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RECEPTOR MECHANISMS IN THE ANTENNAE OF THE  
HERMIT CRAB, PETROCHIRUS CALIFORNIENSIS.

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RECEPTOR MECHANISMS IN THE ANTENNAE OF THE  
HERMIT CRAB, PETROCHIRUS CALIFORNIENSIS

by  
Robert C. <sup>ement</sup>Taylor

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THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my  
direction by Robert Clement Taylor  
entitled Receptor mechanisms in the antennae of the hermit  
crab, Petrochirus californiensis  
be accepted as fulfilling the dissertation requirement of the  
degree of Doctor of Philosophy

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A handwritten signature in black ink, appearing to read "Robert Taylor", is written over a horizontal line. The signature is cursive and somewhat stylized.

#### ACKNOWLEDGMENTS

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## ABSTRACT

Gross dissections and histological techniques have revealed a chordotonal organ in the antennal flagellum of the hermit crab, Petrochirus californiensis. The paired cell bodies lie on the most proximal segment of the flagellum (F1) and the dendrites cross the joint and are embedded in the connective tissue or exoskeleton of the 2nd proximal segment (F2). The receptor cells are arranged in a circle, one cell thick, just below the F1 hypodermis. Separate nerves originate from the dorsal half (50 cells) and the ventral half (30 cells) of the circle.

Separate recording from the two nerves indicates that stimulation of the cells is caused by movement of the joint between the F1 and F2 segments. Single fiber recordings disclose three types of receptor cells, found also in crustacean elastic strand stretch receptors, i.e., position, movement, and intermediate cells. By analyzing the motion around the F1-F2 joint it was found that flexing, and not stretch, was the mechanically transduced event. Depending on the amount of flexion, a cell will respond to movement, differences in position, or both movement and position (intermediate). A comparison between the flagellar chordotonal organ (FCO) and elastic strand stretch receptors suggests that in the elastic strand receptors dendritic flexure is the excitatory phenomenon, and that all responses, except those small amplitude position responses, arise from the same type of cell membrane; the type of response that is produced depends only on the mechanical arrangement between the dendrites

and the elastic strand.

Functionally the FCO is homologous to the lateral line system of fish and amphibians, and is thus considered to constitute a portion of the crustacean acoustic receiving system responding to near-field acoustic stimulation. The FCO is also the "seat" for the antennal texture sense. It also responds to water currents in the environment as well as currents which the organism itself produces (passive echo-location).

## INTRODUCTION

Studies of the structure and function of the crustacean antennae have, in the past, been concerned primarily with those of the lower forms (Abraham & Walsky 1929, Racovitza 1925, Vajdovsky 1901, Wetzel 1935). Most of our knowledge of the decapod antennae comes from behavioral experiments. From these it has been rather conclusively demonstrated that the antennae bear chemoreceptors (van Buddenbrock 1945, 1952) and that vibration sensitivity is present in the antennae (Herter 1925). Tactile sensitivity in the antennae is necessary for a crayfish running a maze (Gilhousen 1927) and is involved in the detection of enemies, prey, and obstacles (Cohen & Dijkgraaf 1961).

Cuticular hairs on the antennae, which are innervated by one or more bipolar dendrites, have been accepted as the units of chemo- and tactile-reception, responding to touch, vibration, water currents or even airborne sound waves. Of particular interest in the present study are the chordotonal organs, a distinct type of internal mechanoreceptor which act as proprioceptors and also participate in special sense organs (Bullock & Horridge 1965). A chordotonal organ is composed of one or more units, each consisting of one bipolar sensory neuron and three associated cells. Chordotonal organs have been observed in the antennae of the Amphipod, Caprella (Wetzel 1935) and at the base of the flagellum of the antennule of the lobster they form a proprioceptor (Laverack 1964). Analysis has revealed that their function is similar to the chordotonal

organs of the leg joints of Garcinus (Wiersma 1959), that is, they signal movement and position.

A chordotonal organ was also found in the basal segment of the antennal flagellum of the hermit crab, Petrochirus californiensis. The present study was undertaken to describe the anatomy of the receptor and the parameters of stimuli to which it will respond. The possible importance of this receptor to the hermit crab is discussed.

## MATERIALS AND METHODS

Histological studies. Adult hermit crabs, ranging in size from 8 to 15 centimeters (measured from rostrum to tip of abdomen) were obtained from the Gulf of California in the vicinity of Puerto Penasco, Sonora, Mexico. The animals were held in aquaria with natural, filtered sea water. Crabs have been maintained in the laboratory for as long as three months with no apparent deterioration when fed a diet of brine shrimp and clams.

Antennae were removed by cutting across the basal segment. For histological work they were cut into convenient lengths and placed for two days in Bouin's solution, embedded in paraffin, serial sectioned, and stained with either Hematoxylin and Eosin (Pantin 1959), or silver using a modification of Holmes' (1942) technique. Reconstructed drawings were made from the serial sectioned material.

Gross dissections also were performed and exposed surfaces stained with reduced methylene blue. However due to the small size of the antennae and the hardness of the surrounding exoskeleton, dissections of living material proved very difficult. Therefore, the following method was developed to allow more suitable dissections with a minimum of internal damage when the exoskeleton was removed.

The antenna was submerged in Bouin's solution for several days after nonessential portions had been cut away to permit better penetration of the fixative. With this treatment the exoskeleton was softened, becoming rather parchment-like, while muscle, connective tissue, nerves

and blood vessels became more rigid, thus maintaining their proper orientation when a portion of the exoskeleton was removed.

Following fixation, the antenna was placed in 95% ethanol and opened, revealing structures stained in various shades of yellow. It was washed several times in 95% ethanol, placed in a 0.5% fast green solution for one to four seconds, and returned to the 95% ethanol bath where the degree of staining was noted. If insufficient, the preparation was dipped for another second or more in the stain. Nerves and blood vessels appeared bluish to bluish green, and muscles and connective tissue light to dark green.

The unwanted tissue was dissected out with hooked insect pins (size 00). As the dissection continued and deeper unstained tissues were encountered, the preparation was dipped for another second or more in the stain. After the organs of interest were exposed, the preparation was cleared in toluene, and permanent mounts made using standard whole mounting techniques. Once the tissues were placed in toluene they hardened and further dissection was impossible. Dissection of the carpopodite and the proximal flagellar segments were made in this way, and during the dissections drawings were made of pertinent structures.

Physiological Studies. The arrangement for stimulating and recording is shown in Figure 1. All recordings were made in aerated sea water, which was changed periodically during recording, or aerated at intervals with pure O<sub>2</sub> through an air stone inserted in the recording bath. Using this method "normal" responses could be obtained for five hours after the antenna had been removed from the animal. However to

ensure a minimum of deterioration artifact, recordings were limited to four hours. Recording usually started within 15 minutes of the time the antenna was removed.

After removal from the animal the dorsal surface of the carpopodite was carefully cut away. The antenna was then attached to the recording dish by a pin through the basal segments. Some muscle and connective tissue were removed, exposing either the dorsal or ventral sensory nerve. The proximal end of the exposed nerve was cut, and fine bundles split off from the nerve using sharp pins (see Wiersma 1959). This process was sometimes facilitated by holding the proximal end of the cut nerve with a micromanipulated clamp just under the surface of the water. The bundles were lifted onto a glass coated, 75 micron platinum, monopolar electrode, and the electrode raised just above the surface of the saline bath. The indifferent electrode was a large silver-silver chloride electrode, which was placed in the sea water bath along with the ground electrode.

Nerve impulses, detected by the platinum electrode, were amplified with a differential A.C. preamplifier (Textronic 122) and displayed on one beam of a dual beam oscilloscope (Textronic 502). Permanent records were made using a Grass C-4 camera.

Movements about the joint between the first (F1) and second (F2) proximal flagellar (Figure 2) segments were also monitored on the oscilloscope. The monitored directions of motion were circular (i.e. angular displacements about the anterior-posterior axis of the antennal flagellum) and radial (i.e. motions along a straight line intersecting at right angles the central anterior-posterior axis of the flagellum).

Figure 1. A schematic drawing of the recording and monitoring apparatus.  
1. loudspeaker; 2. audio amplifier; 3. oscilloscope; 4. physiograph pre-amplifier; 5. 10 turn linear potentiometer; 6. physiograph transducer;  
7a. two cc. syringe with pin to which the flagellum is attached; 7b. ten cc. syringe; 8. preamplifier with recording electrode attached.

