Ionic Mechanisms Underlying the Responses of Off-Center Bipolar Cells in the Carp Retina

I. Studies on Responses Evoked by Light

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ABSTRACT Off-center bipolar cells show hyperpolarizing responses to spot illumination in the receptive field center and depolarization responses to an annulus in the surround. To understand the ionic mechanisms underlying these responses, we examined the current-voltage relationship of these bipolar cells, input resistance changes during their light-evoked responses, and the reversal potentials of these responses. Off-center bipolar cells generally showed inward rectification when they were hyperpolarized and outward rectification when they were strongly depolarized. The membrane potential at which the *I-V* relationship deviated from linearity varied in individual cells. Hyperpolarizing center responses were generally accompanied by a resistance increase, irrespective of signal inputs either from red-sensitive cones or from rods, and the response polarities reversed at greater than +50 mV. Depolarizing surround responses were accompanied by a resistance decrease with a reversal potential at about +28 mV (one case). From the above observations, it is suggested that the center responses are generated by a decrease in sodium conductance (g_{Na}) and the surround response is generated by an increase in g_{Na}.

INTRODUCTION

Bipolar cells in the vertebrate retina can be classified into two types according to their response patterns (Werblin and Dowling, 1969; Kaneko, 1970). The first type, referred to as off-center cells, hyperpolarize when a spot of illumination is presented within a localized area of the retina covering their dendrites; this area is termed the cell's receptive field center. In addition, off-center bipolar cells depolarize when peripheral regions of the retina, i.e., the receptive field surround, are illuminated. The second type, termed on-center

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cells, respond to these sets of stimuli with voltage changes of opposite polarities to those of off-center cells.

Compared with on-center bipolar cells, the membrane properties of off-center bipolar cells have not been examined extensively because of the technical difficulties resulting from their smaller size (Stell et al., 1977; Famiglietti et al., 1977; Kaneko et al., 1979). Furthermore, the reports published so far are not necessarily consistent with each other. One group of investigators (carp: Toyoda, 1973; turtle: Trifonov and Byzov, 1977; tiger salamander: Werblin, 1977), for example, has found that the amplitude of the light response to a spot was enhanced during steady hyperpolarization and was decreased during steady depolarization of the cell by extrinsic current. Other investigators (Richter and Simon, 1975), studying similar questions in the turtle, reported that the response amplitude decreased when the membrane potential was shifted in either depolarizing or hyperpolarizing directions. A third investigator (Nelson, 1973) used mudpuppy retina and did not observe changes in response amplitude during membrane polarization in either direction.

It is the aim of the present papers to clarify the synaptic mechanisms underlying the responses of off-center bipolar cells in the carp retina. The first paper is concerned with studies on the light-evoked responses. Here, we analyzed the effects of membrane polarization on the response of off-center bipolar cells by injecting extrinsic currents through the microelectrode. The second paper (Kaneko and Saito, 1983) will deal with the properties of responses of off-center bipolar cells evoked by electrical stimulation of photoreceptor terminals (cf. Kaneko and Shimazaki, 1976). A preliminary report of some of these experiments was presented at a Meeting of the Physiological Society of Japan (Saito and Kondo, 1979).

METHODS

The experiments were performed on retinas of the carp, *Cyprinus carpio*. The animal was pithed, the eyes were excised, and the retina was detached from the pigment epithelium. The isolated retina was placed receptor side up in a moist chamber equipped with a transparent bottom and penetrated with microelectrodes advanced from above.

Both single- and double-barreled microelectrodes, each filled with 2.5 M KCl solution and of 60–160 MΩ resistance, were used. Double-barreled electrodes were thought to be ideal for this type of study, but these had larger tips than single-barreled electrodes, which lessened the chance of penetrating off-center bipolar cells without damage. Therefore, we had to limit the use of double-barreled electrodes to only a few experiments. The coupling resistance of the double-barreled microelectrodes measured in the vitreous humor was between 0.5 and 2 MΩ.

