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RESPONSES OF BIPOLAR CELLS IN THE RETINA OF THE TURTLE

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SUMMARY

The responses of bipolar cells in the retina of the turtle have been studied by intracellular recording. Two types of bipolar cell have been identified: one gave graded depolarizing and the other graded hyperpolarizing responses to small circles of light (100 μm diameter). The responses of both types of cell were similar in the following respects.

1. Both were extremely sensitive to dim light; the amplitude of response to a small circle of light increased with light intensity more steeply than the cone response.

2. Enlarging the diameter of a spot added an antagonistic effect which decreased response amplitude. This decrease in response amplitude was more apparent at dim than at bright light. Stimulating only distant areas of retina with an annulus produced a response of polarity opposite to that normally produced by a central spot. However, the responses of bipolar cells did not appear to be due to a simple summation of opposite polarity signals contributed from central and peripheral parts of their receptive fields.

3. When small spots or annuli of light were turned off there frequently occurred an overshooting OFF transient. The occurrence of OFF transients depended on the duration of the stimulus. Cones recorded under similar conditions produced an OFF depolarization. The size of cone OFF depolarizations increased with increasing duration of the preceding light; following approximately 3 sec of illumination their maximum amplitude was roughly 1/10 the amplitude of the preceding hyperpolarization. The size of OFF responses in both cone and bipolar cells was increased when horizontal cells were hyperpolarized by light.

It is concluded that bipolar cells produce large responses for very small cone responses, and, as a consequence, a small depolarization in cones following illumination produces large OFF transients in bipolar cells.

Furthermore, the responses of bipolar cells do not appear to represent a simple summation of opposite polarity input from receptor and horizontal cells.

INTRODUCTION

Analysis of the visual image begins in the retina's outer synaptic layer. In this region receptor, horizontal and bipolar cells interact. The responses of receptor and horizontal cells have been extensively studied. Receptors produce a maintained hyperpolarization for light incident on the individual cell (for a review see Tomita, 1972) and receive interactions from neighbouring neurones (Baylor, Fuortes & O'Bryan, 1971; Fuortes, Schwartz & Simon, 1973); horizontal cells respond with a maintained polarization which is determined by the light incident over a large retinal area (Watanabe & Tosaka, 1959; Naka & Rushton, 1967; Simon, 1973). The responses of bipolar cells are, in contrast, poorly understood. They receive synaptic contacts from receptor and horizontal cells (for a recent summary see Lasansky, 1972) and are the only pathway for information to pass from these cells to the amacrine and ganglion cells of the inner synaptic layer. Frequently amacrine and ganglion cells produce transient responses following the commencement and termination of illumination. How these transient responses originate within the retina is not known.

Werblin & Dowling (1969) and Kaneko (1970) have identified two types of bipolar cell: one type depolarized and the other hyperpolarized to receptor input; for both types it was suggested that horizontal cells antagonize the responses contributed by receptors. In these previous studies it was not apparent, however, how the responses of bipolar cells might generate the transient responses of amacrine and ganglion cells. In the present work I have studied the responses of these two types of bipolar cell in the retina of the turtle. The experiments confirm the previous observations that cone and horizontal cells mediate opponent effects on bipolar cells but indicate that the bipolar response is not a simple summation of two types of synaptic input. In addition, the responses of bipolar cells to centred spots and annuli appear sufficient to explain the origin of transient OFF responses in amacrine and ganglion cells.

METHODS

Experiments were performed on the isolated eyecups of turtles (*Chelydra serpentina*) whose carapace lengths were 8–14 in. The properties of cones (Baylor *et al.* 1971) and ON–OFF cells (Schwartz, 1973*a*) previously studied in the turtle *Pseudemys scripta elegans* were determined to be similar in *C. serpentina*. The visual pigments and cone oil droplets for the two species are also similar (Liebman, 1972). *C. serpentina* was preferred for this study because its bipolar cells were easier to penetrate, perhaps due to the slightly larger size of its ocular globe and retinal cells.

The stimulating and recording procedure has been previously described (Schwartz,

1973*a*). A monochromatic light was obtained in all experiments by inserting a 615 nm narrow-band interference filter into the light path. The maximum irradiance delivered to the retina was $1{\cdot}6 \times 10^{14}$ quanta cm^{-2} sec^{-1} and was attenuated with neutral density filters calibrated in optical density units (O.D.). The cross-sectional area of the inner segment of a single receptor is approximately 50 μm^2. The maximum irradiance delivered to a single receptor was, therefore, 8×10^7 quanta sec^{-1}.

