Signal Transformation with Pairing of Sensory Stimuli

DANIEL L. ALKON

From the Section on Neural Systems, Laboratory of Biophysics, National Institute of Neurological and Communicative Disorders and Stroke, National Institutes of Health, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

ABSTRACT Rotation of the isolated nervous system of *Hermissenda* in a caudal orientation causes a synaptic hyperpolarization accompanied by elimination of impulse activity during the steady-state phase of type A but not type B photoreceptors' responses to light. Rotation of the isolated nervous system in a cephalic orientation causes a synaptic depolarization with increase of impulse activity during the steady-state phase of both type A and type B photoreceptors' responses to light. These effects of rotation on photoreceptors are explained by known synaptic interactions. Sufficient redundancy is found to be provided by the neural organization of the visual system and its interaction with the statocyst to preserve much of the visual information in spite of signal transformation in specific photoreceptors resulting from pairing of rotation with light.

INTRODUCTION

Photoreceptors in the eyes of *Hermissenda* are inhibited by impulse activity of the statocyst hair cells (Alkon, 1973 *b*). Hair cells, in turn, may be excited, and/or inhibited by photoreceptors (Alkon, 1973 *b*). A detailed analysis of the specific cell to cell connections responsible for these synaptic effects has been in progress now for some time (Alkon, 1973 *a*, *b*; 1975 *b*). In addition, other studies have demonstrated behavioral modification, mediated at least in part, by the interaction of these two sensory pathways (Alkon, 1974, 1975 *a*).

Although a stimulus (light) to which the photoreceptors are directly sensitive, and the hair cells indirectly sensitive, i.e. via synaptic input, is easily delivered and well-defined, a comparable physiological stimulus for the hair cells has only recently become available (Alkon, 1975 *c*; Alkon and Bak, 1973). This consists of subjecting the isolated nervous system to a centrifugal force generated by a turntable (see Methods).

Thus, it has become possible to monitor intracellular receptor responses to a stimulus, which has a direct effect, when paired with a second distinct stimulus with an indirect effect, i.e. via a synaptic pathway. It will be shown that appropriate pairing of light and rotation can transform responses of specific receptors to their preferred stimuli. This transformation, in turn, will be seen to be dependent on the orientation of the nervous system (and thus, the intact animal) with respect to the center of rotation. It will also be demonstrated that

the neural organization of the visual system and its interaction with the statocyst provides sufficient redundancy to preserve much of the visual information in spite of signal transformation in specific photoreceptors. These data suggest that the design of this neural system allows for modification (at least short-term) by pairing of sensory stimuli without the loss of other information essential to the organism's normal functioning. Such modification is demonstrated and its mechanism analyzed in another, forthcoming study (Alkon, in preparation). This report will be limited to responses to stimuli given only once and not repetitively which was found necessary for modification.

METHODS

Preparation

Hermissenda were provided by Dr. Rimmon Fay of the Pacific Bio-Marine Supply Co. (Venice, Calif.) and Mr. Michael Morris of the Penisula Marine Biological Supply Co. (Monterey, Calif.). Animals were maintained with 6½ h of daily light (cf. Alkon, 1974) in an "Instant Ocean" aquarium at 13°C. The circumesophageal nervous system of *Hermissenda* was dissected and isolated as previously described (cf. Alkon, 1973 *a*; Alkon and Fuortes, 1972).

Type A photoreceptors (Alkon and Fuortes, 1972) were penetrated by placement of the electrode tip in the ventral anterior portion of the eye. That type A photoreceptor in the lateral portion of the eye was used. A silent, nonspiking, unresponsive cell, presumably a pigment cell, was almost always penetrated before impalement of the type A photoreceptor. Following this procedure, it was possible to impale the lateral type A photoreceptor in 95 out of 100 attempts.

Type B photoreceptors were penetrated by placement of the electrode tip in the dorsal posterior portion of the eye. Occasionally a silent cell was encountered before a successful type B impalement was made. Unless otherwise indicated all photoreceptors are dark adapted at least 15 min before light stimuli are given.

Mounting and Stimulation of Preparation

The isolated circumesophageal nervous system is placed, immersed in a few drops of seawater, on a conventional microscope glass slide. Two strips of Vaseline, 1 cm long are placed immediately above and below the preparation. Stainless steel pins are then laid across the connectives of the nervous system. The pins are in direct contact with the surface of the glass slide and are held this way because the ends of the pins are imbedded in one of the Vaseline strips. A ring of Vaseline (approximately 0.4 cm high and 3 cm in diameter) is then spread around the preparation pinned as described between the two Vaseline strips. A Lucite disk, 0.2 mm thick and 3.5 cm in diameter, is then placed on top of the Vaseline ring after it has been filled with seawater. Numerous holes (1.1 mm in diameter) permit passage of microelectrodes. The advantages of this means of mounting for rotation are discussed elsewhere (Alkon, 1975 *c*).

The preparation mounted as described above was placed, ventral side down, on the turntable. Unless otherwise specified (*Excitation with Orientation Reversal* under Results) the caudal end of the axis through the center of the circumesophageal nervous system pointed directly away from the center of rotation.

