

# LOCALIZATION AND ELECTRICAL ACTIVITY OF THE DISTANCE CHEMORECEPTORS THAT MEDIATE PREDATOR AVOIDANCE BEHAVIOUR IN *ACMAEA LIMATULA* AND *ACMAEA SCUTUM* (GASTROPODA, PROSOBRANCHIA)

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## SUMMARY

1. The marine gastropods *Acmaea* (*Collisella*) *limatula* and *Acmaea* (*Notoacmaea*) *scutum* respond to distant predatory starfish (i.e. to starfish scent) by moving up a vertical surface.

2. The distance chemoreceptors that mediate this avoidance behaviour are located on the mantle margin. Heat cauterization of the limpets' mantle margin eliminates their responsiveness to *Pisaster ochraceus* scent, while a similar cauterization of the ctenidium and the osphradia does not diminish the avoidance behaviour.

3. Primary afferent electrical activity can be recorded from the chemoreceptors on the mantle margin that are responsive to starfish scent and also from other physiologically distinct receptors that are responsive to contact with starfish tube feet.

## INTRODUCTION

Many gastropod molluscs recognize and respond to predatory starfish both at a distance (avoidance responses) and upon contact (escape responses) (for reviews see: Bullock, 1953; Kohn, 1961; Feder & Christensen, 1966). The first reports of gastropod responses to predators, however, were of the elaborate behaviour elicited upon contact (Bauer, 1913; Weber, 1924; Hoffman, 1930), and it was against this spectacular standard that early investigators compared possible responses to predators at a distance. As a result, distance responses, if considered at all, were reported as 'weak' or not observed. More recently, however, several reports have implied qualitative as well as quantitative differences between the responses to predators at a distance and upon contact (Feder, 1963; Gore, 1966; Montgomery, 1967; Szal, 1970).

The intertidal gastropods *Acmaea* (*Collisella*) *limatula* Carpenter and *Acmaea* (*Notoacmaea*) *scutum* Eschscholtz respond to waterborne material diffusing from a distant predatory starfish (i.e. to the 'scent' of the starfish) by moving up a vertical surface and by moving downstream. When the animals are required to choose between moving up a vertical surface and moving downstream (by arranging the water current to flow from above) they move up the vertical surface (Phillips, 1974, 1975). These distance chemoreceptor-mediated avoidance responses are strikingly different from the contact

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response reported by several authors (Bullock, 1953; Feder, 1963; Margolin, 1964), in which the limpets simply move away from the point of contact regardless of vertical orientation or the direction of water flow. The primary concern of the present investigation is to locate the distance chemoreceptors responsive to waterborne material diffusing from predatory starfish.

Since chemoreception is such an important and diverse phenomenon in gastropods, the possible sites of distance chemoreceptors in *Acmaea limatula* and *A. scutum* are numerous. These limpets have two osphradia, a ctenidium, mantle tentacles, two cephalic tentacles, and a complex oral region. Each of these structures has been linked with chemoreception in other gastropods: osphradia (Copeland, 1918; Brown & Noble, 1960; Bailey & Laverack, 1966), ctenidia (Szal, 1971), mantle tentacles (Fretter & Graham, 1962, p. 499), cephalic tentacles (Bovbjerg, 1968), and the oral region (Frings & Frings, 1965; Jahan-Parwar, 1972).

There are two basic parts to the following paper: (1) localization of the distance chemoreceptors that mediate avoidance behaviour, and (2) description of the afferent electrical responses from these receptors.

#### MATERIALS AND METHODS

##### *Localization of the distance chemoreceptors*

*Acmaea limatula* and *A. scutum* were collected from the intertidal zone on the day before starting the experiments and ranged in shell length from 18 to 32 mm. Predatory starfish (*Pisaster ochraceus* Brandt) were collected intertidally no more than 3 days before the start of an experiment.

On the day following their collection, 75 limpets were assigned to each of four experimental treatments: sea-water control,  $MgCl_2$  (narcotization) control, ctenidium and osphradia cauterization, and mantle margin cauterization. The groups were then tested on a vertical surface in the light for responses to the scent of *Pisaster* (pre-operative testing).

