

# Characteristics of Bipolar-Bipolar Coupling in the Carp Retina

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**ABSTRACT** ON and OFF bipolar cells were identified in the light-adapted carp retina by means of intracellular recording and Lucifer yellow dye injection. The receptive field centers, determined by measuring the response amplitudes obtained by centered spots of different diameters, were 0.3–1.0 mm for ON bipolar cells and 0.3–0.4 mm for OFF bipolar cells. These central receptive field values were much larger than the dendritic field diameters measured by histological methods. Simultaneous intracellular recordings were made from pairs of neighboring bipolar cells. Current of either polarity injected into one member of a bipolar cell pair elicited a sign-conserving, sustained potential change in the other bipolar cell. The coupling efficiency was nearly identical for both depolarizing and hyperpolarizing currents. The maximum separation of coupled bipolar cells was  $\sim 130 \mu\text{m}$ . This electrical coupling was reciprocal and summative, and it was observed in cell types of similar function and morphology. Dye coupling was observed in 4 out of 34 stained cells. These results strongly suggest that there is a spatial summation of signals at the level of bipolar cells, which makes their central receptive fields much larger than their dendritic fields.

## INTRODUCTION

Bipolar cells, second-order neurons of the vertebrate retina, form a signal pathway from photoreceptors to amacrine and ganglion cells. The receptive field of bipolar cells is roughly circular in outline and contains two areas: a small central area embedded in a much larger antagonistic surround area. It is generally assumed that the responses of bipolar cells to spot illumination covering their central receptive area are directly transmitted from photoreceptors within the circumference of their dendritic fields, whereas the responses to surround illumination are mediated by horizontal cells (Werblin and Dowling, 1969; Kaneko, 1970, 1973; Schwartz, 1974; Richter and Simon, 1975; Toyoda and Tonosaki, 1978; Davis and Naka, 1980).

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There is a notable difference between the central receptive field diameters determined by physiological methods and the dendritic field sizes measured from histological material: the central receptive fields are always larger than the dendritic fields (Werblin, 1970; Kaneko, 1973; Richter and Simon, 1975; Ashmore and Falk, 1980; Saito and Kujiraoka, 1982; Hare et al., 1986). Electrical coupling between photoreceptors (Baylor et al., 1971; Copenhagen and Owen, 1976; Werblin, 1978), which results in the spatial summation of photoreceptors, may be responsible for this discrepancy. In carp (Saito and Kujiraoka, 1982) and salamander retinas (Hare et al., 1986), however, the dendritic and receptive field diameters of some bipolar cells differ by almost an order of magnitude. Such a large difference is too great to be accounted for by signal spread through electrical coupling between photoreceptors (Burkhardt, 1977).

In this study, we simultaneously recorded responses of two neighboring bipolar cells in the carp retina and injected extrinsic currents into one member of each bipolar cell pair to reveal the potential changes of the counterpart. We found that bipolar cells are electrically coupled to neighboring bipolar cells. We propose that there is a spatial summation of signals at the level of bipolar cells, which would make the disparity between the receptive field and dendritic field sizes even larger.

#### MATERIALS AND METHODS

Carp (*Cyprinus carpio*), 25–30 cm in length, were anesthetized with tricaine methanesulfonate (MS 222). Under dim light, the eyes were excised and the retina was detached from the pigment epithelium.

##### *Measurements of the Receptive Field*

The isolated retina was placed receptor side up in a moist chamber. A white light spot at  $\sim 80$  lm/m<sup>2</sup>, whose diameter could be changed from 0.1 to 2.0 mm, was presented from the vitreous side. For the test flash, a spot size of 1 mm diam was usually used. Micropipettes filled with 4 M potassium acetate and having a resistance of 80–150 M $\Omega$  were used for intracellular recording. The electrode placed at the center of the light spot was advanced vertically into the retina from the receptor side, while 350-ms flashes were presented at 3-s intervals. If the electrode penetrated into a bipolar cell, a series of light spots of different diameters was presented to the retina, starting at 2 mm, then going to 0.1 mm, and then returning to 2 mm. A diffuse background illumination of  $\sim 4$  lm/m<sup>2</sup> was given throughout the experiment to keep the retina in the photopic condition.