Rotation of the preparation (13 cm from the center of rotation) was effected by a Garrard turntable (Garrard Co., Swindon-Wiltshire, England, model Zero 92) which had

been reinforced by a 0.5-inch aluminum annulus (Fig. 2). For additional details see Alkon, 1975 *c*.

Light was provided by 10 G. E. lamps (type CM 332, 0.2 A, 6 V, 1 cd each, General Electric Co., Cleveland, Ohio) spaced evenly on a circle, whose center was the center of rotation, 14-cm diameter and 45 cm immediately above the preparation.

Intracellular Recording

As in previous studies, the circumesophageal nervous system was incubated in a solution of a digestive enzyme before intracellular recording. In this study a somewhat milder treatment was used: 17 min of incubation in collagenase (type 1, Sigma Chemical Co., St. Louis, Mo.) solution (0.5–1.0 mg/cm^3).

Intracellular recordings were made with glass micropipettes filled with 4 M potassium acetate (resistances of 60–100 MΩ). The electrode was connected via a silver wire to the input stage of the high impedance amplifier. The reference electrode was a chloride/silver wire. A Wheatstone bridge circuit was used to pass current through the recording electrode. Current was monitored by recording the potential drop across a 10-MΩ resistor in series with the electrode. All experiments were performed at room temperature (approximately 22°C). See Alkon, 1975 *c*, for details concerning the amplifier used for potential recordings.

Cell Selection and Pretreatment

Lateral type A and type B photoreceptors were dark adapted for 15 min before repeated 60-s light steps at 30-s intervals were begun. Most cells responded with an approximately constant number of impulses after the fourth light step, i.e. a steady state of dark adaptation was achieved. Occasionally additional light steps were necessary before such a steady state was reached. A few photoreceptors were discarded which: (*a*) never achieved a steady state of dark adaptation, i.e. progressively fewer impulses occurred during the light response, and/or responded with progressively smaller generator potential amplitudes; (*b*) responded with less than 60 impulses during the light response.

The amplitude of the initial response of the photoreceptors after dark adaptation (using 1-cd lights arranged as described under Methods) ranged between 40 and 60 mV. This range approaches the maximum response range previously observed for photoreceptors (Alkon, 1973 *a*, Alkon and Fuortes, 1972) using a quartz-iodide light source delivering 2×10^5 ergs cm^{-2} s^{-1} to the eyes.

RESULTS

The synaptic effect on photoreceptors resulting from rotation of the isolated nervous system will be described for type A and type B photoreceptors. How this effect varies when rotation is paired with light will then be examined for two different orientations. Finally, examples are given of hair cell responses to rotation with and without a paired visual stimulus.

To introduce these results some mention of the differences between type A and type B photoreceptors should be made. Previous observations provide clear criteria by which the two type A and three type B photoreceptors in each of the two *Hermissenda* eyes can be distinguished from each other. (Alkon, 1973 *a*, *b*; Alkon and Fuortes, 1972). These criteria concern the photoreceptors' spike amplitudes, spontaneous activity, responses to light, and their synaptic relations.

The criteria previously reported are summarized in Table I. Additional criteria are also included in Table I (asterisks) which are now described.

Type A Photoreceptors

Oscillations with a regular periodicity can frequently be observed in the steady-state response to bright lights. Such oscillations can be seen more clearly or are only demonstrated in the steady-state responses of other type A photoreceptors by the application of a weak hyperpolarizing current step (Fig. 1). These oscillations could reflect inhibitory input from type B photoreceptors at least one of which also oscillates (see below).

Slow depolarizing waves occurring in the dark were usually found to increase progressively in amplitude during the first 10–15 min of dark adaptation of type A photoreceptors and then progressively decrease in amplitude and frequency thereafter. The depolarizing responses of type A photoreceptors to moderate and bright light steps are invariably followed by a marked (5–10 mV) and somewhat prolonged (40–60 s) after-hyperpolarization.

Type B Photoreceptors

Oscillations with a regular periodicity (but less frequent than for type A photoreceptors) occur in the steady-state response of at least one type B photoreceptor (Fig. 1). In addition to the previously described spontaneous activity and inhibitory postsynaptic potentials (IPSP's) recorded from type B photoreceptors in darkness (lower trace, Fig. 2), at least one of the three type B photoreceptors

TABLE I
PHOTORECEPTOR CHARACTERISTICS

	Type A (2)	Type B (3)
Location	Anteroventral	Posterodorsal
Average spike amplitude	45 mV	15 mV
Activity in darkness	Slow depolarizing waves*	Spontaneous impulses, IPSP's, EPSP's*
Response to dim lights (dark adapted)	Synaptic hyperpolarization	Depolarizing generator potential with superimposed impulses
Response to moderate and bright lights (dark adapted)	Depolarizing generator potential followed by long-lasting after hyperpolarization,* oscillations during steady-state response*	Depolarizing generator potential followed by depolarizing oscillations with bright flashes. Oscillations during steady-state response (for at least one type B)*
Response to bright lights (light adapted)	Depolarizing response to brief flashes	Hyperpolarizing response to brief flashes
Synaptic interactions	Inhibits type B photoreceptors	Inhibit each other, type A photoreceptors
	Excite and inhibit ipsilateral hair cells	Inhibit ipsilateral optic ganglion cells and hair cells
	Inhibited by hair cells	Inhibited by hair cells

* Characteristics not previously described.

