Neural Organization of a Molluscan Visual System

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ABSTRACT Intracellular recording was used to study the response to light of second order visual cells within the optic ganglion of *Hermissenda crassicornis*. Simultaneous recordings revealed that type B but not type A photoreceptors inhibit the second order cells. Additional details of the neural organization of the visual system were obtained. Possible functional implications of this neural organization are discussed.

INTRODUCTION

Invertebrate second order visual cells are somewhat difficult to study electrophysiologically because of their small size and inaccessibility. Extracellular recording in dragonfly (9) indicated that second order visual cells fire spontaneously in the dark and are inhibited by illumination. More recently, intracellular recording was used to demonstrate hyperpolarizing responses in second order invertebrate visual cells (2, 4, 10). The organization of invertebrate photoreceptor-second order cell interactions has been studied morphologically. Arthropod photoreceptors within the same cartridge of a compound eye were seen in electron micrographs (12) to synapse on the same postsynaptic (second order) element. Synapses between photoreceptors, and between photoreceptors and second order visual cells were identified in electron micrographs of the dragonfly ocellus (6).

The responses and interactions of photoreceptors in the eye of the nudibranch mollusc, *Hermissenda crassicornis* have been studied previously (1, 5). The relative simplicity of the photoreceptor organization suggested a second order visual system amenable to a somewhat detailed network analysis. The present work describes the responses of second-order visual neurons in *Hermissenda* and their relationship to the response of photoreceptors. The organization of photoreceptor-second order visual cell interactions is also examined.

METHODS

Hermissenda were provided by Dr. Rimmon Fay of the Pacific Bio-Marine Supply Co., Venice, Calif. The eyes, statocysts, and optic ganglia of *Hermissenda* are located

symmetrically under the integument at the junction between the pedal and cerebropleural ganglia. A transverse cut immediately beneath the anterior portion (the "head") of the animal causes the integument to retract exposing the entire circumesophageal nervous system. This nervous system (ganglia and sensory organs) was then dissected and immersed in artificial seawater at room temperature (22°C).

A connective tissue sheath enveloping the circum-esophageal nervous system (including the eyes, statocysts, and optic ganglia) was partially digested with Pronase (Calbiochem, Los Angeles, Calif.), a nonspecific protease, to facilitate insertion of the microelectrodes. The micropipettes were filled with 4 M potassium acetate and had a resistance of 80–100 MΩ. Conventional methods were used to record 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.

For Procion injection, electrodes were filled with 6% Procion yellow (in distilled water) (I.C.I. Organics, Inc., Providence, R. I.). These electrodes had resistances of 120–150 MΩ. Cells were marked with 10 nA hyperpolarizing current pulses of 500 ms duration at a frequency of 1/s. The pulses were given for approximately 20 min. The isolated nervous system was then placed in seawater at 4°C for 12 h before fixation in formaldehyde.

RESULTS

Histology

The eyes of *Hermissenda crassicornis* each contain five photoreceptors (7). The optic ganglion has 14 cells (11) whose axons join those of the photoreceptors to form a well defined tract as demonstrated by Epon-embedded sections stained with toluidine blue (Fig. 1). This tract extends approximately 300 μm into the cerebropleural ganglion. The five photoreceptor axons pass within a common sheath through the optic ganglion and end approximately 120 μm from the cell somata in a spray of fine terminal branchings (1). In the same sections we also observed one very large optic ganglion cell which was found to have particular electrophysiologic features. (See below).

Iontophoretic injection of the fluorescent dye Procion yellow revealed two histologic classes of optic ganglion cells. Cells of one class send into the optic tract short axons (approximately 250 μm, cf. Fig. 2) which end with little branching. With other cells it can often be shown that the axon divides in two branches: one ends in the neuropile of the ipsilateral pleural ganglion; the other crosses the brain via a connective joining the two cerebropleural ganglia. The ipsilateral branch of cells which crossed the brain varied in size and extent. Fig. 2 depicts a Procion-injected optic ganglion cell which gives off several fine branches proximal to its soma in the region of ipsilateral photoreceptor terminal endings. Its axon then crosses the brain and ends in a fine