##### *Measurements of Bipolar-Bipolar Coupling*

The isolated retina was mounted flat, receptor side up, on a filter paper. The retina and adherent paper were placed in a Lucite chamber ( $\sim 2$  ml vol) and perfused with physiological saline solution. The solution ( $18 \pm 2^\circ\text{C}$ ) flowed at a rate of 1.0–2.0 ml/min. The composition of the solution (in millimolar) was: 102 NaCl, 2.6 KCl, 2.0 CaCl<sub>2</sub>, 0.8 MgCl<sub>2</sub>, 15 dextrose, and 5.0 Tris (hydroxymethyl) aminomethane. The solution was saturated with pure O<sub>2</sub> and adjusted to pH 7.8 with HCl.

The retina was illuminated from the receptor side every 5 s with a white light spot  $\sim 1.0$  mm in diameter and 500 ms in duration. Two microelectrodes, each filled with 4 M potassium acetate, were mounted on separate micromanipulators and aligned under the microscope at a tip distance of  $\sim 100$   $\mu\text{m}$ . They were advanced independently into the retina from the receptor side, until simultaneous intracellular recordings were made from

two bipolar cells. If a simultaneous recording from the two cells was obtained, extrinsic currents were passed through either of the two microelectrodes. After studying electrical interactions between the impaled cells, we cemented the two microelectrodes to one another and withdrew them simultaneously. The distance between the two electrodes was measured under the microscope. This interelectrode distance was taken as the separation between the two impaled cells.

#### *Intracellular Staining*

Some units physiologically identified as bipolar cells were stained with a fluorescent dye (5% Lucifer yellow dissolved in a 0.1 M lithium chloride solution). The dye was iontophoretically injected into recorded cells with 0.8-s square pulses (1 Hz) of 3–6 nA of negative current. The retinal tissues containing stained cells were fixed for 1 h in an ice-cold mixture of 2% paraformaldehyde and 2.5% glutaraldehyde (buffered with 0.1 M sodium cacodylate at pH 7.4). They were dehydrated in ethanol and embedded in Epon. The block was sectioned tangentially at 10–15  $\mu\text{m}$  with a glass knife. Sections were inspected under a fluorescence microscope.

## RESULTS

### *Spatial Characteristics of Bipolar Cells*

To determine the size of the bipolar cell receptive field, the effect of light spots of different diameters upon the response amplitude of bipolar cells was studied in 20 cells (13 ON and 7 OFF bipolar cells). Fig. 1 shows the relation between the amplitude of responses ( $V$ ) and stimulus diameters. All amplitudes were normalized by the maximum value ( $V_{\text{max}}$ ) of each unit and plotted as a function of log diameter. The response amplitudes of ON and OFF bipolar cells increase with increasing diameter of the light spot to a certain extent and then often decrease with a further increase in stimulus diameter. The spot diameters causing the maximum response amplitude, which was defined as the diameter of the receptive field center, varied from 0.3 to 1.0 mm in ON bipolar cells and from 0.3 to 0.4 mm in OFF bipolar cells. The insets show the number of cells at the spot diameters causing the maximum response amplitude. The decrease in the response amplitude with the larger light spot may be explained by a contribution of the antagonistic surround mediated by horizontal cells, whose receptive field expands far beyond the dendritic field of bipolar cells (Werblin and Dowling, 1969; Kaneko, 1973). Therefore, the central receptive field values may be underestimated, because the response of the receptive field center must be attenuated by the antagonistic response of the receptive field surround.

The ON bipolar cells had a large dispersion of their central receptive field values. This may be caused by the contribution of two types of ON bipolar cells (I and II). Type I and II ON bipolar cells have been identified in the dark-adapted carp retina on the basis of their physiological and morphological properties. The receptive field center of type I cells varied from 0.2 to 0.8 mm in diameter, with a mean value of 0.5 mm, while that of type II cells varied from 0.5 to 1.0 mm, with a mean value of 0.7 mm (Saito and Kujiraoka, 1982). Type I and II cells received input from both rods and cones. In our previous experiments (the mesopic condition), type I and II cells differed greatly in their response waveform, because they had an input ratio different from rods and cones. In the

present photopic condition, however, the response waveform of both cell types resembled one another and could not be distinguished, since the photoresponse of both type I and II bipolar cells reflected the activity of the cones by which they were driven.

