

Responses of Photoreceptors in *Hermisenda*

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ABSTRACT The five photoreceptors in the eye of the mollusc *Hermisenda crassicornis* respond to light with depolarization and firing of impulses. The impulses of any one cell inhibit other cells, but the degree of inhibition differs in different pairs. Evidence is presented to show that the interactions occur at terminal branches of the photoreceptor axons, inside the cerebropleural ganglion. Properties of the generator potential are examined and it is shown that the depolarization develops in two phases which are affected differently by extrinsic currents. Finally, it is shown that by enhancing the differences in the responses of individual cells to a variety of stimuli, the interactions may facilitate a number of simple discriminations.

The nudibranch mollusc *Hermisenda crassicornis* has two small eyes, each containing five photoreceptor cells. The structure of these eyes has been described by Eakin, Westfall, and Dennis (1967) and more recently by Stensaas, Stensaas, and Trujillo-Cenoz (1969) who found that the five cells are arranged as shown in the diagram of Fig. 1 B, taken from their article. Each photoreceptor has an axon, which, after leaving the eye traverses a small optic ganglion and enters the larger cerebropleural ganglion at a distance of perhaps 100 μ from the eye.

The responses of the visual cells of *Hermisenda* were first investigated by Dennis (1967). He classified the photoreceptors in two groups: cells of type I ("complex") produce depolarizing generator potentials and also show evidence of inhibitory impingement from other photoreceptors, while units of type II ("inhibitory") respond to light with hyperpolarizing potentials but do not develop clear depolarization. He concluded that each cell receives "excitatory depolarizing input from its photosensory apparatus" and "inhibitory synaptic input from all the other four cells" and he explained the purely hyperpolarizing responses of type II cells assuming that "in some cases the inhibitory synaptic input . . . is sufficiently effective to overbalance the effect of the photodepolarization" (p. 1461).

The responses of the photoreceptors of *Hermisenda* have been reexamined

in the present article. The organization of the interconnections between the five cells of the eye and the effect of the interactions on the responses produced by illumination are described. Evidence is then presented to show that the interactions occur at terminal branches of the photoreceptor axons, inside the cerebropleural ganglion. The properties of the generator potential are studied and it is shown that the depolarization develops in two phases which are affected differently by extrinsic currents. Finally, the functional consequences of the interactions are investigated.

METHODS

The eyes of *Hermisenda* are located symmetrically under the integument at the junction between the pedal and the cerebropleural ganglia (Fig. 1 A). A transverse cut immediately beneath the anterior portion (the "head") of the animal, causes the integument to retract, exposing the circum-esophageal ganglia and the two eyes. A connective tissue sheath enveloping these structures was partially digested with Pronase (Calbiochem, Los Angeles, Calif.), a nonspecific protease, to facilitate insertion of the microelectrodes. The nervous system (ganglia and sensory organs) was then dissected and immersed in artificial seawater at room temperature (22°C). The micropipettes were filled with 4 M potassium acetate and had a resistance of 80–100 MΩ. Conventional methods were used to record the electrical potentials of the penetrated cells. A bridge circuit was employed in the experiments involving the use of extrinsic currents. Illumination was provided by a quartz iodide incandescent lamp. The intensity of light between 4000 and 8000 Å which reached the preparation from this source was about 2×10^5 ergs cm⁻² sec⁻¹. This intensity will be called intensity 1. The light was attenuated as desired by means of neutral filters.

RESULTS

Cell penetration was signaled by a sudden potential change of approximately 45 mv, and was usually achieved without injury discharge. If this type of discharge occurred and the cell did not recover, the preparation was discarded. On occasions two electrodes were introduced in the same cell. It was then seen that the second penetration did not produce appreciable changes of membrane potential or of the properties of the cell, indicating that, in most cases, impalement does not seriously damage the receptors.

Classification of the Photoreceptors

In studying the responses of the visual cells of *Hermisenda* it soon became evident that there are in the eye two types of cells, distinguished by the size of their spikes. This is shown in Fig. 2 which gives the amplitude distribution of the spikes recorded from 78 cells. Cells giving rise to the larger spikes (about 45 mv peak-to-peak amplitude) were usually penetrated when the electrode was inserted near the lens, in the ventral-anterior region of the eyes and were called class A cells. Other cells produce spikes of about 15 mv, and will be