The absolute value of membrane potential of impaled cells was uncertain due to the unfavourable properties of the high resistance micropipettes (200–400 MΩ) used. Therefore, all voltages were measured as a change from the membrane potential during dark. In a number of experiments, small responses evoked by dim steps of light were investigated. In these cases responses were averaged by a Hewlett-Packard 5480A computer.

The cells described in this study were identified as bipolar cells on the basis of a few marking experiments with Procion Yellow and their opponent responses to small, central spots and large annuli. Bipolar cells in other preparations have been shown to possess graded responses with opponent interaction between central and annular illumination (Werblin & Dowling, 1969; Kaneko, 1970; Matsumoto & Naka, 1972). However, cones also possess an opponent interaction by virtue of a feed-back from horizontal cells (Baylor *et al.* 1971); and it has recently been demonstrated that green-sensitive cones can be hyperpolarized by direct illumination and depolarized by a red annulus (Fuortes *et al.* 1973). It might, therefore, seem possible to confuse responses from green-sensitive cones and centre-hyperpolarizing bipolar cells. It was possible, none-the-less, to distinguish between these cells since bipolar cells produced for a dim, 100 μm spot a large response which decreased markedly as diameter was increased (see Results, Fig. 2) while, in contrast, green-sensitive cones did not generate sizeable responses to a dim 615 nm, 100 μm spot.

RESULTS

Identifying features of bipolar cells were determined with three patterns of illumination which were centred around the micropipette: circles of 100 and 1000 μm diameter and an annulus with inner diameter 400 μm and outer diameter 1600 μm. The irradiance of the annulus was always less than that necessary to produce a response of half maximum amplitude in the underlying red-sensitive cones (i.e. approximately 2·7 O.D.). Intracellular recording showed that with this intensity the red-sensitive cones at the dark centre of the annulus gave no significant response; brighter annuli excited central cones by scattered light.

Responses of bipolar cells

Records from a bipolar cell producing depolarizing responses to central illumination are shown in Fig. 1. The response to a small spot (Fig. 1 *A*) reached a peak amplitude and then frequently, as shown, declined to a plateau; in addition, the response often overshot the dark membrane potential following illumination. A large spot of illumination produced a similar response (Fig. 1 *B*) which was, however, slightly smaller in amplitude. The peak amplitude of response as a function of irradiance for spots of three different diameters is shown in Fig. 2 (continuous lines). Although

the response was depolarizing for all intensities and spot sizes of 615 nm light, increasing the diameter of the stimulating spot decreased response amplitude. This effect was greater with dim than with bright light. Therefore, an annulus added to a small, central, dim spot appeared to exert an opponent interaction (Fig. 1*C*).

Also plotted in Fig. 2 (dashed line) is the average peak response of ten red-sensitive cones to a stimulus 100 μm in diameter. It is seen that at an irradiance of approximately 54 quanta μm^{-2} sec^{-1} the cones produced a maintained response of 1 mV; for the same stimulus the bipolar cell produced a response greater than 10 mV. Although the bipolar cell illustrated was especially sensitive, it was consistently observed that