The central receptive field values obtained here were much larger than the dendritic field diameters measured from histological material: the dendritic diameter of bipolar cells stained with horseradish peroxidase (HRP) averaged 63  $\mu\text{m}$  for type I ON cells, 97  $\mu\text{m}$  for type II ON cells, and 65  $\mu\text{m}$  for OFF cells (Saito et al., 1985).

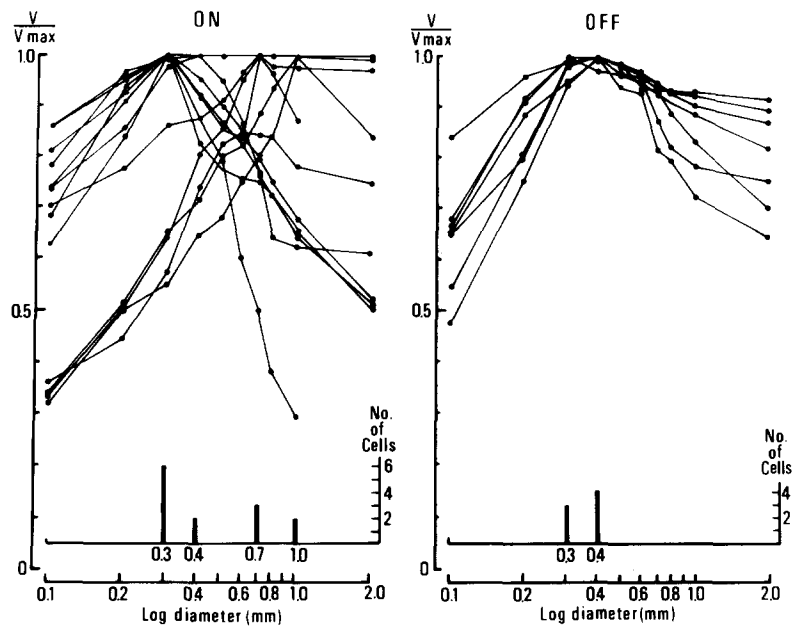


FIGURE 1. The response amplitudes as a function of spot diameter from ON and OFF bipolar cells. The amplitudes plotted ( $V$ ) were normalized with respect to the maximum response amplitude ( $V_{max}$ ) of each unit. The insets show the number of cells at spot diameters causing a maximum response amplitude.

#### *Characteristics of Bipolar-Bipolar Interaction*

Simultaneous intracellular recordings were made from 23 pairs of bipolar cells. To examine interactions between these bipolar cell pairs, extrinsic currents were injected into one member of each bipolar cell pair and the potential changes of the counterpart were recorded. Electrical interactions were found between 15 pairs (13 pairs of ON cells and 2 pairs of OFF cells) separated by  $<130 \mu\text{m}$ . Interactions were not observed in five pairs of ON bipolar cells that were  $>180 \mu\text{m}$  apart and in one pair of ON bipolar cells that was separated by  $\sim 90 \mu\text{m}$ . Two pairs of ON and OFF bipolar cells separated by  $\sim 85 \mu\text{m}$  were apparently not coupled.

Fig. 2 shows examples of electrical interactions in an ON bipolar cell pair (A) and in an OFF bipolar cell pair (B). The timing of current injection is indicated in the bottom trace in each figure. In Fig. 2A, a hyperpolarizing current of  $\sim 10$

nA, applied to the cell whose responses are shown in the lower trace, elicited a hyperpolarization of  $\sim 10$  mV in the other cell, whose responses are shown in the upper trace. A depolarizing current of  $\sim 10$  nA applied to the cell in the lower trace elicited a depolarization of  $\sim 7$  mV into the cell in the upper trace. When we reversed the conditions with respect to current injection and recording cells, essentially identical results were obtained (not illustrated). These interactions disappeared when the microelectrode was withdrawn from one of the two cells and the current was injected into the extracellular space. In Fig. 2B, the basic features of interactions between OFF bipolar cells were similar to those observed in ON bipolar cell pairs: depolarizing and hyperpolarizing currents of  $\sim 10$  nA applied to the lower cell elicited a depolarization and hyperpolarization

