Disturbance of Feeding Behavior
in the Spiny Lobster, *Panulirus argus*,
Following Bilateral Ablation of the *Medulla terminalis**

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Summary. 1. Bilateral eyestalk ablation of spiny lobsters results in:

a) loss of responsiveness to chemical stimulation of antennular chemoreceptors,

b) increased tendency to positive responses following tactile and chemo-tactile stimulation of dactyl receptors,

c) increased tendency to grasp and ingest non-food objects,

d) disturbance of feeding efficiency associated with discoordination of feeding movements and prolonged periods during which food is held but not devoured.

2. Progressive ablation of the eyestalk ganglia indicates that the loss of the innermost, the *medulla terminalis*, is responsible for the above effects. Blinding or optic ganglion removal alone is without significant effect.

3. The observations strongly suggest that the *medulla terminalis* exerts an active regulatory or modulating influence on the spatial-temporal neural constructs responsible for feeding behavior. In this it resembles the functional role ascribed to the amygdala and frontal orbital cortex in mammals.

Introduction

Unilateral ablation of the *medulla terminalis*, the fourth and most proximal ganglion in the eyestalk of decapod Crustacea, disrupts ipsilateral antennular function normally associated with feeding behavior in the Bermuda spiny lobster. *Panulirus argus* (Maynard and Dingle, 1963; Maynard and Yager, 1968). Within the limits of observation, both the function of the antennule on the unoperated side and other aspects of feeding activity appear unaffected by the operation. This paper describes the short term effects of *bilateral* eyestalk ablation on olfactory and feeding behavior. Individual lobsters varied widely in behavior, both before and after eyestalk removal. Nevertheless, the data clearly indicate that bilateral eyestalk removal (which includes ablation of the optic ganglia, the medulla terminalis, and the sinus gland) not only disrupts the normal olfactory function of both antennules, but also interferes with other portions of the feeding process. A preliminary report has been presented (Maynard and Sallee, 1968).

Material and Methods

Fourteen adult *Panulirus argus* Latreille of both sexes were used. Observations were made during June, July and August at the Bermuda Biological Station. As in previous studies (Maynard and Dingle, 1963; Maynard and Yager, 1968) lobsters under observation were kept individually in glass fronted aquaria. Lobsters were fed regularly but sparingly with pieces of fish. They were never fed to satiation.

All lobsters in premolt or postmolt phases at the beginning of the observation period were discarded, leaving only intermolt animals. Since observations lasted several weeks, and since molting in the adult Bermuda population is most common during the summer months, a few individuals passed from the intermolt phase while under observation, and one molted in August. Although premolt lobsters are known to stop feeding (Maynard and Dingle, 1963), these molts were too few and too near the end of the experiment to significantly alter the results.

Normally lobsters maintained at Bermuda remain in excellent health. During these experiments, however, high ambient water temperatures (above 31° C) coincided with difficulties in the sea water supply, and several deaths occurred before the experiment concluded. These deaths were caused by sudden changes in external factors, however, so that observations made a few hours before death remain valid, and are included in the analyses. Table 1 gives the periods of observation and the experimental schedule of the animals studied.

Test Procedures. Responsiveness of antennules and parieopod dactyls to chemotactile stimulation was tested with a cloth swab dipped in a dilute puree of fresh fish ground in sea water. An identical swab dipped in sea water served as a tactile control. At each test period, therefore, responses to four stimulus conditions were obtained. The order of stimulus presentation was not constant. Lobsters were usually tested no oftener than twice per day.

Table 1. *Experimental animals and sequence of operations.*
Observations began on day 1 on intact lobsters

Lobster	Opt. gang. removed	One eyestlk. removed	Two eyestlk. removed	Molted	End obs.
1	day 10		day 21		day 42
2	day 9		day 20		day 41
3	day 10		day 21		day 42
4	day 10		day 21		day 25[a]
5	day 3		day 14		day 21[a]
6	day 19		day 28		day 46[a]
7[b]	day 14	day 18	day 20	day 48	day 56
8			day 8		day 27
9			day 7		day 26
10	day 28				day 31[a]
11					day 15[a]
12					day 7[a]
13					day 5[a]
14					day 2[a]

[a] Lobster died due to external factors.

[b] This lobster was photographed on 16 mm movie film during the course of the experiment.

Responses to stimulation were assigned to one of seven categories:

Positive Responses.

+3. Strong searching and grasping movements with parieopods, associated with forward movements of the lobster. Response immediate and general activity may continue after removal of stimulus swab.

+2. Searching or grasping movements, parieopods reach and grab. Lobster moves forward.

+1. Weak searching or grasping movements, parieopods lifted and move in direction of stimulus, but there is no general bodily advance and activity stops within a few seconds upon removal of stimulus swab.

No Response. No obvious advance or retreat from stimulating swab.

Negative Responses.

−1. Weak advoidance, antennules or parieopods pulled back from stimulating swab, body does not move.

−2. Avoidance, lobster backs away from stimulus swab.

−3. Strong avoidance, lobster backs away violently, using abdominal tail flips as well as parieopods for locomotion.

For some purposes, the above categories were lumped into two groups, positive responses and negative or no responses.

The tendency to manipulate and devour non-food objects was estimated by leaving cleaned rubber stoppers (No. 2, weight approx. 7.5 gm) or short portions of vacuum hose (weight approx. 5.5 gm) in the aquaria overnight. After about 12 hours, stoppers or tubes were taken out, examined for evidence of chewing, and weighed to determine the amount of material removed.

