Intersensory Interactions in *Hermissenda*

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ABSTRACT Hair cells of the *Hermissenda* statocyst respond to photic stimulation. This response requires the presence of at least one of the two eyes. Two principal hair cell responses to light were observed. The activity of photoreceptors in response to a light step is interrupted during firing of contralateral hair cells. The intersensory interactions between the statocyst and visual pathway underlying these responses were examined with simultaneous intracellular recordings. Evidence is presented that the statocyst of *Hermissenda* is an important channel for visual information.

INTRODUCTION

Interaction of visual and gravitational stimuli in determining an invertebrate's behavior has been observed with the molluscs *Lepidochitona cinera* (Evans, 1951) and *Littorina neritoides* (Fraenkel, 1927), and with the crustacean, *Palaemon xiphias* (Alverdes, 1928). Mechanoreceptive responses were first recorded extracellularly in the optic nerve of the crab *Podophthalmus* (Bush et al., 1964). Subsequently, gravitational influence on invertebrate interneurons was observed in the crayfish and rock lobster (Yamaguchi and Wiersma, 1965; Wiersma, 1966). Impulses recorded from fibers in the optic nerve occurred continuously during steady illumination. The receptive fields of a small percentage of these units were observed to change with rotation of the animal. Thus, sensory input to another pathway, probably that of the statocyst, could influence processing of visual information.

A study of the neurophysiologic basis of this type of interaction seemed possible in the relatively simple nervous system of *Hermissenda crassicornis*. In the work presented here I examine the interaction of the *Hermissenda* statocyst with the visual system using intracellular recording techniques. In addition to the nature of such interaction, I shall be concerned with its synaptic basis, the information transmitted, and finally a few functional implications.

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). The typical relationships of the eye, optic ganglion, and statocyst can be seen in Fig. 1 (Stensaas et al., 1968). The characteristic position of the optic ganglion with respect

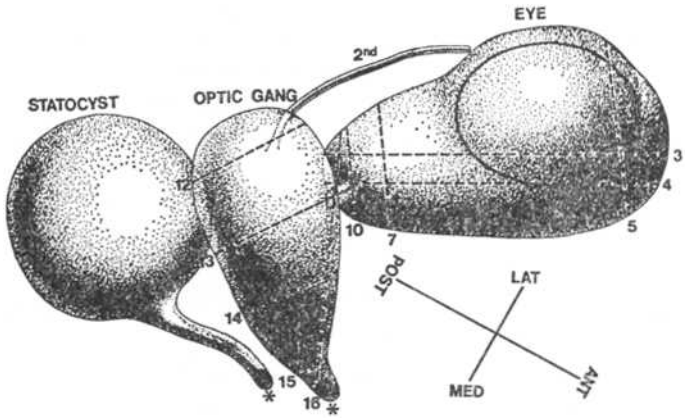


FIGURE 1. Reconstruction based on serial sections of the eye, optic ganglion, and statocyst demonstrating their typical positions as seen from a dorsal perspective. The optic ganglion is approximately 30 μm across. (Stensaas et al., 1968).

to the statocyst (from a dorsal view) is demonstrated by an Epon-embedded section stained with toluidine blue (Fig. 2).

A connective tissue sheath enveloping the circumesophageal nervous system (including the eyes, statocysts, and optic ganglia) was partially digested with Pronase (Calbiochem, San Diego, 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 Ω. 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 4,000 and 8,000 Å which reached the preparation from this source was about 6×10^3 ergs $cm^{-2} \cdot s^{-1}$. This intensity will be called intensity 1. Intensities will be given as optical density units, referring to the optical density of the neutral filters used to attenuate "intensity 1."

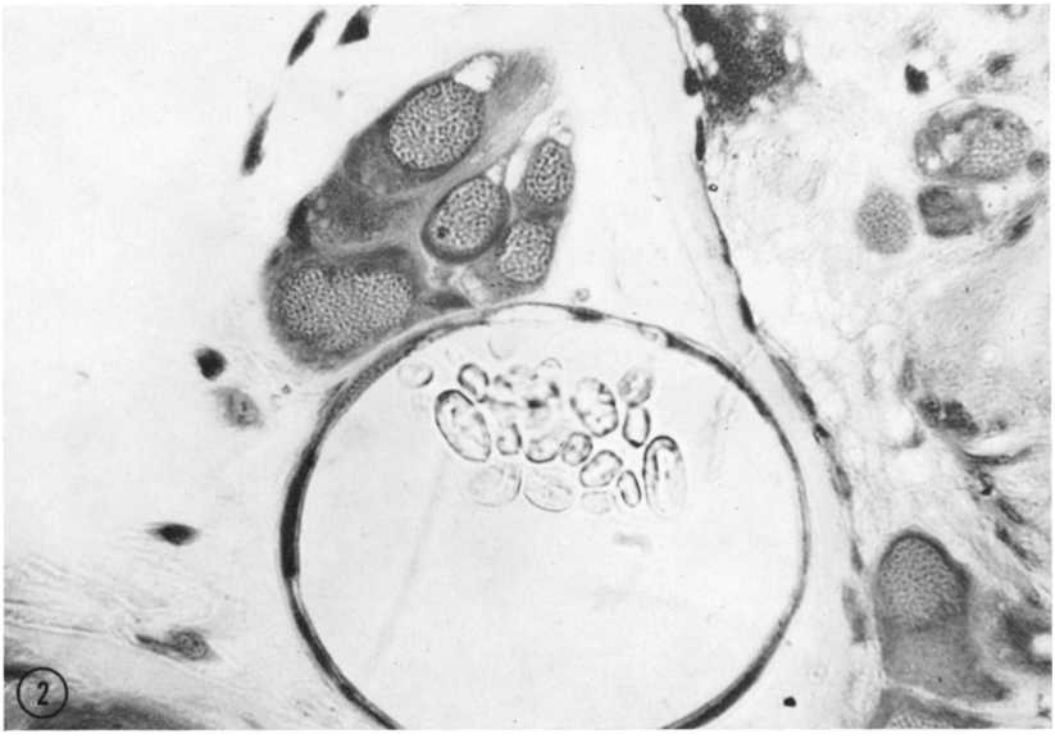


FIGURE 2. 3 μm section of optic ganglion and statocyst stained with toluidine blue. The common border is a typical relation of these two structures. Hair cells comprise the wall of the cyst and statoconia float within. × 750.