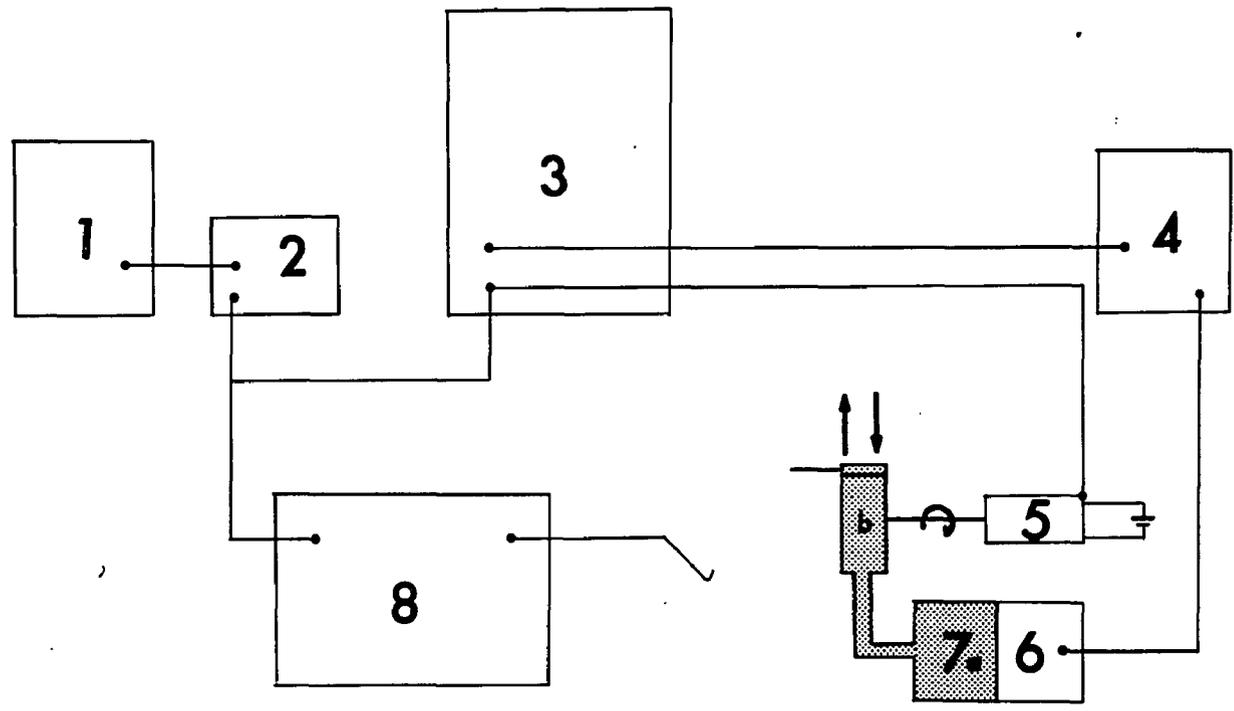


Figure 1. Recording and monitoring apparatus.

The F1 segment was held stationary by a small micromanipulated clamp. This did not affect the nerve activity, and reduced the distance the flagellum had to be moved to evoke a complete range of activity. The distal portion of the flagellum was cut off, and a stainless steel pin with a diameter slightly smaller than the inside diameter of the flagellum inserted into the internal cavity of the flagellum to about the third or fourth segment. The position could be observed by appropriate illumination of the flagellum. The pin was attached by a spring to the plunger of a 2 cc. syringe which was hydraulically driven by a 10 cc. syringe. Oscillations of the hydraulic system were adequately damped with a small amount of vaseline placed on the barrel of the smaller syringe. Plunger movements of the larger syringe were monitored by a B Physiograph muscle transducer, amplified by a Physiograph pre-amplifier, and displayed on the second beam of the oscilloscope. This system produced and recorded radial motion.

The barrel of the smaller syringe was firmly attached to a 10 turn linear potentiometer. Rotation of the potentiometer, and hence the 2 cc. syringe, produced circular motion. The potentiometer was attached to a six volt battery and the output of this circuit monitored on the upper beam along with the nerve activity. Both transducers exhibited a linear displacement with their respective movements.

To produce more rapid displacements the hydraulic system was replaced by the voice coil and cone of a loudspeaker. A glass stylus was attached to the cone and stabilized to eliminate right angle deflections. The stylus was attached directly to the flagellum with a pin

placed in the lumen of the flagellum, or a 22x50 mm. glass cover slip was attached to the stylus to produce water borne vibrations from a distance of several centimeters.

The speaker displacements were measured with an ocular micrometer and the output waveform with a photocell and oscilloscope. Sine wave displacements of one to 100 microns with frequencies from zero to 10,000 CPS were produced. The system had a rise time of about 2 milliseconds for 90% of the total displacement. A slight amount of oscillation in the stimulating system could not be eliminated, but when attached directly to the remaining 20 to 30 mm. of the flagellum it was very slight compared to the rather large natural oscillation of the flagellum. No attempt was made to measure sound intensities in the small recording vessel.

The temperature of the F1-F2 receptor was controlled with a coil of glass tubing attached to cold (8°) and warm (60°) water baths and placed around the F1 segment. By means of valves any mixture of water could be passed through the coil. A separate coil was also placed in the recording bath to hold the bath temperature at a relatively constant 17°C. With this method the preparation temperature could be varied between 10 and 40 degrees centigrade. It was monitored by a small thermometer placed directly next to the preparation or in the opened portion of the carpopodite directly behind the F1 segment. To produce more rapid changes in temperature a heat lamp was focused directly on the F1 segment.

## RESULTS

External Anatomy. The antennae used varied in length from 5 to 7 centimeters, the flagellum composing about 2/3 of the entire length. The antenna possesses the typical crustacean organization (Snodgrass 1952, Balss 1940), with a very small exopodite; the rest of the antenna is derived from the endopodite (Figure 2). The most proximal segment is the coxopodite followed in order by the basipodite, ischiopodite, meropodite, carpopodite, and the flagellum. The flagellum is a multi-segmental, tapered structure probably derived from the dactylopodite.

The joint between the flagellum and the carpopodite allows the flagellum to be moved through 90 degrees in a plane parallel to the wide axis of the carpopodite. The flagellum makes a 180° angle with the carpopodite when fully extended and a 90° angle when fully flexed. The meropodite-carpodite (MC) joint moves about 130° in the same plane as the carpopodite-flagellum (CF) joint. Full flexion of the CF and MC joints allows the flagellum to point posteriorly in a plane parallel to the anterior-posterior axis of the body, and anteriorly when both the CF and MC joints are extended. The remaining, more basal joints allow various degrees of medial, lateral, and radial movements. The resulting total possible motion of the antenna is within a hemisphere, each antenna encompassing its own side of the body, and slightly overlapping anteriorly.

Internal Anatomy. The flagellum (Figure 3) is supplied with a dorsal and ventral blood vessel. The highly branched ventral vessel

Figure 2. External view of the right antenna of P. californiensis. ba. basiopodite; ca. carpopodite; co. coxopodite; F. flagellum; F-1. first flagellar segment; is. ischiopodite; me. meropodite; sq. squame.

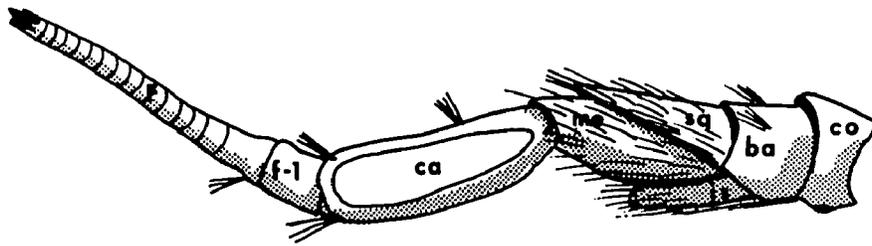


Figure 2. External morphology.

Figure 3. A reconstructed drawing of the internal anatomy of the carpopodite and the first flagellar segment. The base of the antenna is to the left. The inset shows a pair of bipolar sensory cells with their dendrites embedded in the exoskeleton of the next distal segment. Tendons are not shown, or are covered with muscle. V. ventral; D. dorsal.

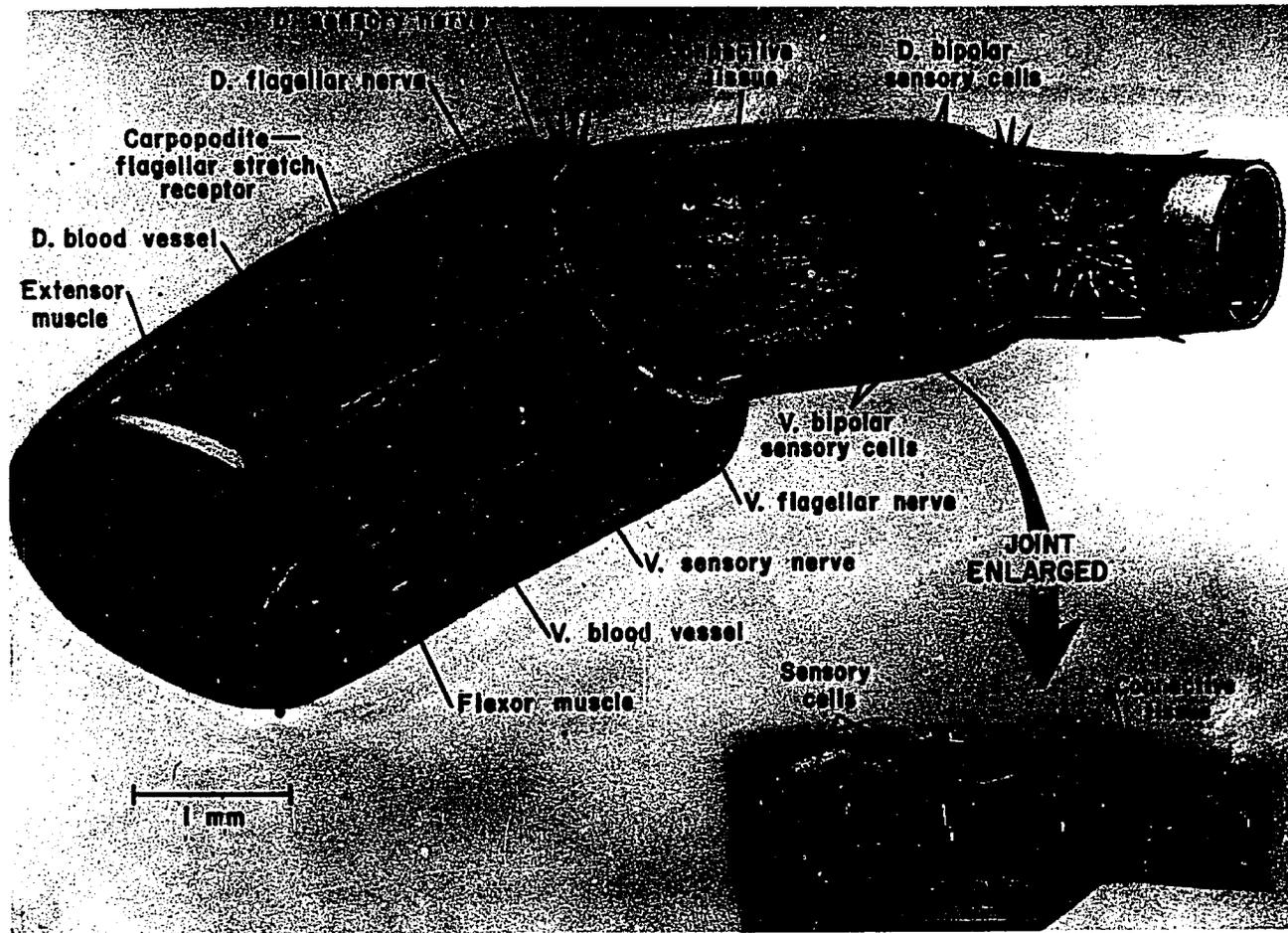


Figure 3. Internal anatomy.

sends small branches dorsally and ventrally to the muscles and nerves of the carpopodite. It passes into the flagellum from the ventral-medial portion of the carpopodite, through the center of the F1-F2 joint and back to the ventral floor of the third flagellar segment where it remains for the rest of its course through the flagellum, intermittently giving off smaller branches. From the amount and direction of branching the ventral vessel is probably an artery and the unbranched dorsal vessel a vein.