Single-barreled electrodes were also used both for recording and for current injection by connecting it to a bridge circuit to cancel the voltage drop across the electrode. In this type of measurement, the records obtained with electrodes that showed strong rectification were discarded.

The photostimulator consisted of a test beam and two background beams, each emanating from a separate quartz-iodine lamp (for details, see Saito et al., 1978). The

test beam could be presented to the retina as a spot (0.4 mm diam at the retinal surface) and an annulus (0.6 mm ID, 2.0 mm OD). One of the background beams was used to present an adapting (white) spot to the receptive field center in order to minimize the effect of scattered light from the annulus to the center. This background beam was combined with the test beam with a half-mirror prism, and both of these stimuli were directed to the retina from the vitreous side. The second background (white) light was delivered diffusely from the receptor side to control the adaptation level of the retina.

RESULTS

Electrical Membrane Properties

MEMBRANE RECTIFICATION *I-V* relationships were studied on 10 off-center bipolar cells by injecting a ramp of current (changing at a rate of ~2.0 nA/s) through one barrel of a double-barreled microelectrode and recording the *I-R* drop through the other barrel. Fig. 1 shows an example of the *I-V*

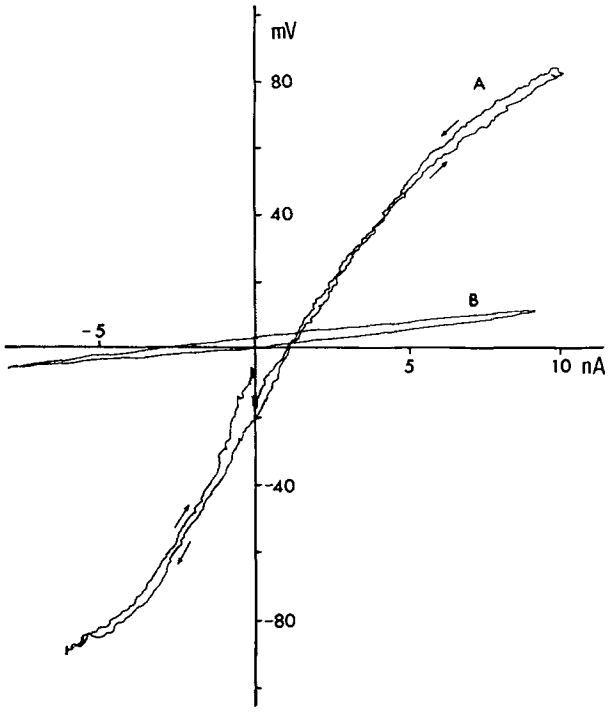

FIGURE 1. Current-voltage relationship of an off-center bipolar cell in the dark. A ramp of current changing at a rate of ~2.0 nA/s was passed through one barrel of a double-barreled microelectrode. (A) Current-voltage curve of the membrane. (B) Coupling resistance of the electrode placed in the vitreous humor. The slope resistance was measured from the slope of the curve of record A in the linear range after subtraction of a voltage drop across the coupling resistance of the electrode (record B).

relationship of an off-center bipolar cell in the dark (i.e., without any background illumination). The cell membrane was first depolarized from the dark resting potential (−18 mV) by injection of outward current, then hyperpolarized by injection of inward current, and finally allowed to return to the original dark level by gradually reducing the amount of current injection. The cell showed an almost linear *I-V* relation between −75 and +30 mV. However, if it was hyperpolarized beyond −75 mV, the membrane slope resistance usually showed an inward rectification, and if it was depolarized above +30 mV, it showed an outward rectification. All 10 cells studied showed outward rectification of the membrane, whereas inward rectification was observed in 6 of them. The slope resistance of the cell of Fig. 1 was ~16 MΩ, in the linear range of the *I-V* relationship (mean ± SD for 10 cells; 15.6 ± 4.5 MΩ).