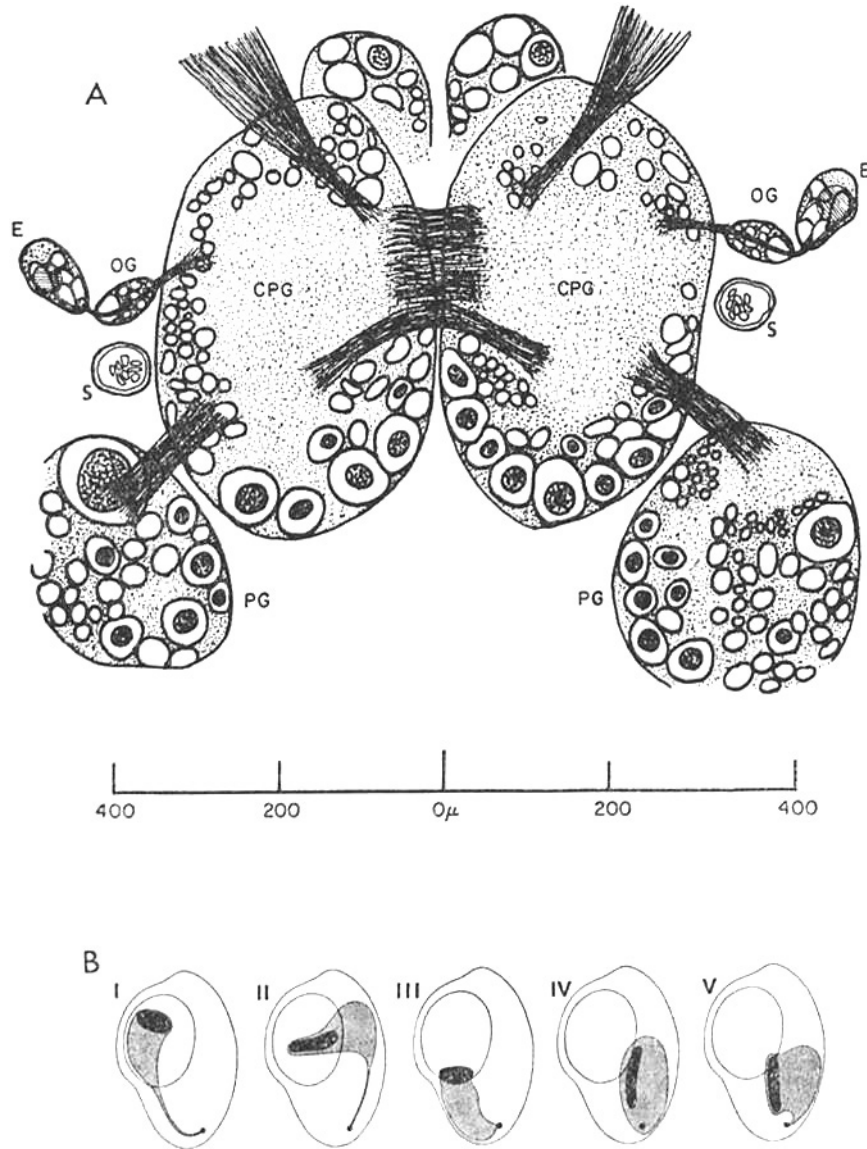


FIGURE 1. Structure of the nervous system of *Hermisenda*. (A), Reconstruction of the circum-esophageal nervous system, retraced from photographs of histological sections. The five axons which emerge from each eye (E) traverse the optic ganglion (OG) and continue into the optic tract, where they are joined by the axons of the optic ganglion cells. The optic tract enters the cerebropleural ganglion (CPG) where the axons form collaterals and terminal branchings. PG is the pedal ganglion and S is the statocyst. (B), Arrangement of the five receptors in the eye (from Stensaas et al., 1969). The black areas show the location of the microvillar membrane and the black dots show the point of origin of the axon.

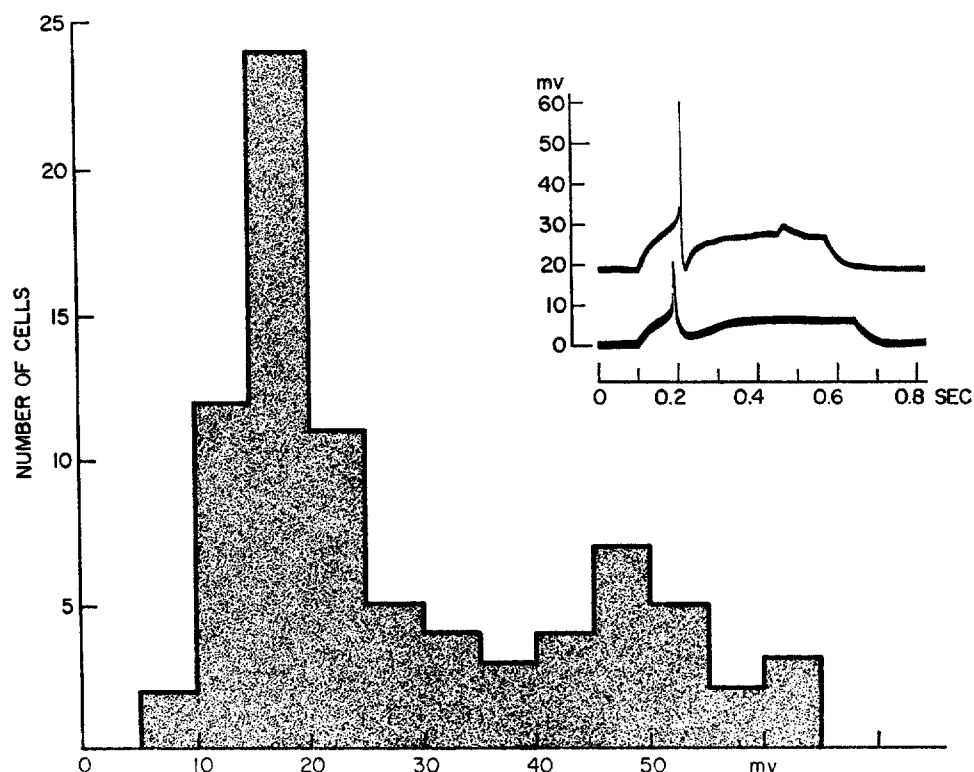


FIGURE 2. Distribution of spike amplitudes. Peak-to-peak spike height was measured in 78 cells. The histogram shows two peaks at 15 and 45 mv, respectively. Typical small and large spikes (evoked by depolarizing current) are shown in the *inset*.

referred to as class B cells. These were usually penetrated when the electrode was introduced in the dorsal posterior region of the eye. Simultaneous recordings from two or three photoreceptors indicates that there are in the eye two class A and three class B cells. It will be seen that A and B cells differ also in the properties of their responses to light and interactions. The location of the microelectrode resulting in impalement of class A cells suggests that they correspond to cells I and II in Fig. 1 B, the class B cells corresponding then to cells III through V.

Inhibitory Interactions

Fig. 3 A shows the results of one experiment in which one class A and two class B cells were simultaneously impaled. It is seen that the spikes produced by depolarizing currents in any of these three cells evoked hyperpolarizing potentials in the other two. Reciprocal interactions however are not always present between A and B cells. In 50 such pairs, the following relations were found: reciprocal inhibition ($A \rightleftharpoons B$) in 22 pairs; inhibition of A upon B

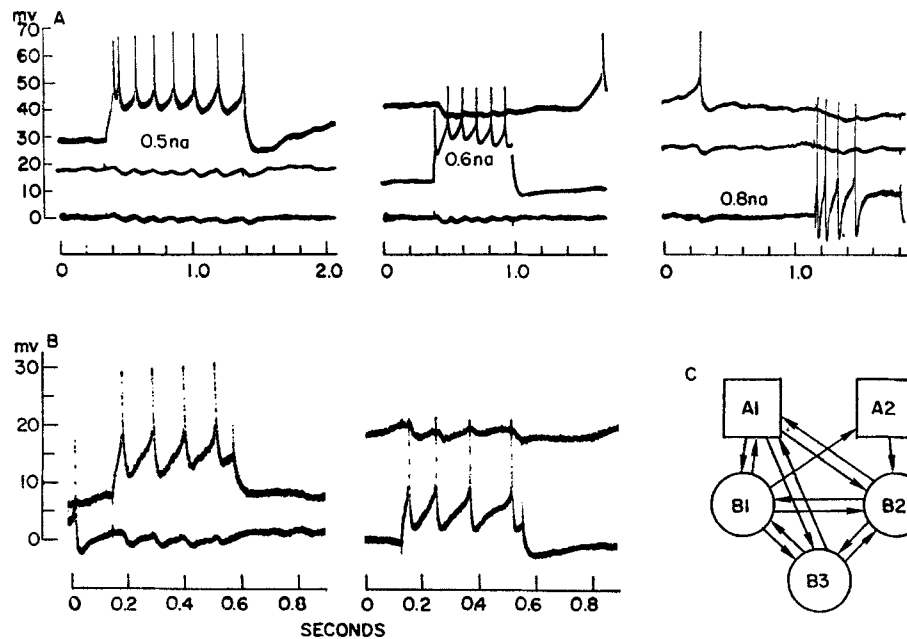


FIGURE 3. Interactions between A and B cells. (A), One type A and two type B receptors were simultaneously impaled. Depolarizing currents through one cell evoke spikes in the same cell and hyperpolarizing waves in the other two receptors. (B), Same as in A but in a pair of type B cells. (C), Presumed diagram of the inhibitory interconnections. Interactions between A cells were regarded as negligible and therefore were omitted. The connections indicated between A and B cells are consistent with the results but should be regarded as tentative. The reciprocal interactions between all B cells are instead well established.