The flagellum is moved by means of two large muscles attached to the flagellum by two tendons. The tendons arise from the mid-lateral and mid-medial region of the proximal rim of the F1 segment. The Muscle Extensor Flagelli is inserted on the medial tendon and the M. Flexor Flagelli on the lateral one (Balss 1940). No muscles occur in the flagellum.

A stretch receptor of the type first studied by Burke (1954) occurs in the carpopodite. Distally it is divided into two branches, the main branch attaching to the medial rim of the F1 segment and the accessory strand to the mid-dorsal rim of F1. Proximally the receptor attaches to the ventral-lateral rim of the carpopodite. Many large bipolar sensory cells are visible on the strand when it is stained with reduced methylene blue. The sensory nerve joins the dorsal nerve at the proximal end of the carpopodite. This receptor would signal flexion-extension motions of the CF joint.

Two large nerves, originating in the flagellum, proceed separately through the carpopodite, each being easily divided into a dorsal and ventral half. The dorsal portion of the dorsal nerve and the

ventral portion of the ventral nerve each originate in the F1 segment. The remainder of each nerve originates more distally in the flagellum.

Passing through the CF joint the nerves are supported by a sheet of connective tissue which constricts just distal to the joint, forming a cone-shaped mass with the large end directed distad and filling the antennal lumen at the F1-F2 joint. Embedded in the connective tissue at the extreme distal end of the F1 segment are two sets of large (40-75 micron in sectioned material) bipolar sensory cells. The dorsal set gives rise to the dorsal fibers (A1 nerve) of the dorsal nerve, and the ventral set to the ventral fibers (B1 nerve) of the ventral nerve.

The dorsal sensory cells, totaling about 50, are arranged in a semi-circle just below the hypodermis on the dorsal side of F1, and the ventral group, totaling about 30, form an antagonistic set on the ventral side. In cross section they appear to form a complete ring of sensory cells, one cell thick, lying just below the hypodermis.

The bipolar cell dendrites extend across the F1-F2 joint and are embedded in the connective tissue or the exoskeleton at the proximal end of the F2 segment. A large bipolar cell (55-75 micron) is usually paired with a smaller (40-55 micron) cell. In silver stained sections it appears that the dendrites of the pair terminate together in a scolopidial structure similar to that described in the elastic strand receptors of Carcinus by Whitear (1962). However, in contrast to the elastic strand receptors in which the cells are all located on the strand and only the elastic strand is intersegmental, in the flagellar chordotonal organ (FCO) the long dendrites of the bipolar cells are intrasegmental.

The FCO also differs from other stretch receptors in that its response is multiaxial. Except for the biaxial elastic strand organ in the first antennule joint of Panulirus argus (Wyse & Maynard 1965) the other elastic strand receptors are uniaxial (Wiersma 1959, Cohen 1963). The flagellum can be moved through a complete circle, and along any radius of the circle when the F1 segment is held stationary.

Functional Localization of the Receptor. Electrophysiological responses also indicate that the motion which excites the receptor cells involves the F1-F2 joint. Whole nerve recordings show no change in the level of background activity from either A1 or B1 when the flagellum is moved by a thread attached to the F1 segment. However when the thread is attached to any segment distal to F1 a response to movement is obtained. The same results are seen when the whole flagellum is moved manually. When all the flagellar segments distal to F2 are removed the same response is obtained, thus localizing the receptor response to F1-F2 joint movement.

Careful dissection while recording also demonstrates the inter-segmental nature of the dendrites. While recording from A1, portions of the dorsal side of the arthrodistal membrane between F1 and F2 were progressively cut away with a hooked, sharpened pin. With each small cut the spontaneous activity progressively decreased until finally when the entire dorsal half of the joint was cut all activity from A1 ceased. Complete section of the membrane between F1 and F2 destroyed all responses in both nerves to movement of the F2 segment.

Fiber Types. Wiersma and Boettiger (1959) have shown that there are three classes of receptor cell types in the elastic strand stretch receptors in the propodite-dactylopodite (PD) organ of the crab Carcinus. One class responds with a phasic discharge to movement of the PD joint; the second class exhibits tonic discharges to different static positions of the joint; and the third, which they termed intermediate, shows characteristics of both types. The motion fibers are unidirectional, firing only to opening or closing of the joint, and the position fibers respond to either the flexed or extended position.

In the FCO there are a few small fibers that show a position response and are unaffected by motion. Many other fibers show a rapidly adapting response to motions of high displacement velocity and little or no response to position. These movement fibers respond unidirectionally which is typical of the crustacean stretch receptors. A continuum of types is found between the movement fibers and intermediate type fibers. The intermediate fibers have a lower displacement velocity threshold and show both phasic discharge to movements and tonic discharge to static displacements of the flagellum.

Patterns of Discharge of Intermediate Fibers. Figure 4 shows a typical recording of the response of an intermediate fiber from the ventral nerve when the flagellum was moved radially. The direction of radial movement of the F2 segment is indicated by the arrow within the circle. The two nerve cells from which the fiber recordings were made is designated by a dot. In Figure 4A the flagellum was moved ventrally in a series of steps while recording from ventral sensory cells. A

Figure 4. A recording from a small fiber bundle containing two active fibers. The large spike is from an intermediate fiber and the smaller is probably a position fiber. The arrow indicates that the flagellum was moved ventrally (in A) and dorsally (in B) in a radial direction. The dot shows the location of the cells from which the recording was made. Records A and B are continuous.



Figure 4. Typical intermediate fiber.

phasic response is evident during movement from one position to the next, and a tonic response during maintained flagellar positions. Record B is continuous with A and shows the response as the flagellum was moved dorsally, i. e. away from the cells. Phasic responses were inhibited and the tonic response had a lower frequency than if the same position had been reached while moving radially from the opposite direction.

The static response frequency is a function of the position in which the flagellum is held when movement is toward the cell (i.e. dorsally for a dorsal cell). In Figure 5 the impulse frequencies for the first four seconds after each movement into a new static position are plotted for eight positions. The high initial peak frequencies are the average frequencies during movement (phasic discharge) and are followed by the slowly adapting responses (tonic discharges). The straight line formed by the frequencies at the end of each four-second interval suggests that the position of the flagellum could be indicated by the FCO if frequency as a function of a fixed interval of time after reaching a static position were recognized as an important parameter by the central nervous system. The phasic responses show a consistent decrease in average frequency as the maximum position is reached. Adaptation to a change in position is complete in twenty to thirty seconds to a spontaneous background discharge. The response appears very similar to that obtained from the Ruffini receptors in the knee of the cat (Boyd & Roberts 1953).

The spontaneous activity was found to be temperature dependent. All background discharge disappears below 12°C and responses to movement

Figure 5. Phasic and tonic response frequencies at eight different positions as the flagellum was moved toward the cells from which the recording was being made. The relative positions are indicated by the lower curve.

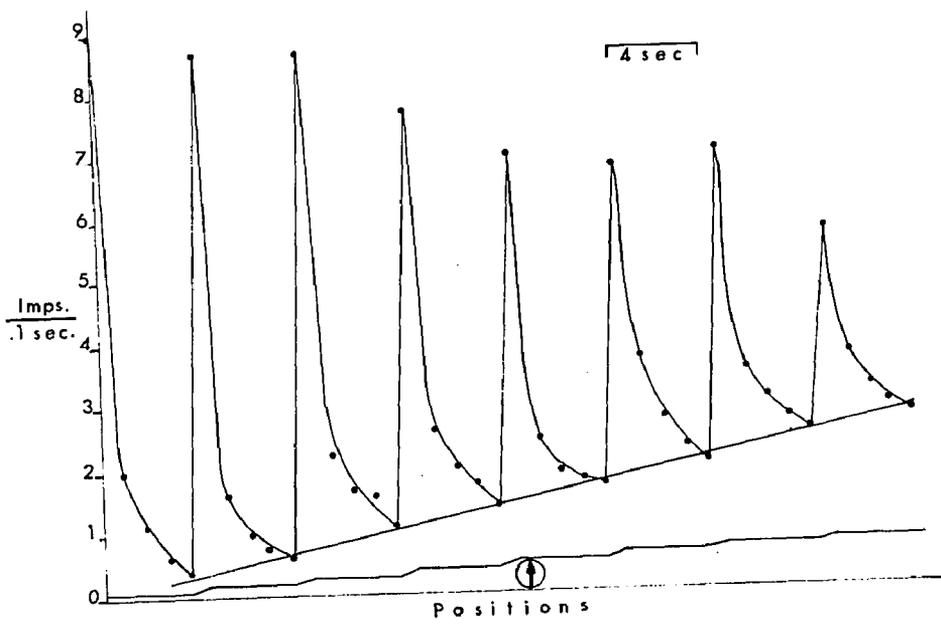


Figure 5. Phasic and tonic responses.

below 10°C. The frequencies of six fibers examined increased from 2-3 impulses per second at 16°C to a maximum frequency of 17 per second at 27°C. All responsiveness disappeared above 30°C in animals adapted to water temperatures of 19-20°C. The highest  $Q_{10}$  obtained between 17°C and 27°C was 6.7. Although this is relatively high compared to most biological activities, the highly sensitive initial response of a temperature receptor was absent. Cohen, Katsuki and Bullock (1953) observed a similar temperature sensitivity ( $Q_{10}$  of 4.5) and the lack of a high initial response in the statocyst of the lobster.