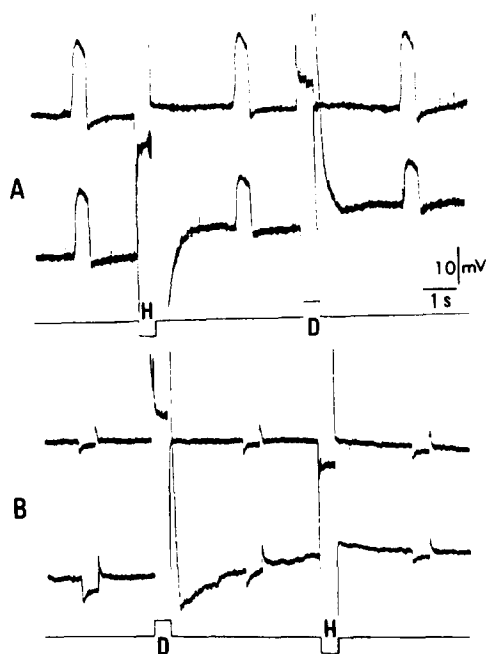


FIGURE 2. Simultaneous intracellular recordings from a pair of ON bipolar cells  $\sim 85 \mu\text{m}$  apart (A) and a pair of OFF bipolar cells  $\sim 80 \mu\text{m}$  apart (B). Extrinsic current pulses of  $\sim 10$  nA and 500 ms were passed into the cell, whose responses are shown in the lower trace. The bottom trace in each panel indicates the timing of current injection. As a monitor of the cell integrity, light stimulation was presented before and after each current injection. H, hyperpolarizing current of  $\sim 10$  nA; D, depolarizing current of  $\sim 10$  nA.

of  $\sim 7$  mV in the upper cell, respectively. In this case, current-evoked potential changes were larger in amplitude than the response evoked by light.

Fig. 3 shows the relation between the amount of current injected into one member of an ON bipolar cell pair and the amplitude of current-evoked potential in the other member. The insets show sample records, which consist of three superimposed response pairs evoked by light and current. The members of this bipolar cell pair were separated by  $\sim 75 \mu\text{m}$ . Depolarizing currents produced slightly smaller changes of membrane potential than hyperpolarizing currents of equal strength. The nonlinearity of the curve may not result from the nature of the coupling pathway itself, but may originate in the somatic membrane of bipolar cells (Toyoda et al., 1978; Saito and Kaneko, 1983).

Fig. 4 shows the electrical interactions between a pair of ON bipolar cells with and without a saturating background light. With no saturating background light, a depolarizing current of  $\sim 10$  nA injected into the cell (lower trace) elicited a

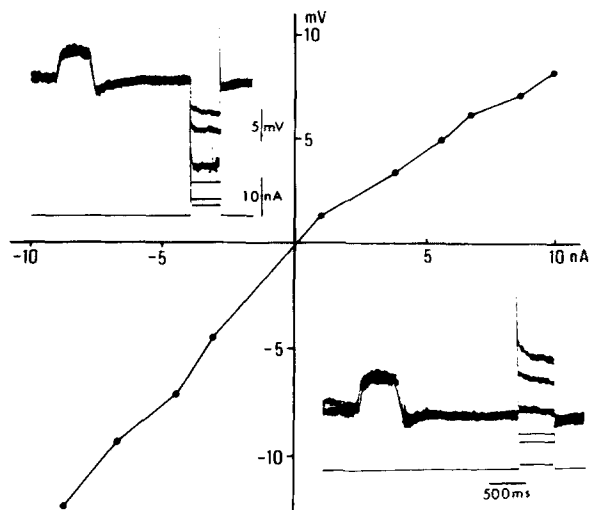


FIGURE 3. Measurement of the current-voltage relation in a pair of ON bipolar cells with current passed into one member of the bipolar cell pair and potential recorded from the other bipolar cell. The insets show sample records, which consist of three superimposed response pairs evoked by light and current.