RESULTS

It was determined in previous studies (Alkon and Fuortes, 1972; Alkon, 1973) that in each eye there are two photoreceptors with average spike size of approximately 45 mV (type A) and three photoreceptors with average spike size of approximately 15 mV (type B). Type B photoreceptors are all closely mutually inhibitory, whereas type A cells have little or no interaction. Second-order visual cells were found to receive inhibition only from B photoreceptors.

Intracellular recording from hair cells revealed characteristic responses (see below) when the preparation was exposed to flashes of light. These responses disappeared when both eyes were removed. To investigate the synaptic basis of the statocyst interaction with the visual system, intracellular recordings were performed in hair cells simultaneously with type A and type B photoreceptors and optic ganglion cells. A train of spikes elicited by a depolarizing pulse in one cell often produced a slow hyperpolarizing wave and/or a cessation of activity in an accompanying cell (see below). The interactions between visual structures and hair cells were found in the present study to

be unidirectional for any given pair of cells. A summary of the interactions (as determined by passage of intracellular currents) is as follows (cf. Table I):

(*a*) Hair cells inhibit ipsilateral and contralateral photoreceptors.

(*b*) Type B photoreceptors weakly inhibit ipsilateral and contralateral hair cells.

(*c*) Type A photoreceptors excite ipsilateral hair cells. They also inhibit contralateral hair cells.

(*d*) Hair cells inhibit and are inhibited by ipsilateral optic ganglion cells.

TABLE I

SUMMARY OF HAIR CELL INTERACTIONS WITH VISUAL CELLS (OBSERVED BY PASSAGE OF INTRACELLULAR CURRENT PULSES)

	Photoreceptors		
	Type A	Type B	Optic ganglion cells
Ipsilateral			
Hair cells inhibit	3	2	2
Inhibit hair cells		3	3
Excite hair cells	3		
Total no. of pairs	17	29	14
Contralateral			
Hair cells inhibit	4	2	0
Inhibit hair cells	0	1*	0
Total no. of pairs	6	7	8

* The only pair (of eight-one) which was reciprocally inhibitory.

Interaction Features

Discrete inhibitory postsynaptic potentials were never observed to occur in hair cells after impulses in visual cells or vice versa. A train of impulses was necessary to elicit hyperpolarization in a receiving cell (Figs. 3, 4, 5). The hyperpolarizing waves evoked in visual cells by stimulating hair cells (Figs. 4, 5), and vice versa (Fig. 3), occurred with a latency (from the onset of a spike train in the presynaptic cell) between 50 and 150 ms. This latency was usually difficult to measure accurately even with maximum frequency of the presynaptic spike train. The hyperpolarizing wave occasionally could be reversed at minus 40–60 mV.

The excitatory effect of type A photoreceptors on hair cells (Fig. 6) had a greater latency than that for inhibitory intersensory interactions. This may be due to the presence of an interneuron (or interneurons), or the weaker nature of this excitation. The excitatory impingement of type A photoreceptors onto ipsilateral hair cells is the only exception to the rule of inhibitory synaptic interaction thus far followed in *Hermissenda*.

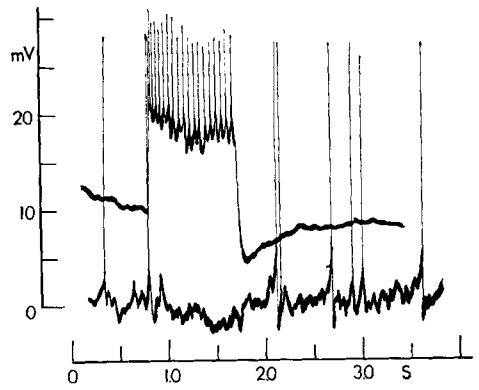


FIGURE 3. (Tracing) Hyperpolarizing wave in a hair cell after a spike train in a type B photoreceptor. The spike train was elicited by a 1.0 s 0.8 nA depolarizing current pulse through the photoreceptor electrode. Baseline frequency of hair cell: 200 impulses/min.

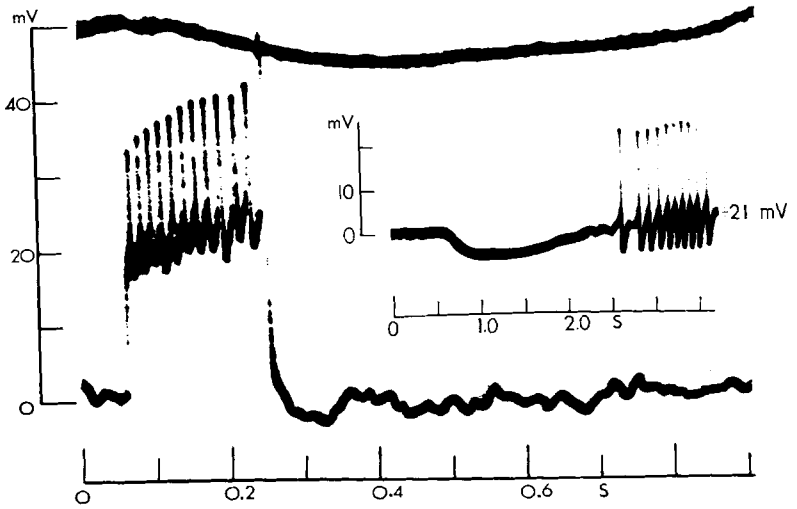


FIGURE 4. Impulses caused by a 1.0 nA, 400 ms depolarizing pulse to the hair cell (lower record) cause a hyperpolarizing wave in an ipsilateral type A photoreceptor (penetrated simultaneously). *Inset* shows the same wave at slower sweep speed when the photoreceptor has been depolarized by 21 mV.