With movement away from the cell the response is of two types. The most frequently encountered is complete inhibition of the phasic response (gaps in record during movement, Fig. 4B), with a reduced tonic response which also disappears when the flagellum reaches the resting (midpoint) position (Fig. 4B). The second type of response is a sudden reduction in frequency after a change in the direction of motion (just prior to 0 in Fig. 7D), followed by a position sensitive response lacking a phasic component associated with rapid movement. This position response is completely inhibited when the rest position (B in Fig. 7D) is passed.

In an animal free in the environment the flagellum would usually be displaced from the rest position, consequently the dorsal and ventral sets of nerves would act as antagonists, one responding to one direction of motion and the other when the direction was reversed. Similarly, nerves of one set will respond differently when the same position is reached from two different directions (Fig. 4A & B). A single receptor cell, functionally similar to the type II receptors in the statocyst of

Homarus (Cohen & Dijkgraaf 1961), would respond to two different stimulus parameters: 1) the direction from which the position was reached and 2) the absolute position relative to the time it was reached.

Adequate Stimulation for the Intermediate Fibers. There is no clear agreement concerning the nature of the sensory transduction processes in the elastic strand organs. Wiersma and Boettiger (1959) have suggested that stretch of the sensory dendrites constitutes the effective stimulation. This view has also been adopted by Cohen (1963) for the myochordotonal organ, and Wyse and Maynard (1965) for the elastic strand receptors in the antennule of Panulirus argus.

Wiersma (1959) has shown that in the CP<sub>2</sub> organ, on the other hand, most of the movement fibers respond to motion of the joint in a direction that causes shortening of the elastic strand. Mendelson (1963) confirmed that the opening units of the PD organ also respond to shortening of the elastic strand. Furthermore he found that either twisting of the strand or tension on off-axis strands of elastic fibers did not contribute to the response.

All of the above studies, however, have depended on gross stretch or shortening of the entire strand. In the FCO stretch or relaxation of the individual dendritic terminals can be easily deduced from the F1-F2 joint motions (Figure 6), which were observed by splitting the F1 and F2 segments in a vertical plane and staining with reduced methylene blue. The flagellum was then suspended under a dissecting microscope and moved by means of a hydraulically driven syringe. On one

Figure 6. A schematic representation of movement around the F1-F2 joint. With the F1 segment held stationary the F2 segment is pictured in the rest position B, and bent in the two extreme positions A and C. The upper and lower cell in each diagram are in their natural positions. The middle cell would also normally be found on the periphery but is displaced to the central axis to illustrate movement of the dendrites during flagellar displacements at right angles to a cell. A comparison of the top cell with the bottom cell will show the antagonistic nature of the response (i.e. one cell is stretched while the other is flexed).

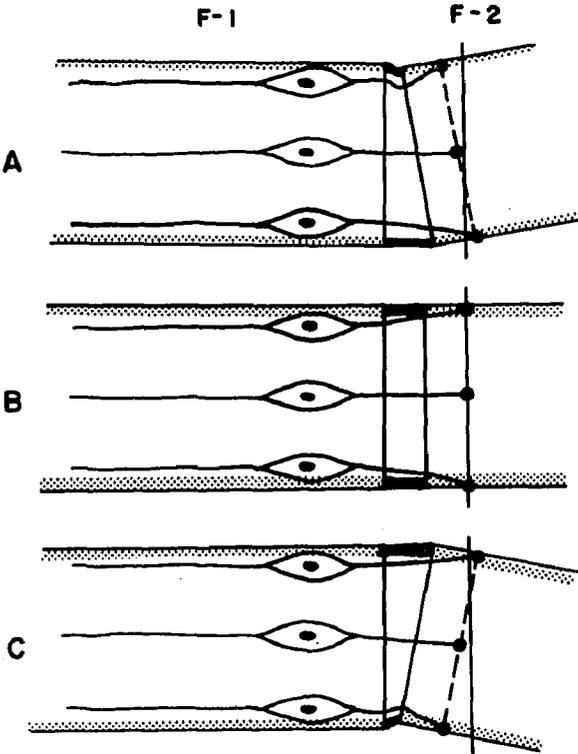


Figure 6. Movement around the F1-F2 joint.

occasion both cells of a pair and their dendrites stained well, but most of the time only one bipolar cell could be observed at the out edge. When motions of the F1-F2 joint were observed externally they appeared to be the same as those seen in the dissected preparations. The dendritic length changes shown in Figure 6 were confirmed by means of a mechanical model. The dendrite of the top (dorsal) cell is stretched maximally in C of Figure 6, shortens as the flagellum (F2) is moved into the resting position (Fig. 6B), and flexes when the flagellum is moved into position A of Figure 6. The dendrites of the bottom (ventral) cell experience the opposite motions as each position is reached.

In Figure 7D the activity of a small fiber bundle from the ventral cells is shown as the flagellum is moved from position C to position A. During the first half of the radial movement the dendrites would be returning to their longer resting position and the activity remains unaffected by movement but appears to be position sensitive. The dendrites would be stretched as the flagellum passes from position B into position A. During this stretch all activity in the two large intermediate fibers ceases, but activity in a very small amplitude position fiber begins.

Different directions of radial motion (Fig. 7A, B, C) also indicate that the excitatory phenomena is not stretch of the complete scolopidia but either flexure of the dendrites or intrascolopidial stretch or compression. In 7A the small and large intermediate fibers show similar phasic and tonic responses as the flagellum moved toward the cells. This movement would result in an increased flexure of the

Figure 7. The discharge of a fiber bundle (at least three active fibers) as the result of radial stimulation at various angles relative to the cell. The dot indicates the approximate position of the intermediate fiber which gives rise to the smaller amplitude spikes in the middle of record B and elsewhere. The largest spikes arise in a ventral nerve cell which about  $90^{\circ}$  to the right of the other intermediate fiber. The very small amplitude spikes, best seen in the later part of D, are those of a position fiber. The amplification in D is higher than in the other three to better visualize the position fiber.

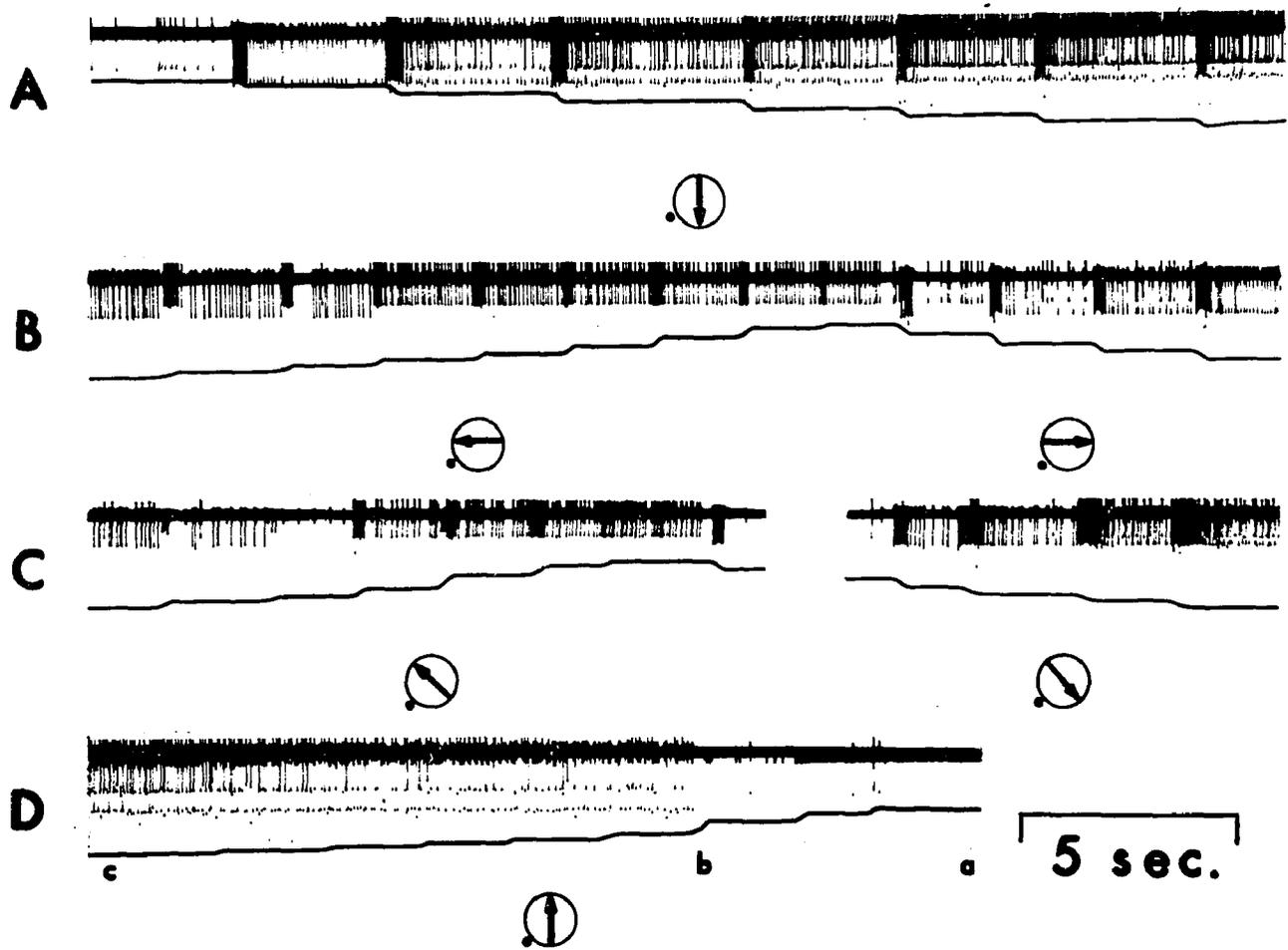


Figure 7. Intermediate fiber response.

dendrites. During radial motions in a horizontal plane (Fig. 7B) the smaller intermediate cell shows the typical phasic and tonic responses as the flagellum is moved toward the cell. In the opposite direction (last third of line 7B) only tonic responses are obtained over the first half of the total range and no response during the second half. The larger cell responds antagonistically (7B) indicating that its position is shifted about  $90^{\circ}$ , but still in the ventral group of sensory cells.