(A \rightarrow B) in 10 pairs; inhibition of B upon A (B \rightarrow A) in 12 pairs, and no interactions in 6 pairs.

Similar experiments performed on seven pairs of A cells showed that trains of spikes in one evoke little or no hyperpolarization in the other. If steady firing is produced in one cell by a sustained depolarizing current, its frequency is not appreciably altered by the firing of the other cell. Thus A cells do not inhibit each other, or at the most they interact very weakly. By contrast, when pairs of B cells were impaled (48 experiments) reciprocal inhibition was always observed (Fig. 3 B), indicating that the three B cells are mutually interconnected. It is concluded from these results that:

- there are in each eye two class A cells and three class B cells;
- the A cells do not inhibit each other, or interact only very weakly;
- the three B cells are all mutually interconnected;
- the interactions between A and B cells can be reciprocal, unidirectional, or less frequently, absent.

These features are incorporated in the diagram of Fig. 3 C. This diagram

should be regarded as tentative because the interactions between individual A and B cells could not be unequivocally established. Any alternative scheme satisfying the experimental observations listed above would however be largely analogous to the scheme proposed in the figure.

Responses to Light

As already noted by Dennis (1967) the interactions between cells complicate the properties of the responses to light, since these will include depolarizing waves produced by the light impinging on the cell itself and hyperpolarizing potentials resulting from the activity of surrounding cells. In these conditions, sensitivity to light and strength of the interactions will both control the properties of the responses. An example of the results of this interplay is shown in Fig. 4. The records were obtained by delivering flashes of different intensities while recording from one A and one B cell.

A dim flash of light evoked depolarization of the B photoreceptor but had no effect on the A cell. A brighter flash produced spikes in B and evoked in A a hyperpolarizing wave with superimposed wavelets, each of which followed

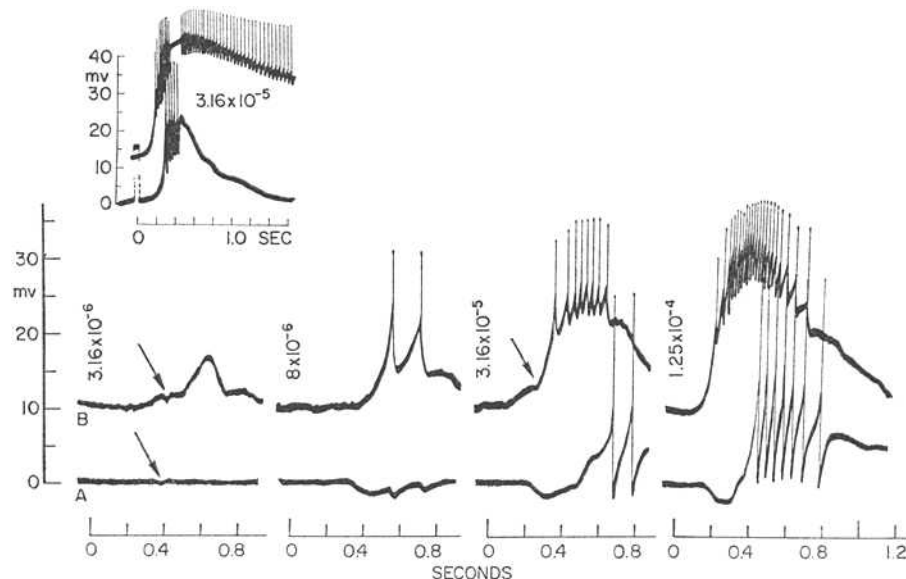


FIGURE 4. Responses of A and B cells to flashes of light. A dim flash (3.16×10^{-6}) produces a noisy depolarization in the B cell (upper trace) with no effect on the A cell. Note small hyperpolarizing potential (arrows) appearing simultaneously in the two cells. With a flash of intensity 8×10^{-6} the B cell produces two spikes and the A cell develops a hyperpolarizing wave with two superposed wavelets. The onset of the hyperpolarization of the A cell precedes the depolarization of the B cell. Brighter flashes evoke firing of the A cell, associated with interruption or slowdown of the discharge of the B cell. *Inset*, same experiment in another pair of A-B cells, showing interruption in the firing of the B cell in coincidence with the discharge of impulses in the A cell. Flash intensity 3.16×10^{-5} .

closely a spike of the B cell. Apparently, the spikes of the impaled B cell produced hyperpolarization of the A cell, but depolarization in the absence of spikes (as in record on the left) had no effect in this case. Hence, the early part of the hyperpolarizing wave must have been evoked by the activity of B cells other than the one that was impaled. It may be concluded, therefore, that the A cell in the records was inhibited by the impaled B cell and also by others. Numerous observations on A-B pairs showed that at least one B cell is always more sensitive to dim lights than either A cell, explaining the observation that responses of A cells to dim lights always include an early hyperpolarizing wave. Brighter flashes evoke depolarization and firing of the A cell. It is seen then that the discharge of the B cell is decreased or stopped in coincidence with the firing of the A cell.

Sensitivity to light differs considerably also in individual B cells, leading to results such as those illustrated in Fig. 5. The dimmest flash evoked a large generator potential in one B cell and initial hyperpolarization, followed by a depolarizing wave in the other. With brighter flashes the initial change was depolarizing also in the second cell but the developing depolarization was soon interrupted by a hyperpolarizing wave apparently produced by the firing of the cell in the upper records. The firing of the first cell was interrupted in coincidence with the discharges of the second cell, as one might expect, since the inhibitory interactions between B cells are always reciprocal. Nonuniformities in the sensitivity to light and in the strength of inhibitory interconnections seem therefore to be important features of the design of the eye of *Hermissenda*. These features will then control the characteristics of the message produced by the five cells in response to different illuminations.

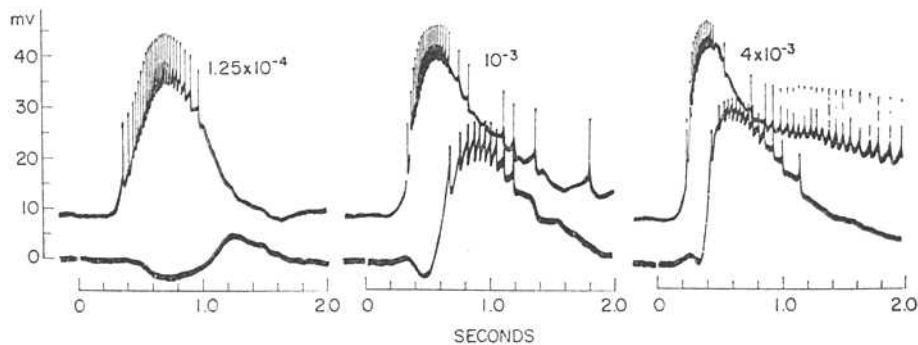


FIGURE 5. Responses of B cells to flashes of light. The more sensitive cell in the upper trace responds to a flash of intensity 1.25×10^{-4} with large generator potential while the cell in the lower trace develops a hyperpolarizing wave which delays the visible onset of the generator potential. With brighter flashes the generator potential in the lower cell starts early but is interrupted by a hyperpolarizing wave which becomes smaller as flash intensity increases. The firing of the more sensitive cell is decreased in coincidence with the peak of the response of the lower cell.