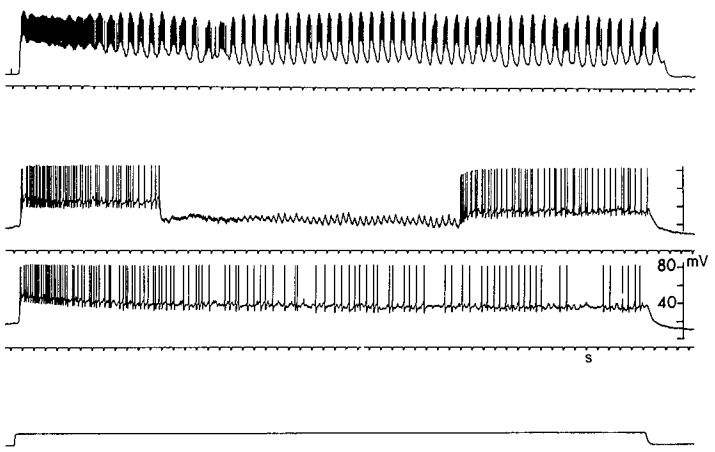

FIGURE 1. Steady-state response to light of type A and B photoreceptors. A weak negative current (0.5 nA) in a type A photoreceptor demonstrates oscillations in middle record not readily apparent in the type A response to light (lower record). Upper record shows oscillations during the light response of a type B photoreceptor. Note that these oscillations occur somewhat less frequently than those in the type A cell. Bottom trace indicates duration of light stimulus. Tops of impulses in middle and lower records are not included in record.

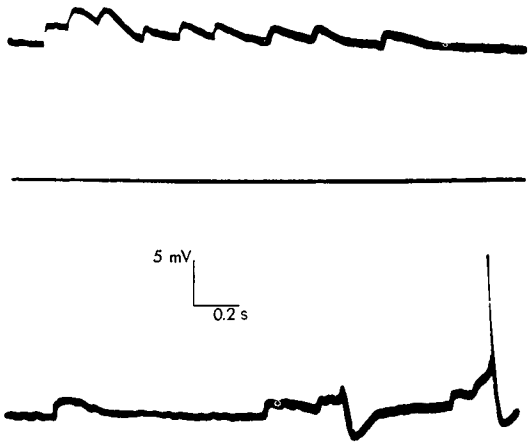

FIGURE 2. Excitatory postsynaptic potentials (EPSP's) during dark adaptation of type B photoreceptors. Upper record shows a train of EPSP's. Lower record includes EPSP's, an IPSP, and a spontaneous impulse.

receives frequent trains of excitatory postsynaptic potentials (EPSP's) (upper trace, Fig. 2).

Rotation Control

Rotation in the dark produced no measurable effect on photoreceptors when both statocysts were destroyed (Fig. 3). Rotation of such a preparation also

caused no change of membrane potential or decrease of impulse activity of the type A Photoreceptor during its steady-state response to light (Fig. 4). Occasionally some regularity of impulse activity not present without rotation was suggested in the steady-state response of these photoreceptors during rotation. This

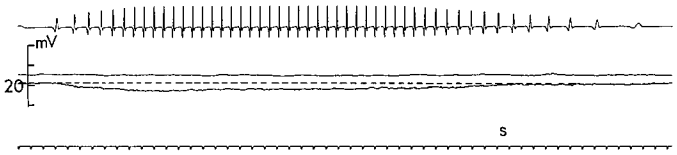

FIGURE 3. Effect of rotation on type A photoreceptors in darkness. The upper of the two cell records is that of a type A photoreceptor in preparation from which both statocysts had been removed. Lower tracer shows hyperpolarization produced by rotation in type A photoreceptor in preparation with intact statocysts. Note the hyperpolarization begins to decrease before the onset of deceleration. Dashed line indicates level of resting membrane potential for lower record. The amplitude of monitor signal (top trace) is proportional to the angular velocity of the turntable. The interval between monitor signals equals the period of the turntable's rotation.