The statocyst nerve was seen under the light microscope to pass through a region within the cerebropleural ganglion ($\sim$30 μm from its lateral border) thought to contain the synaptic endings of photoreceptors (Alkon and Fuortes, 1972). The site of ipsilateral intersensory interactions might not be far, therefore, from the site of interactions within the visual pathway (Alkon, 1973). With regard to contralateral interactions, it has been mentioned that hair cells often inhibit contralateral photoreceptors. It might be inferred,

therefore, that hair cells send a process across the brain to the contralateral optic tract forming synapses approximately 30 μm from the lateral border of the contralateral cerebropleural ganglion. Procion yellow injections of hair cells confirm that hair cell axons do cross to the contralateral side via the connective joining the two cerebropleural ganglia (Detwiler and Alkon, in preparation).

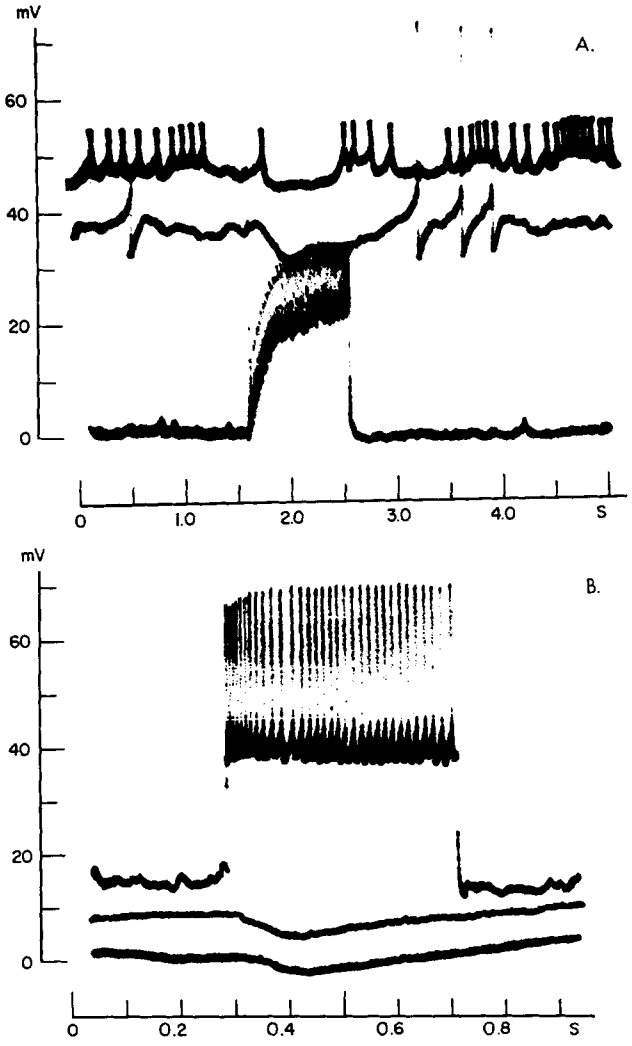


FIGURE 5. A. Type B photoreceptor (upper record) penetrated simultaneously with a type A photoreceptor (middle record) and a contralateral hair cell. A 1.0 nA, 0.85 s depolarizing current pulse in the hair cell hyperpolarizes the contralateral photoreceptors which are firing in response to a light step (3.6 OD). B. As above. Impulses caused by a 1.0 nA, 0.85 s pulse to the hair cell (now upper record) cause a hyperpolarizing wave in the two contralateral photoreceptors.

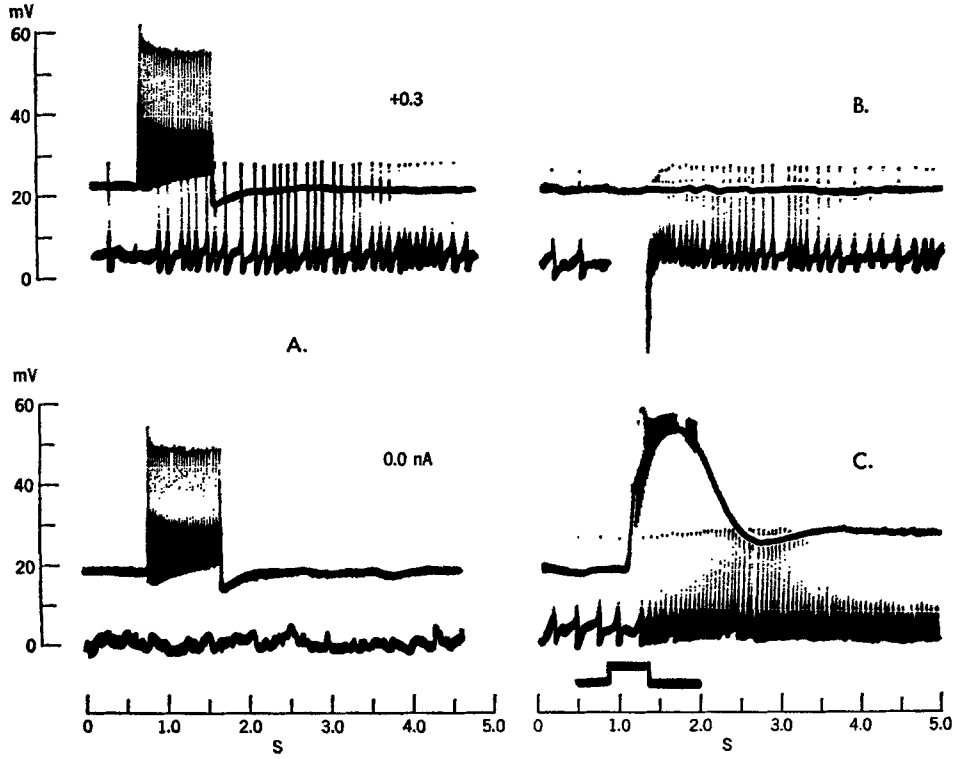


FIGURE 6. A. Type A photoreceptor (upper record) spike train, produced by a 1.2 nA. 0.9 s depolarizing current pulse, causes a delayed excitation in an ipsilateral hair cell (penetrated simultaneously). This effect is apparent only when a steady depolarizing current, 0.3 nA, is applied to the hair cell. B. A hyperpolarizing current pulse (2.0 nA) delivered to the hair cell is followed by an increased frequency of firing (0.3 nA applied to hair cell). Type A photoreceptor (upper record) is unaffected by firing of hair cell (lower record). C. Response of hair cell (lower record) to a 1.2 OD flash is, in this case, mainly depolarization. Baseline impulse frequency in the hair cell averaged 162/min (0.3 nA applied to hair cell).