Site of the Interactions

Eakin et al. (1967) and Stensaas et al. (1969) have examined the anatomical relations between the photoreceptors of *Hermisenda*. They found contacts between the somata and also between the axons as they run through the optic ganglion. Vesicles were often observed near these areas, but in no case did the areas of contact have the typical structure of synapses. Thus, the site of the interactions remained uncertain. Eakin et al. (1967) suggest that the synapses are located at the soma or axon hillock while Stensaas et al. (1969) regard it as probable that they are at the infoldings of the axons in the eye or in the optic ganglion.

In order to obtain information on this question electrodes were simultaneously introduced in the soma of a photoreceptor and in its axon, at the point of entry into the cerebropleural ganglion. The results of one such experiment are illustrated in Fig. 6. They show that spikes are larger, and earlier in the axon, while the generator potential is larger at the soma. Synaptic potentials are larger and have shorter time to peak at the axon. Steps of current were passed through one electrode while recording from both. It was found that the resulting potential drops decayed from axon to soma somewhat less than the synaptic potentials.

These observations strongly suggest that the generator potential arises at the soma; the spikes originate in the axon and do not invade the soma (as already concluded by Dennis, 1967) and the synaptic interactions occur in the vicinity of the axonal electrode. Since intracellular injection of Procion yellow (I.C.I. Organics, Inc., Providence, R.I.) showed that all photoreceptor axons form extensive branchings just inside the cerebropleural ganglion, it seems reasonable to suggest that these arborizations may be the site at which the interactions occur. Supporting this conclusion it is seen that both the spikes and the inhibitory synaptic potentials disappear if the nerve is cut between the optic ganglion and the cerebropleural ganglion. In these conditions, currents through one cell do not evoke any appreciable potential drop in neighboring cells, indicating that no effective electrical junctions are present in the structures isolated by the cut. Generator potentials however can still be produced by illumination (see Fig. 8 B).

Nature of the Inhibitory Potentials

Dennis (1967) established that the inhibitory potentials can be reversed by hyperpolarization of the membrane but could not determine the potential at which reversal occurs. In order to perform this measurement, his experiments were repeated in a slightly different form. After impaling two cells, a burst of spikes was evoked in the first by means of a depolarizing current, and steps of hyperpolarizing current were delivered to the second. As shown in Fig. 7, the

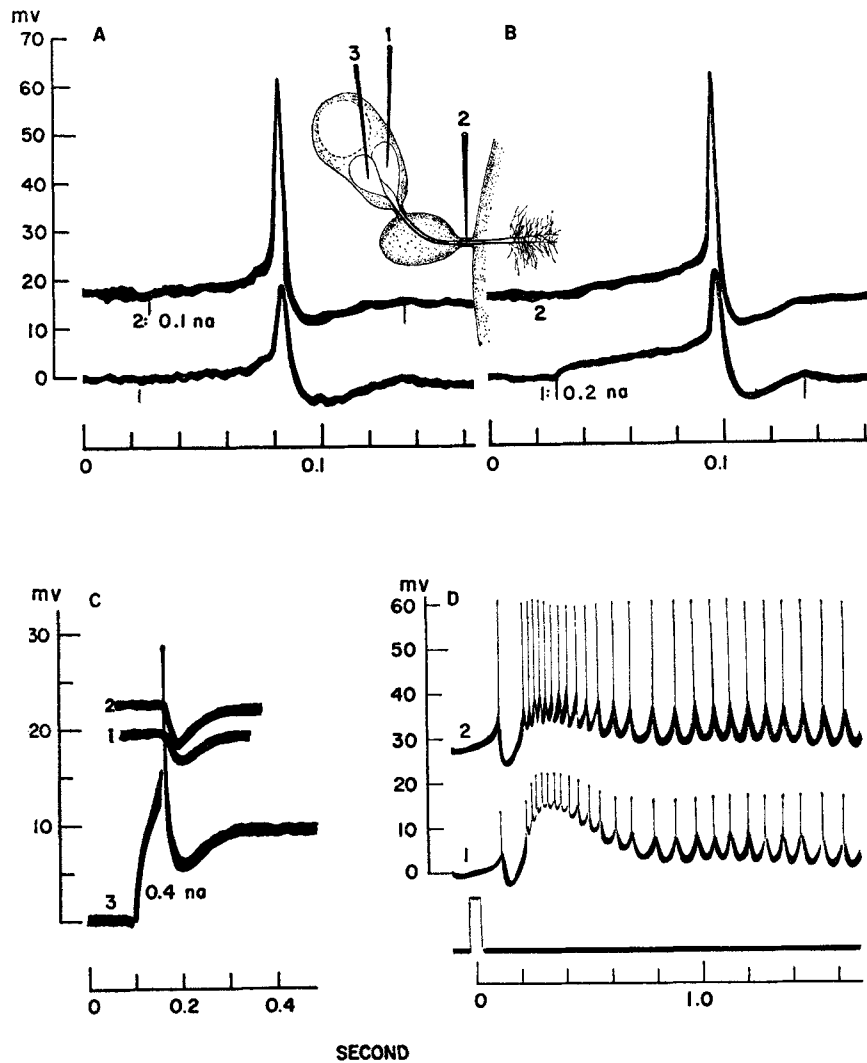


FIGURE 6. Responses recorded from soma and axon of same cell. The distance between the two electrodes was 80–100 μ . (A), Responses to a step of depolarizing current through axonal electrode; (B), response to a step of current through the soma electrode. In either case the spike is larger and earlier in the axon; (C), two electrodes were inserted respectively in the soma and axon of one receptor and a third electrode was inserted in the soma of a second receptor. A step of depolarizing current through this third electrode evokes a spike in one receptor and a hyperpolarizing synaptic potential in the other. The synaptic potential is larger and has shorter time to peak in the axon. (D), Responses to a flash of light. The generator potential is larger at the soma (lower trace) while the spikes are larger at the axon. Down-going bars in (A) and (B) indicate timing of current steps.