In the test procedure, 25 limpets were placed along a horizontal strip halfway up the front glass of an 8 gal aquarium supplied with running sea water through a manifold located on the bottom. The limpets were then subjected either to control sea water or to water flowing over six *Pisaster ochraceus* (approximately 1440 g total wet weight) in a 4.5 l tub feeding water to the test aquarium. After 15 min, the number of limpets moving up and down was recorded. The test criterion for a positive response was increased upward movement by the limpet population in starfish-scented water, and only those animals moving more than 1 cm up or down were included in the results. It should be noted, however, that both in control water and in scented water, a substantial number of limpets did not move during the experimental period and were therefore not included in the results. For each group of limpets, test and control runs were about 7 h apart with half of the animals experiencing control water first and half experiencing *Pisaster*-scented water first.

On the next day, operations were performed with 75 limpets (3 groups of 25 limpets) representing each of the four experimental treatments as follows.

(1) Sea water-control groups were left undisturbed in their storage tub with running sea water.

(2) The  $\text{MgCl}_2$  (narcotization)-control groups were placed in a 1:1 mixture of sea water and isotonic (7.5%)  $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$  for 2 h. They were then returned to running sea water where they began to revive within an hour.

(3) The ctenidium-and-osphradia-cauterization groups (surgical controls) were placed in the sea water: $\text{MgCl}_2$  mixture for 1–2 h. The relaxed limpets were held in a clamp ventral side up and tilted forward slightly. In this position, the limpet's head could be flexed against the foot and the entire mantle cavity became accessible to the heat-cautery unit. All of the ctenidial filaments and both osphradia were then cauterized. Each animal was immediately returned to sea water after its operation. Operations on 25 limpets took about 1 h.

(4) Mantle-margin-cauterization groups were placed in the sea water:  $\text{MgCl}_2$  mixture for 1–2 h; an animal was clamped ventral side up, and then the mantle margin was cauterized all around. In addition to the mantle tentacles, approximately 2 mm of tissue proximal to the tentacles was destroyed. Each animal was returned to sea water after its operation. Operations on 25 limpets took about 1 h.

On the day following the operations, groups of limpets were again examined for responses to the scent of *Pisaster* (postoperative testing) using the same procedures described for preoperative testing. After this final testing, the limpets were maintained in aquaria for several weeks to observe their general health and the long-term effects of the cauterization.

The heat-cautery unit used in these experiments consisted of two insulated, flexible copper leads with a tip of 30-gauge tungsten wire soldered to the leads. The copper leads passed through an 8 cm length of glass tubing (2 mm inside diameter) so that the completed unit could be held like a probe and the 1 mm wide tip controlled accurately. Line voltage was reduced with two variable transformers in series so that the voltage delivered to the leads was between 2 and 5 V. The exact voltage required to heat the cautery varied with the amount of mucus caked on the tip and the state of erosion of the tungsten wire.

Details of the experimental apparatus and testing procedures have been described elsewhere (Phillips, 1974, 1975).

#### *Afferent activity in the pallial nerve*

A large limpet (29–34 mm shell length) was carefully removed from its shell and pinned to the wax bottom of a plexiglass recording chamber (14 × 6.5 × 4.5 cm). Enough sea water was added to just cover the limpet, and then the buccal apparatus, the entire visceral mass, and all of the presumed sensory structures except the mantle margin were removed. The pallial nerves, which innervate the mantle margin (Fretter & Graham, 1962), were cut just distal to the pleural ganglia, and the central nervous system was removed. The end result of this procedure was a preparation consisting of the foot, the mantle margin, and the pallial nerves. Finally, a pallial nerve was selected for recording, and the cut distal end was teased apart using sharpened watchmaker's forceps.

Afferent chemosensory responses from the frayed pallial nerve were recorded in a Faraday cage with non-polarizing  $\text{Ag}/\text{AgCl}_2$  glass-capillary, suction electrodes (20–40  $\mu\text{m}$  diameter tips). Input from the recording and indifferent  $\text{Ag}/\text{AgCl}_2$  wires was first led to a preamplifier (Grass P8 A.C.) and then to a two-channel oscilloscope

(Tektronix type 502A). Oscilloscope tracings were initially recorded on a tape recorder (Magnecord 728) from which permanent records were made on moving film (Nihon Kohden PC-2A camera).