Hair Cell Input to Photoreceptors

The technique developed thus far for mechanically stimulating hair cells while recording intracellularly (Alkon and Bak, 1973) only produces transient generator potentials with several superimposed impulses. Such stimuli produce little or no effect in photoreceptors (synaptic or otherwise). Simultaneous penetration of hair cells and photoreceptors, however, revealed a rather clear inhibition of photoreceptors after excitation of hair cells by current (Fig. 4). Steady firing of photoreceptors (in response to a light step) could be interrupted by a train of impulses elicited by depolarizing current in a simultaneously penetrated hair cell (Fig. 5).

Hair Cell—Optic Ganglion Cell Interactions

Optic ganglion cells were hyperpolarized and their spontaneous activity interrupted by a train of impulses in an accompanying hair cell. Inhibition of a similar nature was also observed in the opposite direction but never in both directions for a given hair cell and an ipsilateral optic ganglion cell. Hair cells were never found to interact with contralateral optic ganglion cells.

Light Responses in Hair Cells

TYPES Two main types of hair cell responses to a brief step of light (2–10 s) were observed:

(A) *Hyperpolarization and Cessation of Spontaneous Activity during Illumination* (*Fig. 7 A*). Usually the cell resumes firing if the light continues for more than 10–20 s. An initial increase of firing frequency occurs immediately after the light step.

(B) *An Initial Hyperpolarization Followed By a Prolonged Depolarization* (*Fig. 7 B*) Little change in firing frequency is seen when darkness resumes. For this response type, the frequency of firing during the depolarizing phase is a direct function of the intensity of illumination (Fig. 8). Occasional variations of these two types were also encountered.

Effect of Current

The response to light usually became more obvious if the cell was somewhat depolarized (Fig. 9). Hyperpolarizing the hair cell invariably abolished both phases of the light response, but reversal of the hyperpolarizing response was never clearly observed. As the hair cell membrane potential approaches the reversal potential of the hyperpolarizing wave, (with progressive hyperpolarization) this wave would be expected to diminish and eventually be abolished. It is not as clear, however, why progressive hyperpolarization does not increase the depolarizing phase of the hair cell light response. This would happen if the depolarizing wave were a local response (cf. Hodgkin, 1938) or if it resulted from a decrease in conductance of an ion with a negative equilibrium potential.

Origin of the Light Response

A. HYPERPOLARIZING PHASE Simultaneous recording of a hair cell with type A and/or type B photoreceptors demonstrates that the hyperpolarizing wave in the hair cell light response must, at least in part, arise from inhibition exerted by type B photoreceptors. It has been previously shown (Alkon and Fuortes, 1972) that at least one type B photoreceptor is always the most sensitive receptor in each eye. The more sensitive type B photoreceptors