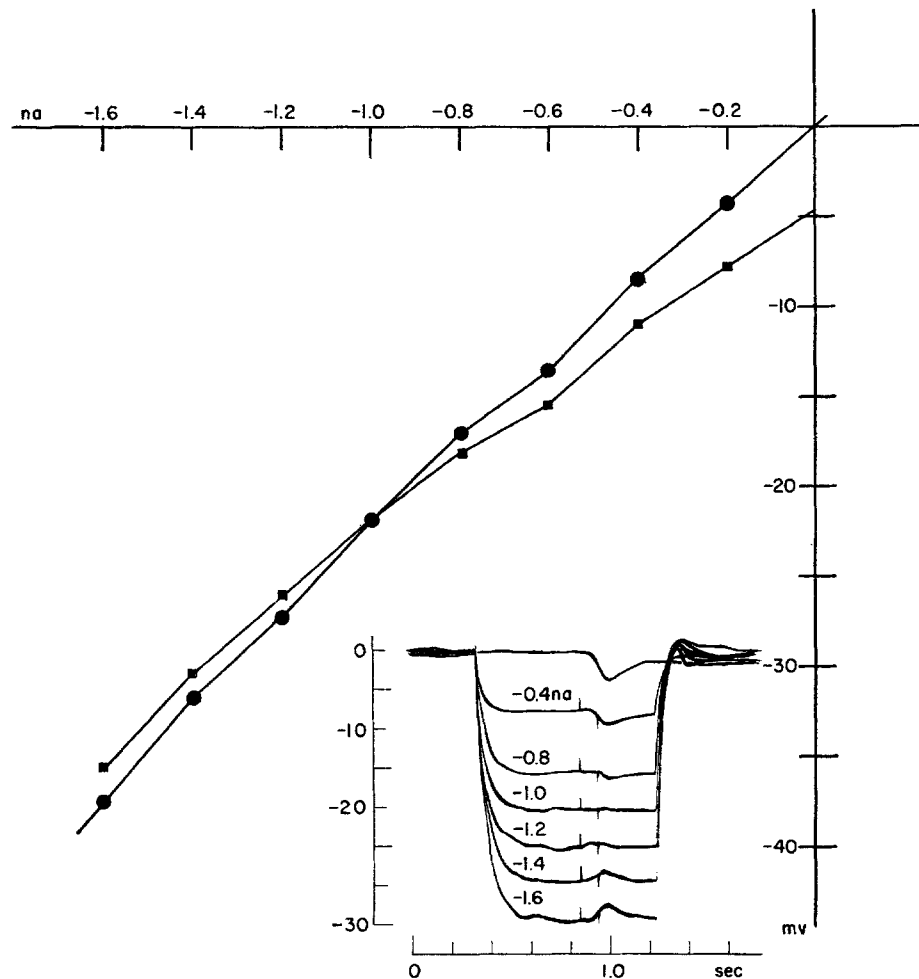


FIGURE 7. Reversal of the synaptic potential. Two receptors were impaled. Depolarizing current pulses of 2×10^{-9} amp through one of them consistently evoked a burst of four spikes. The records from this receptor are not shown, but the timing of the depolarizing current is indicated by on and off artifacts. Steps of hyperpolarizing current (intensity indicated near each record) were applied to the second receptor giving the records illustrated in *inset*. The synaptic potential reverses when the hyperpolarization of the soma exceeds 20 mv. Plot is of the voltage just before (circles) and at the peak (squares) of the synaptic potential, as a function of the intensity of the applied current.

inhibitory potentials reversed polarity when the soma of the second cell was hyperpolarized by about 20 mv. Assuming that the inhibition occurs at some distance from the soma and that the potentials of the soma decrease to about one-half at the synaptic sites (as indicated by the results illustrated in Fig. 6 C) this finding leads to the conclusion that the inhibitory potentials reverse when the subsynaptic membrane is hyperpolarized by about 10 mv.

Dual Nature of the Depolarizing Wave

Having gained some understanding of the properties of the interactions, it is useful to reexamine the responses to light in order to determine how the depolarization is brought about. In the cells which do not show prominent signs of inhibition, the generator potentials evoked by flashes of moderate or bright intensity have a fairly simple form, not unlike that of other invertebrate photoreceptors. When the cell is hyperpolarized by extrinsic currents, amplitude of these potentials increases as would be expected if the response were brought about by an increase of membrane conductance. These features of responses to bright flashes are illustrated in the records and plot of Fig. 8.

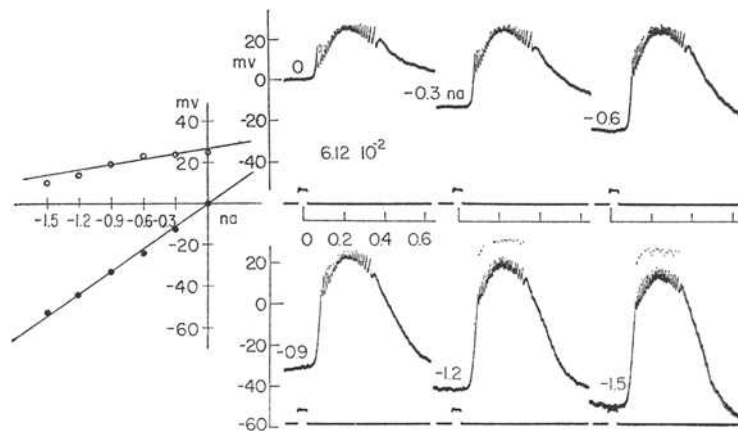


FIGURE 8. Effects of extrinsic currents on responses to bright flashes. Flashes of intensity 6.3×10^{-2} were applied at time 0 while the cell was hyperpolarized by extrinsic currents (intensity shown near each record). With these bright flashes, no inflection is seen in the rising phase of the generator potential. Response amplitude increases progressively with hyperpolarization. The plot at left measures the potential changes evoked by the currents in darkness (filled circles) and at the peak of the response (empty circles).

The responses to dim flashes, however, reveal more complex features. The third record in Fig. 4 (3.16×10^{-5}) shows that the response of the B cell develops in two steps: an early, slow depolarization followed (at the arrow) by a larger wave with superposed spikes. The early, slow component can be isolated using dim flashes, as in the experiment of Fig. 9 A. In this case the same flash intensity evoked on two occasions only a small, irregular wave while in the third record the response included both components. The second component can be abolished (or at least can be strongly depressed) by hyperpolarizing currents. In the experiment of Fig. 10 a dim flash was applied while the photoreceptor was hyperpolarized by extrinsic currents of different intensities. The early wave was not greatly changed by the hyperpolarization; the