Sea-water at approximately 13 °C continually flowed into the plexiglass recording chamber through a series of stopcocks that directed the flow from either of two aquaria. Water was delivered to the chamber at a rate of 1.25 ml/sec through a single, submerged glass inlet tube (2 mm inner diameter), which was positioned close to the limpet to direct a water flow along either side of the mantle margin. An exit hole kept the water depth in the chamber at about 1 cm. The aquaria were maintained at 10 l capacity with water from the running seawater system.

Three different methods were used to introduce the scent of starfish into the recording chamber. In the most common method, one aquarium contained nine *Pisaster ochraceus* (approximately 2700 g total wet weight) in sea water while another aquarium contained only control sea water. Water flowing through the recording chamber initially came from the control aquarium. Then, by turning two stopcocks, scented water was shunted into the recording chamber from the *Pisaster* aquarium, and the water flow from the control was stopped. In the second method, water was continuously siphoned from only one aquarium, and, after a period of control sea-water flow, several *P. ochraceus* were added to this aquarium. In the third method, control sea water flowed into the recording chamber while either a glass probe or one *Pisaster* tube foot was held in front of the inlet tube, directing water over the mantle margin. To avoid possible excitation of photoreceptors, experiments using the first two methods of stimulation were always conducted in total darkness.

## RESULTS

### *Localization of the distance chemoreceptors*

Normal *Acmaea limatula* and *Acmaea scutum* on a vertical surface in the light respond to a flow of control sea water from below by moving down the vertical surface. In contrast, they move strongly up the vertical surface under these conditions when the water first flows over the predatory starfish *Pisaster ochraceus* (Phillips, 1975).

The distance chemoreceptors that mediate this avoidance behaviour were localized by comparing the responses of normal limpets with the responses of limpets that had had particular sensory areas destroyed by heat cauterization. In Table 1, comparisons are made between the responses of limpets on a vertical surface before and after receiving the following treatments: sea-water control, MgCl<sub>2</sub> (narcotization) control, ctenidium and osphradia cauterization (surgical control), and mantle margin cauterization. Although 75 animals represented each treatment group, only the limpets that moved more than 1 cm up or down are included in Table 1.

Before the operations (pre-operative testing), all four prospective treatment groups showed characteristic responses to control water and to water that had previously flowed over *Pisaster ochraceus* (*Pisaster*-scented water). In a flow of control water, the limpet populations moved down the vertical surface; when *Pisaster* scent was present in the water, the limpets moved in the opposite direction (upward).

After the operations (postoperative testing), the group with the mantle margin cauterized no longer responded to the scent of *Pisaster*. The distributions of *Acmaea*

Table 1. *Localization of receptors mediating avoidance behaviour*

(Each treatment group contained 75 limpets, but only those animals moving more than 1 cm up or down are included, the test criterion for a positive response was increased upward movement by a population in starfish-scented water.)

	Preoperation tests				Postoperation tests			
	Control		Pisaster		Control		Pisaster	
	Up	Down	Up	Down	Up	Down	Up	Down
<i>Acmaea limatula</i>								
Sea-water control	13	28	28	8	5	27	49	3
MgCl <sub>2</sub> control	7	27	42	6	13	18	32	1
Ctenid + osph cauterized	12	32	36	5	13	12	48	0
Mantle margin cauterized	4	36	36	5	4	22	7	20
<i>Acmaea scutum</i>								
Sea-water control	9	30	51	6	8	44	37	6
MgCl <sub>2</sub> control	12	37	54	3	11	32	36	6
Ctenid + osph cauterized	14	27	45	6	18	17	42	3
Mantle margin cauterized	16	23	34	6	10	36	9	30

*limatula* and *A. scutum* in *Pisaster*-scented water after the operations were significantly different from their distributions under the same conditions before the operations ( $P < 0.001$  by a chi-square test corrected for continuity). Additionally, the postoperative distributions of these limpets in the presence of *Pisaster* scent were not significantly different from their postoperative distributions in control sea-water ( $P > 0.05$ ). In contrast, the sea-water-control group, the MgCl<sub>2</sub>-control group, and the ctenidium-and-osphradia-cauterization group continued to respond to the scent of *Pisaster* after the operations. Differences between the distributions of these groups in control sea-water and in *Pisaster*-scented water remained highly significant ( $P < 0.001$ ).