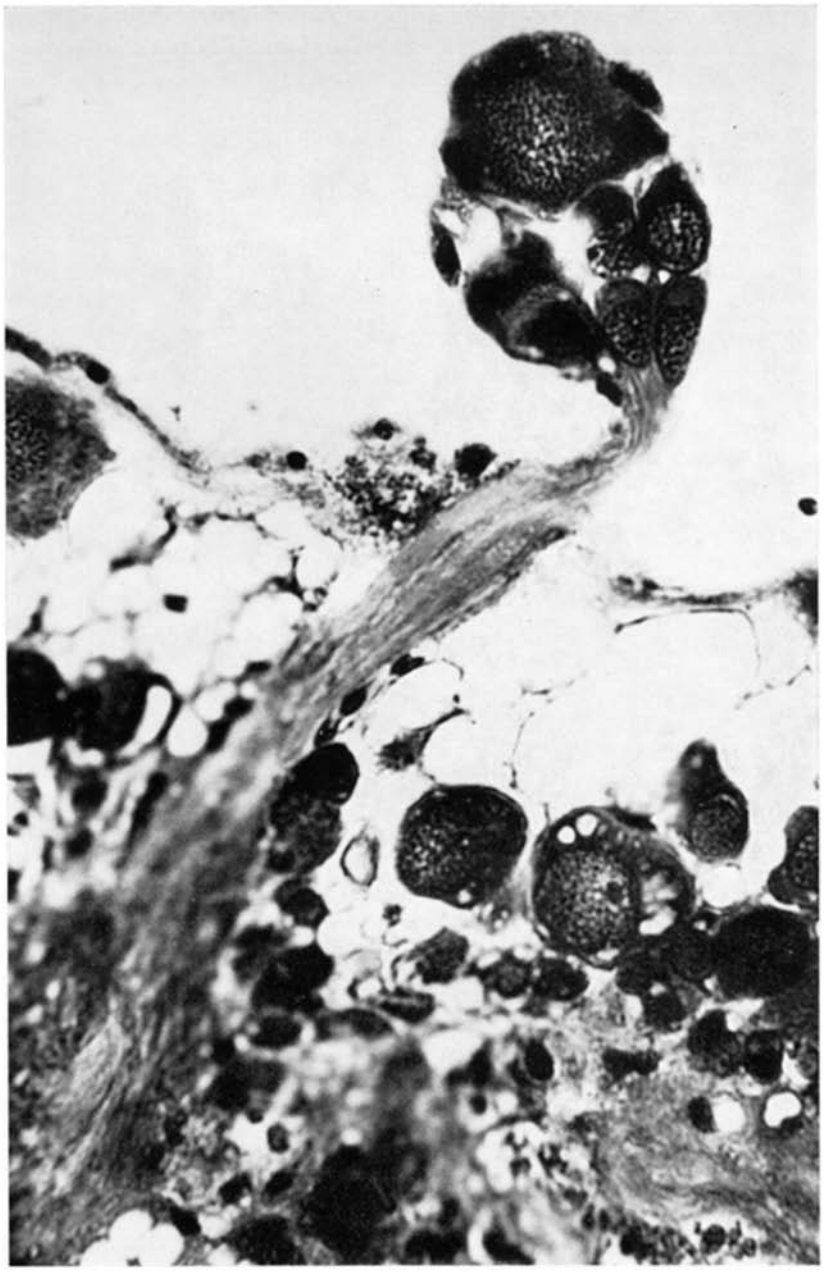

FIGURE 1. 25 $\frac{1}{4}$ μm thick section stained with toluidine blue showing the optic ganglion (40 μm across) and "optic tract." The largest cell is unresponsive to light.

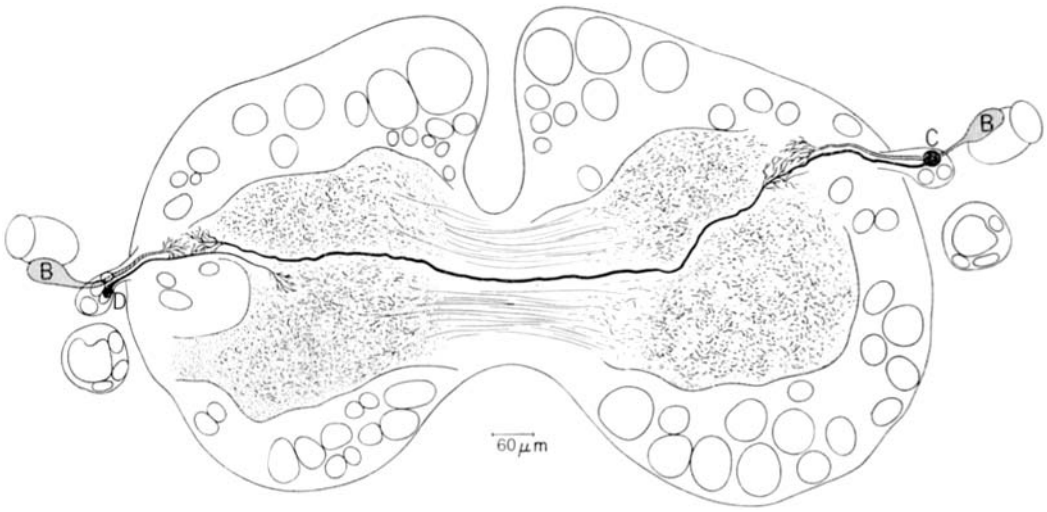

FIGURE 2. Sketch based on serial sections of type B photoreceptors and optic ganglion cells marked with Procion yellow. The optic ganglion cell which crosses the brain (C) presumably receives synaptic input from ipsilateral type B photoreceptors near its soma and contralateral type B photoreceptors on its terminal branches. The optic ganglion cell which crosses the brain inhibits contralaleral optic ganglion cells (D).

arborization close to the lateral border of the contralateral pleural ganglion in a region that contains the fine endings of the contralateral photoreceptors.

Optic Ganglion Cell

PENETRATION Almost invariably cell penetration was accompanied by injury discharge. If this discharge was allowed to continue, the cell usually soon lost the ability to produce spikes although it could still generate slow potentials. The initial discharge could, however, be depressed by hyperpolarizing currents through the microelectrode. In a number of instances the conditions of the cell became stable after a few minutes and it was then possible to remove the hyperpolarizing current. Firing frequency in darkness varied then between 20 and 200/min in different cells.

Responses to depolarizing currents, typical of many optic ganglion cells, are depicted in Fig. 3. The largest cell in the optic ganglion is quiet in darkness and has large (50–70 mV) slow spikes which rapidly inactivate.

One type of cell fires frequently in darkness in bursts of double and triple spikes (Fig. 9 D). Weak depolarizing currents in this type of cell, subsequently referred to as the "C" (contralateral) cell, cause small aborted spikes (Fig. 4). Stronger currents produce full spikes with two different initial time-courses.

RESPONSE TO LIGHT Most optic ganglion cells hyperpolarize with a cessation of firing in response to illumination. The relation of light intensity to the latency of the hyperpolarizing response in optic ganglion cells followed

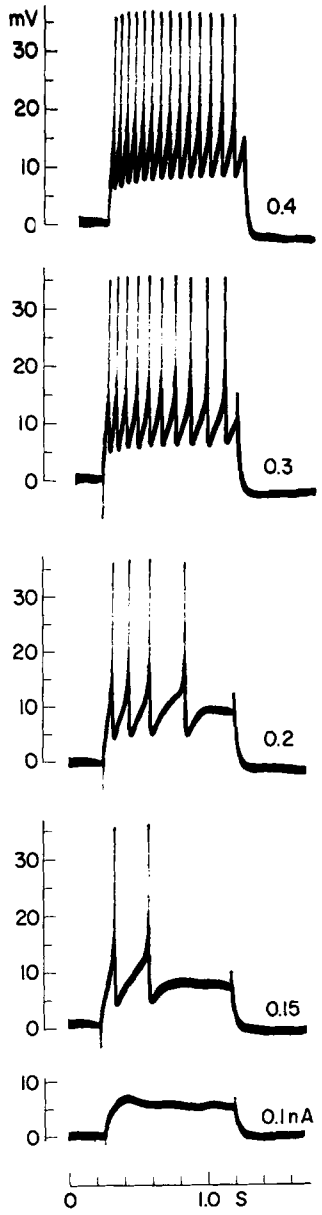

FIGURE 3. Response of non-"C" cell to increasing depolarizing current. Note absence of aborted spikes, spike doublets, and differences in initial time-course of the spikes.

closely that of the depolarizing type B (see below) photoreceptor response (Fig. 5). The synaptic origin of this hyperpolarizing response is further confirmed by its abolition when the eyes are removed.