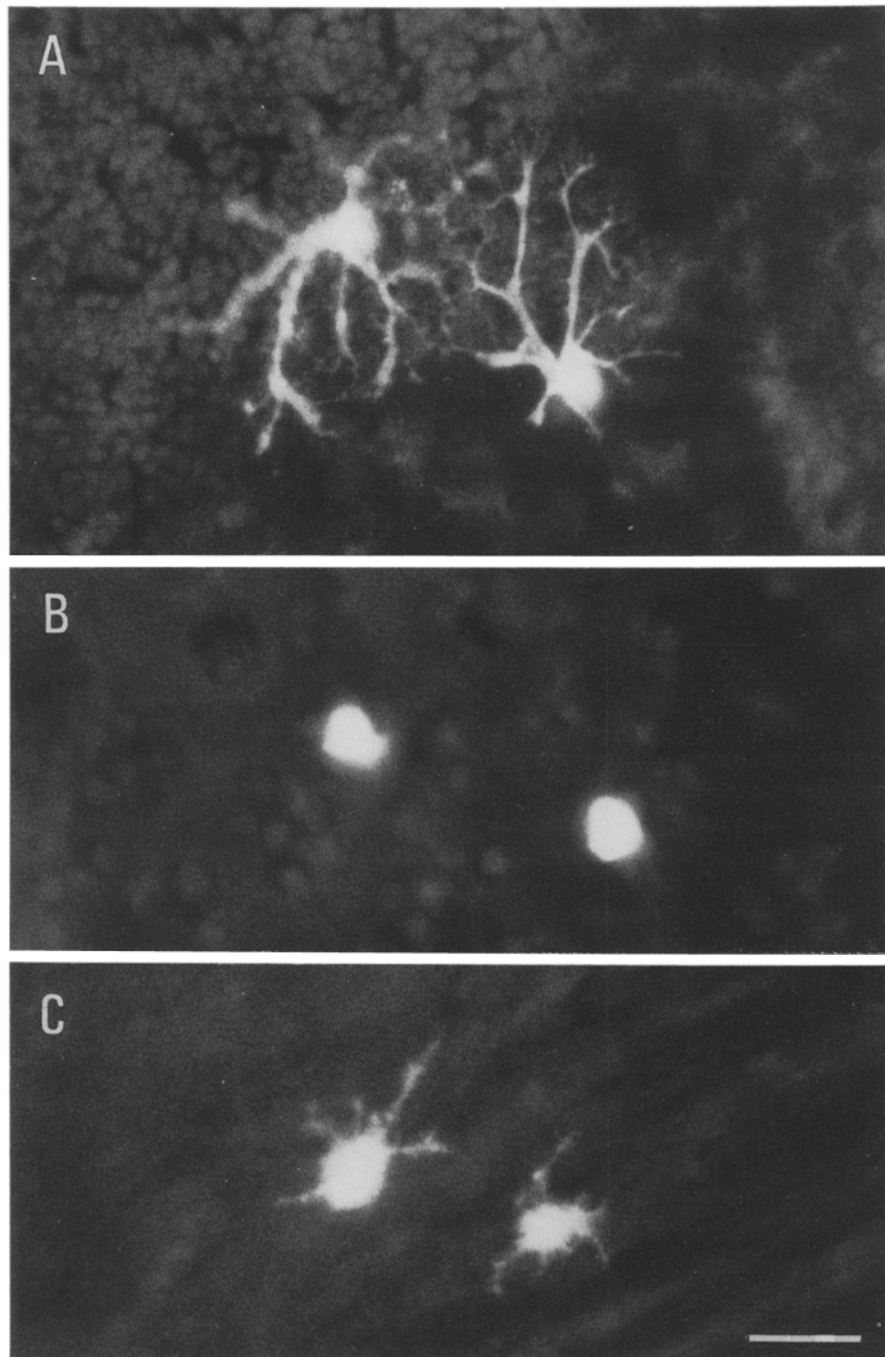
depolarization of  $\sim 5$  mV in the other cell (upper trace). Switching on the background light produced a maximum depolarization of the membrane. When depolarizing current was passed while the light was delivered, the current-evoked potential summed with the light-evoked response. There was no significant difference in amplitude between the current-evoked responses with and without the background light, which suggests that the apparent conductance changes brought about by light are very small. This observation is consistent with our previous finding that the photoresponse of ON bipolar cells is brought about by at least two conductance changes of opposite sign (Saito et al., 1979).