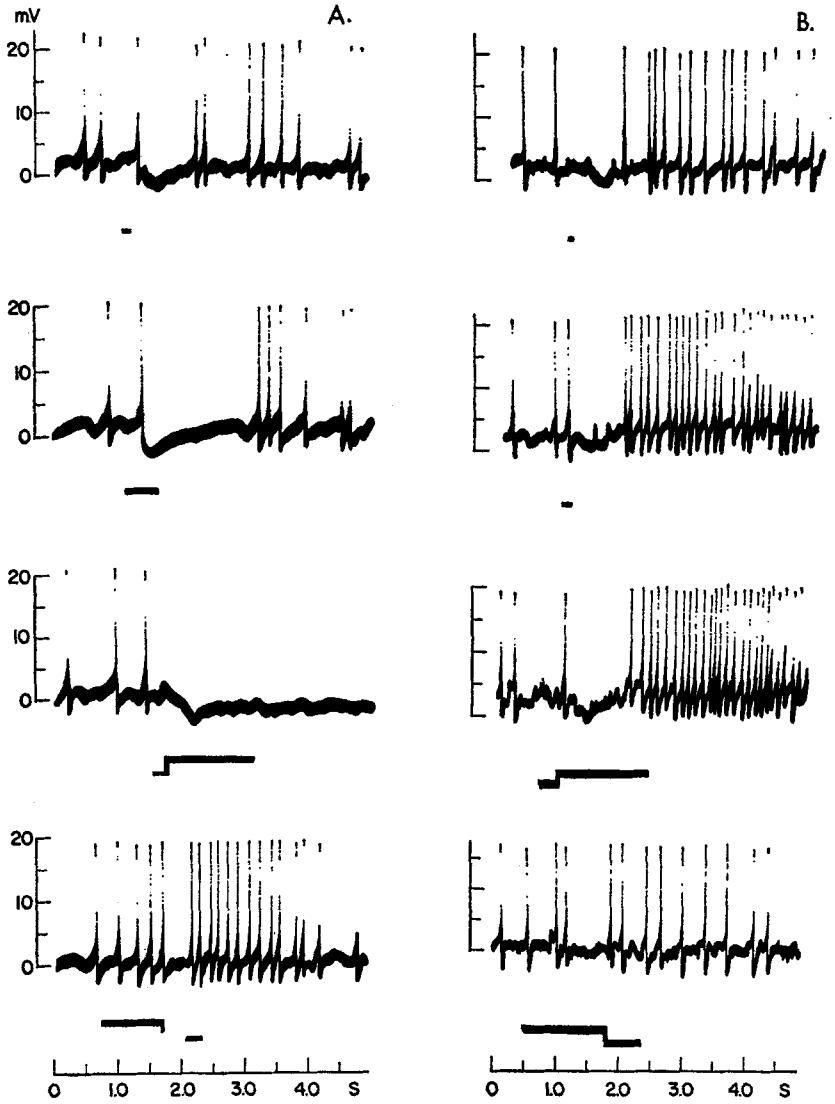


FIGURE 7. A. Hair cell "Off" response to light. Bar signals duration of light flash. In the two lower frames, vertical bars signal when steady light is turned on and then off. Light intensity 2.4 OD. Hair cell stops firing for 10 s light step then gradually resuming spontaneous activity. An increase in firing frequency occurs when light step is turned off. Frequency of spontaneous activity (upper most frame): 135/min. B. Hair cell "On" response to light. Light signals and intensity as above. An initial hyperpolarization is followed by an increase in frequency of impulses. No apparent change in activity occurs when a long step is turned off. Frequency of spontaneous firing (lowest frame): 170/min.

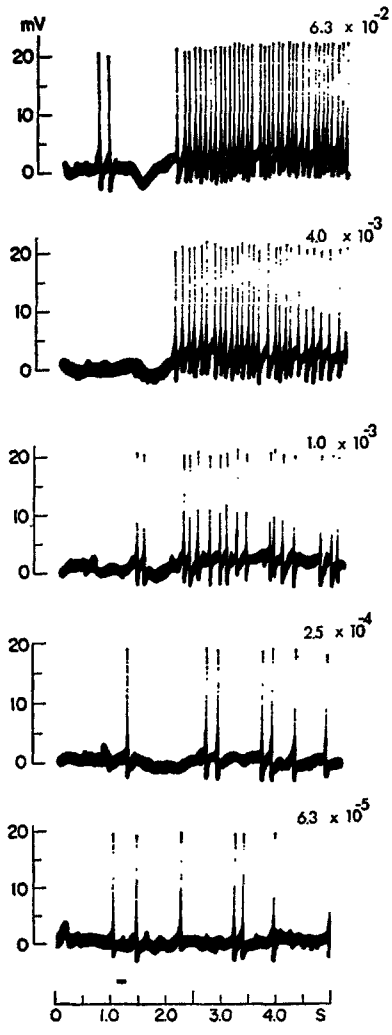


FIGURE 8

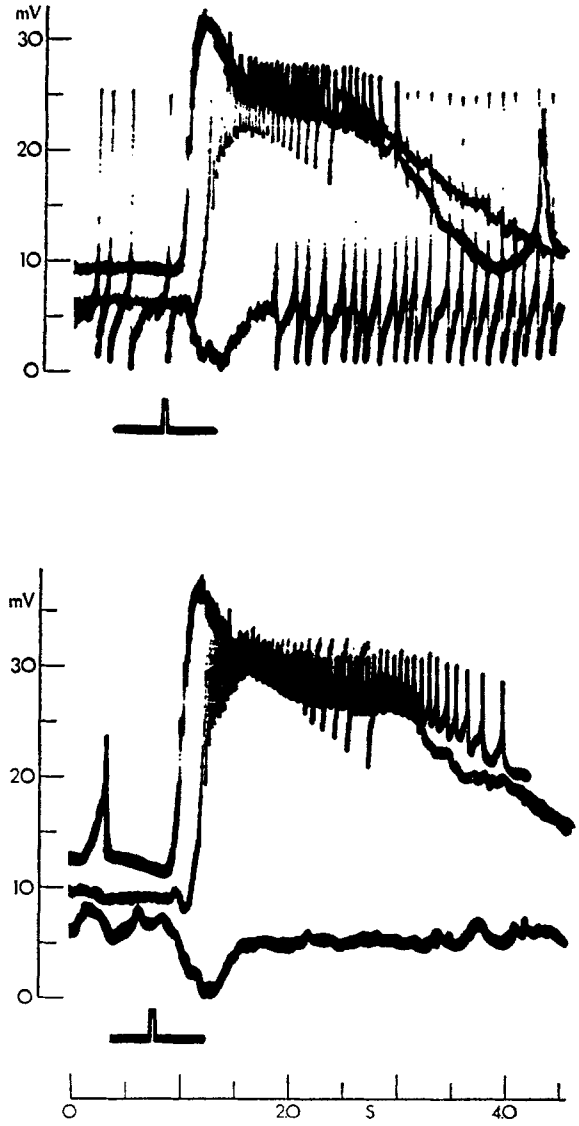


FIGURE 9

FIGURE 8. Hair cell "On" response as a function of light intensity. Firing frequency increases with increasing intensity (Brightest light at top of figure.) Bar at bottom signals duration of light flash. Spontaneous firing frequency (lowest record): 90/min. Note initial hyperpolarization followed by slight depolarization and marked increase in firing for bright flashes.

FIGURE 9. Response to light of type B photoreceptor (upper record), type A photoreceptor (middle record), and ipsilateral hair cell penetrated simultaneously. In upper figure, when the hair cell was depolarized approximately 5 mV, the increased frequency of firing with a light flash (1.2 OD) is apparent. Marker at lower left of each figure indicates duration of flash.

inhibit type A photoreceptors, causing the initial hyperpolarization with dim flashes. This hyperpolarization with dim lights in type A photoreceptors usually coincides with the hyperpolarization in simultaneously impaled hair cells (Fig. 10). Furthermore, impulses (elicited by depolarizing current) of type B but not type A photoreceptors produce a small hyperpolarizing wave in hair cells.