To investigate the origin of the hyperpolarizing response, one or two photoreceptors were penetrated simultaneously with an optic ganglion cell. A

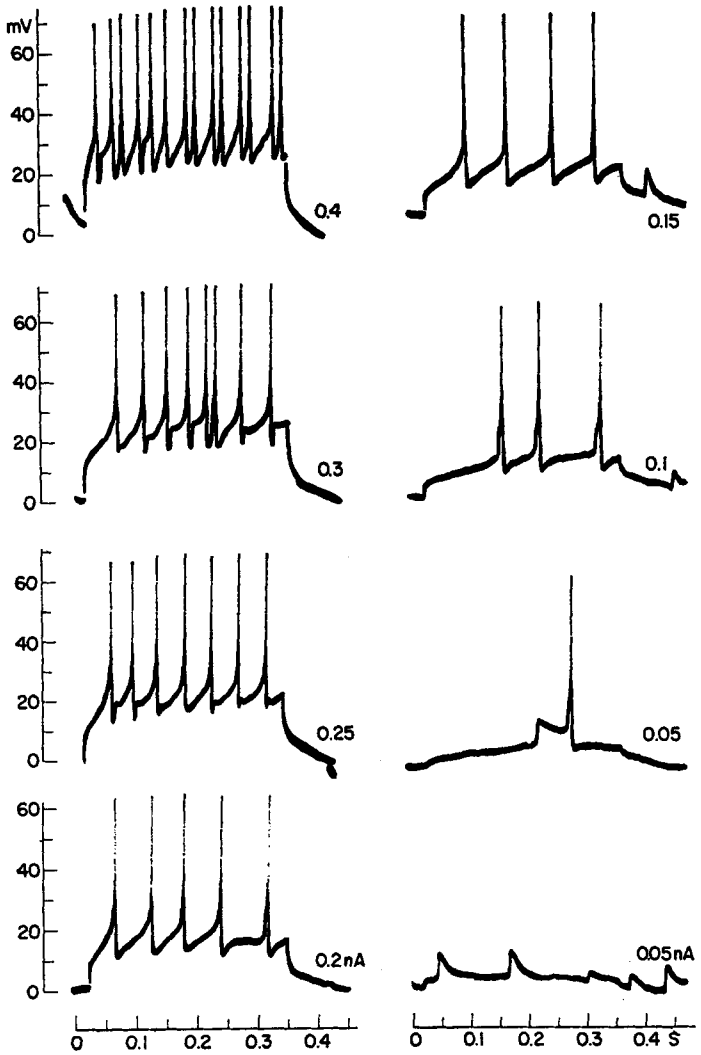

FIGURE 4. Response of the "C" cell to increasing depolarizing current. Note appearance of aborted spikes with 0.05 nA. Full spikes with rapid initial time-course occur with 0.05–0.1 nA. Spikes with more gradual initial time-course are produced by pulses of 0.15 nA or greater. Spike doublets begin to appear at 0.30 nA. 0.1 nA steady hyperpolarizing current was applied to reduce spontaneous activity.

previous study (1) indicated that in each eye there are two type A photoreceptors, with average spikes of 45 mV, which have little or no inhibitory effect on each other and three type B photoreceptors, with average spikes of 15 mV, which are all mutually inhibitory. In 52 out of 57 experiments, firing (produced by depolarizing current) of a B photoreceptor caused hyperpolarization of a simultaneously impaled optic ganglion cell (Fig. 6). Conversely,

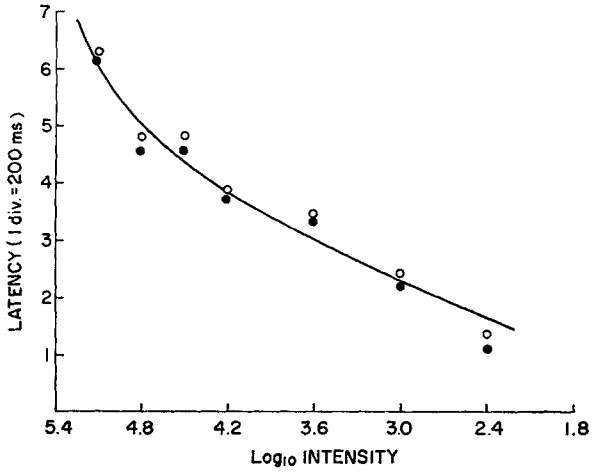

FIGURE 5. Onset latency of response to flashes of light in type B photoreceptor (closed circles) and in optic ganglion cell (open circles) penetrated simultaneously vs. $\log_{10}$ intensity. The onset of the optic ganglion cell hyperpolarizing response follows closely the onset of the B photoreceptor generator potential.

the discharge of A photoreceptors caused no hyperpolarization in an accompanying optic ganglion cell in 29 of the 31 cases explored. Two type A photoreceptors caused a weak and intermittent hyperpolarization in an accompanying optic ganglion cell. Simultaneous recordings from two type B photoreceptors and an optic ganglion cell were performed in 15 preparations. In 14 cases, both inhibited the optic ganglion cell; in the remaining experiment, only one had a clear inhibitory action. With these triple recordings frequently one photoreceptor had a stronger inhibitory effect on the optic ganglion cell than the other photoreceptor. Often simultaneous inhibitory impingement from a third receptor could be seen in the optic ganglion cell and two photoreceptors (Fig. 7). Thus, optic ganglion cells were observed to receive inhibitory input only from type B photoreceptors, and the results suggest varying degrees of convergence of this synaptic input.