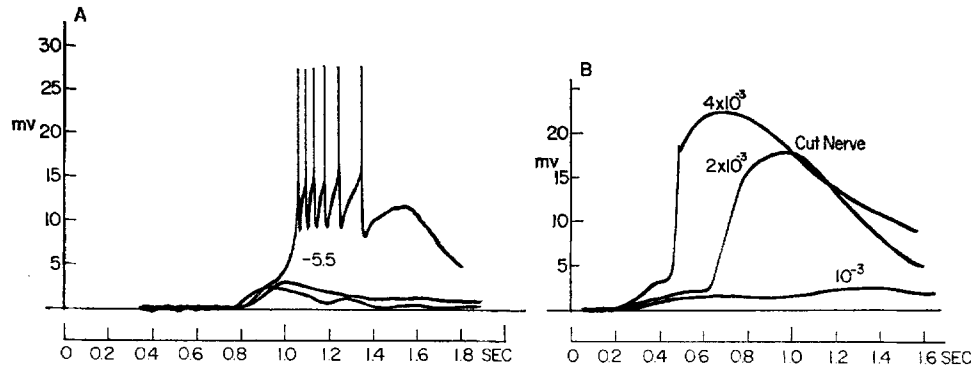


FIGURE 9. Development of generator potentials. (A), Dim flashes (intensity 3.16×10^{-6}) were applied at time 0. On two occasions the cell developed only small, slow depolarizing waves. On the third trial, the generator potential started in a similar manner but later developed an additional, larger wave with superposed spikes. (B), Cut-nerve preparation. The optic nerve was sectioned between optic and cerebroleural ganglia, to abolish nerve impulses and synaptic interactions. Flashes of increasing intensity (as indicated) applied at time 0. With the brighter flashes a large depolarizing wave develops some time after the start of a slow generator potential. This preparation was unusually insensitive to light although other cut-nerve preparations had normal sensitivity.

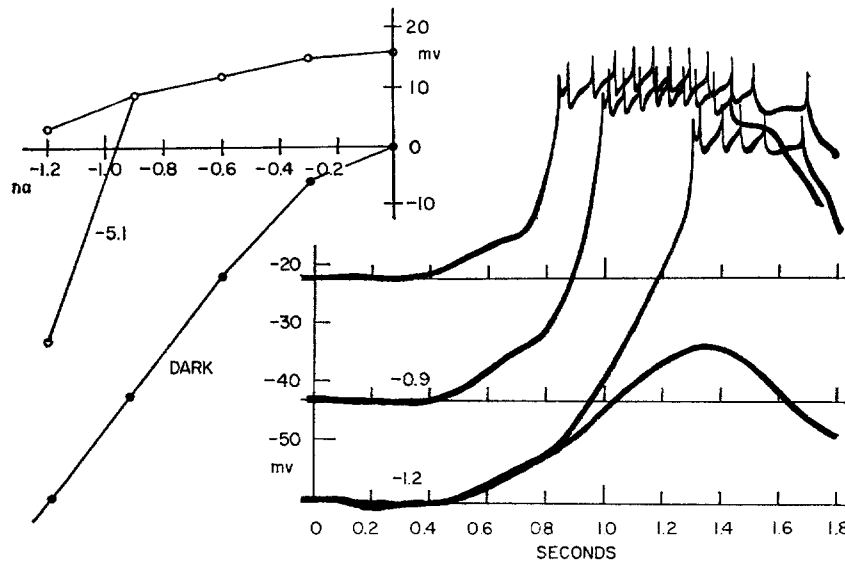


FIGURE 10. Effects of currents on responses to dim flashes. The records show responses to dim flashes (intensity 8.0×10^{-6}) applied at time 0, in the presence of hyperpolarizing currents of the intensities indicated. The early phase of the generator potential is not systematically increased by the hyperpolarization. The later phase is delayed and increased in amplitude, but it is critically blocked by currents of intensity 1.2 na. The plot at left measures the potentials in darkness (filled circles) and at the peak of the generator potential. (1 na = 10^{-9} amp.)

second wave instead was increased and delayed until, at a critical level, it suddenly broke down. These effects of currents were observed both in A and in B cells. They are evident only in the responses evoked by dim flashes, perhaps because with bright lights the two waves merge and the second component is more difficult to abolish. The second wave cannot be duplicated by means of depolarizing currents indicating that it is not controlled by membrane voltage exclusively. The two components of the generator potential persist and often become more obvious after cutting the optic nerve (Fig. 9 B). This indicates that the second wave is not related to spike discharge or to the inhibitory interactions. Fig. 11 shows that the effects of extrinsic currents on the generator potentials obtained after cutting the nerve are similar to those described in the intact preparations.

Consequences of the Interactions

The basic consequence of these inhibitory interactions is that the cells which respond more vigorously to a given illumination will decrease the response of other cells. With uniform illumination, differences in the responses due to different sensitivities of individual cells will be enhanced by the interactions.

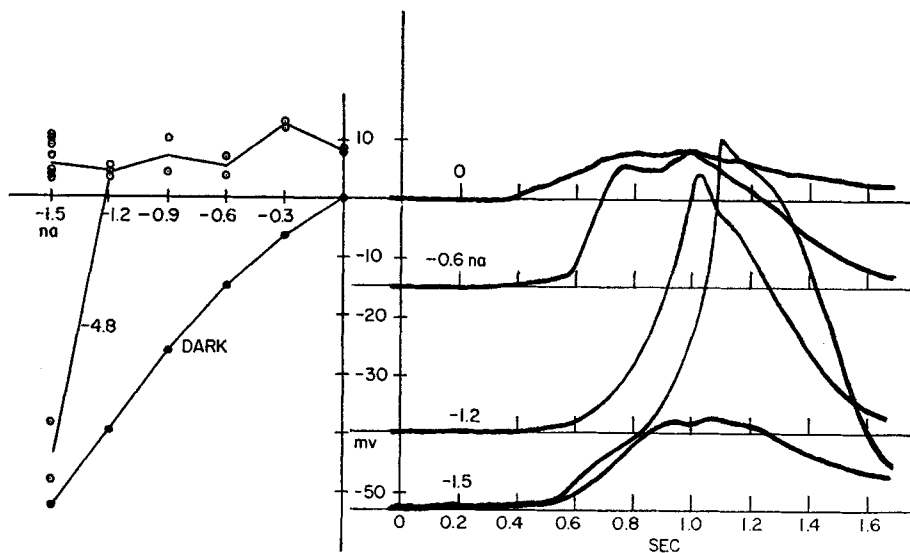


FIGURE 11. Action of currents on responses evoked after section of the optic nerve. Same experiment as in Fig. 10 in a preparation with the optic nerve cut between the optic and the cerebropleural ganglia. As in the previous figure, the early part of the generator potential does not become larger with hyperpolarizing currents. The later wave however is first increased and then critically blocked by the current. The plot at left measures the potential drop evoked by the current in darkness and at the peak of the responses.

Light Adaptation

In dark adaptation B cells respond more readily to dim lights and, therefore, they inhibit type A cells, as shown in Fig. 4. Type A cells, however, recover from light adaptation more rapidly and may then become more sensitive to light than B cells. After a bright flash, type B cells remain depolarized and discharge impulses for many seconds, whereas type A cells repolarize within a few seconds. A second bright flash delivered at this time produces a depolarizing generator potential with superposed impulses in the A cell but elicits a large hyperpolarizing wave in the B cell (Fig. 12).