When the flagellum is moved radially at right angles relative to the smaller intermediate cell, the response is also the result of flexure or shortening. If the movements of the dendrites of the middle cell in Figure 6 are compared with the nerve responses in Figure 7C it is evident that the activity in the smaller intermediate fiber is associated with flexing of the dendrites during the second half of the radial movement in either direction. Moving from A or C to B (resting position in Fig. 6) results in stretch of the dendrites, with the typical inhibition of response.

The response obtained during circular motion (Fig. 8) shows the additive effect of vectors representing radial displacements toward the cell (dendritic flexure) and the right angle radial displacement (also resulting in flexure). Figure 8B is a fiber bundle response to circular displacements. The average frequencies during this movement are plotted in 8C. Curves with an initial steep slope preceeding a gradual decrease and sudden termination of activity are those that would be predicted if the response were due to the magnitude or velocity of the component vectoral radial displacements of the circular motion. Right angle radial displacement could account for the small hump on the falling

Figure 8. Whole nerve (A) and bundle (B) recordings of responses to circular movements. The arrows indicate the direction of circular motion, the dot the nerve cells from which recordings were made and the size of the circle the relative size of the circle through which the flagellum was moved. The graphs plot the frequency of response against the movement in degrees. In graphs a and b the flagellum was moved from  $270^{\circ}$  (9 o'clock) to  $0^{\circ}$  (12 o'clock) and in c and d from  $90^{\circ}$  (3 o'clock) to  $0^{\circ}$  (12 o'clock). In each case rotation away from the cell resulted in reduction or cessation of nerve activity.

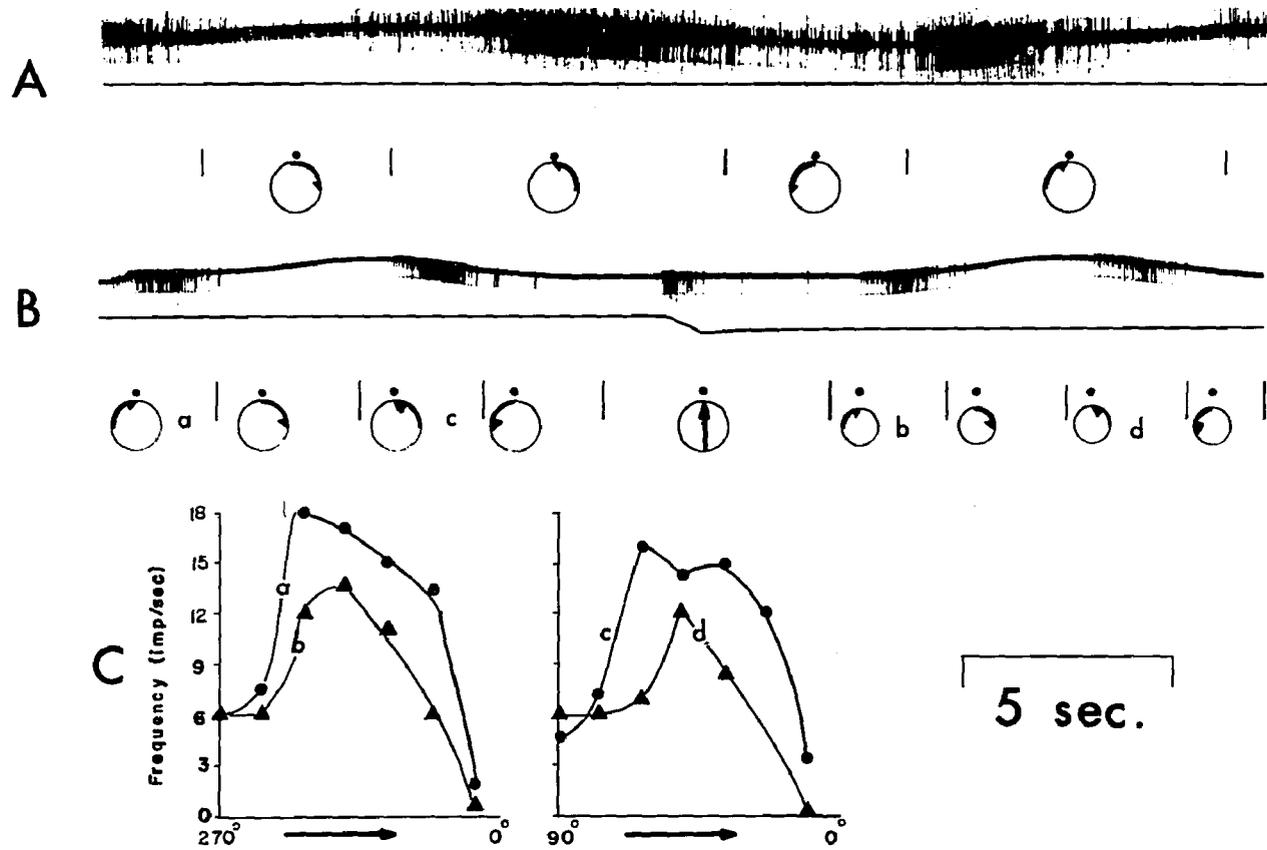


Figure 8. Response to circular movement.

phase of a and c as the F-2 segment moves through the rest position to position A or C of Figure 6.

Since the velocity is slower in the b, d circle of Figure 8 than the a, c circle the resultant vectors would also have a lower velocity and hence the frequency of discharge would be lower than for the a, c circle. However, while passing through the smaller circle, the flagellum is also passing through an area where the response of the cell to radial movement is typically of a lower frequency.

To separate the effects of position and velocity of displacement the flagellum was moved continuously through a series of positions at different velocities. The results of a typical experiment are given in Figure 9. Increases in velocity cause a linear increase in the frequency of the response (distance between curves), but the response is also affected by the position through which the flagellum is moving (slope of curves). Unlike pure movement fibers which show a relatively constant discharge frequency at different rates of displacement (Bush 1965a) these fibers are evidently affected by the velocity of movement and position.

Phasic Fiber Types. Although smooth velocity changes were difficult to obtain with the stimulating arrangement some estimates of the types of responses could easily be made. The ideal pure movement fiber would have a curve similar to a rectangular hyperbola, with a steep initial slope that flattens off rapidly (Bush 1965a). They should respond also to motion in only one direction with a constant frequency for movement at a steady rate (Wiersma & Boettiger 1959). Figure 10

Figure 9. A plot of the impulse frequency as the flagellum is moved continuously through four positions (four positions equal to a full range of flagellar movements). The flagellum is moved at four different but constant velocities. In position 1 the flagellum is bent maximally away from the cells and moves toward the cells to position 4.

Figure 10. Three types of responses of phasic nature to different displacement velocities. The inset shows the response to acceleration of the fiber represented by the squares. The numbers on the three curves are velocities in mm/second. Note the decrease in slope at 25mm/second. As the displacement velocity is decreased still further the response becomes position dependent and the slope of the curve becomes positive.

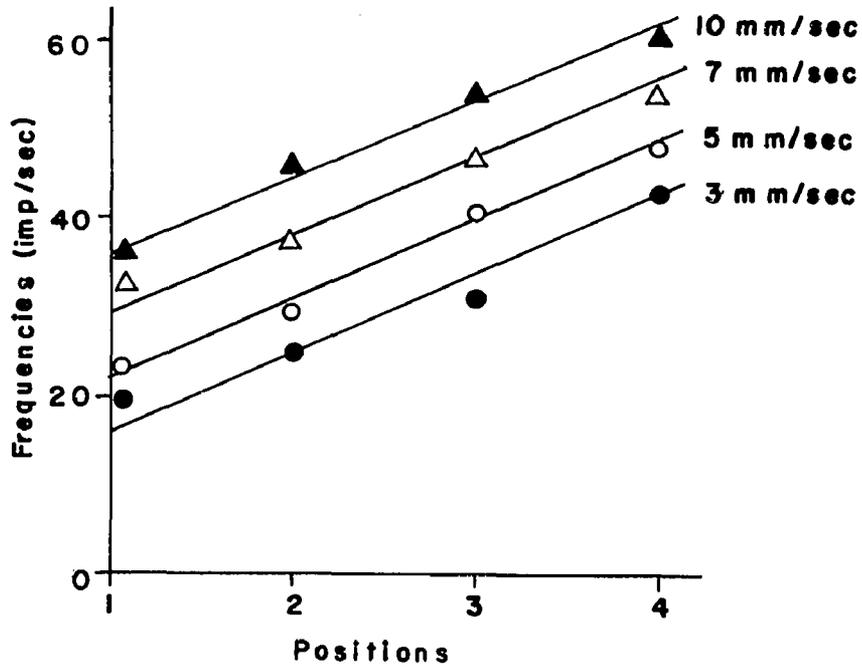


Figure 9. Frequencies as a function of position.