If two type B photoreceptors, both of which inhibited an optic ganglion cell, were depolarized and fired simultaneously, a greater hyperpolarization was produced in the optic ganglion cell than if either photoreceptor were depolarized individually with the same current inputs (Fig. 8). Due to the mutual inhibition of the B photoreceptors, the same current input causes fewer impulses in each receptor when both are stimulated simultaneously than individually. Nevertheless the combined number of impulses in both receptors is greater than either produces alone, accounting for the slightly greater hyperpolarization. In seven triple recordings, the "C" cell, which fires in darkness in bursts of double and triple spikes (see "optic ganglion cell characteristics"), was inhibited by type B photoreceptors in both the ipsilateral and in the con-

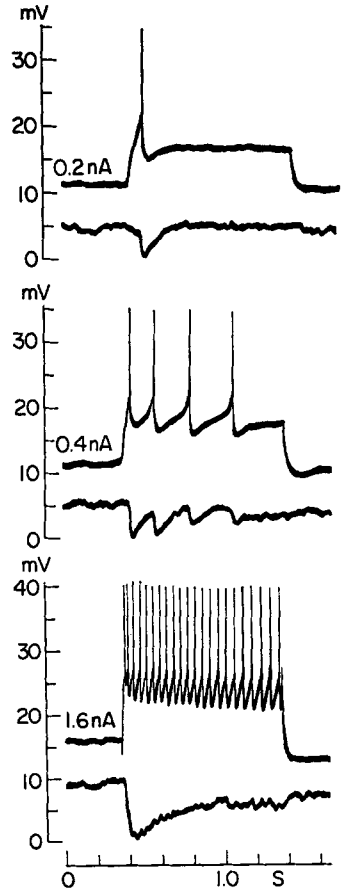

FIGURE 6. Depolarizing currents to type B photoreceptor produce impulses associated with IPSP's in simultaneously impaled optic ganglion cell.

tralateral eye (Fig. 9). In 12 pairs of type B photoreceptors and contralateral optic ganglion cells which did not have the "C" cell characteristics no connections were found. Since photoreceptor axons end shortly after entering the *Hermissenda* brain (as determined by Procion yellow iontophoresis) the "C" cell is one of those optic ganglion cells which send axons across the connective joining the two halves of the brain. Presumably this cell receives input from ipsilateral photoreceptors near its soma and from contralateral photoreceptors on the fine branches of its axon's termination (cf. Fig. 2).

Optic ganglion cells did not feed back onto photoreceptors. In 25 pairs of optic ganglion cells, within the same optic ganglion, no cells were connected. This was not true with pairs of optic ganglion cells in each of the optic ganglia on either side of the brain (Alkon, work in progress). An example of such an interaction is seen (Fig. 10) where a "C" cell inhibited (with one spike causing

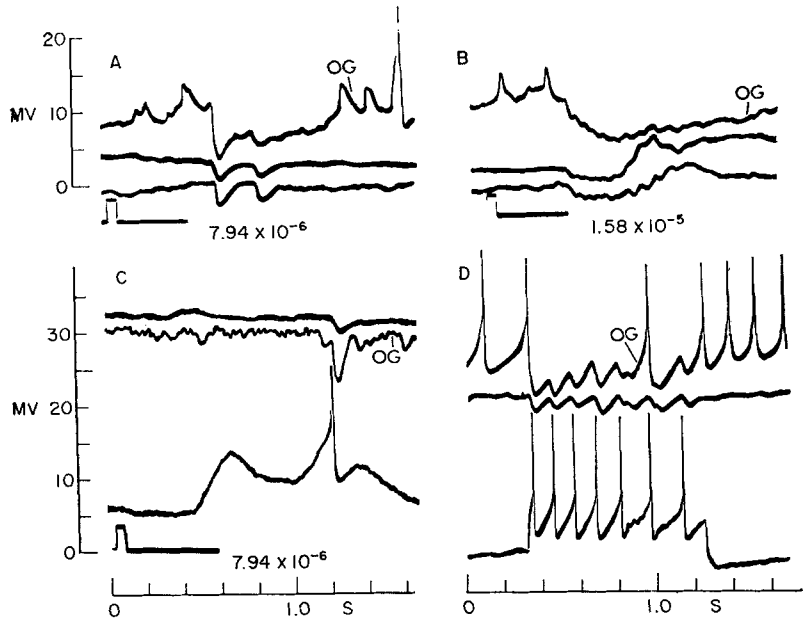

FIGURE 7. (A, B), Responses to dim flashes of type A photoreceptor (middle record) type B photoreceptor (lowest record), and optic ganglion cell (OG) penetrated simultaneously. IPSP's occur simultaneously in all three cells. (C), Simultaneous IPSP in type A photoreceptor (upper record) and optic ganglion cell (middle record) associated with spike in type B photoreceptor (lowest record) penetrated simultaneously. Response to dim flash. (D), Simultaneous IPSP's in type A photoreceptor (middle record) and optic ganglion cell (upper record) associated with spikes in type B photoreceptor (lowest record) penetrated simultaneously. Depolarizing pulse to B photoreceptor. Optic ganglion cell IPSP's are larger and have a faster rise to peak amplitude than IPSP's in type A photoreceptor.