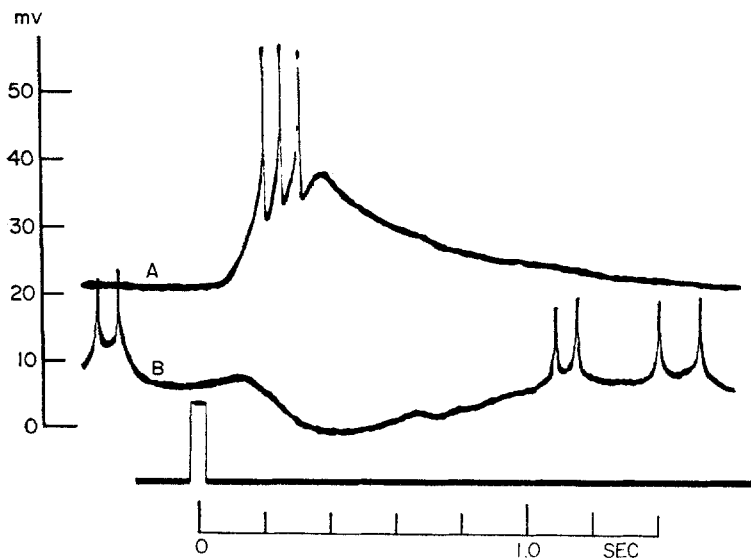


FIGURE 12. Responses to flashes during light adaptation. A bright light was applied to the preparation for 1 min. Records taken from an A cell (upper trace) and from a B cell (lower trace) 20 sec after returning to darkness. The A cell has recovered its normal membrane potential, but the B cell is still depolarized and discharges impulses. A flash of bright light delivered at this time evokes a generator potential with spikes in the A cell and a large hyperpolarizing wave in the B cell.

In the experiment of Fig. 12, the hyperpolarizing potential preceded the firing of the A cell suggesting either that another cell also delivered inhibitory impingement or that in these special conditions, the generator potential itself contributed to the inhibitory action. It is also possible, however, that the hyperpolarizing wave is not a simple synaptic potential but is brought about (at least in part) by other mechanisms.

Oscillations

Oscillations often arise in the responses to bright lights as one would expect to occur as a consequence of the interactions between cells. Fig. 13 shows

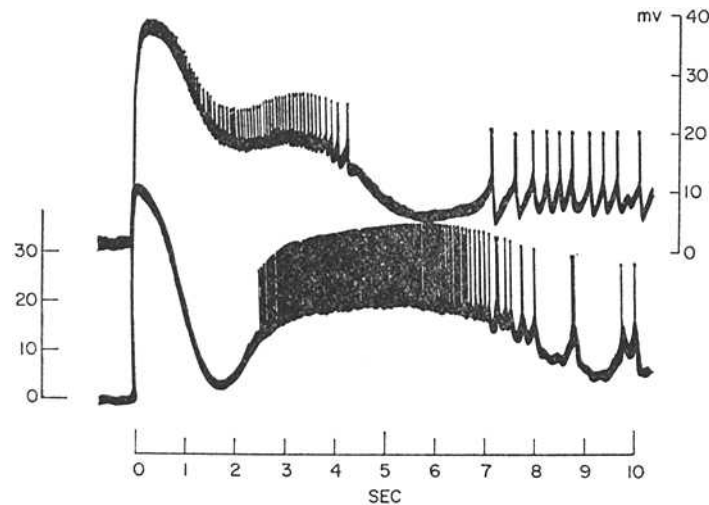


FIGURE 13. Oscillations in B receptors. A bright flash of light applied at time 0 evokes oscillatory generator potentials of long duration. The oscillations are largely out of phase in the two receptors.

responses to a bright flash recorded from two B cells which were interconnected by strong reciprocal inhibition. In this case the oscillations were out of phase. Conversely the phase shift was usually small or negligible in the two A cells, and this observation is consistent with the conclusion that A cells do not inhibit each other effectively.

Directional Sensitivity

If the stimulating light is localized rather than diffuse, the magnitude of photoreceptor responses depends on the position of the light, indicating that the lens can preferentially concentrate the light on individual receptors. In these conditions, the eye will generate different responses for different positions of the light, as shown by Dennis (1967). With experiments of this sort it is difficult, however, to establish what role is exerted by the interactions, while easier interpretations can be derived from experiments involving movement of the stimulus. In the absence of interactions, and provided that the stimulus does not produce light adaptation, moving a light at uniform speed, first in one and then in the opposite direction would give identical responses in all the cells and only their relative timing would differ. Interactions between cells, however, can change the whole structure of the responses, and in this way they may increase directional sensitivity. This possibility was confirmed by experiments in which an edge whose image was focused on the eye was moved at uniform speed in front of the field lens from right to left and then from left to right. Records from pairs of cells showed then the features illustrated in Fig. 14 where it is seen that the responses can be appreciably different for the two directions of movements. It seems, therefore, that the inhibitory

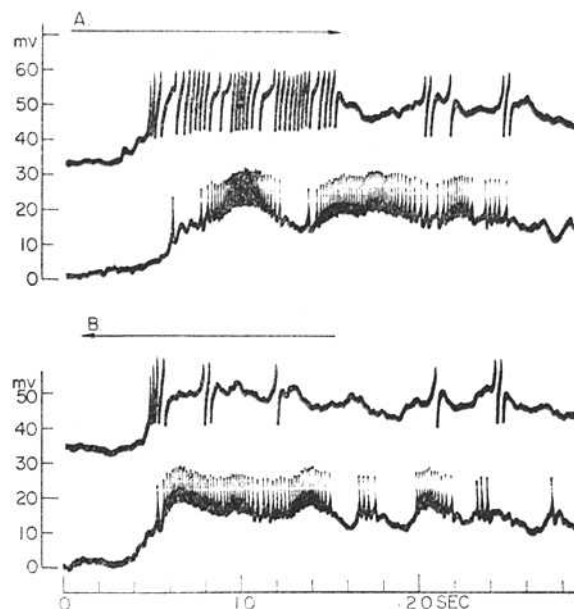


FIGURE 14. Responses to opposite directions of movement. A rectangular image was moved across the eye at uniform speed first in one direction (A) and later in the opposite direction (B). Responses were simultaneously recorded from one A cell (top traces) and from one B cell (bottom traces). The responses were always complex, as would be expected in the presence of multiple interactions, and were consistently different for the two directions of movement.

interactions increase the difference in the patterns of discharge evoked by opposite directions of movement.