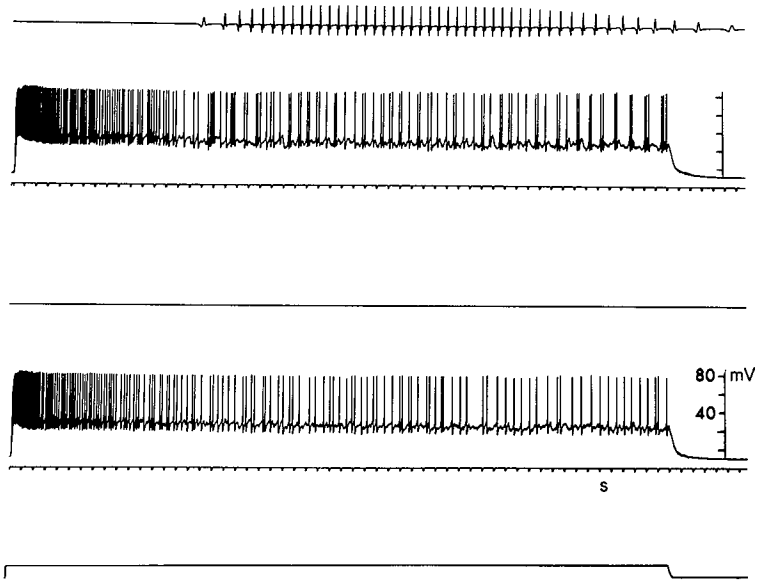

FIGURE 4. Effect of rotation on type A photoreceptor during its response to light when the statocysts are removed from the circumesophageal nervous system. Lower record is response to light alone. Upper record is response to rotation with light. Note the absence of any change in membrane potential or decrease of impulse activity associated with rotation. Bottom trace indicates duration of light stimulus. The amplitude of monitor signal (top trace) is proportional to the angular velocity of the turntable. The interval between monitor signals equals the period of the turntable's rotation.

was due to a small shadow produced by the slip ring mounting (pictured as in Alkon, 1975 *c*). It was clear from this control, then, which was repeated for 12 preparations, that the type A photoreceptors do not respond to rotation without the presence of intact statocysts.

Synaptic Effect in Photoreceptors Produced by Rotation

Rotation produces a clear hyperpolarization in type A photoreceptors (Table II, Fig. 3) via the synaptic input from hair cells. Note that the hyperpolarization reaches a maximum with maximum acceleration, but shows some decay (as would be expected of a synaptic effect) before the onset of deceleration. Many type B photoreceptors are not affected by rotation (Table II) although in some cells a slight hyperpolarization and/or a decrease in spontaneous activity can be observed.

Pairing of Light and Rotation

The hyperpolarization produced in type A photoreceptors by the synaptic effect of rotation was usually increased during the steady-state response of the receptor to light. The hyperpolarization, in addition, is accompanied by a complete cessation of the receptor's impulse activity (Figs. 5, 7). For those type B photoreceptors which hyperpolarized with rotation this was not the case. During the steady-state response (to moderate as well as bright lights) of the type B photoreceptor, rotation, at most, produced a transient and/or slight decrease in impulse activity (Fig. 6). Thus, for no type B photoreceptors was impulse activity abolished or markedly reduced when rotation was paired with moderate to bright ($^1/_3$ to maximal intensity) light, whereas for the great majority of type A photoreceptors impulse activity in response to light was abolished by the synaptic input of hair cells in response to rotation. If for these same type A photoreceptors rotation was begun first and then a light step was given during the rotation, impulse activity was never entirely abolished although it was significantly reduced (Figs. 7, 8).

TABLE II

PHOTORECEPTOR RESPONSES TO ROTATION

	Type A photoreceptors	Type B photoreceptors
Caudal Orientation		
No Response	2	13
Hyperpolarization and/or decrease in impulse activity	56	10
Cessation of impulses during steady-state response to light	55	0
Total no. of cells	58	23
Cephalic Orientation		
Depolarization in dark	8	5
Increase in impulse activity during steady-state response to light	8	5
Total no. of cells	8	7

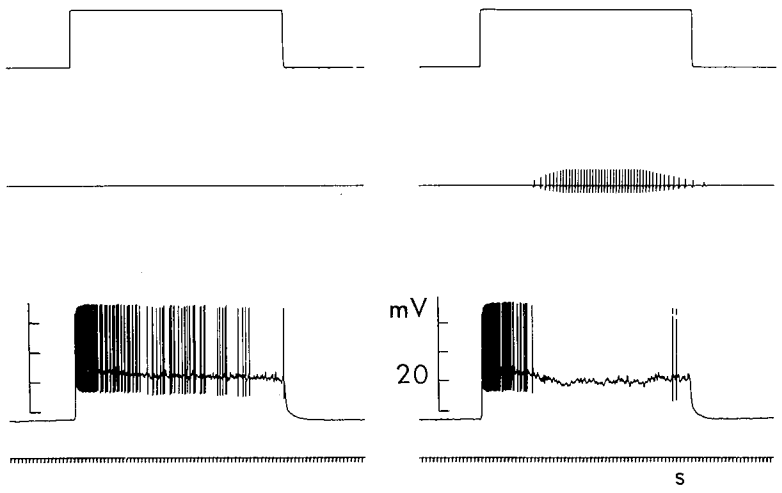

FIGURE 5. Effect of rotation on a type A photoreceptor during its response to light. Record on left shows response to light alone. Record on right shows response to light and rotation. Top trace indicates duration of light stimulus. The amplitude of monitor signals (middle trace) is proportional to the angular velocity of the turntable. The interval between monitor signals equals the period of the turntable's rotation.