Fig. 2A shows the *I-V* relationship of another off-center cell in the dark

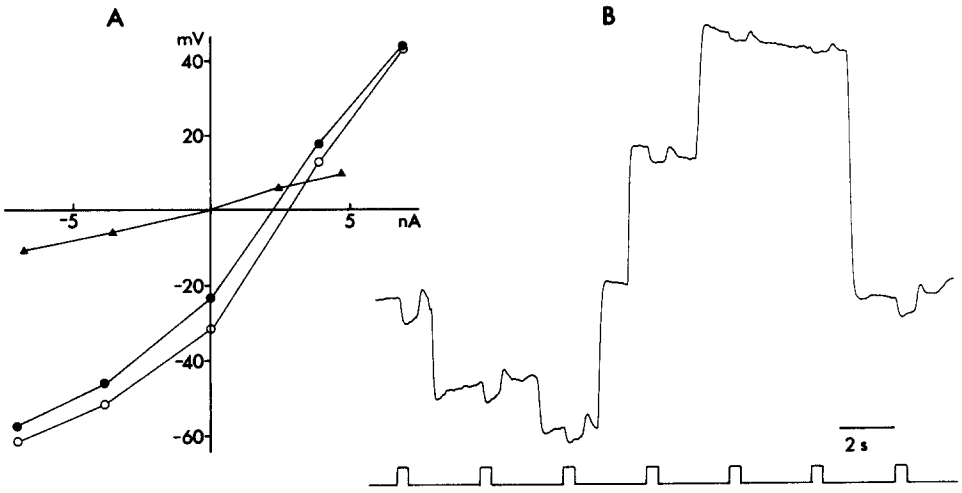

FIGURE 2. Effects of membrane polarization of an off-center bipolar cell. (A) Current-voltage curves plotted from record B. (●) Membrane potential in the dark, (○) at the response peak to spot illumination, (▲) coupling resistance of the electrode in the vitrous humor. (B) Effects of membrane polarization on the center responses. The vertical axis of record A also applies as a voltage calibration for record B.

(filled circles) and during spot illumination (open circles), plotted from the results of Fig. 2B. As shown in Fig. 2B, the cell was polarized by increasing steps of hyperpolarizing or depolarizing current and spot illumination was superimposed on current steps. Transition from the linear *I-V* relation to inward rectification was found near the dark potential level in this cell. A slight outward rectification seemed to be present when this bipolar cell was depolarized beyond +20 mV.

MEMBRANE INPUT RESISTANCE CHANGES Changes in membrane input resistance during light-induced responses were measured on 54 off-center cells by passing constant current pulses through single-barreled microelectrodes

and detecting the membrane *I-R* drop using a bridge circuit. The results are summarized in Tables I and II. In response to white spot illumination, off-center bipolar cells showed either one of three types of resistance changes. As shown in Table I, group A cells (26 out of 54 cells), which showed a resistance increase, were encountered most frequently. Group B cells (12 cells), which showed a resistance decrease, were encountered the least frequently. In group C cells (16 cells), we could not detect a resistance change. Fig. 3 illustrates the recordings from two off-center cells, one (A) from group A, and the other (B) from group B.

Illumination of the receptive field surround evoked an antagonistic depolarization in many of the cells studied (19 out of 54 cells). When depolarizing surround responses were observed, they were accompanied by either resistance decrease (8 cells) or no resistance change (11 cells). We found no example in

TABLE I

MEMBRANE RESISTANCE CHANGES DURING HYPERPOLARIZING (SPOT) AND DEPOLARIZING (ANNULUS) RESPONSES (WHITE LIGHT)

	Resistance change to spot illumination		
	Increase (Group A)	Decrease (Group B)	No change (Group C)
	26	12	16
Resistance changes to annulus illumination			
Increase	0	0	0
Decrease	6	2	0
No change	4	2	5
Not examined*	16	8	11

* Antagonistic surround response was not obtained.

which depolarizing surround responses were accompanied by resistance increase.

More than half of the cells studied (35 out of 54) did not show a depolarizing surround response to the annulus, but showed a hyperpolarizing response that was smaller in amplitude than those produced by spot illumination. Several factors might be responsible for the lack of antagonistic response in the surround, such as the inappropriate adjustment of stimulus parameters or cell deterioration. Within the limited time in which we held the cell, we were not able to optimize the size and intensity of the annulus presented to each cell so as to detect the antagonistic surround response.