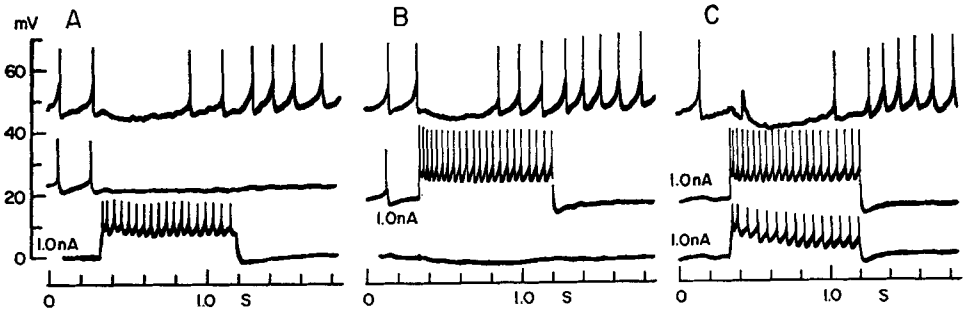

FIGURE 8. Two type B photoreceptors penetrated simultaneously with optic ganglion cell (spike tops not visible). (A), 1.0 nA current pulse to first type B photoreceptor; (B), 1.0 nA current pulse to second type B photoreceptor; (C), 1.0 nA current pulse to each type B photoreceptor. Although mutual inhibition reduces the number of spikes for a given current pulse in each photoreceptor when the two pulses are given simultaneously, the hyperpolarization in the optic ganglion cell is greater than if either photoreceptor is fired separately.

one inhibitory postsynaptic potential [IPSP]) a non-"C" cell in the contralateral optic ganglion.

The interruption of spontaneous firing in optic ganglion cells associated with the hyperpolarizing response to light does not appear to be adequate for

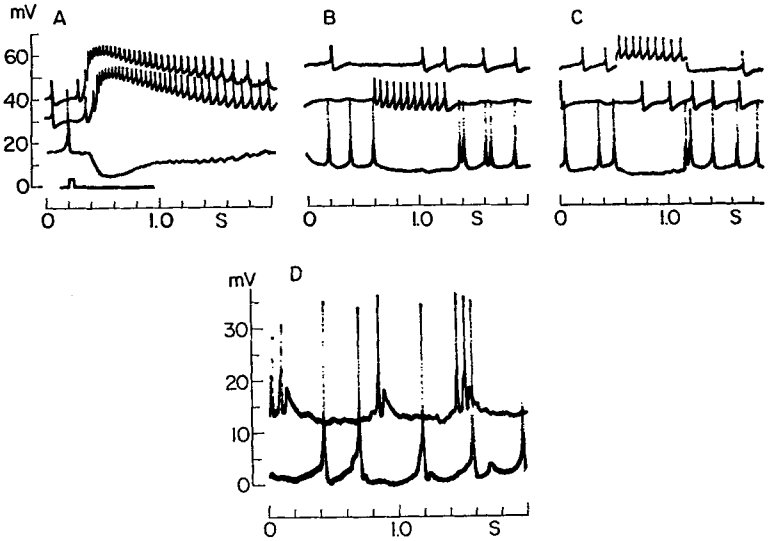

FIGURE 9. "C" optic ganglion cell penetrated simultaneously with a type B photoreceptor in each of *Hermissenda's* two eyes. (A), Response to bright flash. (B), Firing in contralateral photoreceptor causes cessation of the "C" cell activity. (C), Firing in ipsilateral photoreceptor also prevents "C" cell from firing. Note double spikes typical of the "C" cell. (D), Spontaneous activity of "C" (upper record) and non-"C" cell penetrated simultaneously.

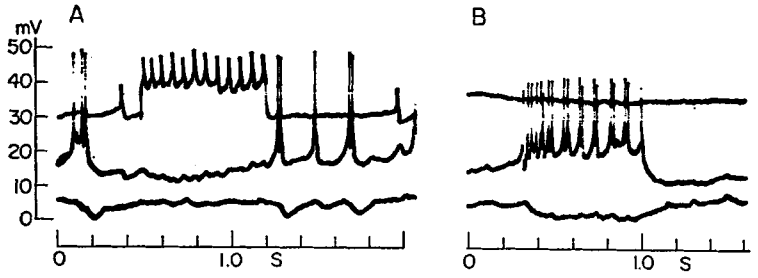

FIGURE 10. A nonspiking optic ganglion cell on the right side of the *Hermissenda* brain is penetrated simultaneously with a type B photoreceptor and "C" optic ganglion cell which are both on the left side. The right eye has been removed. (A), impulses in the "C" cell are associated with hyperpolarizing waves in the contralateral optic ganglion cell. Firing in the type B photoreceptor prevents the "C" cell from firing as well as preventing the hyperpolarizing waves in the contralateral optic ganglion cell (which must not be a "C" cell since the type B photoreceptor causes no hyperpolarization). (B), A train of impulses in the left "C" cell is associated with a long hyperpolarizing wave in the right optic ganglion cell.

signaling differences in stimulus strength. Both the photoreceptor generator potential and spike frequency vary directly with light intensity (Figs. 11 and 12 A). The duration of the ganglion cell hyperpolarizing response, however, does not increase with light intensity except with bright flashes (Figs. 13 and 14). With dim to moderate lights optic ganglion cell impulses briefly cease during the hyperpolarizing response and then resume firing at an initial frequency much greater than that of a dark-adapted cell (Figs. 11, 12 B, 13). Bright flashes cause a greatly prolonged cessation of impulse activity (Fig. 14). With bright flashes the ganglion cell hyperpolarization was diphasic, mirroring the diphasic response of type B photoreceptors.