#### *Morphological Appearance of Electrically Coupled Cells*

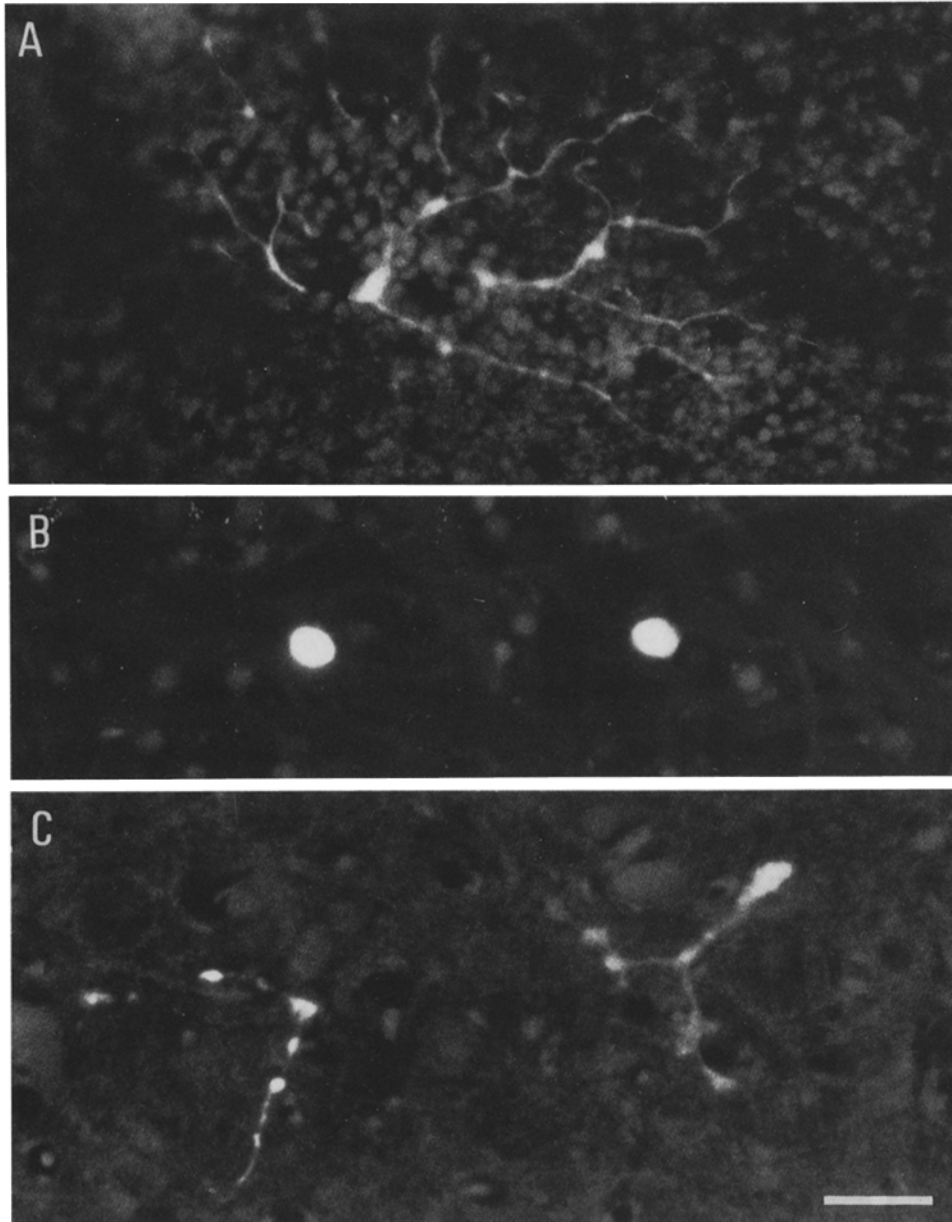
It is essential to demonstrate that the coupling described above is not due to interactions between the two parts within the same bipolar cell, such as the cell body and the axon terminal. To localize the positions of the electrode tips, we marked bipolar cell pairs with Lucifer yellow after observing their electrical interactions. Three pairs of ON bipolar cells were successfully stained. The photomicrographs in Fig. 5 show the morphological properties of a pair of cells in tangential sections. Dendrites from the two cells are stained side by side (A). Some of the dendritic processes of these cells cannot be seen because of the



FIGURE 4. Summation of responses evoked by light and by current through a neighboring bipolar cell. Current pulses of  $\sim 10$  nA and 500 ms were applied to the lower cell before and during the response of the upper cell to light. L, light; D, depolarizing current of  $\sim 10$  nA.