MEMBRANE RESISTANCE CHANGES ACCOMPANYING SPECTRAL RESPONSES IN OFF-CENTER BIPOLAR CELLS The results presented thus far show that, in response to spot illumination, group A cells and group B cells show resistance changes of opposite sign. In on-center bipolar cells, it has been demonstrated that the synaptic inputs from rods and red-sensitive cones are different in their ionic mechanisms (Saito et al., 1978, 1979, 1981). A similar suggestion has been made concerning L-type horizontal cells of the tiger salamander (Skrzy-

pek and Werblin, 1981). Since it is known that converging inputs from both rods and red-sensitive cones produce responses of identical polarity in off-center bipolar cells (Kaneko and Tachibana, 1978), we asked whether the variety of resistance changes observed in the present study were induced by synaptic inputs from different type of photoreceptors.

To find out the type of photoreceptors driving off-center bipolar cells, we measured the responses of 21 off-center bipolar cells to monochromatic spots of equal quantal flux. As summarized in Table II, two types of response

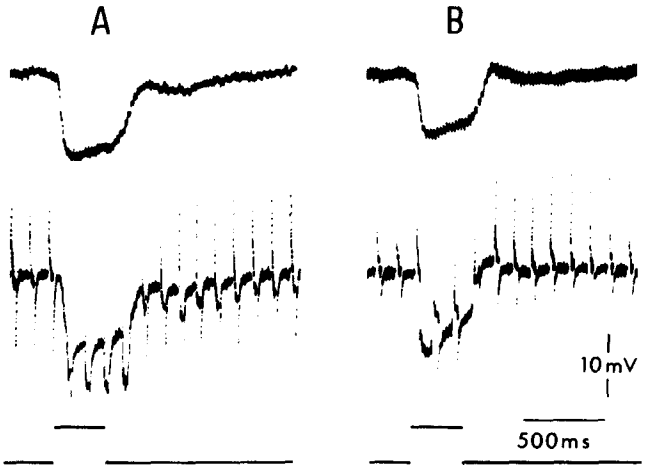

FIGURE 3. Resistance changes during responses to spot illumination. A train of negative current pulses of ~1.0 nA and of 30 ms duration was applied at a frequency of 10 pulses/s. The bridge was balanced before giving a flash. Note that the response in record A is accompanied by a resistance increase (downward deflection of pulses), and the response in record B has a resistance decrease (upward deflection of pulses).

TABLE II

MEMBRANE RESISTANCE CHANGES DURING HYPERPOLARIZING RESPONSE TO SPOT ILLUMINATION (MONOCHROMATIC LIGHT)

Spectral response peak	Resistance changes			Total
	Increase	Decrease	No change	
nm				
575	9	4	2	15
625	3	1	2	6
Total	12	5	4	21

spectra were observed, one peaking at ~575 nm (15 cells), and the other peaking at ~625 nm (6 cells). Judging from the difference spectrum of carp rod pigment extracts (532 nm; Munz and Schwanzara, 1967) and the spectral sensitivity of carp red-sensitive cones (623 nm; Tomita et al., 1967), it seems possible that the former type of cells was driven by both rods and red-sensitive

cones, and the latter type mainly by red-sensitive cones. As seen in Table II, however, we could not find any significant correlation between the spectral sensitivity and the type of resistance changes measured during light responses.

To confirm the above conclusion, we attempted another experiment. If we assume (*a*) that rods and cones converge onto single off-center bipolar cells, (*b*) that illumination of cones produces a decrease in the membrane resistance of the bipolar cell, and (*c*) that illumination of rods results in a resistance increase in the bipolar cell, we might expect to see an augmentation of responses in the blue-green region of the spectrum and a reduction of the response amplitude in the red region of the spectrum when the bipolar cell is steadily hyperpolarized by extrinsic current. Conversely, if illumination of cones results in a resistance increase, the steady hyperpolarization might enhance responses in the long-wavelength region of the spectrum. Fig. 4 shows