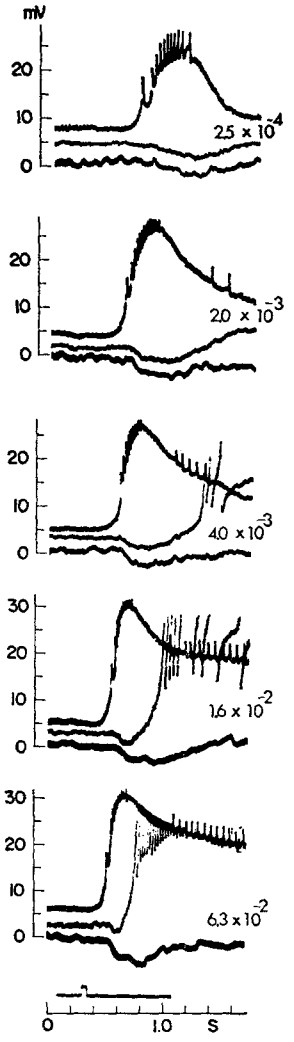
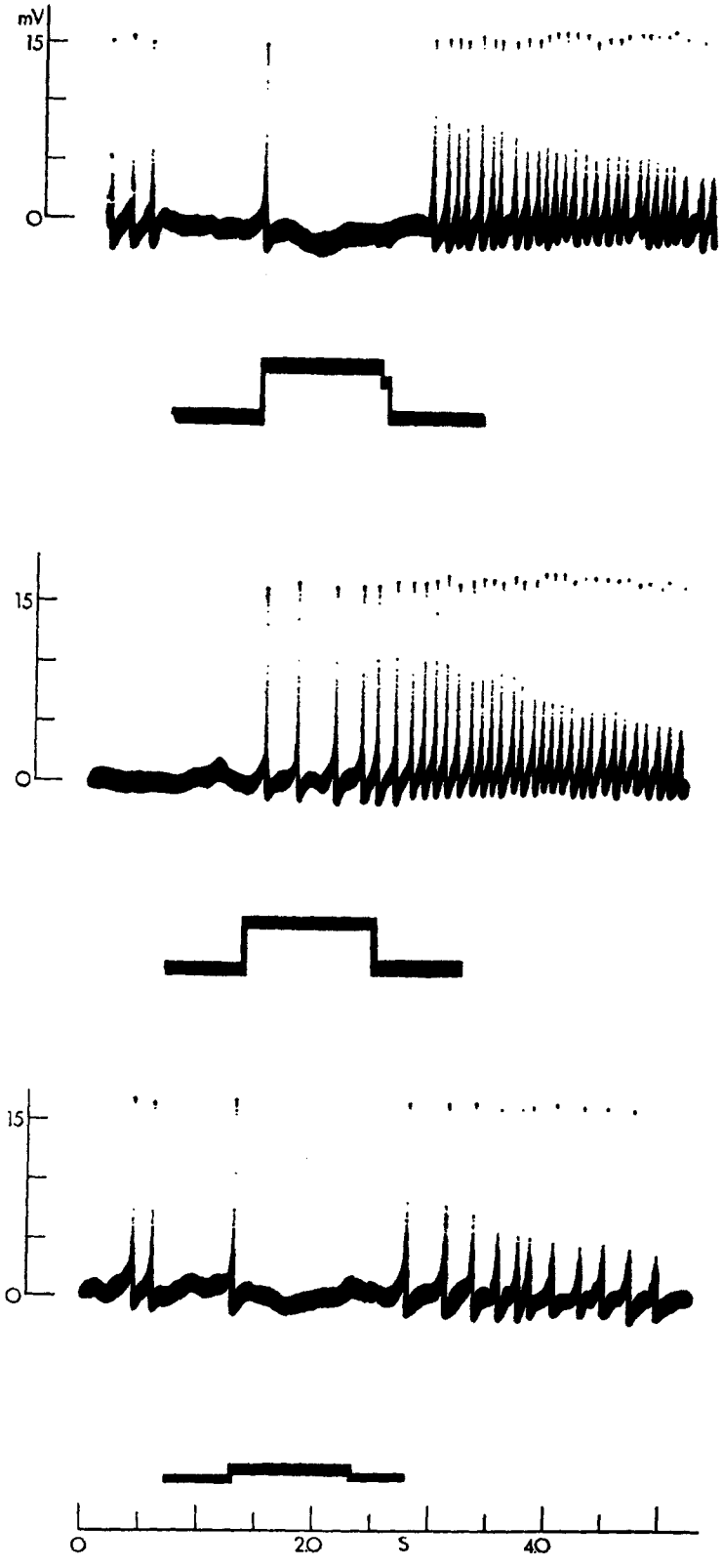


FIGURE 10. Response to light of type B photoreceptor (upper record), type A photoreceptor (middle record), and ipsilateral hair cell penetrated simultaneously. Flashes are of increasing intensity from top to bottom. Hyperpolarizing wave in type A photoreceptor and hair cell follows closely the depolarizing generator potential of the type B photoreceptor. Bar at lower left indicates duration of light flashes. Only the ipsilateral eye was illuminated.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B. DEPOLARIZING PHASE Three actions may contribute to the depolarization of hair cells in response to light.

1. *Overshoot after the Initial Hyperpolarization Caused By type B Photoreceptors* The depolarization and increased firing of hair cells usually followed an initial hyperpolarization or cessation of spontaneous activity in response to light. Hyperpolarizing current pulses in hair cells also are followed by a slight depolarization and briefly increased frequency of firing (Fig. 6).

2. *Disinhibition Due To Cessation of Spontaneous Activity of Inhibitory Optic Ganglion Cells* Ipsilateral optic ganglion cells inhibit hair cells (see above). Because second order visual cells in the optic ganglion are spontaneously active, some hair cells must be continuously inhibited in the dark and disinhibited in response to light.

3. *Delayed Excitation from Ipsilateral type A Photoreceptors* (See above.)

To further examine the origin of the hair cell light response, two light spots were made sufficiently small so as to stimulate one eye without stimulating the other. Table II summarizes the data from responses of 28 hair cells to illumination of the ipsilateral and contralateral eyes. It is readily apparent that depolarizing synaptic input to hair cells arises predominantly from the ipsilateral eye (cf. Table II). Although a small depolarization (Fig. 11) occasionally followed an initial hyperpolarizing wave with stimulation of the contralateral eye, this depolarization was never observed in isolation nor was it ever of a magnitude comparable to that resulting from illumination of the ipsilateral eye. Conversely, seven hair cells depolarized with little or no preceding hyperpolarization upon illumination of the ipsilateral eye (Fig. 11). The great majority of hair cells with a light response are hyperpolarized by the contralateral eye. Ipsilateral hyperpolarizing input was common but not observed as frequently as contralateral input.