**FIGURE 5.** Photomicrographs showing two ON bipolar cells identified by intracellular injection of Lucifer yellow after observing their electrical interaction. Two microelectrodes were filled with 5% Lucifer yellow in 100 mM lithium chloride. Each cell was marked by passing 3 nA of negative current for 2 min. (A) Dendrites; (B) cell bodies; (C) axon terminals. The scale bar represents 20  $\mu\text{m}$ .



**FIGURE 6.** Photomicrographs showing two ON bipolar cells obtained by intracellular injection of Lucifer yellow into a single cell. The cell on the left was marked by passing 5 nA of negative current for 5 min. (A) Dendrites; (B) cell bodies; (C) axon terminals. The scale bar represents 20  $\mu\text{m}$ .



obliquity of the plane of sectioning. The dendritic arbores of the two cells appear to overlap to some extent. The two stained cell bodies are  $\sim 10 \mu\text{m}$  in diameter and their center-to-center distance is  $\sim 50 \mu\text{m}$  (*B*). The shape and level of the stained axon terminals are quite similar (*C*). Judging by the large swelling of the axon terminals, both cells are likely to be classified as type I ON cells (Saito and Kujiraoka, 1982). Two other Lucifer yellow-labeled pairs of cells were also of the type I ON cells.

#### *Dye Coupling*

To elucidate whether or not dye coupling takes place among bipolar cells, Lucifer yellow was iontophoretically injected into single bipolar cells with a negative current of  $\sim 5 \text{ nA}$  over a period of 3 min. Only cells that continued to respond to light after injection of the dye were used for histological examination. Out of 45 bipolar cells stained, 38 cells were recovered (26 ON bipolar cells and 12 OFF bipolar cells). In 34 cases, there was no evidence for dye coupling of bipolar cells. In the remaining four cases, the dye injected into a single ON bipolar cell stained one neighboring bipolar cell. An example is shown in Fig. 6. Unfortunately, not all of the dendrites of the two cells are shown, because the tangential sections were obliquely oriented. However, the two stained cells seem to be similar in their dendritic pattern (*A*). The two cells are also similar in the size and level of the cell body (*B*) and in the shape and level of the axon terminal (*C*).

#### DISCUSSION

We demonstrated, by impaling pairs of bipolar cells, that the same morphological and functional types are coupled to one another. This coupling is sign-conserving, reciprocal, and summative. The maximum separation of coupled bipolar cells, so far detected, was  $\sim 130 \mu\text{m}$ .

Two possible ways by which bipolar cells might exchange signals are (*a*) via interneurons in the pathway such as horizontal cells or amacrine cells, and (*b*) via a direct pathway between bipolar cells. Horizontal cells, since they are thought to be presynaptic to bipolar cells, may mediate bipolar interactions. Extrinsic current injected into the horizontal cells elicited potential changes from both ON and OFF bipolar cells (Trifonov and Byzov, 1978; Marchiafava, 1978; Toyoda and Tonosaki, 1978; Sakuranaga and Naka, 1985). However, these interactions were complementary in the two bipolar cell types, sign-conserving for ON bipolar cells and sign-reversing for OFF bipolar cells. Therefore, this excludes the possibility that the horizontal cells provide a pathway by which bipolar cells can exchange signals. Amacrine cells may be possible candidates for bipolar-bipolar interactions, since they are both pre- and postsynaptic to bipolar cells. Extrinsic current injected into bipolar cells produced sign-conserving responses in amacrine cells (Kujiraoka et al., 1986). These bipolar-amacrine interactions had a delay characteristic of chemical synapses. In the present and previous (Kujiraoka and Saito, 1986) experiments, however, such a delay could not be detected at interactions between bipolar cells. It therefore seems more likely that signals spread directly between bipolar cells.

Gap junctions between neurons are supposed to be the anatomical substrate for electrical coupling. In the fish retina (Witovsky and Stell, 1973; Van Haesendonck and Missotten, 1983), these junctions have been observed at the level of bipolar cell axons, between adjacent axon terminals, or between collaterals that extend outward from the axon terminal. However, in the present intracellular staining experiment, three paired bipolar cells, which showed electrical coupling, appeared to be separated from each other at their axon terminals or collaterals. On the one hand, fine dendritic processes of these coupled bipolar cells seemed to overlap each other. Therefore, dendritic processes of some bipolar cells may constitute the direct pathway by which bipolar cells can interact with one another. In the outer plexiform layer of the retina of primates (Raviola and Gilula, 1975), freeze-fracture analysis has revealed many minute gap junctions on bipolar cell dendrites, although the precise identity of the partner cell in the junctions is not known.