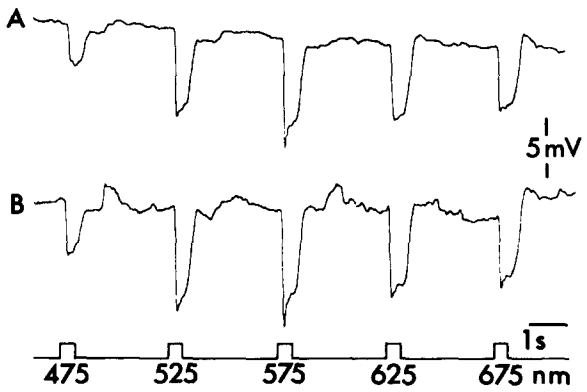

FIGURE 4. Effect of hyperpolarizing current on the spectral responses of an off-center bipolar cell to monochromatic spots of equal quantal flux. Wavelength was changed stepwise from 475 to 675 nm in 50-nm steps. (A) Control spectral responses of the receptive field center obtained without membrane polarization. The cell showed a spectral response maximum at ~575 nm. (B) The spectral responses obtained during steady hyperpolarization of the cell. Note that the wavelength at which the cell showed the maximum response remained unchanged during steady hyperpolarization of the cell.

that when the mixed spectral type of off-center bipolar cell is hyperpolarized by extrinsic current, the responses to all wavelengths increased in amplitude (Fig. 4B) in comparison with the control responses (Fig. 4A). From this type of experiment we concluded that in contrast to on-center bipolar cells, off-center cells show similar resistance changes regardless of the type of photoreceptor inputs.

REVERSAL POTENTIAL OF OFF-CENTER BIPOLAR CELL RESPONSES One method of identifying the ionic species that contribute to the generation of light responses is correlating the reversal potential of a given response with the equilibrium potential of known ionic species. In the present experiments, reversal potentials of the center and surround responses were measured by shifting the cell membrane potential with various amounts of extrinsic current

delivered through one barrel of a double-barreled microelectrode. 23 cells were studied.

The membrane resistance of 18 of these cells increased with spot illumination, and the amplitude of their receptive field center responses was increased by hyperpolarization and decreased by depolarization within the limited range of membrane potential changes (approximately −80 to +50 mV). Beyond the above-mentioned range of membrane hyperpolarization, however, the amplitude of the center responses of many of these cells started to decrease with more hyperpolarization of the membrane, but never reversed, even with a strong hyperpolarization. This type of change is presumably brought about by membrane rectification.

In six of these cases, the polarity of center responses reversed when the cells were depolarized past approximately +50 mV (+49 ± 13 mV; mean ± SD, $n = 6$). A typical example is shown in Fig. 5. The response reversed its polarity somewhere between +58 and +81 mV. The *I-V* curve of this cell in darkness and that at the peak of the response to light intersected at about +62 mV.

In the other 12 cells the center responses became small in amplitude or almost undetectable at strong membrane depolarizations (+30 to +80 mV). When we attempted to increase further current injection, the response became very noisy. Therefore, we were unable to depolarize these cells enough to demonstrate the reversal potential.

Of 23 cells studied, the remaining 5 cells, in which the center responses were accompanied by a resistance decrease, were characterized by a decrease in the amplitude during either depolarization or hyperpolarization of the membrane. They showed a strong inward rectification of the membrane and their responses did not invert even with the maximal applicable polarization of either polarity. The cell illustrated in Fig. 2B is an example.

Reversal potentials for surround responses were examined in seven cells. In every case, the surround response was decreased in amplitude by steady depolarization, and in one cell, the response reversed when it was strongly depolarized (Fig. 6). The reversal potential was estimated to be +23 mV by the same procedure mentioned above. In the other six cells, the surround response could not be reversed even when these cells were strongly depolarized. In these cases, extrapolation of the *I-V* curves indicates an estimated reversal potential of +63 ± 21 mV ($n = 7$).