DISCUSSION

The results reported in this study confirm Dennis's (1967) basic finding that inhibitory connections are present between the five photoreceptors of *Hermisenda*. In addition, the present observations show that the inhibitory interactions are not uniformly distributed but probably are organized as in the scheme of Fig. 3. The experiments involving simultaneous recordings from soma and axon (Fig. 6) as well as the results obtained after cutting the nerve, give convincing evidence that the synaptic interactions occur at the neuropile formed by optic nerve branchings, inside the cerebropleural ganglion. It seems doubtful therefore that the contacts at the soma, axon hillock or axon have a synaptic function.

Records such as those of Fig. 3 show that the impulses of one cell may evoke inhibitory potentials in other cells. It is not clear however if the generator potentials themselves, in the absence of spikes also contribute to the inhibitory interactions. In the records of Fig. 4 a dim flash produced a small depolariza-

tion in one cell but no appreciable hyperpolarization of the other. It is possible however that larger depolarizations may produce inhibitory potentials even before spikes are discharged. This suggestion is consistent with the observation that the voltage decrement from the soma to the terminal regions of the axon is not very great (Fig. 6) and might explain the smooth hyperpolarizing wave of Fig. 4 and Fig. 12. Since the hyperpolarizing potentials can be reversed by hyperpolarizing currents, it is most likely that they are brought about by a conductance change as it is the case in other synapses.

The origin of generator potentials, remains obscure. When they are elicited by bright flashes (Fig. 9), their size is increased by hyperpolarizing currents without appreciable changes in wave form. Their origin could then be interpreted as it was proposed for *Limulus* (Fuortes, 1959) by assuming that light produces an increase of membrane conductance leading to depolarization.

Study of the potentials evoked by dimmer flashes, however, reveals that they include two components: an early slow wave which is not appreciably changed by currents, and a later wave which increases both in amplitude and delay when the cell is hyperpolarized.

These results suggests that the generator potentials of *Hermisenda* (and perhaps of other preparations) are brought about by a rather complex sequence of processes. This question however was not investigated in this work.

With regard to the functional significance of the interactions, it is useful to keep in mind that a primitive eye containing five overlapping receptors may not be able to carry out operations comparable to those performed by such highly developed structures as the composite eye of arthropods or the camera eye of vertebrates, with their regular mosaic of thousands or millions of receptor cells. Thus, it would not be surprising if the "lateral inhibition" subserved substantially different operations in *Hermisenda* or in *Limulus*.

In *Limulus*, the inhibitory interactions enhance the resolution of spatial contrast (see Hartline, Ratliff, and Miller, 1961; Ratliff, 1965). This task is best performed with uniform sensitivity of the receptors and symmetrical inhibitions because in these conditions the enhancement of contrast is invariant with respect to the direction of the gradient of illumination. With nonuniform sensitivities, as in the eye of *Hermisenda*, contrast enhancement will instead be directional: it will operate effectively if the more sensitive cell receives the brighter light, but not in the reversed situation.

Considerations of this sort suggest that neither the structure nor the organization of the eye of *Hermisenda* are suitable for performing complex operations such as those required for resolving the details of an image. They may be adequate instead for generating specific and easily recognizable messages, corresponding to different stimuli (possibly few) whose recognition is important for survival.

The observations described in this paper suggest that the interactions in the eye of *Hermisenda* can facilitate discrimination of light intensities, recognition of direction of movement, and perhaps of the position of a stimulus. With uniform illumination of all the cells the inhibitory interconnections will increase the range of dim light over which the message is carried only by the most sensitive cells; with bright lights, they may produce typical patterns, such as the oscillations illustrated in Fig. 13. Both effects may simplify the task of distinguishing gradation of intensity over a wide range.

Responses of the same size may be evoked by a dim light in conditions of dark adaptation or by bright lights in a state of light adaptation. Mechanisms preventing possible confusion, however, exist in *Hermisenda*, as shown by the experiments of Figs. 4 and 12: in dark adaptation B cells response more readily than A cells but the situation is reversed when the eye is light-adapted.

There is some evidence that the animal can detect the direction of an object's movement. Preliminary behavioral experiments (performed by Mr. Douglas Bowling) showed that the freely swimming animal avoids a shadow approaching from one direction by withdrawing in the opposite direction. Movement of a light across the whole visual field of the eye results in preferential illumination of one cell after another. The cell illuminated first will then be in favorable condition for developing its response unencumbered by inhibitions. Opposite directions of movement will then give responses in individual cells which differ not only in their relative timing but also in their overall structure, as indicated by the results of Fig. 14. Identification of the direction of large movement will thus be simplified by the interactions. Limited movements, covering only a small part of the visual field, will of course be much more difficult to recognize, and the usefulness of the interactions for these more refined tasks is doubtful.

It appears, therefore, that the organization of the eye of *Hermisenda*, although too primitive for fine discriminations, may be suitable for generating a number of clearly distinct messages, corresponding to different stimuli. In several instances the inhibitory interactions increase the difference of the responses brought about by these different stimuli and thereby facilitate their recognition.

SUMMARY

(a) The five photoreceptors in the eye of *Hermisenda* can be classified in two types: class A: (two cells) producing spikes of approximately 45 mv and class B: (three cells) producing spikes of approximately 15 mv.

(b) All photoreceptors respond to the light they absorb with a depolarizing generator potential from which spikes may arise.

(c) The organization of the eye was investigated by recording simultaneously the activity of two or three photoreceptors. The following inhibitory interactions were observed: very weak or absent between A cells; reciprocal

and roughly symmetrical between B cells; reciprocal, unidirectional or absent between different pairs of A and B cells.

(d) Individual photoreceptors have different sensitivities to light. In dark adaptation, at least one B cell is more sensitive than either A cell and therefore the response of A cells to dim lights includes an early hyperpolarizing wave caused by inhibition from B cells. A cells, however, recover more rapidly than B cells from exposure to bright lights. A flash of light delivered in these conditions produces a generator potential with spikes in A cells and a hyperpolarizing potential in B cells.

(e) Simultaneous records from the soma and axon of the same photoreceptor showed that the generator potential is larger at the soma while the spike and synaptic potential are larger at the axon. Such observations suggest that the spikes arise in the axon and the synaptic potentials arise in terminal branchings inside the cerebropleural ganglion. This conclusion is confirmed by the finding that when the optic nerve is cut, the generator potential persists, but the spikes and the synaptic potentials are abolished.

(f) In both A and B cells, the generator potentials evoked by dim flashes include two components: an early, slow depolarization followed by a larger, more rapid wave. These two components remain after cutting the optic nerve. The second wave can be abolished or depressed by large hyperpolarizing currents.

(g) The response to bright flashes of light usually includes oscillations. These are out of phase in pairs of B cells and in phase in pairs of A cells.

(h) Receptor cells respond differently to an edge moved in opposite directions across the eye, suggesting that the interactions increase directional sensitivity.

(i) It is concluded that although the eye of *Hermissenda* is too primitive for fine discrimination, its organization is adequate for generating specific signals reflecting light intensity, the eye's state of adaptation, the general direction of the illumination, and direction of movement.

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