

## Non-visual Functions of Crustacean Eyestalk Ganglia\*

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*Summary.* Ablation experiments demonstrated that in several crustacean groups, the proximal eyestalk ganglia are important in a variety of behavior patterns:

1. Chemical elicitation of feeding via the antennules is altered in lobsters, hermit crabs, and some brachyuran crabs by bilateral eyestalk ablation; the ablation of one antennule and the contralateral eyestalk is effective in lobsters and hermit crabs;

2. increased chewing of inedible objects occurs in all three groups following eyestalk ablation;

3. postural alterations in lobsters and hermit crabs occur following eyestalk ablation;

4. escape responses in lobsters occur only after considerable tactile input in eyestalk-less animals;

5. shell entry by hermit crabs takes much longer following complete eyestalk ablation, in contrast to control operations in which just the distal elements of both eyes are removed.

It is suggested that all of the behavioral alterations seen following eyestalk ablation can be considered a result of the removal of temporal attenuation of stimulus input by the *medulla terminalis*.

### Introduction

The stalked eyes of decapod crustacea contain four ganglia between the retina and the nerve tract leading to the brain. The neurosecretory complex of X-organ and sinus gland are also located in the eyestalks. While it is obvious that visual information will be transmitted and partially analyzed in the eyestalks (Waterman and Wiersma, 1963; Wiersma, Bush, and Waterman, 1964; Wiersma and Yamaguchi, 1967), the involvement of the neurons in the eyestalks of crustacea in non-visual activities is not so expected. Bush, Wiersma, and Waterman (1964) recorded from some neurons in the eyestalks of the crab *Podophthalmus vigil* which transmit tactile information from several parts of the crab's body and Watermann and Wiersma (1963) reported upon

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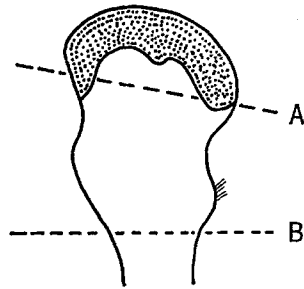


Fig. 1. Outline of eyestalk of *Panulirus japonicus*. Line A indicates control (distal) ablations, line B complete eyestalk ablation. Scale line 3 mm

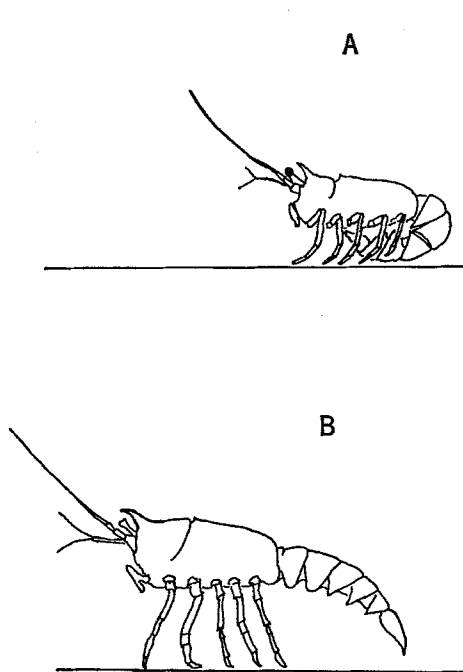


Fig. 2. Typical posture of (A) intact and (B) eyestalk-less individuals of *Panulirus japonicus*

An exception to this postural alteration was seen in one female *P. japonicus* which had spawned and attached the eggs to her pleopods following the removal of one eyestalk and one antennule. Subsequently

when the remaining eyestalk was removed, the posture-activity level appeared to be unchanged. The female cleaned the eggs with her pereopods and aerated the eggs by fanning the pleopods in an apparently normal fashion.

*Scyllarides squammosus*. A few specimens of this slipper lobster were available for testing at the Institute of Marine Biology in Hawaii. Ablation of both eyestalks or ablation of one eyestalk and the contralateral antennule eliminated the sustained feeding responses initiated in intact animals via distance chemoreception.