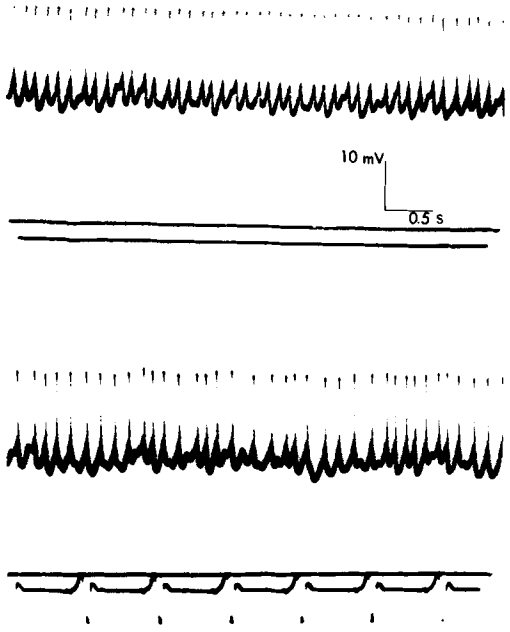

FIGURE 6. Effect of rotation on a type B photoreceptor during its steady-state response to light. Upper record shows steady-state response to light alone. Lower record shows steady-state response to light with rotation. Bottom trace artifacts monitor rotation, here 78 rpm.

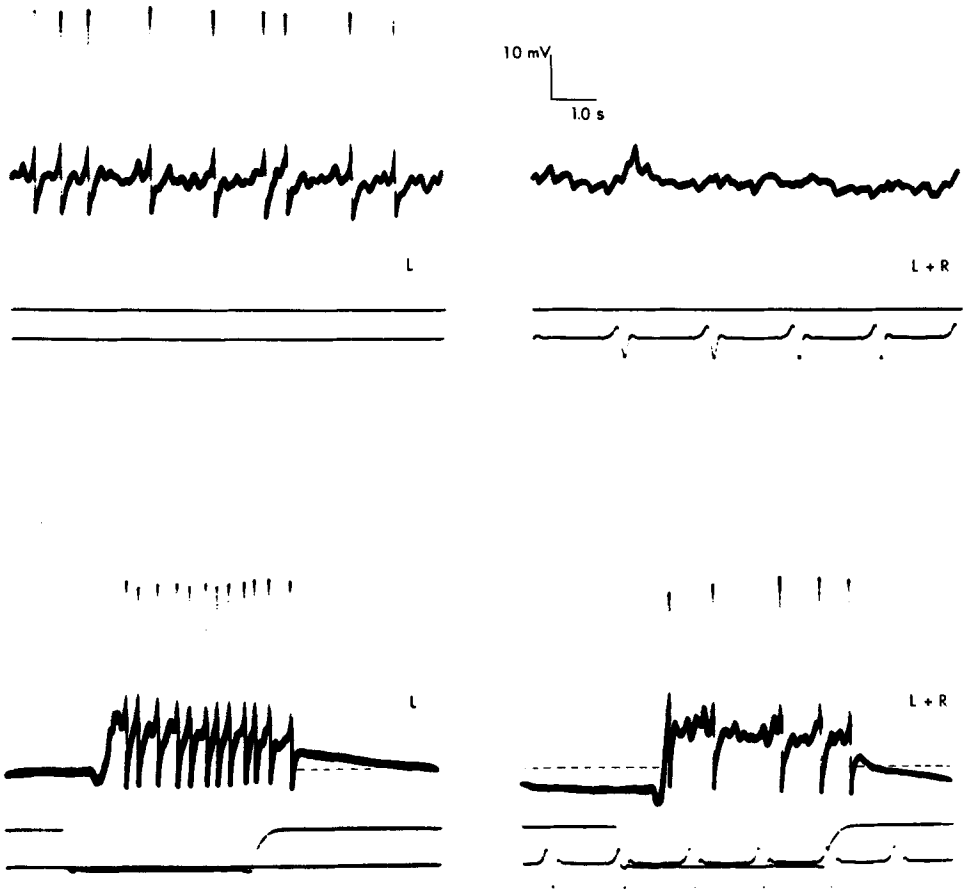

FIGURE 7. Effect of rotation on a type A photoreceptor during its response to light. Upper records show activity of a type A photoreceptor during its steady-state response to light alone (left) and light with rotation (right) begun 10 s after the onset of the light. Lower records show response of a type A photoreceptor (after 8 min of dark adaptation) to light alone (left) and light with rotation (right) begun 40 s before the onset of the light. In lower frames the middle trace indicates the duration of the light stimulus. In frames on the right the artifacts in the bottom trace monitor rotation.

Excitation With Orientation Reversal

The results above were obtained when the preparation was oriented with the caudal end of the axis through the center of the circumesophageal nervous system pointing away from the center of rotation (caudal orientation). When the circumesophageal nervous system was turned 180° with respect to the center of rotation (cephalic orientation) the effect of rotation was to excite both type A and type B photoreceptors. This excitatory effect is manifest in darkness as a small depolarization (with no firing) of the type A cell and a slight depolarization and increase in firing of type B cells. During these cells' steady-state responses to