The limpets' mantle margin, therefore, contained the chemoreceptors detecting distant *Pisaster*. Furthermore, cauterization of the mantle edge knocked out the avoidance response so completely that it appeared that these distance chemoreceptors were in large numbers only on the mantle edge. Since the cautery always destroyed both the mantle tentacles and a narrow ring of mantle tissue proximal to the tentacles, this experiment cannot, however, determine whether the chemoreceptors are actually located on the tentacles or on the mantle margin just proximal to the tentacles.

Following the postoperative tests, 50 limpets from each treatment group except the MgCl<sub>2</sub> control were placed in aquaria and examined periodically for mortalities and regeneration of cauterized tissue. More than 90% of the mantle-margin-cauterization group were still alive after the first week, and, by the end of the third week, many of these limpets had regenerated minute tentacles around the mantle edge. By the end of the ninth week, almost all of the limpets had mantle tentacles and some had completely regenerated the mantle margin. Mortality in the ctenidium-and-osphradia-cauterization group, however, was virtually 100% within one week. All the limpets in the sea-water-control group were alive at the start of the third week and 90% survived to the tenth week.

*Afferent activity in the pallial nerve*

Stimulation of the mantle margin of *Acmaea scutum* with water that had flowed over the predatory starfish *Pisaster ochraceus* produced an increase in afferent electrical activity in the pallial nerves. Since the recordings were made with suction electrodes on the cut distal end of a pallial nerve and since there were no peripheral ganglia between the mantle margin and the pleural ganglia, this chemically elicited output most likely represented primary afferent activity.

Recordings of responses using three different methods of stimulus presentation are shown in Fig. 1. The three sources of starfish scent (water from an aquarium containing starfish, starfish suddenly introduced upstream, and tube feet held near the mantle margin) all produced similar increased afferent electrical activity in the pallial nerve. The recordings in Fig. 1 were continuous and therefore probably represented the same receptor(s). In contrast to this increased activity after chemical stimulation, photostimulation of the mantle margin or tactile stimulation with a glass probe during these recordings did not induce receptor activity. The results clearly indicate that distance chemoreceptors sensitive to natural concentrations of *Pisaster* scent are located on the mantle margin of *A. scutum*.

These distance chemoreceptors showed several interesting physiological characteristics. First, impulses often occurred in doublets or bursts. This can be seen in Fig. 2, which is the same nerve recording as Fig. 1A but photographed at a higher speed to separate individual impulses. Secondly, in a continuous flow of *Pisaster*-scented water, impulse frequency remained high for about 45 sec (Fig. 1), indicating that these receptors adapt rather slowly. Considerable activity was still present after 5 min. Thirdly, the impulse frequency of a unit was low (less than 1.5 impulses/sec).

In addition to the distance chemoreceptors responsive to starfish scent, chemoreceptors responding specifically to actual contact with the tube feet of certain predatory starfish occur on the mantle margin. A continuous recording of electrical responses to contact with a glass probe and the tube feet of several species of echinoderms is presented in Fig. 3. The tube feet of five echinoderms were tested, *Strongylocentrotus purpuratus* Stimpson, *Patiria miniata* Brandt, *Pisaster ochraceus*, *Pisaster brevispinus* Stimpson, and *Pycnopodia helianthoides* Brandt, as well as a filtered homogenate of *P. ochraceus* tube feet (1 mg tube ft/ml sea water).

As can be seen in Fig. 3, strong responses were given upon contact with *P. ochraceus*, *P. brevispinus*, and *Pycnopodia*, all of which are predators. Whereas responses to the glass probe, *Patiria* (a scavenger), *S. purpuratus* (an herbivore), and the extract of *Pisaster* tube feet were extremely weak. Since positive responses were given to the three predators and negative responses were given to the three 'non-predators', these chemoreceptors showed considerable specificity by making the correct predator/non-predator distinction in six out of six cases. In addition, they were never observed to respond to an extract of tube feet or before actual contact.