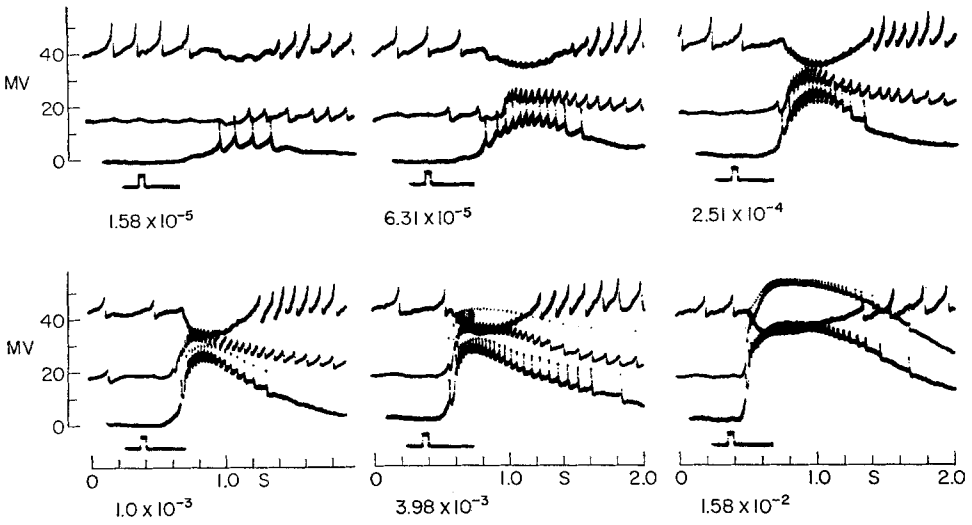

FIGURE 11. Responses of two type B photoreceptors and an optic ganglion cell penetrated simultaneously to light flashes of increasing intensity.

Site of Receptor-Optic Ganglion Cell Synapses

In the majority of cases one spike of a type B photoreceptor produced one inhibitory synaptic potential in a receiving optic ganglion cell; with sufficiently high frequencies the individual synaptic potentials fused into a smooth hyperpolarizing wave (Fig. 6). Recording of IPSP's produced by spikes in one photoreceptor occurring simultaneously in an optic ganglion cell and a second photoreceptor (Fig. 7) demonstrates that the optic ganglion cell IPSP is larger and has a faster rise to peak. This is consistent with the optic ganglion cell electrode being closer to the synaptic sites than the photoreceptor electrode.

Simultaneous recordings from the soma and axon of a photoreceptor (1), and experiments in which the photoreceptor axon was cut, indicated that the site of the synapses between photoreceptors is a region of their terminal

branchings, identified by Procion staining, approximately 30 μm from the lateral border of the pleural ganglion within the optic tract. It seems reasonable that receptor impingement onto optic ganglion cells would also occur at the same site within the optic tract.

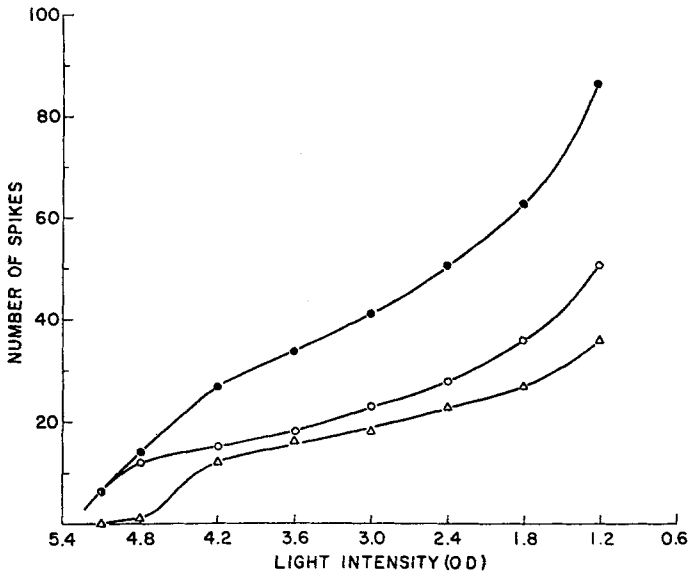

FIGURE 12 A. Plots of number of photoreceptor spikes (cf. Fig. 11) in 1.0 s interval after onset of depolarizing response to light vs. $\log_{10}$ intensity. Upper plot is sum of two lower plots for each type B photreceptor.

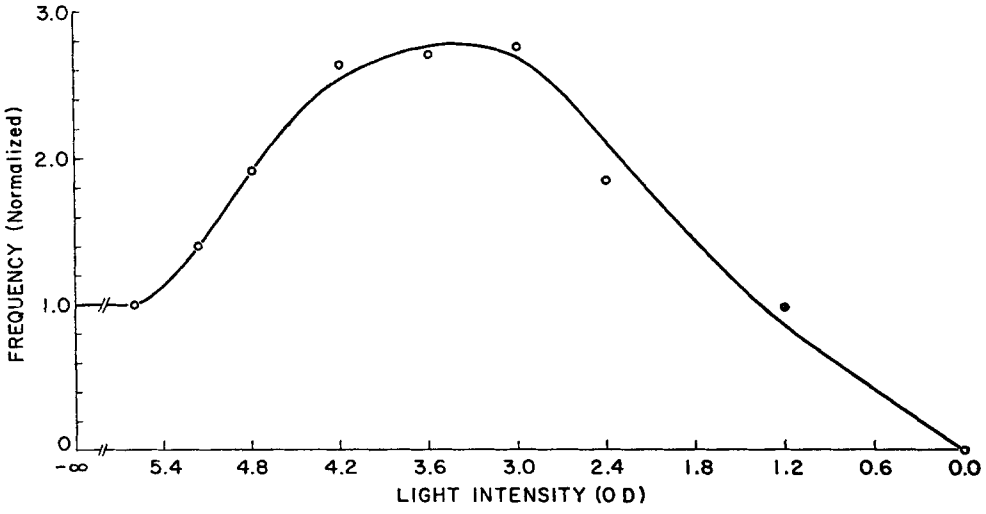

FIGURE 12 B. Plot of frequency of firing during 2.0 s interval after hyperpolarizing response (average of four optic ganglion cells) vs. $\log_{10}$ intensity.