Intact animals, those with one eyestalk and one antennule removed, and those with both antennules removed would not chew on plastic tubing placed in contact with their maxillipeds. Eyestalk-less *S. squammosus* chewed on tubing for 10–40 seconds (four tests).

Intact slipper lobsters were very inactive during the day and remained in a lowered position with the abdomen pulled tightly under the cephalothorax, usually backed into a corner of the holding tank. Rapid, swimming retreat by flexion of the abdomen was rather easily elicited by tactile input on various parts of the body. Eyestalk-less *S. squammosus* slowly wandered about the aquaria almost continuously, with body elevated and unflexed abdomen, similar to eyestalk-less *P. japonicus*. In addition, when a walking leg was poked or pinched, that particular leg would move away but no tail flexion escape occurred. Escape by rapid tail flexion could be elicited by more vigorous agitation of legs and abdomen, but tactile input that would elicit escape in normal or one eyestalk-one antennule animals was not effective in lobsters with both eyestalks removed.

#### *Section Brachyura*

*Libinia emarginata*. This majid crab was shipped from Woods Hole, Massachusetts to Ann Arbor, Michigan. Removing both eyestalks (five specimens) eliminated the feeding responses elicited via antennule chemoreceptors in the normal animal. However, these crabs did not show any other behavioral alterations.

*Leptodius sanguineus*. This xanthid crab was tested at the Hawaii Institute of Marine Biology. The feeding activities initiated via the distance chemoreceptors of the antennules in the intact animals were not elicited in eyestalk-less animals (six specimens). However, feeding elicitation appeared normal in crabs with one antennule and the contralateral eyestalk removed (five specimens).

Normal animals would not chew on a piece of plastic tubing placed in their maxillipeds, while eyestalk-less crabs chewed the plastic for an average of 66 seconds (range 4 to 180 seconds). Body posture in eyestalk-less crabs appeared normal except that the chelipeds were held away

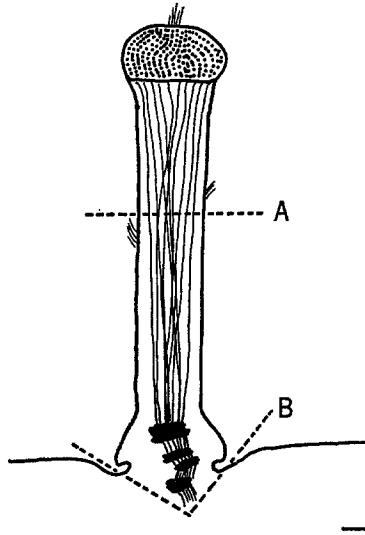


Fig. 3. Schematic outline of eyestalk of *Petrochirus diogenes* based on methylene blue preparations. Line *A* indicates control (distal) ablations, line *B* complete eyestalk ablation. Scale line 3 mm

mistakes in the form of movements or in the sequence of the acts involved in shell entry. All unsuccessful attempts to enter a shell were due to improper orientation of the crab's body with respect to the shell aperture. That is, the crab executed shell entry movements while in various positions on the shell; intact crabs always orient with respect to the aperture of the shell before executing any of the other behavior patterns. Most of the time the crabs just sat quietly on the outside of the shell.

Frequently specimens were prodded in the abdomen with a metal pointer after many minutes of inactivity. The crabs reacted to this tactile stimulation by moving the abdomen and ambulatory legs thus touch was still a stimulus for these animals. However, the movement was much slower than that of an intact naked crab when poked in the abdomen. These prodding movements by the observer did not seem to quicken shell entry attempts. In addition to this general inactivity, postural differences were noted. When outside a shell, normal hermit crabs hold the abdomen either against whatever surface the crab is clinging to or tightly curled forward under the body (Fig. 4a). In the case of eyestalk-less crabs, the shell was not tightly grasped by the ambulatory legs and the abdomen was held "loosely", not flexed forward or pulled against any surface (Fig. 4b). After shell entry, several of the eyestalk-less animals