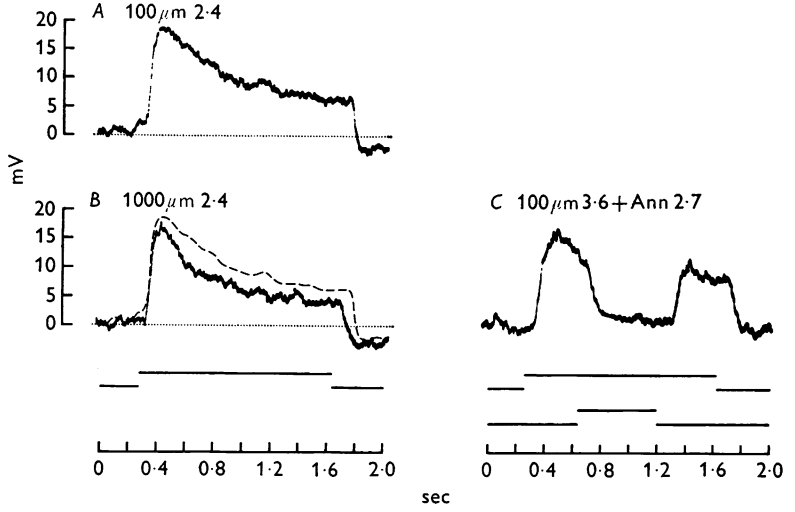

Fig. 1. Responses from a centre-depolarizing bipolar cell. At the left are responses to 100 μm (above) and 1000 μm spots (below). The response to the 100 μm spot is retraced below as the dotted line for comparison with the 1000 μm spot. Both a small and large spot of illumination produced the same polarity of response. At the right, the upper timing trace indicates the duration of a 100 μm spot and the lower timing trace the duration of an annulus. The response demonstrates an opponent interaction between illumination of the centre and an annular surround.

depolarizing and hyperpolarizing (as described below) bipolar cells produced responses to dim illumination which were significantly larger than the responses recorded from cones under identical conditions. It, therefore, appears that transmission across the receptor-bipolar synapse produces a large increase in signal amplitude.

It may be queried whether the observed great sensitivity of bipolar cells was due to the activity of rods. This is unlikely. For the 615 nm wave-length, 100 μm diameter light, red-sensitive cones are the most sensitive receptors in turtle retinae. For

a 100 μm spot, the gain (i.e. time integral of the response) per absorbed photon of rods is four times greater than that of cones (Schwartz, 1973*b*). However, turtle rods absorb 615 nm wave-length light 10 × less well than red-sensitive cones (Baylor & Hodgkin, 1973). Therefore, for these conditions the responses of rods are expected to be less than half that of cones. Responses of rods to 615 nm light confirm this expectation but also demonstrate an interaction mediated by cones which becomes apparent when spot diameter is increased (personal observation).

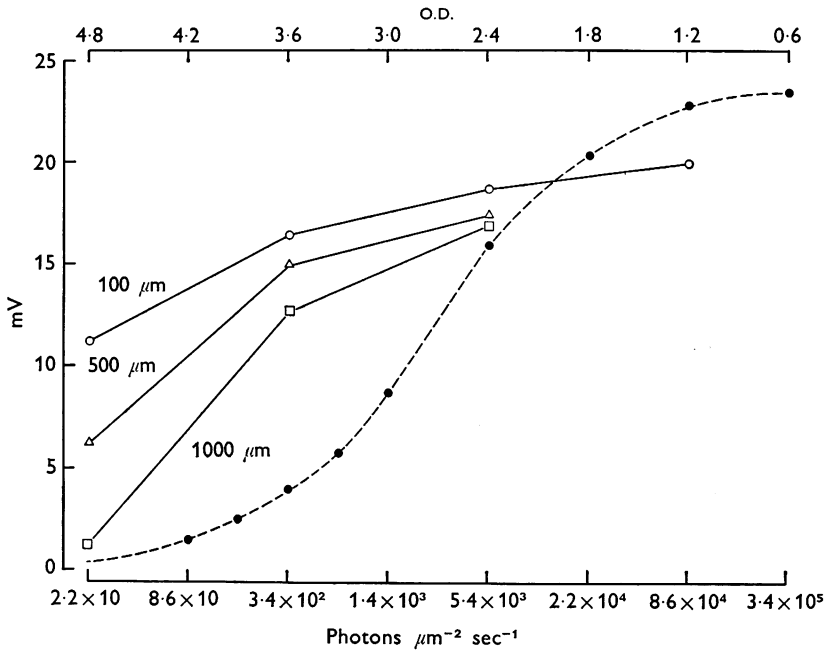

Fig. 2. Irradiance response relationships of a bipolar cell for stimuli of varying diameter. Open symbols plot the peak amplitude of response of the bipolar cell shown in Fig. 1 for circles of light 100, 500 and 1000 μm in diameter. Increasing the diameter of the stimulating spot decreased the bipolar response; the effect was greater at dim than bright light. The filled circles plot for a 100 μm stimulus the average peak response of ten consecutively penetrated red-sensitive cones with maximum responses greater than 20 mV. For fewer than approximately 100 quanta μm^{-2} sec^{-1} the amplitude of the cone response is linear with light intensity (Schwartz, 1973*b*; Baylor & Hodgkin, 1973) allowing the curve to be readily extrapolated backward for dimmer light.