DISCUSSION

Membrane Rectification

In the present study, we found that the current-voltage (*I-V*) curve of off-center bipolar cells shows inward and outward rectifications both in the dark and during presentations of spots of light to their receptive field centers. Inward rectification similar to that found in the present study has also been reported for rods (Bader et al., 1978; Werblin, 1979) and for horizontal cells (Trifonov et al., 1974; Werblin, 1975; Tachibana, 1981). Trifonov et al. (1974) have localized the nonlinear *I-V* property of horizontal cells to the nonsynaptic

membrane from an experiment in which the synaptic transmission had been interrupted. Strong inward rectification has been found also in solitary horizontal cells isolated from the goldfish retina (Tachibana, 1981). It seems highly possible that these nonlinear properties of nonsynaptic membranes strongly modify the light-evoked responses of horizontal or bipolar cells.

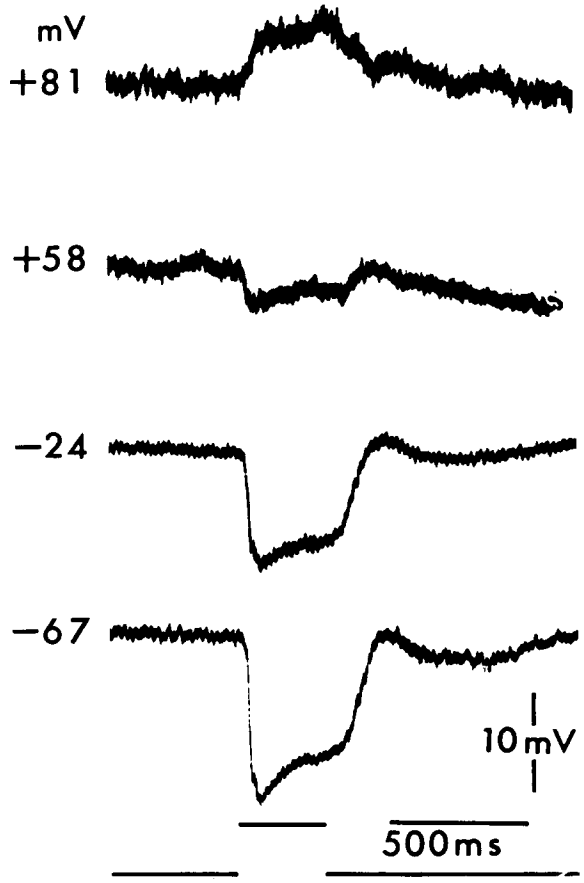

FIGURE 5. Effects of membrane polarization on responses of an off-center bipolar cell to spot illumination (white light). The membrane potential in the dark was −24 mV. The figure attached to each trace indicates the membrane potential before giving a flash. When the membrane was hyperpolarized, the response amplitude increased, and when it was depolarized, the amplitude decreased. Note that the response polarity reversed between +58 and +81 mV. The current-voltage curves obtained from this cell in darkness and at the response peak during light intersected at +62 mV (the reversal potential).

The degree of both inward and outward rectification observed in off-center bipolar cells varied considerably from one cell to another. Furthermore, the potential level at which the membrane became rectifying varied from cell to cell. For example, the *I-V* relationship of the cell of Fig. 1 is more or less linear

within the wide range of membrane voltage (−75 to +30 mV), whereas that of the cell of Fig. 2 became inwardly rectifying when the cell was slightly hyperpolarized from the resting (dark) membrane potential. It may be asked why the membrane potential at which off-center bipolar cells show the inward rectification differed from one cell to the other. One of the possible interpre-