Behavior

Certain behavioral features were observed in the large majority of more than 50 animals studied. If *Hermissenda crassicornis* is gently dropped into a tank of seawater, it follows a stereotyped behavioral sequence. It lands with its "foot" (the entire undersurface of the animal) touching bottom or quickly

FIGURE 11. Hair cell response to light. In the lowest record illumination of the contralateral eye alone causes a hyperpolarization followed by a slight increase of firing frequency. Illumination of the ipsilateral eye alone (middle record) causes depolarization and increased firing of hair cell. Illumination of both eyes simultaneously (upper record) consists of an initial hyperpolarization and a subsequent depolarizing response. Baseline firing frequency: 120/min. Bars indicate duration of light flash (1.2 OD intensity).

TABLE II

SUMMARY OF HAIR CELL RESPONSES (RECORDED INTRACELLULARLY) TO SEPARATE ILLUMINATION OF THE IPSILATERAL OR CONTRALATERAL EYE

	Illumination	
	Ipsilateral	Contralateral
Hyperpolarization	12	18
Depolarization (without preceding hyperpolarization)	7	0
Depolarization (after hyperpolarization)	3	5 (Slight)
Hyperpolarization with illumination of either eye		7
Hyperpolarization with illumination of contralateral eye and depolarization with illumination of ipsilateral eye		8
Number of cells responding to light		21
Total number of cells:		28

achieves this position after landing. It then will crawl in the direction of steepest incline until it finds a tank wall, i.e. a vertical surface, which it will crawl up. Often, upon reaching the water's surface, it will turn over, (i.e., "foot up"), and swim on its back for at least a short period of time. Swimming in this position, or crawling with its foot touching bottom, the animal moves quickly into a spot of light. It will travel 15 cm or more to reach such a spot and is often able to execute brisk turns to maintain a direction of swimming toward the light.

DISCUSSION

Intersensory Interactions

It was seen that hair cells receive synaptic input from the visual pathway and that photoreceptors are influenced synaptically by hair cell activity. The synaptic organization underlying this interaction (cf. Fig. 12) appears rather specific. The weakness of the hyperpolarization produced in a hair cell by a train of impulses in a type B photoreceptor might in part account for the infrequency with which it was observed. In response to a light flash, it is, however, often quite marked. This was often true even with light so dim as to excite only one or two type B photoreceptors in each eye. The hyperpolarizing wave may often be appreciable even with dim light because (*a*) firing frequency of a type B photoreceptor in response to a dim flash is often greater than that achieved with current passed through an intracellular electrode; (*b*) additional transmitter release might be associated with the generator potential itself; and/or (*c*) contralateral photoreceptor input might summate with the hyperpolarization produced by an ipsilateral type B photoreceptor. The infrequency of recordings from synaptically related pairs,

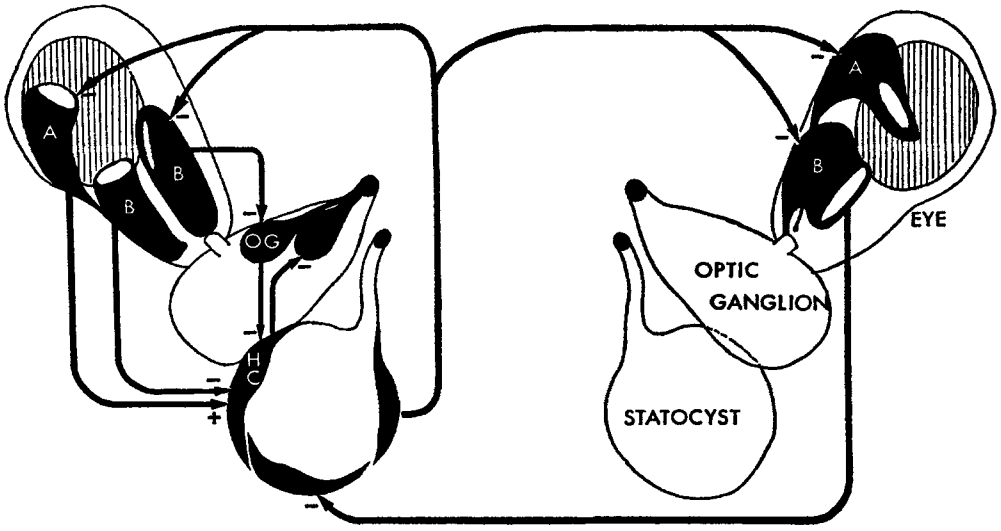

FIGURE 12. Interactions between hair cells and the visual system. The three symmetrical structures represented are 1.0–1.5 mm apart *in situ*. All interactions are inhibitory (−) with the exception of type A photoreceptors' excitatory effect (+) on ipsilateral hair cells. All interactions are unidirectional. Optic ganglion cells do not interact with contralateral hair cells.

however, does suggest that there is little convergence for any one type of ipsilateral visual synaptic input to hair cells, although a given hair cell may be affected at the same time by different types of ipsilateral synaptic input; (i.e., a type A photoreceptor, a type B photoreceptor, and an ipsilateral optic ganglion cell). Furthermore, a given hair cell can inhibit more than one contralateral photoreceptor (Fig. 5), indicating possible convergence for this interaction.

Two principal hair cell visual responses were found: (*a*) hyperpolarization and cessation of firing, and (*b*) hyperpolarization followed by depolarization and increased firing. Single-eye illumination demonstrated that the depolarizing visual input to hair cells is largely from the ipsilateral eye. The hyperpolarizing input arises from both eyes, but more frequently from the contralateral eye (cf. Table II).

