteristics of horizontal cell responses suggest that GABA is the chemical transmitter in the feedback pathway from L-type cells to cones (Lam et al., 1978). This suggestion is also supported by recent studies on the carp retina (Murakami et al., 1978). After the depolarizing response of horizontal cells elicited by transretinal current, a small hyperpolarizing response appears in cones. This response is abolished by application of an excess of GABA or its antagonist to the retina.

The effect of hyperpolarization of L-type horizontal cells on red cones was also studied in the present experiments. In 2 out of more than 10 pairs recorded, a small depolarizing response in cones was detectable when the field potential due to the extracellular current spread was subtracted from the records. The results suggested a certain kind of interaction between these cells but the effect was so small that we were reluctant to accept them as convincing enough to indicate the synaptic connection. Difficulty in detecting a depolarizing response of cones to an annular illumination and to hyperpolarization of horizontal cells, especially in the cyprinid fish retina, led Byzov et al. (1977) to assume that the feedback is mediated by electric current. According to them, the current generated by horizontal cells flows in part through the photoreceptor terminal and elicits a voltage drop across the presynaptic membrane, which in turn causes a change in the ionic permeability of the membrane and the amount of the transmitter released.

Table I summarizes the present results. In this table, the effects of hyper-
polarization of horizontal cells on both on-center and off-center bipolar cells are listed. The effects of depolarization of horizontal cells are shown in parentheses. Generally, the transmitter is assumed to be liberated by depolarization of presynaptic elements. In the feedback pathways, therefore, the transmitter acting on bipolar cells must be liberated from photoreceptors when horizontal cells are hyperpolarized by current. In the feed-forward pathways, the transmitter must be liberated by depolarization of horizontal cells. The possible actions of the transmitters released at the last stage of both feedback and feed-forward pathways are also listed in the table.

Recent physiological studies on the on-center bipolar cells suggest that the transmitter from red cones acts to increase the conductance of subsynaptic K⁺ and/or Cl⁻ channels and the transmitter from rods acts to decrease the conductance of subsynaptic Na⁺ channels (Saito et al., 1979; Saito and Kondo, 1978). The possible actions of transmitters listed in the table are consistent with these observations, when it is assumed that each type of horizontal cells makes a feedback connection to those photoreceptors from which they receive inputs: L-type cells to red cones and intermediated horizontal cells to rods. It has been suggested that RG-type cells receive direct inputs from green and blue cones (Stell and Lightfoot, 1975). Thus there will be a feedback connection from RG-type cells to green as well as to blue cones. As seen in the table, the action of the transmitter from green or blue cones could be different from that of red cones.

The responses of off-center bipolar cells to illumination have been reported to show a positive reversal potential (Toyoda, 1973; Trifonov and Byzov, 1977; Saito and Kondo, 1979). It is reasonable to assume, therefore, that the transmitter liberated from photoreceptors in the dark acts to increase the

### Table I

Summary of the Effect of Hyperpolarization (or Depolarization) of Horizontal Cells on Bipolar Cells

| Bipolar cell | Horizontal cell | Response elicited | Reversal potential | Possible pathways | Action of transmitter |
|--------------|-----------------|-------------------|-------------------|-------------------|----------------------|
| On-center    | L-type horizontal cell | Hyperpolarization (depolarization) | - | a. Feedback to red cones b. Feed-forward | Inhibitory |
|              | Intermediate horizontal cell | Hyperpolarization (depolarization) | + | a. Feedback to rods b. Feed-forward | Disfacilitatory |
|              | RG-type horizontal cell | Hyperpolarization (depolarization) | + | a. Feedback to green cones b. Feed-forward | Disfacilitatory |
|              | All three types of horizontal cells | Depolarization (hyperpolarization) | + | a. Feedback to photoreceptors b. Feed-forward | Excitatory |

Responses elicited in bipolar cells by hyperpolarization of horizontal cells are shown without parentheses and those elicited by depolarization are shown in parentheses. The presumed action of the transmitter listed is of that liberated at the last stage which affects bipolar cells directly. In the feedback pathways, it is the transmitter from photoreceptors. In the feed-forward pathways, it is the transmitter from horizontal cells. The transmitters are assumed to be liberated by depolarization of presynaptic terminals.
conductance of subsynaptic Na\(^+\) channels. This is consistent with the excitatory action of the transmitter proposed in Table I. Thus, the feedback hypothesis can explain the present results reasonably well.

The presence of a negative feedback from horizontal cells to rods in the toad (Brown and Pinto, 1974) and in the turtle (Copenhagen and Owen, 1976) is seriously questioned, although its presence in the toad is suggested by Norman and Pochobradsky (1976). Horizontal cells in these retinae receive inputs from both rods and cones. Therefore, the conclusion derived in these animals may not apply to the cyprinid fish.

In the feed-forward pathways, on the other hand, we have to further assume three different ionic mechanisms; some of them are simple but some are rather complex. The effect of intermediate and RG-type horizontal cells on on-center cells is the simplest. The transmitter liberated by depolarization of these horizontal cells must be excitatory. The effect of L-type cells on on-center cells is the most complex. The transmitter must act to decrease the conductance of subsynaptic K\(^+\) and/or Cl\(^-\) channels (disinhibition). In other pairs, the transmitter must act to decrease the conductance of subsynaptic Na\(^+\) channels (disfacilitation).

In summary, the simplest explanation of the present results is to assume the presence of feedback pathways. But, since not all of these pathways have been confirmed, a contribution of feed-forward pathways in some pairs cannot be excluded. The identification of transmitter substances will help elucidate the overall mechanisms.

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