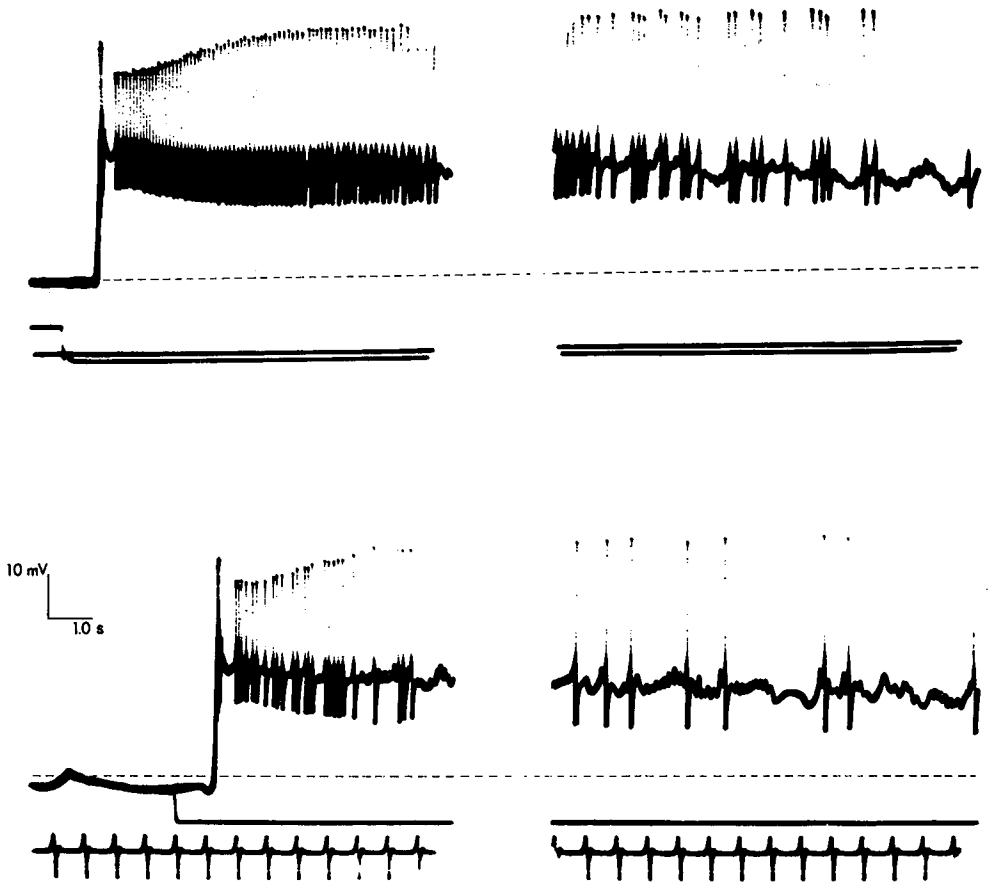

FIGURE 8. Effect of rotation on a type A photoreceptor during its response to light. Upper records show response to light alone. Lower record shows steady-state response to light with rotation begun 40 s before the onset of the light. Signals in bottom trace (lower frame) monitor rotation, here 78 rpm. The other trace in all frames indicates duration of light stimulus. Dashed line indicates level of resting membrane potential.

light an increase in firing is produced by rotation (Fig. 9). Thus, not only is the response to light of a given photoreceptor, e.g. the lateral type A cell, affected by synaptic input resulting from statocyst stimulation, but it is affected specifically by which part of the statocyst is maximally stimulated by the centrifugal force. The synaptic interactions responsible for this excitation of photoreceptors by hair cells are discussed below.

Hair Cell Responses to Rotation and Light

Hair cells are known to respond in at least two ways to photic stimulation of the *Hermissenda* eyes: hyperpolarization with cessation of firing and depolarization with increase in firing (Alkon, 1973 *b*). The synaptic effect of light was observed

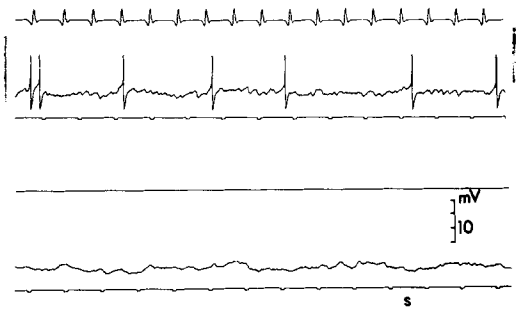

FIGURE 9. Effect of rotation on responses of a type A photoreceptor (cephalic orientation) to light step. Lower record: response to light step alone (1/3 maximum intensity). Upper record: response to light step paired with rotation (indicated in top trace by artifacts). Note presence of IPSP's arising from type B photoreceptors (Alkon, 1973 *a*) when light is paired with rotation. Tops of impulses in upper record are not included in record. Signals in top trace monitor rotation.

to augment the response to rotation of some hair cells and to diminish the response of other hair cells.

Thus cessation of firing produced by light was also effected in some hair cells during the cells' own depolarizing response to rotation. In other hair cells the primary receptor response to rotation was similar to the synaptic effect of light (e.g. in some cells rotation caused an increase in firing in addition to the increased firing caused by light).

DISCUSSION

Hyperpolarizing Response to Rotation

That a greater number of type B photoreceptors (in the caudal orientation) than type A cells are unresponsive to rotation is consistent with previous observations (Alkon, 1973 *b*). In those previous experiments hair cell inhibition of photoreceptors was demonstrated by simultaneous intracellular recording and current passage in photoreceptor-hair cell pairs. Only 4 in 36 type B-photoreceptor-hair cell pairs as compared to 7 in 23 type A-photoreceptor-hair cell pairs showed inhibition of photoreceptors by hair cells. Impulse trains elicited by depolarizing current pulses in these hair cells produced hyperpolarizing waves in the photoreceptors. Other factors could influence the efficacy of hair cell inhibition of photoreceptors and thus account for the different effects produced by rotation on the type A and type B photoreceptors particularly during their responses to light. These include the proximity of hair cell synaptic input to the photoreceptor impulse focus, the absolute magnitude of the inhibitory effect, and the processes responsible for impulse inactivation.