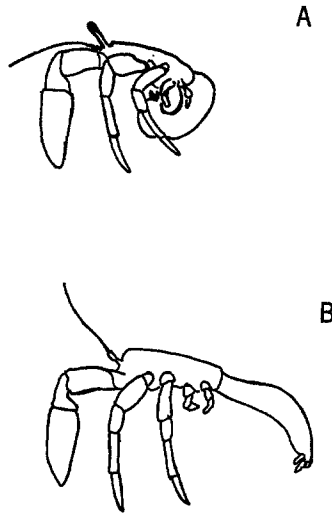


Fig. 4. Posture of (A) intact and (B) eyestalk-less individuals of *Petrochirus diogenes* when outside a gastropod shell

left the shells simply by walking forward and not pulling the shell along, suggesting improper abdominal posture even when the crab was in a shell.

A shell fight was observed between a large and a smaller eyestalk-less *Petrochirus diogenes*. The larger grasped the smaller with its ambulatories, moved forward without pulling its shell along (thus exposing most of its abdomen), and executed two raps (see Hazlett, 1966 for a description of shell fighting in the related genus *Dardanus*). Before the smaller could respond in any way to the rapping, the larger grasped one of the smaller's chelipeds with its own and crushed it. The cheliped was autotomized and then eaten by the larger crab. Such physical violence has been observed in intact specimens of this species (Hazlett, in press) but only after long shell fights involving a large number of raps.

### Discussion

The effects of proximal eyestalk ablation observed in this study are summarized in the Table.

The particular eyestalk ganglia responsible for the behavioral deficits seen can not be designated for the species observed in this study. Selective ablation of the terminal three ganglia without the disruptions described are needed to establish the *medulla terminalis* ganglion as the

could readily execute shell entry, but individuals were apparently not "stimulated" to do so. Anthropomorphically, they were not 'aware' they were shell-less. The information from proprioceptors in the abdomen (Chapple, 1966) that signal lack of shell inhabitation in intact crabs were probably still functional, however, the sensory input was not effective (in the normal amount of time). It is important to remember that a hermit crab does not periodically (spontaneously) show shell entry behavior when it is already in a gastropod shell. Thus the eyestalk-less hermit crabs that did eventually show this behavior were apparently responding to input from the abdominal proprioceptors, although on a different time scale. The actual execution of the movements involved in shell entry were normal both in path of movement and in speed of execution.

In each of the behavior patterns observed, the proximal eyestalk ganglia appeared to serve a similar function—that of a temporal multiplier: (1) For antennule elicitation of feeding, the normal animal shows feeding behavior for many seconds after initial excitation by chemical input to the antennules while eyestalk-less animals showed no response or only a brief one. (2) It would appear that chewing activity can be elicited by tactile input from receptors in the mouthparts. In the normal animal, chewing on inedible objects is probably inhibited by the lack of proper chemical input; this chewing is eventually inhibited in eyestalk-less animals, but not as quickly. (3) Chewing on edible objects is maintained by proper chemical input, i.e. food stimuli; maintenance of chewing is erratic or lacking in eyestalk-less animals. (4) The execution of escape reactions in intact animals is stimulated by tactile input which is quickly "multiplied in importance" by the CNS; eyestalk-less lobsters can show escape reactions (the motor patterns are present), but only after tactile input multiplication at the level of the abdominal receptors. (5) The shell entry of hermits was discussed above. All of these proposed functions of the eyestalk ganglia can be categorized as temporal multiplication, although other interpretations could be given.

It is not necessary to assume that the eyestalk ganglia in any way circuit the specific information involved in a behavior pattern. The multiplication function of this region need not carry particular information about specific input. Rather it just turns on and accentuates (multiplies) the input that is going to another region of the central nervous system. The fact that particular behavior patterns are attenuated can be due simply to the fact that the input goes to the appropriate part of the CNS. Thus, chemical stimulation from the antennules could go (separately) to the area(s) concerned with feeding; this area would be sustained in its activity by attenuation from the eyestalk ganglia. Attenuation from the eyestalk ganglia could be simultaneously going to

other "centers", but since these had not been activated by sensory input the attenuation is ineffective.

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