These neurophysiological studies were primarily carried out on *A. scutum*, because of the relative abundance of large specimens (29–34 mm shell length). However, *A. limatula* were also examined and gave similar results. Distance chemoreceptors responsive to the scent of predatory starfish were present on the mantle margin of *A. limatula* as were chemoreceptors responsive to contact with predatory starfish.

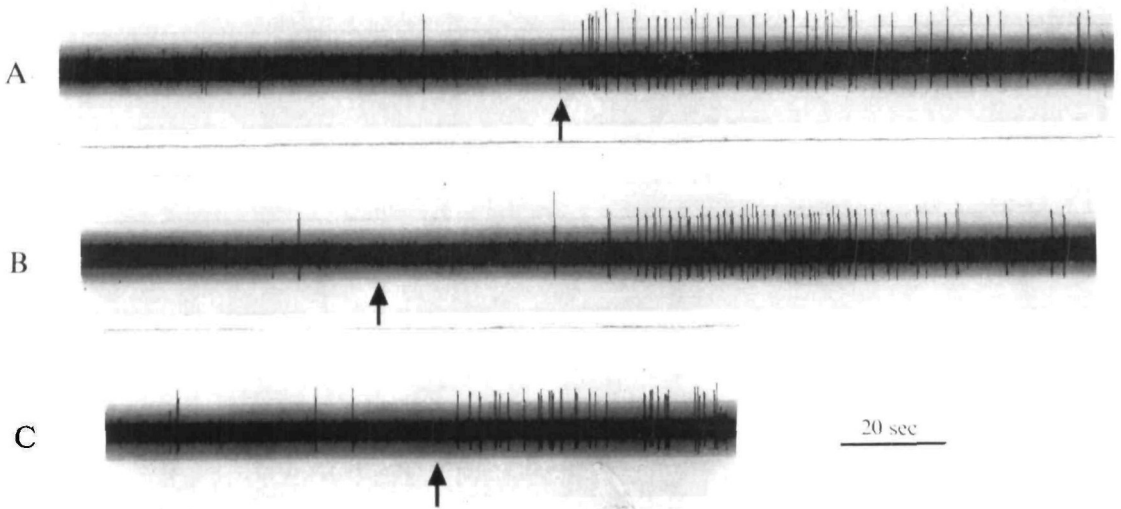


Fig. 1. Primary afferent electrical responses to the scent of *Pisaster ochraceus* recorded from a pallial nerve of *Acmaea scutum*. In this continuous recording, *Pisaster* scent was introduced in three ways with approximately 20 min between stimulus presentations. A, Control sea water, then, at the arrow, sea water came from a tank containing several *Pisaster*. B, Control sea water from an aquarium, then, at the arrow, *Pisaster* were added to the aquarium. C, Control sea water with a glass probe held near the mantle margin, then, at the arrow, one *Pisaster* tube foot was held near the mantle margin.