The presence of gap junctions between cells has been correlated with the capacity to transfer low-molecular-weight fluorescent dyes. Lucifer yellow injected into a horizontal cell normally diffuses to several neighboring horizontal cells through gap junctions (Stewart, 1978; Piccolino et al., 1982; Kaneko and Stuart, 1984; Teranishi et al., 1984*a*). Such dye coupling has also been observed among amacrine cells (Teranishi et al., 1984*b*). One would therefore expect dye coupling to occur between bipolar cells. In the present study, however, most stained cells did not show the dye coupling. In a few cases, the dye injected into a single cell stained one neighboring bipolar cell. The amount of dye injected seemed to be large enough to reveal dye coupling, because the same amount of dye injected into horizontal cells or amacrine cells usually stained a group of cells around the injected one. Since this staining pattern was not obtained when bipolar cells were injected with dye, and since in most cases only one bipolar cell was stained, we cannot exclude the possibility that the rarely observed dye coupling of bipolar cells was an artifact.

On the other hand, it should be mentioned that neighboring photoreceptors are electrically coupled, but evidence of their dye coupling has not yet been obtained. Therefore, the lack of spread of the dye does not mean that the cells of a network are not coupled. Bipolar cells, as well as photoreceptors, may have a lower density of gap junctions per unit area of cells and/or smaller dimensions of gap junctions than horizontal cells or amacrine cells have. It will be necessary to carry out further experiments, loading cells with larger amounts of dye, in order to detect dye coupling.

In the present and previous (Saito and Kujiraoka, 1982) articles, we found that the diameters of the central receptive fields of carp bipolar cells are larger than those of their dendritic fields; the difference is almost an order of magnitude in some cells. ON bipolar cells had a larger dispersion of their central receptive field sizes than OFF bipolar cells, because of the fact that two types of ON bipolar cell are involved (Saito and Kujiraoka, 1982). Thus, a comparison between the mean diameters of receptive and dendritic fields is more reliable for OFF bipolar cells. The dendritic field of OFF bipolar cells marked with HRP averaged 65  $\mu\text{m}$  diam (Saito et al., 1985), while their receptive fields were 300–400  $\mu\text{m}$  diam

(Fig. 1). A similarly large difference between dendritic and receptive field diameters was found in the tiger salamander (Hare et al., 1986). Such a discrepancy between dendritic and receptive field diameters might be attributable to several experimental errors, such as light scattering, misalignment of the electrode, retinal shrinkage during the histological procedure, and a failure of the dye to infiltrate the smallest dendritic branches or to be visualized in the branches under the microscope. However, it seems more likely that lateral interactions between photoreceptors or bipolar cells, which mediate spatial summation of their photoresponses, make the receptive field of the bipolar cells much larger than the dendritic field. Baylor et al. (1971) showed that turtle cones were summatively coupled over distances of up to 50  $\mu\text{m}$ . Rods of the snapping turtle exhibited a similar coupling over more than twice that distance (Copenhagen and Owen, 1976). Burkhardt (1977) reported that the photoresponse of perch cones increased appreciably, with an increase in stimulus diameter up to  $\sim 100 \mu\text{m}$ . If the extent of signal spread through the receptor network is  $\sim 100 \mu\text{m}$  diam, the mean receptive field center of carp OFF bipolar cells can be estimated to be  $\sim 165 \mu\text{m}$  diam. This value is still less than half the value of the mean receptive field center, which we measured by the expanding light spot method. The maximum separation of coupled bipolar cells we have found so far is  $\sim 130 \mu\text{m}$ . If the receptive field center of the bipolar cells is determined by signal spread of both photoreceptors and bipolar cells, the estimated and measured receptive field center diameters are thought to be in good agreement.

Electrical coupling of bipolar cells, as well as that of photoreceptors in other investigations, would appear to degrade the spatial resolution of the eye. There must be other mechanisms, still unknown, that may offset such a loss of resolution.

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