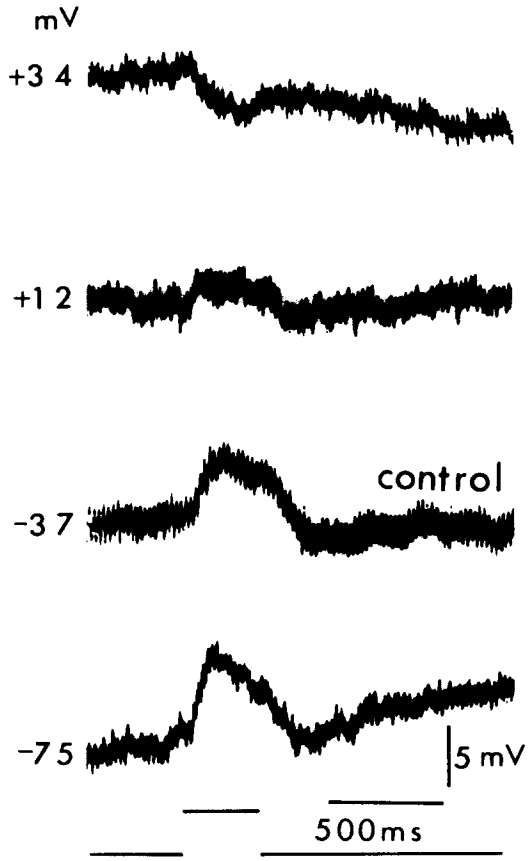

FIGURE 6. Effects of membrane polarization on responses of an off-center bipolar cell to an annulus. The surround response was recorded under illumination of the receptive field center with a steady spot in order to minimize the effect of scattered light from the annulus to the receptive field center. This procedure hyperpolarized the membrane and increased the amplitude of the surround response. The resting potential in the dark was −37 mV.

tations is that during injection of extrinsic current the subsynaptic region of bipolar cells may not be as polarized as the cell body. In fact, variation in cell morphology is extensive (Stell et al., 1977; Kaneko et al., 1979).

In our samples, the resistance increase during the center response and the resistance decrease during the surround response were observed most frequently. These changes are similar to those reported by Toyoda (1973). Those cells whose membrane resistance decreased or did not change measurably

during hyperpolarizing center responses, and those whose membrane resistance did not change during the surround response, were not the majority.

It seems highly possible that the variety of resistance changes observed in the present study is due to various mixtures of two types of membrane resistance changes: one is that of the subsynaptic membrane, which increases in resistance during illumination; another is the inward rectification at the nonsynaptic membrane. In cells in which the former component is predominant, the total input resistance may increase in response to illumination, whereas in cells in which the latter component is dominant, the total resistance may decrease. Variety in changes in response amplitude during hyper- or depolarizations of the cell can be interpreted similarly.

One of the most useful clues to understanding the ionic mechanisms underlying the light-evoked response of retinal neurons is the measurement of a reversal potential. No direct measurements of the reversal potential have so far been made on off-center bipolar cells. In the present work we were able to demonstrate reversal of both the center and surround responses during membrane depolarization. The reversal potential for the center response was +49 mV (average of six cells) and that for the surround response was +23 mV (one cell). These values are close to those reported by Toyoda (1973) (+5 mV in carp) and by Werblin (1977) (+50 mV in tiger salamander), who indirectly estimated the reversal potential by extrapolating *I-V* curves in the dark and during spot illumination.

The reversal potential of the off-center bipolar cell responses seems to be close to the equilibrium potential for Na^+ rather than that for Ca^{2+} estimated in other preparations (cf. Schanne and Ceretti, 1978). It is therefore reasonable to suppose that the center and surround responses of off-center bipolar cells are mediated by changes in the membrane conductance to Na^+.

It may be asked whether substitution of external Na^+ with impermeable cations would eliminate the light response of off-center bipolar cells, if the response is Na^+ dependent. Indeed, with substitution of Na^+ to choline, the responses invariably disappeared and the membrane potential of most of the cells hyperpolarized (Kaneko and Saito, 1983). However, it has been reported that in the low-Na^+ medium, photoreceptors hyperpolarize and their light responses disappear (Cervetto, 1973; Brown and Pinto, 1974; Kaneko and Shimazaki, 1975). Therefore, it is doubtful for the above-mentioned reasons that the changes seen in off-center bipolar cells are the primary ones. In the following paper (Kaneko and Saito, 1983), we will analyze the responses of off-center bipolar cells evoked by brief transretinal current pulses. We assume that the current depolarized photoreceptor terminals and let them release the endogenous transmitter independent of external Na^+.

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