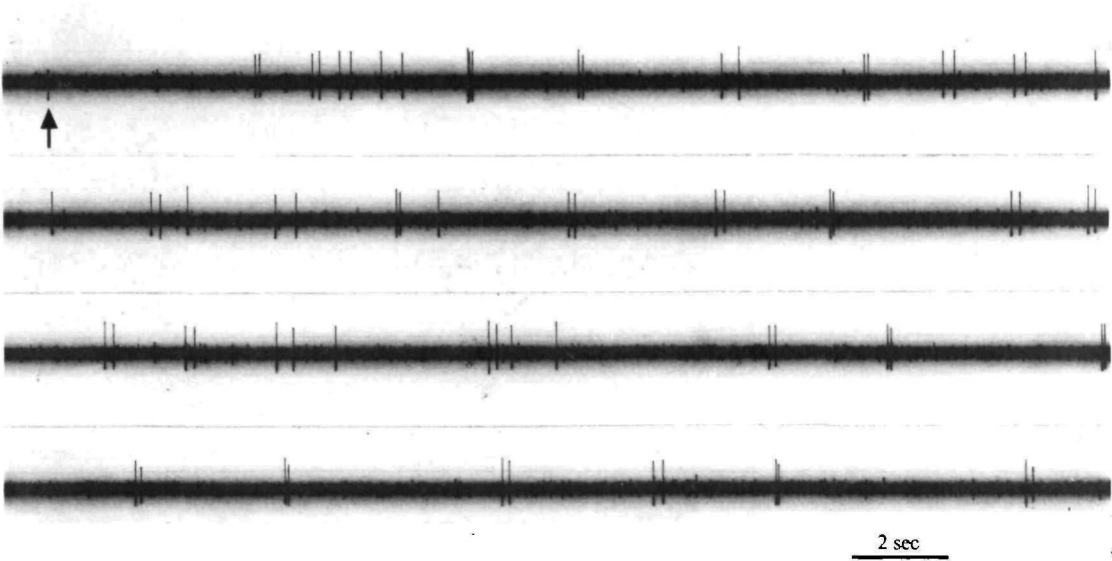


Fig. 2. Primary afferent impulse pattern in response to the scent of *Pisaster*. Impulses often occur in doublets or bursts as can be seen in this segment of Fig. 1A photographed at a high speed.