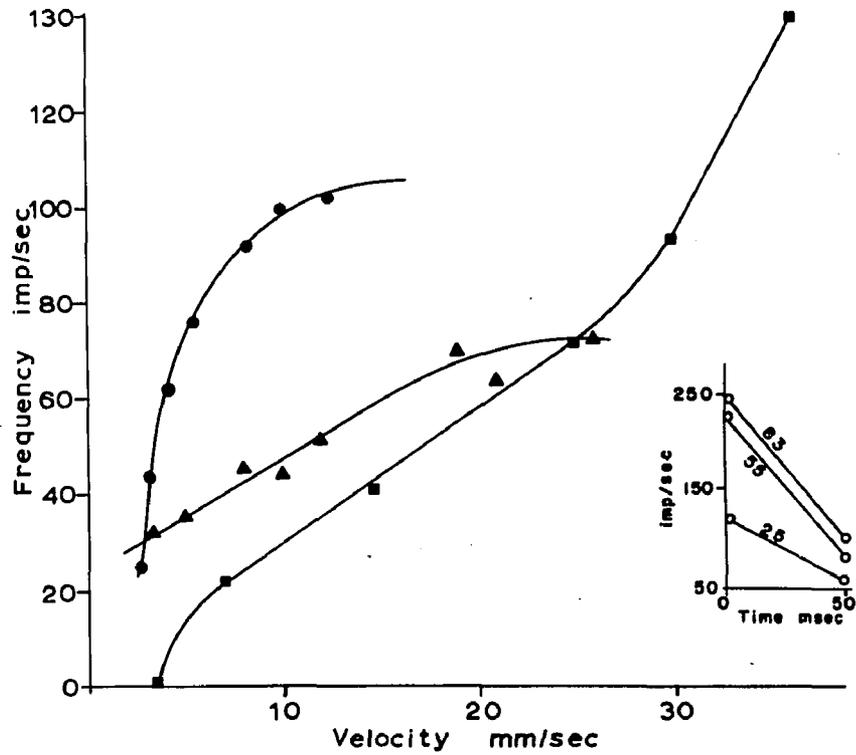


Figure 10. Three types of movement fibers.

shows the mean frequency of discharge as a function of the velocity of displacement for three flagellar chordotonal organ receptors. The lower curve (filled squares) appears to be a type of acceleration fiber described by Bush (1965a). The discharge frequency at rapid displacement rates is very high initially and decreases steadily with continued steady displacement (inset Fig. 10). Also typical of this type of fiber is the relatively linear form of the curve and the steep slope. However at low displacement velocities its discharge frequency tends to be affected by position, as is illustrated by the change in slope at 25mm per second. The upper curve (filled circles) shows the typical movement receptor curve. At the higher velocities, indicated on the curve, the initial response is very high (200 impulses per second) and is followed by a rapid decrease in frequency, typical of acceleration fibers. At very low velocities the response is position dependent, the discharge frequency increasing as the flagellum is moved toward the cells. In the mid-velocity ranges it gives an ideal movement response, firing at a constant frequency for constant rates of displacement.

All of the phasic receptors exhibit the unidirectional response of the intermediate fibers, responding when the flagellum is displaced toward the cells and inhibited by movement in the opposite direction. They differ from the intermediates only in their threshold velocity and rates of adaptation.

Movement Sensitivity and Frequency Response. Because the entire flagellum is supported by the F1-F2 joint membrane any displacement of

the relatively stiff flagellum results in a small movement in the F1-F2 joint. Except for medial-lateral movements, the CF joint is not affected due to the unidirectionality imposed upon it by the uniaxial hinge joint.

The minimum displacement of the flagellar chordotonal organ that will initiate a response is a one to three micron sine wave movement applied 22 millimeters distal to the F1-F2 joint. Measurement made on sectioned material indicates that the dendrites are attached about 100 microns distal to the F1-F2 joint in the F2 segment. Assuming that the flagellum is a stiff rod this amount of movement would result in a dendritic displacement of about  $10^{-6}$  to  $10^{-7}$  centimeters. However since the flagellum is somewhat flexible the actual amount of movement would be even less.

Responses to displacements of the flagellum at different frequencies were studied either with the speaker cone stimulator attached directly to the flagellum, or with the stimulator placed in or on the surface of the saline bath. Figure 11A shows the discharge of the whole nerve to surface ripples produced by a 22x50 mm. cover slip attached to the stimulator stylus and placed 100 mm. from the antenna on the surface of the bath. For a ripple frequency of 1 per second a burst of compound spikes are produced with a burst frequency of 1 per second. The several compound spikes in each burst occurred at a frequency of 50-70 per second, probably resulting from the natural resonance of the flagellum. At higher stimulus frequencies the response became more consistent. When stimulated at 25 per second (Fig. 11B) bursts of three different sets of fibers occur at 25 per second. As the

Figure 11. Whole nerve responses to surface ripples of 1/sec in A; 25/sec in B; a gradual change from 15 to 40/sec in C. D is the response to near-field acoustic vibrations of 20/sec, and E of 65 and 85/second. Stimuli are recorded as pulses on the lower trace in each record.

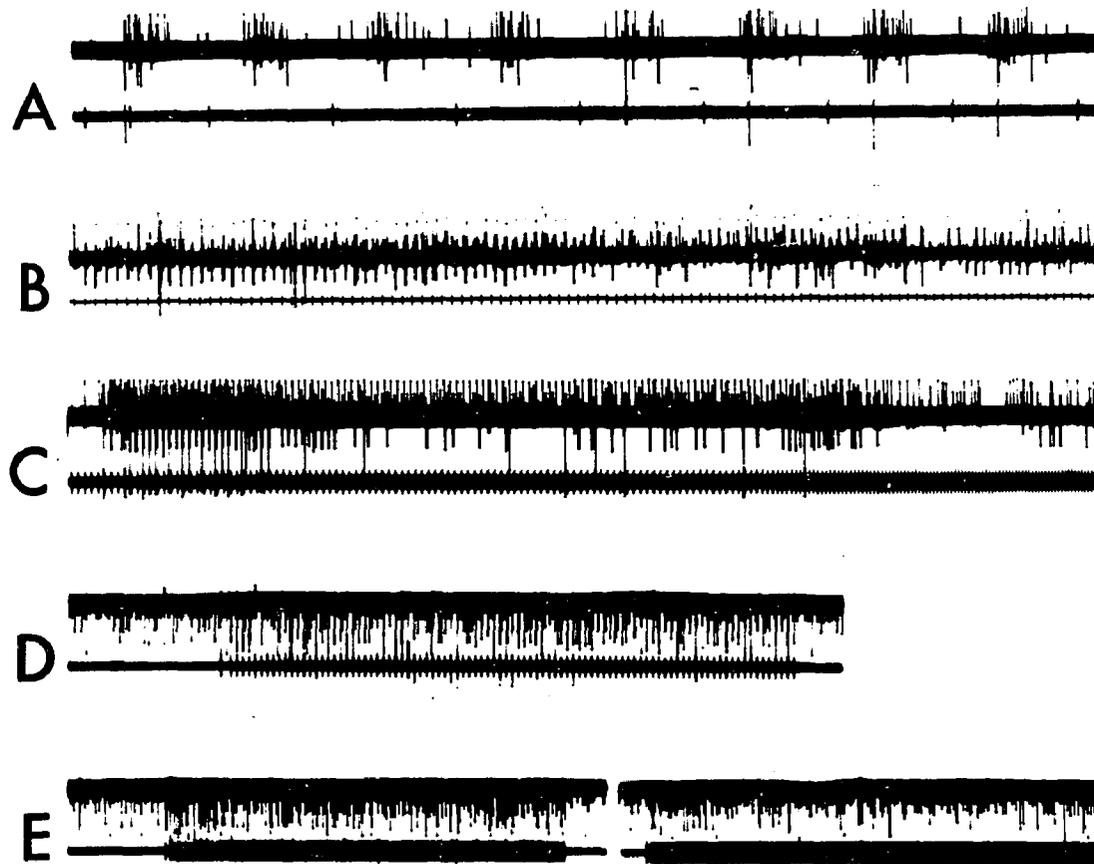


Figure 11. Whole nerve responses.

frequency increases above 20 per second the amplitude of the compound spikes decreases and the overall frequency drops (Fig. 11C).

The response to water borne vibrations was studied using the same stimulating apparatus. Both the flagellum and the stimulating stylus with the cover slip attached were positioned below the surface of the saline bath. The cover slip was placed 10 mm. away from and parallel to the long axis of the flagellum. To a stimulation of 20 per second (Fig. 11D) the nerve responds with large compound spikes of variable amplitude but in synchrony with the stimulus. At 65 per second (11E) the spontaneous activity becomes modulated, the smaller spike frequency becoming very low and the large spikes firing in synchrony with the stimulus during the first few moments. At 85 per second (11E) the activity is asynchronous but modulated to a certain extent.

To evaluate the actual frequency response characteristics in the absence of standing waves and similar interference phenomena the flagellum was attached directly to the stimulator. Single fiber recordings (Fig. 12A) show synchronous discharges to stimulation at 50 per second. At higher frequencies the response is often synchronous for the first few stimuli and then becomes asynchronous (12A). Fibers continue to respond to stimulation at frequencies up to 1000 per second, but always asynchronously although occasionally the first two spikes are in phase. A result of the initial synchronization and then loss of synchronization with time is the decline in the amplitude of the compound spikes (Fig. 12B). This phenomena called equilibration has also been observed in the mammalian VIIIth nerve and nerves from

Figure 12. Responses from the FCO with the stimulator attached directly to the flagellum. A. single fiber response at 50 and 80/second. B-G are whole nerve responses at 100 and 270/second B; 10/sec C; 30/sec D; 200/sec E; 400/sec F; 1000/sec G. Calibration is 100 msec, except for B where it is 1 second.