The general properties of centre-hyperpolarizing bipolar cells were similar to those of centre-depolarizing cells. The responses of a hyperpolarizing bipolar cell are shown in Fig. 3. These cells responded with a sustained hyperpolarization to central illumination which was antagonized by an annular surround. Similar to depolarizing cells, these cells were extremely sensitive to small spots and the effect produced by an annulus

was greater when the centre was dimly illuminated (compare the effect of the annulus in Fig. 3*B* with 3*A*). These cells also frequently produced a transient depolarization when the light was turned off. Thus, both cell types were extremely sensitive to small spots, decreased response amplitude with increasing spot size and frequently produced overshooting OFF transients.

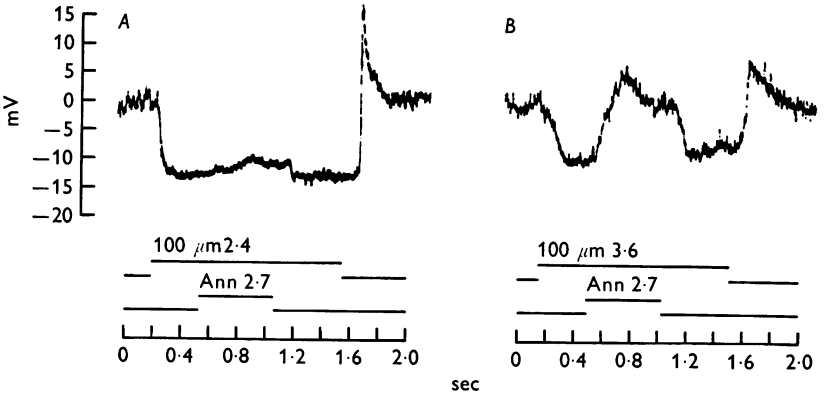

Fig. 3. Responses from a centre-hyperpolarizing bipolar cell. The upper timing traces indicate the duration of a 100 μm diameter spot of irradiance 2·4 O.D. (left) or 3·6 O.D. (right). The lower timing traces indicate the duration of an annulus of irradiance 2·7 O.D. The annulus produced little effect when added to a bright, central spot (left). The same annulus produced a large decrease in response amplitude when added to a moderate intensity, central spot (right).

Occurrence of OFF responses in cones and bipolar cells

A moderate intensity 100 μm spot of light produced no measurable response during recording from horizontal cells. Thus, the response of a bipolar cell to this stimulus was presumably determined only by the receptors with which it was directly connected. It was consequently of interest to determine the responses of bipolar cells to 100 μm stimuli and to correlate these with the responses of cones.

The ability of a 100 μm spot to produce an OFF transient in bipolar cells depended on its duration. In Fig. 4*A* are shown responses of a centre-depolarizing cell to a 100 μm spot of different durations. For a short duration, no OFF transient occurred. When the duration was increased a characteristic OFF transient was produced. Transients following the off of a 100 μm spot (Figs. 1 and 3) occurred after the stimulus was lengthened beyond a minimum time; the minimum duration of light necessary to produce transients varied from approximately 0·5–3 sec.

Cones recorded under similar conditions also produced an afterpolarization. In Fig. 4*B* are shown the responses of a red-sensitive cone to two

durations of a 100 μm spot. Both stimuli produced the same amplitude hyperpolarization at the onset of illumination. At the offset of the light there occurred a small, transient depolarization. The longer duration stimulus produced a larger depolarization. The amplitude of the depolarization which occurred in this cone following a light of varying duration is