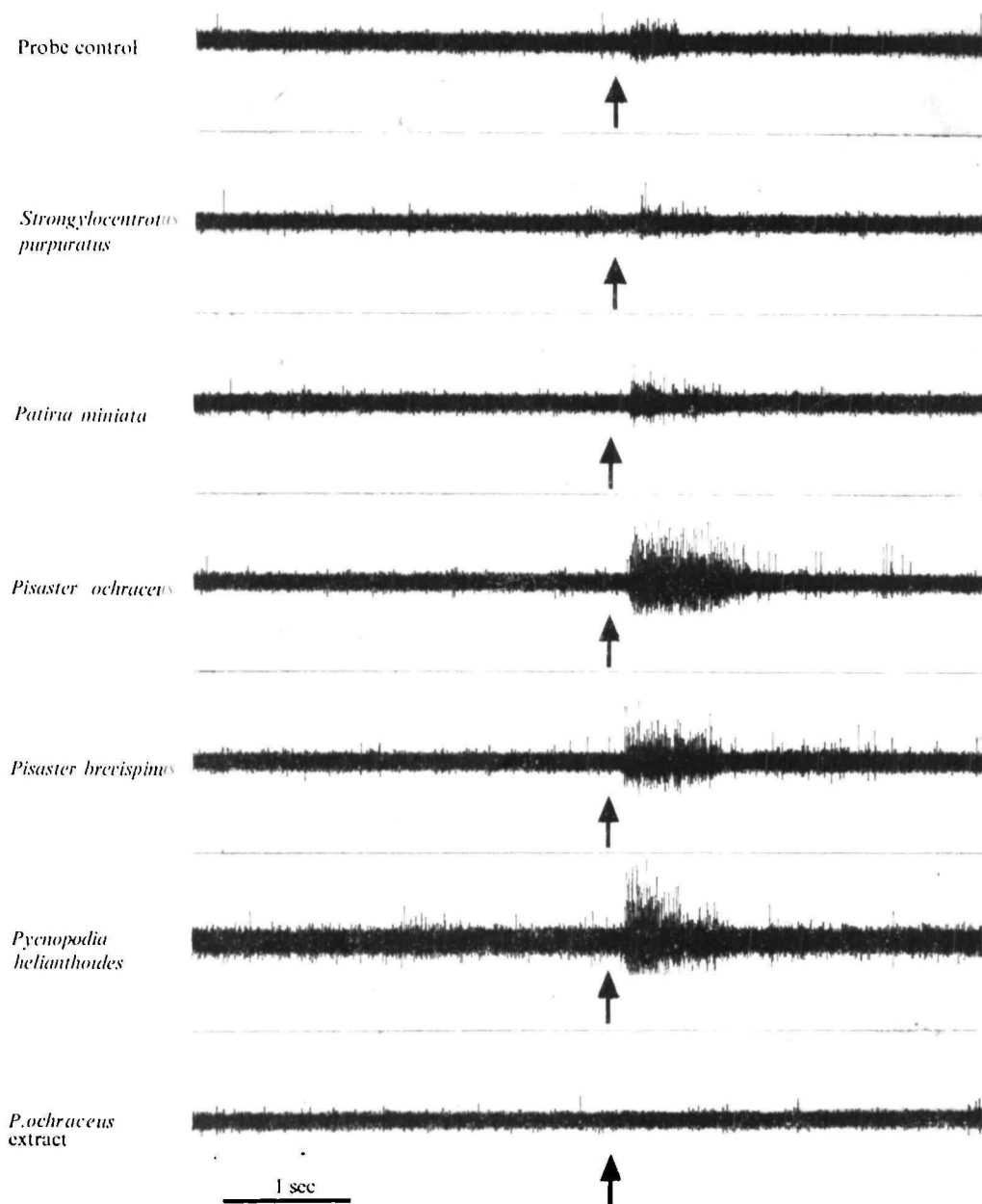


Fig. 3. Afferent responses to contact with echinoderm tube feet. The recordings are continuous, and the same location was touched once quickly in each trial. There were approximately 2 min between trials.



## DISCUSSION

Cautery of the limpets' mantle margin eliminated avoidance behaviour. The animals' general health and sensory-motor capabilities did not appear to have been significantly impaired by this treatment, however, and several points support this conclusion. First and foremost, limpets without functional mantle margins were nevertheless active in the presence of *Pisaster* scent, but they moved down instead of up. Thus, their capabilities for movement were not impaired, but they responded as if they were in unscented (control) water. Secondly, the limpets without functional mantle margins responded with normal, vigorous escape behaviour when they were touched on a cephalic tentacle by a *Pisaster* tube foot after the experiment. Thirdly, the surgical control of cauterizing the ctenidial filaments and the osphradia appeared to be a much more damaging treatment than cauterizing the mantle margin; most of the limpets with cauterized ctenidial filaments and osphradia died within a few days of the end of the experiment. However, limpets in this extremely severe surgical control responded well to the presence of *Pisaster* scent. The distance chemoreceptors that mediate avoidance responses to *Pisaster* scent are, therefore, located on the mantle margins of the limpets.

Receptors sensitive to starfish scent have been localized in this manner for only one other gastropod: Szal (1970, 1971) found chemoreceptors responsive to starfish scent on the ctenidium of the archaeogastropod *Tegula funebris* in small, ciliated pockets, which he called bursicles. Furthermore, bursicles were found throughout the prosobranch order Archaeogastropoda with the exception of the suborders Patellacea (containing the acmaeids) and Neritacea. Since cauterization of the ctenidial filaments did not affect the avoidance behaviour of *A. limatula* and *A. scutum*, we can conclude that the starfish-sensing function as well as the bursicles are absent from the ctenidia of acmaeids. Bursicles are also absent in the orders Mesogastropoda and Neogastropoda. These 'higher' gastropods do, nevertheless, respond to starfish at a distance (Gore, 1966).

In the evolution of the higher gastropods, bursicles may have been abandoned with the advent of the monopectinate gill and the invasion of waters containing large amounts of suspended sediments, which easily foul the bursicles (Szal, 1970). Their absence in the Acmaeidae, which have the more primitive bipectinate ctenidia and are firmly committed to life on rocky shores, is more difficult to explain. The simplest assumption is that the limpets have lost the bursicle structure but have retained its chemoreceptive function in a different location.

Location of the chemoreceptors on the mantle margin instead of on the ctenidium may provide several advantages for limpets. (1) In animals that are dorso-ventrally flattened, receptors around the periphery will generally be alerted to approaching starfish well before more centrally located receptors. (2) With receptors surrounding the periphery of the limpet and separated on opposite edges by as much as 3 cm, stimulus direction could be accurately detected by differential stimulation of the receptors. With receptors on the ctenidium, it would appear that any sense of stimulus direction (separate from the direction of the water flow) would be lost. (3) Receptors lining the periphery also present a larger sensory target area than a group of receptors localized in the mantle cavity. (4) Finally, when a limpet is mostly out of water or

when it is periodically splashed during tidal changes, it is the mantle margin and not the ctenidium that is primarily in sensory contact with the water and would thereby be more likely to sense predatory starfish in the vicinity.