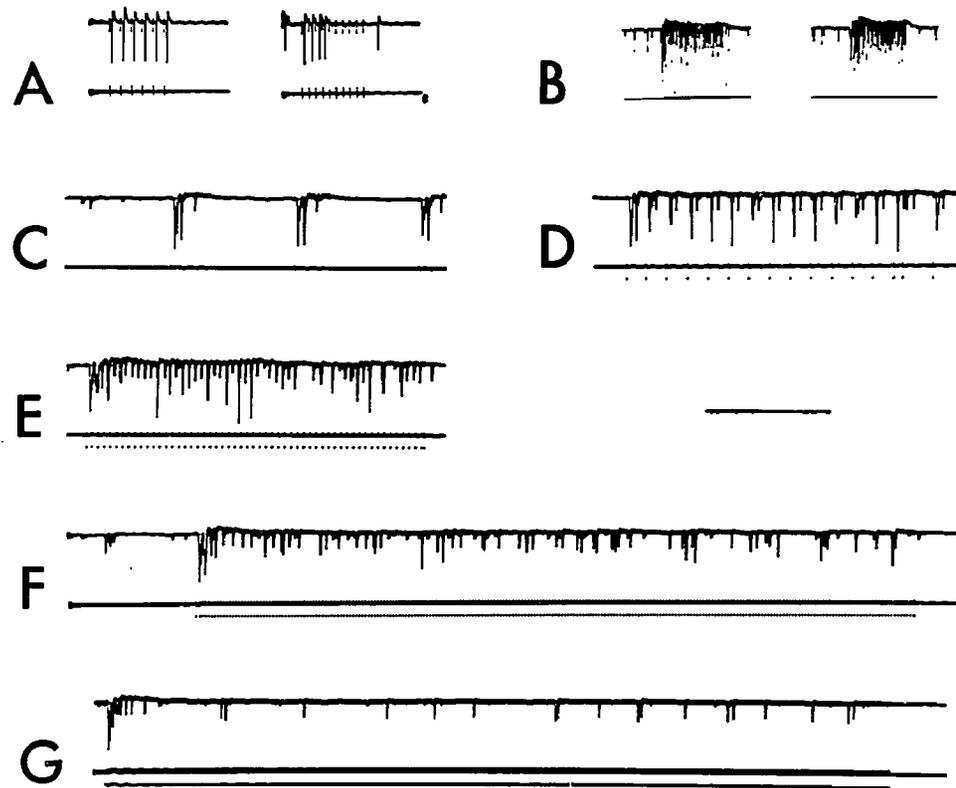


Figure 12. Responses to vibration.

the cercal hairs of certain insects (Dethier 1963). Dethier interprets this as a result of the lengthening of the relative refractory period of each fiber. At lower frequencies the response is often two or three spikes for each stimulus (12C), probably in response to flagellar resonance. At higher frequencies the response is usually synchronous up to 200 per second (12E) and then becomes asynchronous up to 1000 vibrations per second (12 F and G).

## DISCUSSION

Sensory Transduction Events. The responses from the flagellar chordotonal organ and the movements of the dendrites as the flagellum is moved through a series of static positions are summarized in Figure 13. The point to be emphasized is that increased flexure appears to be the mechanically transduced event and stretch either inhibits the phasic response, or the tonic position-sensitive response continues until the resting position is reached whereupon additional stretching brings about inhibition of discharge.

Similar dendritic deformations have been shown to be excitatory to other Arthropod groups. The trichobothrium of the Arachnids is excited when the nerve endings are inclined over the border of the "helmet" (Gorner 1965). In the hair plate sensilla of the honey bee transverse movements relative to the hair terminals result in excitation (Thurm 1965). Thurm suggests that the compressional component is the adequate stimulating event. In the FCO receptors, dendritic hence scolopidial, stretch has been shown to be inhibitory to phasic discharges and to temperature sensitive background discharges. Since dendritic flexure would result in stretch on one side and compression on the other side of the dendrite, it is probable that here also the compressional component of dendritic flexure is the stimulating event at the cellular level. Bending of the scolopale, which encloses the

Figure 13. A schematic representation of nerve fiber activity in a, the dendritic movements in b, and the relative position the flagellum was held in c.

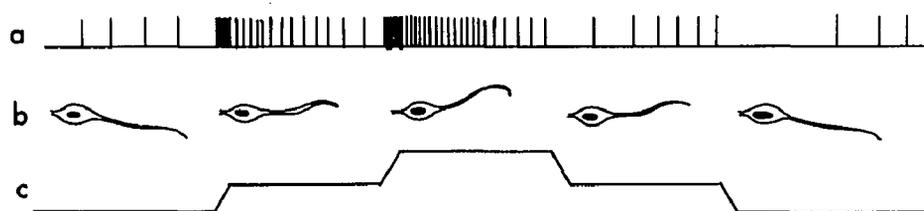


Figure 13. Nerve responses and dendritic movements.

terminal processes of the dendrites, could also cause a flattening of the terminals and hence compression.

Responses from the FCO strongly resemble those obtained from the periopod stretch receptor organs of other Decapod Crustaceans. The FCO differs in that it is circular rather than linear, and at any one moment the output of the individual cells tends to be different, depending upon the direction of displacement of the flagellum, in contrast to the output of the cells in the elastic strand organs which tends to be similar for the same degree of stretch.

All three types of cells observed in stretch receptors are found in the FCO. Small amplitude position receptors, of rare occurrence, respond in the extreme positions when the dendrites are maximally stretched. They are non-adapting and unaffected by movement. Phasic and intermediate fibers are the most abundant, the distinction between them being only in the velocity threshold and adaptation rate.

If the sensory transduction processes found in the FCO are to be applied to other chordotonal organs two basic assumptions must be made: 1) that the scolopidial structure observed in silver stained sections are homologous to those observed by Whitear (1960, 1962) with the electron microscope in the periopod receptors of Carcinus and 2) that unidirectional movement responses and most position responses (the exception being the small amplitude discharges of pure position fibers) are not a function of any specific membrane type but are rather a function only of the mechanically transduced events occurring at the scolopidial endings (Mendelson 1963).

The first assumption awaits confirmation with the electron microscope. However, in silver stained sections, a scolopidial structure with scolopale and sheath cell nuclei encompassing the dendritic endings appeared to be present.

The second assumption is based on the fact that in all of the chordotonal organs studied, movement and position cells never fall into two distinct groups but there are always cells more or less intermediate between the two. Hartman and Boettiger (1965) found that movement cells are sensitive to position when the elastic strand is shortened by increments of 25-100 microns. Thus over a small range pure movement fibers would even be classified as intermediate fibers. The FCO was similar in that intermediate fibers in some positions respond as pure movement receptors and in other positions as position receptors. Phasic fibers also occur but the difference between them and the intermediate fibers is not very distinct.

The typical movement response from the FCO intermediates is associated with a flexing of the scolopidia from the stretched position. With stretch from the rest position a complete inhibition of all activity occurs. If the mechanical arrangement of the dendrites in an elastic strand receptor limited the dendritic movements to the two former flexing and stretching movements, bipolar cells would exhibit a typical unidirectionality, responding in one direction to movement and showing little or no tonic activity. If the mechanical arrangement allowed a greater amplitude of dendritic flexure a movement response with some tonic response in the extreme positions would be obtained (Bush 1965a, b, Wiersma & Boettiger 1959, Wyse & Maynard 1965). With

greater flexion of the dendrites the intermediate type of response having both phasic and tonic characteristics would occur. Certain records in all the papers cited above show different degrees of this condition.

That the adequate stimulus is flexing of the dendrites, as initially proposed by Mendelson (1963) and later by Bush (1965a), is supported by the responses of the six pericard stretch receptors that have been studied (summarized in Bush 1965b). Two respond only to relaxation of the strand (MC2 & CP2), two have more fibers which respond to shortening than to lengthening of the strand (MC1 & CP1), and two have equal numbers of relaxation and extension fibers (CB & PD).

If the dendrite lies parallel to the elastic strand it would be stretched when the strand is stretched and flexed when the strand returns to the least stretched position. This would result in a movement response when the dendrites are flexed (strand relaxation) and an inhibition of response when it is stretched (i.e., a unidirectional movement response).

Movement fibers sensitive to strand stretch can also be explained by using a flexing hypothesis. The body of the strand contains relatively inelastic connective tissue cells mixed with extracellular bundles of collagen fibers. The periphery of the strand is surrounded by an amorphous connective tissue (Whitear 1962). As a result, stretch applied to the strand would result in different amounts of movement per unit of elastic tissue, the outside probably being displaced less per unit length than the inside. If the excitatory region of the dendrites crosses the interface of the two types of connective tissue

it would be flexed during stretch and straightened during relaxation. Scolopidia within the interior of the strand, if not parallel, might also experience flexion with strand stretch. Unequal displacements have been observed externally by Wiersma (1959).

Dendritic flexure during stretch would probably be less efficient however, than dendritic flexure occurring with strand relaxation. Wiersma and Boettiger (1959) did observe that the threshold of the most sensitive opening (relaxation) fibers of the PD organ is lower than for the most sensitive closing (stretch) fiber. FCO and PD movement receptors are also similar in that they both show a position dependence at velocities of displacement slightly above threshold.