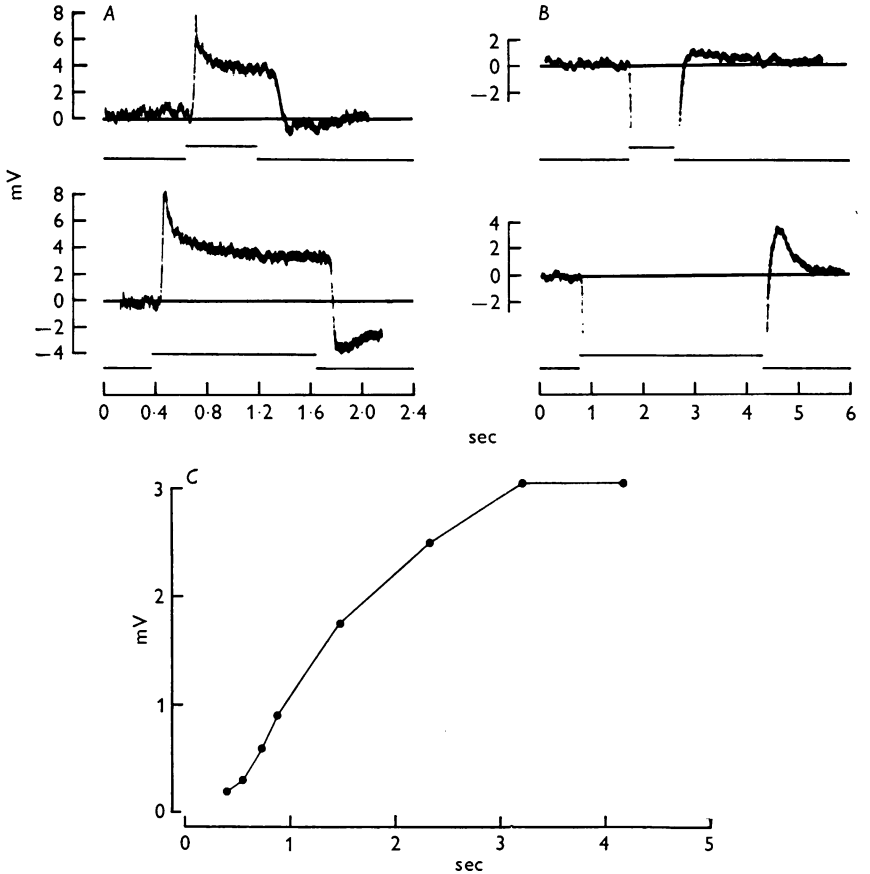

Fig. 4. OFF responses in bipolar cells and cones depend on the duration of the stimulus. *A*: responses from a centre-depolarizing bipolar cell to a 100 μm, 3·6 O.D. light. For stimuli of short duration no OFF transient occurred. For stimuli of longer duration a prominent OFF transient occurred. Transients usually reached a maximum amplitude following stimuli of 3 sec duration. *B*: responses from a red-sensitive cone for a 100 μm, 1·8 O.D. light. The peak hyperpolarization for this irradiance was 20·5 mV; the maximum hyperpolarizing response to a bright light was 26 mV. As the duration of the stimulus was increased the amplitude of the OFF depolarization increased. *C*: amplitude of the cone afterpolarization for stimuli of varying duration. The peak height of the afterpolarization is plotted as ordinate against stimulus duration as abscissae. The cell and stimuli are the same as in part *B*.

plotted in Fig. 4*C*. The maximum amplitude of the cone OFF depolarization was generally about 1/10 the size of the preceding hyperpolarization.

The responses of the cone in Fig. 4*B* were elicited by relatively bright light which allowed depolarizing afterpolarizations to be easily seen in single responses. Afterpolarizations were not dependent, however, on a large preceding hyperpolarization. They also occurred at intensities which produced small cone responses (Fig. 5). Following dim illumination both cone and bipolar cells produced OFF transients which increased with