In addition to initiating predator avoidance, chemoreception in gastropods has been reported to initiate many other types of behaviour, including food finding, mating, homing, and settlement (for reviews see: Charles, 1966; Kohn, 1961; Laverack, 1968). Despite great interest in gastropods as neurobiological preparations (e.g. Kater & Rowell, 1973) and the prominent role played by chemoreception in some of these studies (Mpitsos & Davis, 1973; Willows, Dorsett & Hoyle, 1973*a, b*), only a few recordings have been made from gastropod primary afferents that are sensitive to chemical stimuli (Jahan-Parwar, 1972; Field & MacMillan, 1973). This study presents the first definite recordings from distance chemoreceptors mediating avoidance behaviour and distinguishes these receptors from the contact chemoreceptors mediating escape behaviour.

Unfortunately, distinctions between specific contact responses, specific distance responses, and unspecific body contractions resulting from general damage have often been neglected in studies of molluscan defensive behaviour. This is unfortunate since the sensory modes and neural pathways involved in these phenomena may be as different as those responsible for taste, smell, and pain in terrestrial vertebrates, although on a different level of complexity. Attention to these distinctions will be particularly important in clarifying and extending preliminary work on the starfish substances that naturally elicit defensive reactions in gastropods (e.g. Mackie, 1970).

The distance chemoreceptors that mediate avoidance behaviour in *Acmaea scutum* appear to be quite different from the contact chemoreceptors that mediate escape behaviour in this limpet. Different parts of the limpet's body are responsive to the scent of a distant starfish (mantle margin) and to contact (head, cephalic, tentacles, foot, and mantle margin) (Phillips, 1974). In addition, the respective behaviours differ fundamentally: in the presence of starfish scent, the limpets move downstream and up a vertical surface, whereas upon contact with the starfish they move directly away from the point of contact regardless of the waterflow direction or vertical orientation. These behaviours also have somewhat different specificities: the limpets respond weakly or not at all to the scent of *Pisaster brevispinus*, but they respond vigorously upon contact with members of this species (Phillips, 1974). The present study further supports the distinction between avoidance and escape behaviour and the chemoreceptors that mediate them. Chemoreceptors responsive to contact with starfish were never observed also to respond to tube feet held at a distance or to an extract of tube feet.

The initial recordings from *Acmaea scutum* and *A. limatula* immediately reveal a level of complexity in the chemosensory input from the mantle margin. For instance, the presence of impulse pairs or groups is a common feature of the chemoafferent activity in a constant concentration of starfish scent. The intrinsic afferent 'burstiness' may be of interest to neurophysiologists in terms of neuronal oscillators and the synchronization of sensory input. The observed impulse patterns, however, could result from a number of different neuronal phenomena indistinguishable by extra-cellular recording.

There is also a great deal of complexity in the combined sensory input from the mantle margin. Although the chemoreceptors responsive to predatory starfish were

The primary concern of this investigation, it should be properly noted that the mantle margin is not solely concerned with the recognition of predators. It is a general sensory structure, and, during the course of this study, afferent pallial nerve activity was routinely recorded from other receptors including 'off'-photoreceptors (active when the light intensity was reduced) and tactile receptors (active when mantle tentacles were either touched or deflected by a water current).

This complexity of the combined sensory input from the mantle margin raises the possibility of peripheral synchronization and integration. It has previously been reported that light and the direction of water flow modify the limpets' avoidance behaviour in the presence of *Pisaster* scent, and all of these effects can be overridden by contact with the starfish (Phillips, 1974, 1975). Photoreceptors, tactile receptors, and the distance chemoreceptors mediating avoidance behaviour are all found on the limpet's mantle margin, as are the chemoreceptors that mediate responses upon contact with starfish. The simplest assumption is certainly that the pallial nerve activity reported in this paper represents unmodified, primary afferent activity. However, peripheral interactions between receptors have been observed in other gastropods (e.g. Detwiler & Alkon, 1973; Dennis, 1967), and nerve cell bodies are often found scattered along molluscan nerves instead of organized into discrete ganglia. Furthermore, limpets have a well-defined nerve completely encircling the mantle margin (the circumpallial nerve) that could provide an excellent integrating pathway for sensory input.

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