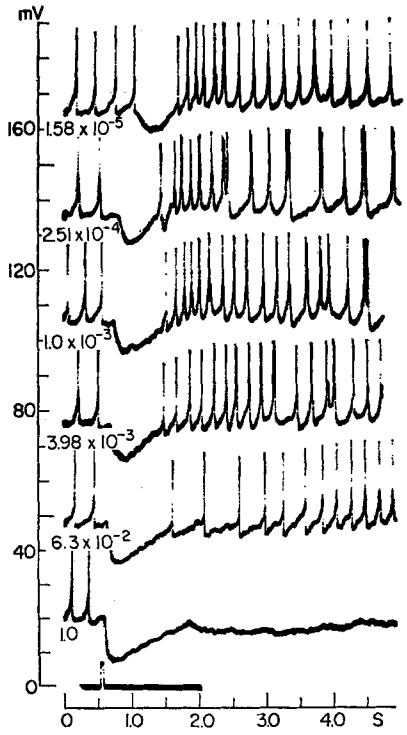

FIGURE 13. Responses of "C" cell to light flashes of increasing intensity. Note increased frequency of firing after the hyperpolarization for dim to moderate flashes. The duration of hyperpolarization with cessation of firing increases only for the brighter flashes.

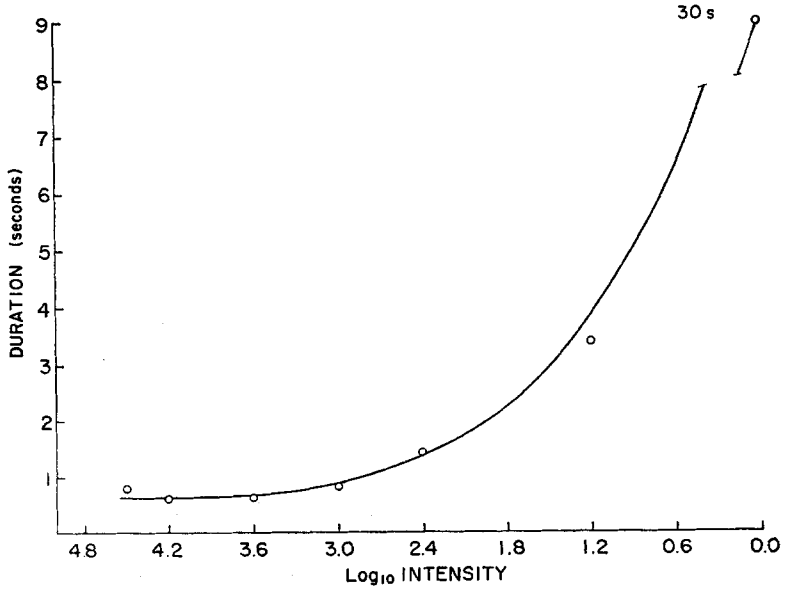

FIGURE 14. Plot of duration of optic ganglion cell hyperpolarizing response to light vs. $\log_{10}$ intensity.

IPSP's produced in the "C" cell for each spike of a type B photoreceptor in the contralateral eye were less frequently observed, although a brief train of spikes in the contralateral B photoreceptor invariably causes hyperpolarization with a cessation of firing in the "C" cell (Fig. 9). Individual IPSP's would be expected to decay significantly, however, if the contralateral photoreceptor made synapses on the terminal branchings of the "C" cell, more than 1.0 mm from its soma.

Nature of the Hyperpolarizing Response

Current pulses in optic ganglion cells caused a smaller potential change during the hyperpolarizing response to light than in darkness (Fig. 15) indicating a conductance increase during the response.

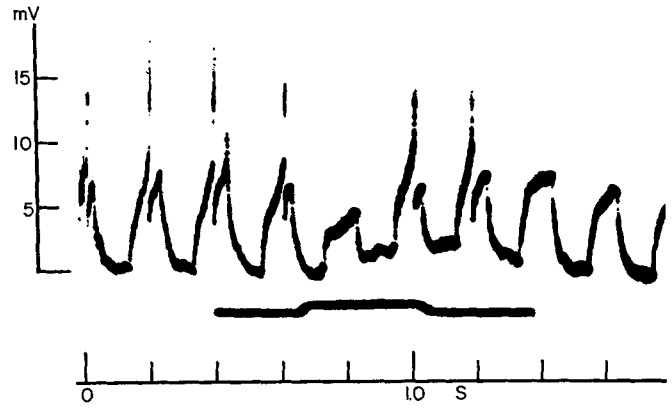

FIGURE 15. Current pulses to a spontaneously firing optic ganglion cell cause a smaller potential change during the hyperpolarizing response to light than in darkness.

Reversal of the hyperpolarizing response to light occurred when the optic ganglion cell soma was hyperpolarized by 30–35 mV. Assuming that the synaptic inhibition causing the hyperpolarizing response occurs at some distance from the soma adjacent to the terminal branchings of the photoreceptors (cf. Fig. 2), and that the potentials of the soma decrease by 30% at the synaptic sites (based on estimates for photoreceptors, see Alkon and Fuortes [1]), reversal of the hyperpolarizing response occurs when the subsynaptic membrane is hyperpolarized by 20–25 mV.

The maximum hyperpolarizing response to light was usually 15–20 mV. Allowing for an approximate 30% decrement from the synaptic locus to the recording electrode the potential change of the subsynaptic membrane would be 20–25 mV—very close to the probable reversal potential of the subsynaptic membrane. The magnitude of the hyperpolarizing response increased rapidly with intensity for dim lights, but by small increments, if at all, for moderate and bright flashes. Thus, although the number of photoreceptor impulses

increases more or less linearly with these intensities (Fig. 12 A), the synaptic effect of each impulse apparently decreases rapidly.

DISCUSSION

Organization of Photoreceptor-Optic Ganglion Cell Connections

Simultaneous recording from pairs of photoreceptors with optic ganglion cells, and pairs of optic ganglion cells with photoreceptors, indicate that type A (large spikes) photoreceptors do not impinge on, nor do they receive impingement from optic ganglion cells. Type B photoreceptors inhibit optic ganglion cells. Each optic ganglion cell most likely is inhibited by at least two and often by three type B photoreceptors. For a given optic ganglion cell the inhibition may be strongest from one photoreceptor. The double-spiking "C" cell receives input from all three type B photoreceptors in both the ipsilateral and contralateral eyes. Optic ganglion cells do not feed back onto photoreceptors nor do they interact with each other within the same optic ganglion, but they do interact across the *Hermissenda* "brain." These data suggest a wiring diagram of the visual system summarized in Fig. 16.