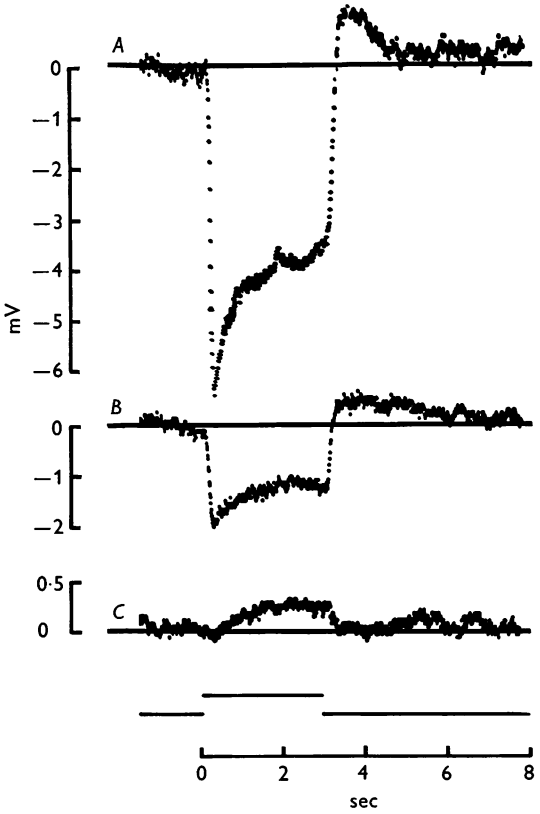

Fig. 5. Cones produce OFF depolarizations for dim stimuli. The traces are the computer averaged responses of sixteen or thirty-two repeated stimulus presentations. In trace *A* the stimulus was a 100 μm, 3·6 O.D. light. In trace *B* the light was dimmed to 4·2 O.D. and the response during and following illumination decreased. The pipette was then withdrawn from the cell (upward deflexion of trace not indicated) and the 100 μm, 3·6 O.D. stimulus repeated. A small (note $\times 2$ increase of gain) extracellular field potential was recorded in trace *C*. Comparison of traces *A* and *C* indicate that the OFF depolarization of cones is an intracellular potential. The maximum response of this cell was 21 mV.

increasing duration of the light. In addition, results similar to Fig. 2 indicate that transmission from receptors to bipolar cells produced a large increase in signal amplitude. It, therefore, appears likely that small changes in ambient light can elicit transient OFF responses in receptors which produce larger transient responses in bipolar cells.

Although OFF responses in cones and bipolar cells both increased in amplitude with increasing duration of the preceding light, there existed considerable variability in time course and size of OFF transients. Furthermore, not all bipolar cells produced OFF transients, and OFF transients were sometimes less obvious for central compared to annular (see below) fields. Because of this variability, quantitative comparison of responses of cells from different preparations was not possible.

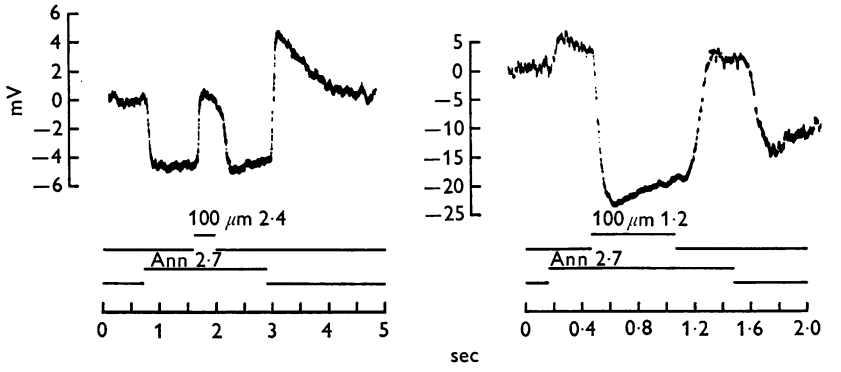

Fig. 6. Responses to an annulus while the centre was dark and then subsequently illuminated. The left record is from a centre-depolarizing cell; the right record is from a centre-hyperpolarizing cell. An annulus produced a polarity of response opposite to that of a central spot. In addition, there occurred after cessation of the annulus an overshooting OFF transient. The upper timing traces indicate the duration of a 100 μm spot and the lower timing traces the duration of an annulus.

The influence of horizontal cells

It was shown in Fig. 2 that enlarging the area of illumination decreased the amplitude of bipolar cell responses. The antagonistic effect which was added by enlarging the area of illumination could be isolated as the response to an annulus if care was taken to avoid scattered light at the dark centre of the image (Fig. 6). For both centre-depolarizing and centre-hyperpolarizing cells, an annulus produced a response of polarity opposite to that produced by central spots. In addition, there frequently occurred an overshooting OFF transient which was of opposite polarity to the OFF transient that normally occurred following centred spots. The occurrence of this OFF transient also depended on the duration of the light.

An annulus produced large horizontal cell responses without directly stimulating central receptors. The responses of bipolar cells to annular illumination observed in this study are consistent with the notion proposed by Werblin & Dowling (1969) that horizontal cells mediate an effect which is opponent to that normally contributed by central receptors. Werblin & Dowling (1969) have suggested that this occurs by a direct synaptic connexion from horizontal cells on to bipolar cells. The evidence for this