Hair cells located on that part of the *Hermissenda* statocyst away from the center of rotation (i.e. in front of the centrifugal force vector) depolarize and increase firing in response to rotation (Alkon, 1975 *c*). Those in back of the vector hyperpolarize slightly and decrease firing with rotation. The hyperpolarizing waves in photoreceptors produced by rotation, then, must be the result of a

net increase in firing of those hair cells which inhibit the photoreceptors.

IPSP's (previously shown to result from type B photoreceptor impulse activity) are usually observable during the hyperpolarizing response of the type A photoreceptors to light paired with rotation (Fig. 7). Inhibition of photoreceptors by hair cells, unlike inhibition by other photoreceptors (cf. Alkon, 1973*a*, *b*), never consists of discrete IPSP's, but a hyperpolarizing wave produced by a train of hair cell impulses. This indicates first that type B photoreceptor activity is not substantially reduced by rotation. In addition it suggests that the site of synaptic input from the type B photoreceptor onto the type A cell is sufficiently remote from the site of synaptic input from the hair cells onto the type A cell to prevent significant shunting of one synaptic effect by the other.

Regardless of the sequences, rotation first and then light or vice versa, the hyperpolarization recorded in the soma of type A photoreceptors, although substantial, would not be expected to cause such a marked inhibition of spike activity unless the site of the synaptic input from the hair cells is much closer to the spike-generating zone than to the recording electrode. The evidence accumulated to date supports this interpretation (Alkon and Fuortes, 1972; Detwiler and Alkon, 1973).

These data demonstrate that for a specific cell, hair cell, or photoreceptor, a synaptic input in response to a sensory stimulus can modify the effect of another sensory stimulus to which that cell is directly responsive. Particular attention was paid to the differences between the synaptic effects of rotation on type A and type B photoreceptors. Rotation abolishes impulse activity during the steady-state light response of type A but not type B photoreceptors. Thus, visual information can still be transmitted during rotation by the type B photoreceptors to optic ganglion cells, since it has been shown (Alkon, 1973*b*) that only type B but not type A photoreceptors synapse on optic ganglion cells.

Depolarizing Response to Rotation

Provided a hair cell was located on that part of the statocyst away from the center of rotation, the cell's response to rotation was depolarizing, independent of the nervous system's orientation with respect to the center of rotation. Unlike the hair cell responses, the synaptic response of photoreceptors to rotation was hyperpolarizing for the caudal orientation and depolarizing for the cephalic orientation. Recording and current passage from 59 hair cell-photoreceptor pairs (Alkon, 1973*b*) however, revealed only one synaptic effect of hair cells on photoreceptors: inhibition. The excitation produced in photoreceptors by rotation can be easily explained if the hair cells which inhibit photoreceptors are located in the caudal, but not the cephalic part of the statocyst. When the nervous system has a cephalic orientation, the caudal hair cells, now located toward the center of rotation, hyperpolarize as their own response to rotation (Alkon, 1975*c*) as well as in response to synaptic inhibition from the cephalic hair cells. Since hair cells on opposite sides of the statocyst are mutually inhibitory (Detwiler and Alkon, 1973), when the cephalic hair cells are excited by centrifugal force, they inhibit the caudal hair cells and thus further disinhibit the photoreceptors. It should be noted that this excitation produced by rotation,

presumably by disinhibition, is ineffective for type A photoreceptors in darkness, but causes a change in impulse activity when paired with a light/step. Here, again, an effective signal in a receptor is the resultant of both sensory stimulation and synaptic input.

Physiological Significance

What meaning might the neural organization presented here have for the animal? The centrifugal force generated by the turntable is 0.9 *g*. If the animal is moving upward, i.e. directly opposite to the direction of the earth's gravitational force, 1.0 *g* will be exerted on those hair cells in the caudal portion of the statocyst. This corresponds almost exactly to the caudal orientation of the circumesophageal nervous system with respect to the center of rotation in the experiments of this study. Therefore, when the animal moves upward, the activity in the type A photoreceptor will be the resultant of excitation from ambient light and inhibition from the caudal hair cells. When it moves downward, the reverse holds: the type A photoreceptor will be disinhibited by excitation of cephalic hair cells. If the animsl moves in that direction which maximizes the type A cells' impulse activity, the animal could be expected to approach the water's surface during daylight. At or near the surface a change from a vertical to a horizontal position could increase type A activity still more by reducing excitation of the caudal hair cells and thus inhibition of type A photoreceptors. At night, the activity of type A photoreceptors, which are unresponsive to dim light (Alkon, 1973 *a*) would no longer determine the direction of movement of the animal, which in any case becomes quiescent during the dark period of its diurnal rhythm (Alkon, 1974).