"C" Cell

Depolarizing currents in the "C" cell first caused aborted spikes and then full spikes with two different initial time-courses. An interpretation consistent with these findings would attribute the two types of spikes to at least two excitable foci. If indeed, there are two excitable foci, they may be located close together or far apart on the same axon. Alternatively, the two foci may occur on two different branches of the cell. Many of the cells (stained with Procion yellow) which crossed the brain gave off at least one sizeable branch ipsilaterally. The "C" cell was shown to have contralateral photoreceptor input and therefore must cross the brain since photoreceptors terminate soon after entering the cerebropleural ganglion. It thus is quite possible that the "C" cell has at least two branches on each of which is located an excitable focus. Each of these foci might be located near a site of photoreceptor synaptic impingement (from ipsilateral and contralateral eyes) where such impingement could be most effective in influencing spike activity.

Information Processing by Optic Ganglion Cell

A. INTENSITY It was seen that the correlation of the optic ganglion cell response with light intensity is poor. Dim to moderate lights are distinguishable from bright lights, but there is no information concerning gradation of light intensity from dim to bright. The bright flashes do cause a progressively prolonged hyperpolarization related to light intensity (Fig. 14).

There was some indication that the optic ganglion cell impulse frequency immediately after the hyperpolarizing response progressively increased for

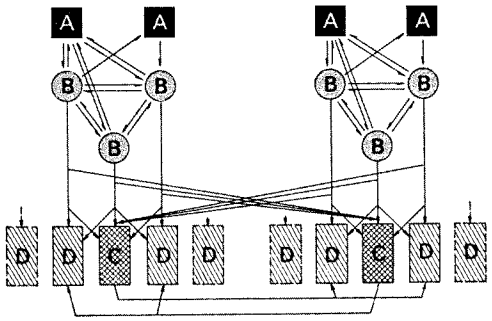

FIGURE 16. Diagram of interactions in the *Hermissenda* visual system. Each arrow represents inhibitory input. The two squares on each side are the type A photoreceptors, the three circles on each side, the type B photoreceptors. The type B photoreceptors are seen to inhibit with varying degrees of convergence the optic ganglion cells (the rectangles); five cells of each optic ganglion are represented here. At least one optic ganglion cell on each side, the "C" cell, is inhibited by the three type B photoreceptors in each eye. The "C" cells inhibit contralateral optic ganglion cells. The interactions of optic ganglion cells across the *Hermissenda* brain must be regarded as tentative and will be the subject of a future report.

dim to moderate light intensities. If the responses of several optic ganglion cells are averaged the increase is quite consistent unil moderately bright intensities (cf. Fig. 12 B). Thus, two competing coding processes might be present in the optic ganglion cell response to light: one involving an increase in optic ganglion cell firing (after the flash), the other involving prolonged absence of optic ganglion cell firing (for bright lights).

B. POSITION AND MOVEMENT DETECTION Experiments have been conducted (1) in which the image of an edge was moved across the *Hermissenda* eye. Specific photoreceptor responses occurred for opposite directions of movement. If movement detection is possible in each eye, as suggested by the responses of photoreceptors, a more specific organization of primary and secondary visual cells seems necessary to preserve this information. The extent of convergence of type B photoreceptor impingement onto optic ganglion cells, as well as the poor correlation of the optic ganglion cell response with light intensity, suggests, therefore, the existence of second order visual cells outside the optic ganglion.

Position and movement perception would be facilitated by comparison of visual input to the two eyes whose longitudinal axes are oriented at approximately 90° to each other. Provision for such comparison is apparent from the wiring diagram of Fig. 16. If for example the right eye alone were first illuminated the left "C" cell would hyperpolarize. The left "D" cells (ipsilaterally innervated) would fire more rapidly due to the disinhibition from the contralateral "C" cell which was hyperpolarized. Thus, the difference between the "C" and "D" cells' activity would be enhanced by the synaptic organization. This difference between C and D cell activity could signal the approach of a

moving shadow or light. A freely swimming *Hermissenda crassicornis* is able to turn and/or withdraw in a direction opposite to that of a moving shadow. With dim background illumination the animal will follow a moderate to bright light source often executing brisk turns to maintain a direction of swimming toward the light. For the execution of such a turn, the interaction of the optic ganglion cells on either side of the "brain" would permit coordination of the other side.

Convergence of visual information from two sides of a brain at the second order cell level is not found in vertebrates. Investigation of the visual and statocyst pathways in *Hermissenda crassicornis* as discussed here and in subsequent studies confirms the view (8) that integrative functions reserved for central nerve cells in vertebrates are often performed more peripherally in invertebrates. A detailed understanding of neural circuitry in this simple nervous system, therefore, may afford insights into synaptic functions of some relevance to the more inaccessible and complex central nervous systems of higher animals.

SUMMARY

(*a*) Intracellular recording of second order visual cells within the optic ganglion of *Hermissenda crassicornis* was performed. These cells are spontaneously active in darkness. They hyperpolarize and stop firing in response to a flash of light. Often an increased frequency of firing occurs immediately after the hyperpolarizing response.

(*b*) The second order visual cell response is not a simple function of the log of intensity of illumination.

(*c*) Simultaneous recordings revealed that type B photoreceptors inhibit the second order cells but type A photoreceptors do not. Additional details of the neural organization of the visual system were obtained.

(*d*) Iontophoretic injection of Procion yellow demonstrated two classes of optic ganglion cells. Cells of one class give rise to axons which end ipsilaterally; other cells send axons across the *Hermissenda* brain to the contralateral optic tract.

(*e*) A type of second order visual cell was identified which was inhibited by both ipsilateral and contralateral type B photoreceptors.

(*f*) Functional implications of the neural organization of this visual system are discussed. The existence of other second order visual cells was suggested.

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