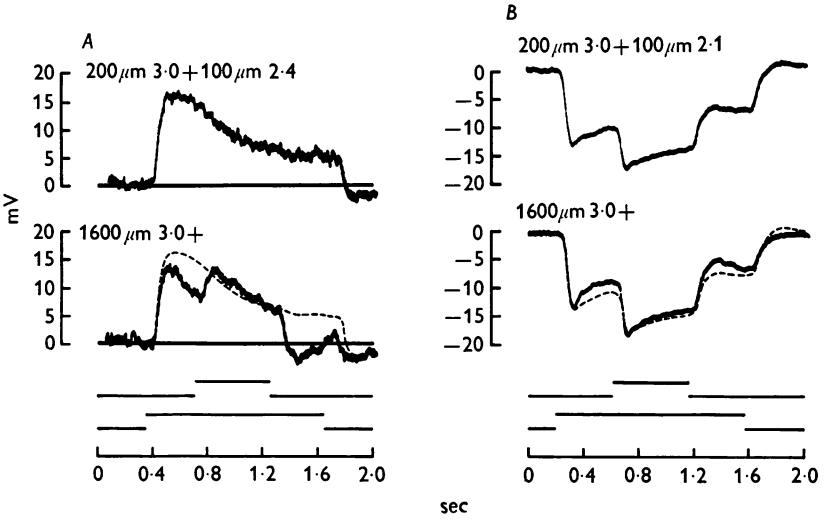

Fig. 7. The generation of OFF responses in cones and bipolar cells was modified by a continuous background. *A*: same cell as in Figs. 1 and 2. In the upper trace a 200 μm, 3·0 O.D. background was applied and then a 100 μm, 2·4 O.D. spot was added. As predicted from Fig. 2, the background light evoked a near maximum response. The light added to the centre was 0·6 O.D. brighter but without effect. In the lower trace a 1600 μm, 3·0 O.D. background was applied and then the same 100 μm, 2·4 O.D. spot was added. The response shown above is dotted in for comparison. As predicted from Fig. 2 the background light evoked a slightly smaller response than previously; when light was added at the centre there occurred a small additional depolarization and a transient overshoot following its termination. *B*: responses from a red-sensitive cone. In the upper trace a 200 μm, 3·0 O.D. background was applied and then a 100 μm, 2·1 O.D. spot was added. In contrast to bipolar cells under similar stimulus conditions, the added test light produced an additional response. In the lower trace a 1600 μm, 3·0 O.D. background was applied and then the same 100 μm, 2·1 O.D. spot was added. The response shown above is dotted in for comparison. At the onset of the background lights the responses reached the same peak amplitude; afterwards the response to the 1600 μm background was smaller due to the depolarizing feedback of horizontal cells (Baylor *et al.* 1971). When the test spot was then added to the larger background and subsequently removed it produced a slightly larger OFF depolarization.

synaptic pathway is not compelling, however; and, observations presented in this report are also difficult to reconcile with this simple scheme (see Discussion). The situation may well be more complex.

Responses in horizontal cells did not always decrease the responses of bipolar cells to central illumination. The OFF responses of bipolar cells were actually enhanced during maintained hyperpolarization of horizontal cells. In Fig. 7*A* are shown responses from a centre-depolarizing bipolar cell which were produced when a test spot 100 μm in diameter was added to two different diameters of background illumination. The light under the test spot was the same for the two stimulus conditions. The backgrounds, however, differed by the annular field which extended from 200 to 1600 μm diameter. When this annular field was added an increased hyperpolarization was recorded in horizontal cells. During this hyperpolarization the test spot produced a large amplitude OFF transient. The same result was also obtained with centre-hyperpolarizing bipolar cells.

A similar phenomenon was seen in the responses of cones (Fig. 7*B*). Enlarging the area of background illumination increased the size of the cone afterpolarization produced by the added test spot. The responses from cones were, however, less dramatic in demonstrating this property than were the responses of bipolar cells. This may have happened because the penetration of a cone by a micro-pipette decreased the feedback action of horizontal cells which normally occurs in unmolested cones (see Fuortes *et al.* 1973). The responses of impaled cones may only approximate those of cones not damaged by a micropipette. The observed responses do indicate, none-the-less, that a change in the horizontal cell membrane potential can affect the size of cone afterpotentials. Whether this is sufficient to account completely for the observed responses of bipolar cells is uncertain. The mechanisms for the generation of an OFF depolarization in cones and for the influence of horizontal cells is not known. The origin of the OFF depolarization of cones is a subject which should repay further investigation.

DISCUSSION

From the results of this study, it is concluded that bipolar cells are extremely responsive to small changes in receptor input. A small change of the cone potential away from the dark level produced a large bipolar cell response. Consequently, a small afterpolarization in cones can produce a sizeable OFF transient in bipolar cells. Transient OFF responses, therefore, can originate within receptors and be transmitted to bipolar cells with a large increase in amplitude. They need not be ascribed to 'reciprocal' synapses of the inner plexiform layer as suggested by Werblin & Dowling (1969) and Werblin (1972).