When the dendrites in the FCO are returned to the resting position from a more flexed position, a response of lower frequency, dependent only on position and either unaffected or inhibited by movement, is obtained (Fig. 7D & 4B). Wiersma and Boettiger (1959) describe a commonly encountered type of fiber from the PD organ which shows this response. The fiber discharges with a  $10^\circ$  movement of the joint in one direction (dendritic flexure) but responds with reduced frequency for only one half of the return distance (dendritic stretch through the rest position). The movement in 7A and 7D would produce exactly this response if the high frequency response during motion in 7A were absent. Laverack (1964) and others, however, do discuss position receptors which possess phasic responses of a relatively high frequency to motion. The FCO phasic responses, which are not position dependent, can be eliminated at slower velocities (Fig. 9), which would thus give a phasic position response to movement identical to that recorded from the above-mentioned

fiber of the PD organ. Since the scolopidia of the stretch receptors are embedded in a rather compact mass one would not expect to obtain the initial high frequency phasic responses which require a rapid flexure of the dendrites. This also agrees with the finding that in the elastic strand stretch receptors the more distal position sensitive cells are more closely associated with the connective tissue than the more loosely held movement receptors.

Functional Aspects of the FCO. Variation in the threshold of movement fibers result in essentially two overlapping input channels, one responding phasically to relatively small, rapid displacements and the other phasically to slower displacements and tonically to position. The dorsal and ventral sets of sensory cells respond antagonistically to give a directional component to both input channels. The advantages of separate channels for phasic and tonic information have been discussed by Cohen (1960, 1963, 1964). He concludes that an organ with these channels can provide precise information about rate, velocity, and direction of movement in addition to indicating fixed position.

Since the various chordotonal organs all appear to be capable of the same type of afferent discharge to a similar stimulus, the relevant fraction of the environment sensed by a particular organ appears primarily dependent on the physical location of the receptor and the frequency limitation imposed by the appendage or organ with which they are associated. The importance of the FCO to the total sensory input of the crab would then depend on what fraction of the environment the antennal flagellum came in contact with.

With rapid movements of the crab's body the antennae, due to their own inertia, would be displaced rapidly, producing a phasic response in the FCO. A minute or more after their return to the resting position all activity disappears. This eliminates the possibility that the FCO could also signal static directions of gravity. The magnitude and direction of water currents would be signaled by the tonic position fibers and any change in direction of current by a change in the phasic and tonic fibers which are active.

Antennal tactile orientation have been described in the crayfish (Gilhousen 1927). He found that animals which had mastered a maze attempted to turn prematurely after their antennae were cut off. A FCO type of receptor would signal a corner with a phasic response if the antennae had been held against the wall as the animals moved along the passage. If it had been tapped along the wall, as is the habit of the hermit crab, the corner would be signaled by the lack of discharge. Tactile orientation of this type would also prove helpful in turbid or poorly lit waters.

Both tactile stimulation (Hertz 1932) and shell weight (Reese 1962) have been shown to be of significance in the choice of gastropod shells by hermit crabs. Small and medium sized P. californiensis are always found in highly sculptured murex shells although other shells of equal size but smoother and of less weight are available, probably in greater numbers. The antennal texture sense resides mainly in the FCO, as immobilization of the F1-F2 joint of a blinded hermit crab abolishes the antennal withdrawal response when the flagellum is touched with a

vibrating rod. Prentiss (1901) also found vibrational sensitivity reduced when the antennae were removed. Vibration sensitivity is resolved into a texture sense, when a hermit crab encounters a shell or another hermit crab, by moving the antennae obliquely across the shell surface for a short distance. As the antennae passes over irregularities on the surface a phasic response similar to low frequency vibratory stimuli would be produced, the duration and frequency of each burst depending respectively on the size of and the distance between sculptures.

Vibration reception is defined by Cohen and Dijkgraff (1961) as a sensitivity to sound or vibrations reaching the animal through the solid substrate. Although the FCO responds to vibrational stimuli of this type it also responds to contact vibratory stimuli (tactile) and to small amplitude water borne vibrations (sound reception). Thus, in accepted terminology, the FCO cannot be defined precisely but is representative of a group of sensory fibers, discussed by Bullock (1965), that show overlap in the quality of the stimulus to which they are sensitive. The FCO responds to some parameter of both sound and vibration and is limited only by the magnitude of possible flagellar displacements which can be caused by the various stimulus parameters. The range of excitatory displacements of the FCO is in the range of displacement of the hair cells in the vertebrate lateral line and the cutaneous receptors of fishes. Functional homologies with the vertebrates, rather than the insects, is a common occurrence in the Crustaceans. The statocysts are very similar to the vertebrates non-acoustic labyrinth (Cohen & Dijkgraff 1961) and the MC myochordotonal organ is analogous to the muscle spindle of the vertebrates (Cohen 1965).

A comparison of responses from the FCO and the lateral line show their afferent discharges to be almost identical. Both respond with several spikes per cycle to water-borne vibrations of a low frequency (less than 25/sec), one spike at frequencies of 25-50 per second, and with irregular responses at still higher frequencies up to several hundred per second (Katsuki, et al. 1951). In Ameiurus (Hoagland 1933) the nerve spikes synchronize with stimuli up to about 100 per second, in Fundulus to about 180 per second (Suckling & Suckling 1950), and in the FCO to about 200 per second. Modulation of spontaneous activity, as found in the FCO, also occurs in the lateral line of Xenopus (Dijkgraaf 1956). In Raja (Sand 1937) some fibers respond to perfusion of the canal from the head to the tail and others from the tail to the head depending on the direction the kinocilium of each hair cell is pointing relative to the flow of water (Warsall, Flock & Lundquist 1965). The unidirectional nature of the response is also evident in the FCO due to the arrangement of the two sets of bipolar cells. The response to surface ripples in the FCO also resembles the ripple response from the lateral line (Dijkgraaf 1956).

Harris and van Bergijk (1962) demonstrated that the lateral line organ responds to near-field displacements of sound sources, such as those created by swimming fish, wave motions, currents, and tides and thus concluded that the lateral line is indeed a portion of the acoustic system of the vertebrates. The similarity in response characteristics of the lateral line and the FCO indicate that the FCO, along with other joint receptors (i.e. antennule receptors, Laverack 1964) and various

hairs (Laverack 1962, 1963) will probably be found to constitute the acoustic receiving system of the Crustaceans (Autrum 1963).

The near-field effect is caused by the vectoral displacements of water molecules by a vibrating body as compared to the better known scalar pressure waves. The displacements decrease as the square of the distance from the vibrating body, consequently the distance involved is equal to about one wave length. At the lower frequencies (e.g. 100/sec) this distance would be about 5 to 10 meters. Acoustic responsiveness has been observed in the spiny lobster within this distance (Lindburg 1955). The stridulatory noise produced by a captured lobster caused all other individuals within 1 to 2 meters to retire into their hiding places. Near-field effects would be detected by displacement receptors.

It has been known for years that chemical and mechanical stimuli originating at a distance from the animal are effective in evoking complex behavioral responses (Laverack 1964). "Distant touch" was observed in 1897 when it was found that blinded Carcinus could detect moving objects at some distance. Blinded hermit crabs also possess this ability which is considerably reduced when the F1-F2 joint is immobilized, or the nerves from the FCO are cut. A large volley of spikes is recorded when an object is placed in the saline bath at a distance of 20 centimeters from the antenna.

The importance of the ability to detect moving objects at some distance is self evident. The amplitude of a near-field pulse from a swimming fish depends on the volume of the fish and the frequencies on the speeds of the fish (van Bergijk 1964). Thus large predatory fish

could be detected at a distance great enough so that the rapid escape reaction of the crustaceans would allow it to retreat to safety. In Petrochirus this consists of a rapid withdrawal into its shell. Sound production as a warning to others of the same species appears to be of significance (Lindberg 1955), and the other varied devices which the Crustaceans use for sound production will most likely be found to have a similar significance to the animals (Schmitt 1965).

Variation in the water currents produced by the beating of the crabs own scaphgnothites is a sufficient stimulus for the FCO receptors. If an object is placed in the path of water current pulses produced by the beating scaphgnothites interference phenomena in the outgoing waves would be set up, which the hermit crab would be able to detect as changes in frequency and/or amplitude of the pulses. This would result in what Vincent (1963) called passive echolocation. A few successful experiments with intact hermit crabs showed a large decrease in the compound spike amplitude, and a flattening of the interspike interval curve when a transparent sheet of plastic, supported on a micromanipulator, was placed 3 to 5 centimeters in front of a hermit crab who was actively pumping. Schroeder (1960) had demonstrated passive echolocation in a freshwater cladocera, with the reception of the swimming movements occurring in the first pair of antennae.

## SUMMARY

1. A chordotonal organ in the basal segment of the antennal flagellum of the hermit crab Petrochirus californiensis is described.
2. Adequate stimulation is flexion or intrascopoidal compression of the dendrites. Stretch of the dendrites inhibits responses from the bipolar sensory cells.
3. A theory for the adequate stimulation of the flagellar chordotonal organ (FCO) is applied to periopod elastic strand stretch receptors. A mechanism that results in flexion of the dendrites in response to strand stretch or relaxation is proposed to account for the responses obtained from the other chordotonal organs.
4. It is suggested that movement responses, most position responses and responses that are intermediate, could arise from a single type of cell, and would depend only on the physical arrangement of dendrites within the strand.
5. Responses from the FCO are analagous to responses from the vertebrate lateral line and the FCO is thus considered to be a portion of the crustacean acoustic receiving system.
6. A temperature dependent background discharge is modulated by water borne vibrations. Vibrational stimuli applied directly to the flagellum

produce synchronous compound spikes up to 200 cps and asynchronous responses to 1000 cps.

7. The possibility that the FCO can be used for the detection of water currents, body displacements, texture, and near-field acoustic stimuli including passive echolocation is discussed.

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