Hermissenda exhibit a clear negative geotaxis after gentle dropping into a container of seawater, i.e. they crawl in the direction of steepest incline until reaching a vertical surface which they then ascend, moving in a direction opposite to that of the earth's gravitational force (Alkon, 1973 *b*). They then remain at the water's surface for some time or float, dorsal side down. This would be consistent with the discussion above. The negative geotaxis could result if the animal oriented (after disorientation such as might occur with dropping, shaking, or oceanic turbulence) so as to maximize the activity of the caudal hair cells. The animal's direction of movement after disorientation, then, could be the resultant of two determinants: the activity of type A photoreceptors (accounting for positive phototaxis [Alkon, 1974]) and the activity of the caudal hair cells (accounting for negative geotaxis).

If the animal were repeatedly disoriented, as it might be with turbulence at the water's surface, the following might occur. After each disorientation, the animal would follow the sequence described above: dropping, vertical orientation, approach toward maximal light near the water's surface, disorientation, and dropping with shaking or turbulence. Each time this occurred the animal would be maximizing inhibition (by the caudal hair cells) of type A photoreceptors during stimulation with light. These conditions resemble those of the associative training already described (Alkon, 1974, 1975 *a*). Repeated pairing in a type A photoreceptor, then, of a depolarization produced by light with a hyperpolariza-

tion produced by rotation or turbulence might be expected to play a role in the persistence of behavioral and correlated neural modification. Such a role is, in fact indicated in another report (Alkon, in preparation). If this is so, the neural design just described is well suited for allowing a type of short-term associative training in some cells, i.e. involving type A photoreceptors and hair cells, while preserving essential visual information in other cells, i.e. the type B photoreceptors and consequently the optic ganglion cells.

Daily sequential migrations and their dependence on geotactic and phototactic reflexive behaviors have been studied for other intertidal gastropods (Newell, 1970). Behavioral sequences comparable to that proposed here for *Hermissenda* were observed for these animals. To further analyze the behavioral significance of the electrophysiological findings in the present study, intact animals could be exposed to the same centrifugal acceleration stimulus used for the isolated nervous system. Such a stimulus could be associated with (*a*) diffuse illumination, (*b*) darkness, (*c*) a light focused at the axis of rotation, (*d*) a light annulus at the periphery of the rotating table. All of the conditions could be used with and without immersion of the animal in a seawater bath. Observation of *Hermissenda* in their natural setting and/or a simulated natural setting in the laboratory would undoubtedly add additional valuable information.

SUMMARY

(*a*) Characteristics distinguishing type A and type B photoreceptors are presented.

(*b*) Rotation of the isolated nervous system of *Hermissenda* (in a caudal orientation) causes a hyperpolarization accompanied by elimination of impulse activity during the steady-state phase of the type A photoreceptor's response to light.

(*c*) If the statocysts are destroyed, rotation of the isolated nervous system causes no hyperpolarization in type A photoreceptors nor any decrease of impulse activity during the steady-state response to light (caudal orientation). This result together with previous findings proves the synaptic origin of the hyperpolarizing response of type A photoreceptors to rotation.

(*d*) Rotation may cause no hyperpolarization in type B photoreceptors. When such a synaptic effect is present it is never sufficient to eliminate impulse activity during the steady-state response to light.

(*e*) Rotation of the isolated nervous system (cephalic orientation) causes a depolarization accompanied by an increase of impulse activity during the steady-state phase of type A and B photoreceptors' responses to light.

(*f*) For certain hair cells, as for type A photoreceptors, a synaptic input in response to a sensory stimulus can signficantly modify the effect of another sensory stimulus to which the cells are directly responsive.

(*g*) The results demonstrate that the neural organization of the visual system and its interaction with the statocyst provides sufficient redundancy to preserve much of the visual information in spite of signal transformation in specific photoreceptors resulting from pairing of rotation with light.

Received for publication 22 May 1975.

REFERENCES

ALKON, D. L. 1973 *a*. Neural organization of a molluscan visual system *J. Gen. Physiol.* **61**:444.

ALKON, D. L. 1973 *b*. Intersensory interaction in *Hermissenda*. *J. Gen. Physiol.* **62**:185.

ALKON, D. L. 1974. Associative training of *Hermissenda*. *J. Gen. Physiol.* **64**:70.

ALKON, D. L. 1975 *a*. Neural correlates of associative training in *Hermissenda*. *J. Gen. Physiol.* **65**:46.

ALKON, D. L. 1975 *b*. A dual synaptic effect on hair cells in *Hermissenda*. *J. Gen Physiol.* **65**:385.

ALKON, D. L. 1975 *c*. Responses of hair cells to statocyst rotation. *J. Gen. Physiol* **66**:507.

ALKON, D. L., and A. Bak. 1973. Hair cell generator potentials. *J. Gen. Physiol.* **61**:619.

ALKON, D. L., and M. G. F. Fuortes. 1972. Responses of photoreceptors in *Hermissenda*. *J. Gen. Physiol.* **60**:631.

DETWILER, P. B., and D. L. ALKON. 1973. Hair cell interaction in the statocyst of *Hermissenda*. *J. Gen. Physiol.* **62**:618.

NEWELL, R. C. 1970. Biology of Intertidal Animals. American Elsevier Publishing Co., Inc., New York.