Afterpolarization of cones may be considered a phenomenon of adapta-

tion but the mechanism by which it occurs is unknown. Post-illumination afterpotentials have also been noted to occur in invertebrate photoreceptors (in *Limulus* by Benolken, 1961 and Kikuchi, Naito & Tanaka, 1962; in the dragonfly by Naka, 1961; in the barnacle by Koike, Brown & Hagiwara, 1971). For the photoreceptors of the barnacle (Koike *et al.* 1971) and *Limulus* (Brown & Lisman, 1972), evidence has been presented consistent with the notion that afterpolarization is produced by an electrogenic sodium pump. The membrane and ionic mechanisms contributing to an afterpolarization of vertebrate cones should be further investigated.

The intensity-response relationship of bipolar cells (see Fig. 2) requires a comment on how receptor and horizontal cells might influence bipolar cells. Although the response of a bipolar cell to a 100 μm, moderate intensity light is similar to that produced by bright light of the same diameter, the responses to these two stimuli are affected very differently when an annulus is added. An annulus antagonizes the response produced by a moderate intensity spot but does not antagonize the response produced by a bright spot (Fig. 3). In both cases the annulus produces nearly the same response in horizontal cells. The opponent interaction produced by an annulus would, therefore, appear not to depend directly on either the membrane potential of the bipolar cell produced by the central spot or on the response of horizontal cells to the annulus. What differs between the two stimulus situations is the response of the cones under the central spots. How can this difference account for the observed responses of bipolar cells? It might be suspected that the failure of an annulus to be effective when added to a bright spot could be ascribed to shunting by a large synaptic conductance associated with the larger cone responses. However, it has been claimed (Toyoda, 1973) that hyperpolarizing bipolar cells exhibit an increase in membrane resistance during illumination by a small, central spot. In this case it is then difficult to understand how horizontal cells could contribute directly to bipolar cells. It is possible that the effect of an annulus is not mediated by a direct input of horizontal cells on to bipolar cells but rather by a feedback of horizontal cells on to cones. Negative feed-back of horizontal cells on to cones has been discovered by Baylor *et al.* (1971). Recent experiments by Fuortes *et al.* (1973) show that horizontal cell feed-back has a profound effect on the cone response and, with an appropriate stimulus, can even depolarize cones. How horizontal cells influence bipolar cells is still obscure – particularly, what information bipolar cells receive from direct synaptic contacts with horizontal cells and what information is transferred indirectly by feed-back on to cones. It is, as yet, not possible to assess the relative importance of these two pathways. But it is unlikely that direct connexions primarily determine bipolar cell responses in turtle retinae.

The composite effect of both pathways is for horizontal cells to decrease bipolar cell responses to large fields of illumination. Thus the responses of bipolar cells to small diameter stimuli are accentuated. This result is not exactly the same as that achieved by the 'centre-surround' organization of retinal ganglion cells (Kuffler, 1953; Barlow, 1953). For certain ganglion cells, a small spot of light in the periphery can interact with small spots of light at the centre. This interaction, which is revealed by determining responses with small spots of light, is not mediated by horizontal cells but by central and peripheral bipolar cells (Schwartz, 1973*a*). In contrast, stimulation with a large diameter spot can produce a ganglion cell response which differs from that produced by a centred, small diameter spot. The difference has been attributed to the horizontal cell response added by stimulating a large area of retina (Naka & Nye, 1971). We may then distinguish a 'centre-surround' interaction determined by relative position and a 'local-global' interaction determined by the expanse of area stimulated. It appears that the local-global computation involves horizontal cells and occurs in the outer synaptic layer and the centre-surround computation involves a comparison between spatially separated groups of bipolar cells (and may include amacrine cells as interneurones) and occurs in the inner synaptic layer. Bipolar cells should, therefore, reflect a local-global interaction and consequently may be considered as detectors of contrast across their receptive field centres, i.e. detectors of local contrast. Thus, given a completely dark background, they produce greater responses for small compared to large, uniform fields (Fig. 2); and, given backgrounds of light of varying diameter, they produce greater responses when spot and background differ in size than when they are similar (Fig. 7).

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