The intersensory interactions, observed recording within cell somata, are uniformly weaker than the visual intrasensory interactions. This may be a function of hair cell geometry and membrane characteristics, or indeed represent a weaker synaptic effect.

Information Processing

Different features of the hair cells' visual input suggest that the statocyst of *Hermissenda* provides an important channel for visual information. In a

previous report (Alkon, 1973) optic ganglion cells were shown to be inhibited by type B photoreceptors. No part of the optic ganglion cell response to light (neither the magnitude and duration of the hyperpolarizing wave nor the frequency of firing immediately after this wave) varied systematically with light intensity. By contrast, one type of hair cell light response, the "on" response (Fig. 8), was a direct function of light intensity (Fig. 13).

If movement and/or position discrimination is possible within each eye alone (Alkon and Fuortes, 1972), the information would not be transmitted to the optic ganglion cells due to the convergence of synaptic input from

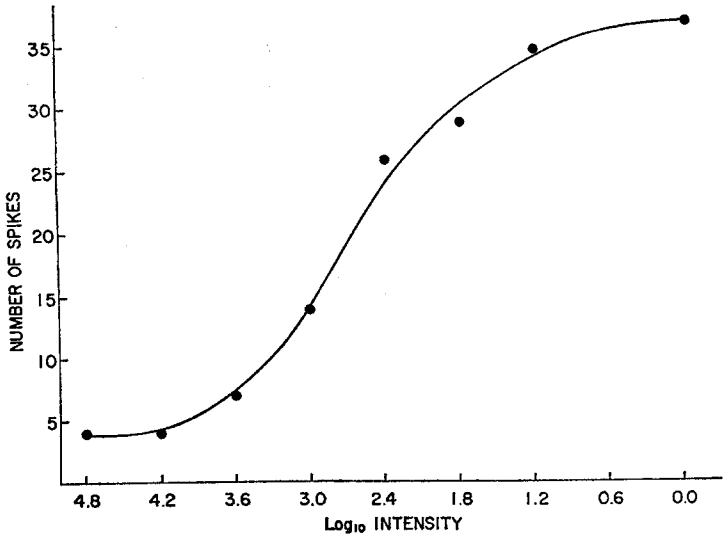

FIGURE 13. Number of impulses occurring in a 2.5 s interval after the initial hyperpolarizing response to light of a hair cell ("On" response) as a function of log light intensity.

type B photoreceptors (Alkon, 1973). The data accumulated thus far suggest less ipsilateral convergence of photoreceptor input onto hair cells. Thus, the information for movement and/or position discrimination may be preserved by the organization of the statocyst interaction with the visual pathway.

Finally, unlike optic ganglion cells which all hyperpolarize and stop firing during a light step, the hair cells have at least two different types of response to a short (2–10 s) step of light: (*a*) cessation of firing, and (*b*) increased firing during the step.

Temporal Association of Stimuli

Reference to Table I and Fig. 12 reveals that optic ganglion cells do not interact with the contralateral statocyst. Photoreceptors, however, commonly receive inhibition from contralateral hair cells. Photoreceptors, except for

occasional spontaneous activity, are quite in darkness. Hair cell inhibition of photoreceptors in darkness, therefore, would have little effect on the optic ganglion cells. If, however, the hair cell inhibition is associated in time with illumination (cf. Fig. 5), the activity of the photoreceptors (and thus the postsynaptic optic ganglion cells) will be significantly altered. Similarly, those hair cells which are least active will be least influenced by photic input. It was seen (Fig. 9) that depolarization may bring out the hair cell response to light. The state of depolarization of a penetrated cell could of course vary with the injury associated with impalement. Since, however, the hair cell also depolarizes with movements of the statocyst, (Alkon and Bak, 1973) and presumably with changes in orientation, hair cell activity will be more significantly altered when the visual stimulus is associated in time with the appropriate gravitational stimulus.

When the animal is floating in an upside-down position, different hair cells will be preferentially stimulated than when the animal is crawling. Those hair cells most depolarized for a given orientation of the animal would be expected to be most affected by light. Certain motor neurons might be directly or indirectly influenced by hair cell activity for the animal to move toward light when it is floating and other motor neurons when it crawls. If indeed the hair cells are an important channel for visual information, the animal's position and movement at any given time would be expected then to influence further movements in response to visual stimulation.

Responses to light of *Littorina neritoides* (Fraenkel, 1927) change with the animal's orientation. *Hermissenda*, however, was observed to seek light whether in a floating or crawling position. For *Hermissenda*, then, the dependence of a final movement command upon a temporal association of specific visual and gravitational stimuli might account for the positional independence of the animal's phototaxis.

SUMMARY

(*a*) Hair cells of the *Hermissenda* statocyst respond to photic stimulation. This response was present only when at least one of the *Hermissenda* eyes remains.

(*b*) Two principal hair cell responses were observed during a 10.0 s light step:

(1) "Off" response. Cessation of firing and increased firing when the step is turned off.

(2) "On" response. A brief initial hyperpolarization followed by an increased frequency of firing. This increase in firing frequency was a direct function of the log of light intensity.

(*c*) The activity of photoreceptors in response to a light step is interrupted during firing of contralateral hair cells.

(*d*) The intersensory interactions between the statocyst and visual pathway underlying the above responses were examined. Intracellular recording was performed for two or three cells simultaneously and currents were passed using a bridge circuit.

(*e*) A wiring diagram was formulated for connections between the two pathways. The principal interaction was a unidirectional hyperpolarizing wave associated with a train of impulses in the presynaptic cell.

(*f*) The "On" response was found to consist of two phases:

(1) A depolarization resulting largely from illumination of the ipsilateral eye.

(2) A hyperpolarization arising from both eyes but more commonly from the ipsilateral eye.

(*g*) Whether floating on its back or crawling on its foot, *Hermissenda* was observed to actively move toward and enter a spot of light.

(*h*) The dependence of certain visual responses in hair cells on a temporal association of visual and gravitational stimuli may account for the positional independence of the animal's phototaxis.

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