Protocol. In the basic experiment the responses of a group of 5 normal lobsters to chemo-tactile stimulation and non-food objects were followed for 3—10 days. Both eyestalks of each lobster were then opened (Maynard and Yager, 1968), and the distal optic ganglia were removed. The group was observed for 11 days before the remaining eyestalk ganglia were removed by cutting off the eyestalk. Finally, responses of the eyestalkless lobsters were observed for 21 days or until death (see Table 1, Lobsters 4 and 5). Two other lobsters received similar treatment, but with varying intervals between operations. In one, eyestalk removal was accomplished in two steps, permitting confirmation of earlier observations on unilateral ablations. In another group of two lobsters the initial operation, removal of optic ganglia, was omitted. (Table 1, Lobsters 8 and 9).

Although observations were continued well beyond the period required for recovery from the trauma of operations, no truly long-term observations were made in these experiments. No deaths resulted from the operations or the experimental treatment.

Most responses were recorded on a portable tape recorder or transcribed immediately to a record book. One individual (No. 7, Table 1) was also observed intensively and photographed periodically at 32 fraims/second for subsequent detailed analysis.

Histological Controls. Ablated eyestalks were fixed in Bouins, embedded in paraffin-celloidin, and serially sectioned. They were examined to determine the extent of the initial ablation of optic ganglia.

Results

Bilateral eyestalk ablation produces extensive behavioral and physiological alterations in decapod Crustacea. The observations reported here deal only with those changes relating to the feeding act and to respon-

siveness to mechanical and chemo-tactile stimulation of dactyl and antennular receptors. They are also limited in time to intervals of days or weeks following eyestalk removal.

As described by Maynard and Dingle (1963) the typical, complete feeding act involves a sequence of stimuli and responses. Application of fish juice to antennular chemo-receptors results in approach and reaching movements with the parieopods directed toward the stimulus site. This normally leads to stimulation of the chemoreceptors on the parieopod dactyls, and the intensity of the parieopod reaching and grasping increases until the odorous object is touched and grasped. It is then brought toward and grasped by the maxillipeds and finally conveyed to the mandibles. The object is held and manipulated by maxillipeds and parieopods while being chewed and ingested. The total feeding act, therefore, can be considered to consist of three major stages: a) *Initiation*, in which stimulation of antennules or dactyls leads to searching, grasping activity. b) *Feeding*, in which the object is grasped by parieopods and transported to the mouthparts. c) *Ingestion*, in which the object is chewed and ingested while being held and manipulated by maxillipeds and parieopods.

The full sequence does not always occur. For example, if the object touched by the parieopods following antennular stimulation is not itself odorous or tasty, it may not be grasped, or it may be conveyed to the mouthparts and then discarded. Thus the second or third stages of the sequence may be lost. However, if the feeding drive is low, or the lobster otherwise disturbed, the feeding sequence may break up through loss of the first or second stage. A chemical or chemo-tactile stimulus that is ineffective when applied to the antennules may elecit the remainder of the sequence when applied to the parieopod dactyls, or to the mouthparts.

The intensity and completeness of the feeding act and the nature of the responses to chemo-tactile stimulation varied widely among intermolt lobsters, and over time within any one individual. Some rarely gave positive responses to antennular stimulation with fish juice, whereas others nearly always responded vigorously. We made no attempt to preselect individuals on the basis of behavior.

Initiation of Feeding

Results of experiments testing the initiation of feeding may be expressed in several ways, all leading to essentially the same conclusions.

Total Responsiveness. The percentage of all stimulus presentation trials for all lobsters that resulted in positive responses, e.g. approach and grasping reactions, may be lumped (see Table 2 A). Since several

Table 2. *Responses to stimulation under normal and experimental conditions*

Nature of measure of responsiveness	Locus of stimulus	Nature of stimulus	Percent feeding responses		
			Normal	Opt. gang. removed	Med. term. removed
A. Total number of responses	dactyls	control	37% (116)	35% (94)	77% [a] (95)
		fish j.	78% (114)	78% (94)	93% [b] (95)
	antenn.	control	9% (116)	2% (87)	0% [c] (95)
		fish j.	55% (116)	44% (87)	0% [a] (95)
B. Number of dominant lobsters	dactyls	control	55% (14)	14% (8)	100% [a] (9)
		fish j.	79% (14)	86% (8)	100% (9)
	antenn.	control	7% (14)	0% (8)	0% (9)
		fish j.	57% (14)	37.5% (8)	0% [c] (9)

n is given in ( ) beneath the percent positive responses.

[a] $p =$ less than 0.01 for Norm. *vs* Med. term. or (Norm. + Opt. gang.) *vs* Med. term.

[b] $p =$ less than 0.05 for Norm. *vs* Med. term. or Opt. gang. *vs* Med. term.

[c] $p =$ less than 0.025 for Norm. *vs* Med. term.; NS for Opt. gang. *vs* Med. term.

trials were usually given each individual, and since the number of trials per individual varied, the appropriate statistic is not altogether obvious. Nevertheless, if independence between trials is assumed, then it is evident that whereas removal of the outer optic ganglia produced no significant change in response, subsequent removal of the remaining optic ganglia fragments and the medulla terminalis produced A) a significant increase in positive responses to dactyl stimulation with either control or test swabs, and B) a complete loss of feeding responsiveness to antennular stimulation (Chi-square test, significance at 0.05 level or better).

Dominant Behavior of Individuals. Lobsters did not always give consistent positive or negative responses (as defined above) to the same kind of stimulus when repeatedly presented over a period of several days. An individual lobster was considered dominantly positive when the number of trials producing positive responses exceeded the number producing negative responses. Table 2 B lists the percentages of dominantly positive lobsters for various experimental conditions. Though not always statistically significant by a Chi-square test, these values parallel those of Table 2 A.
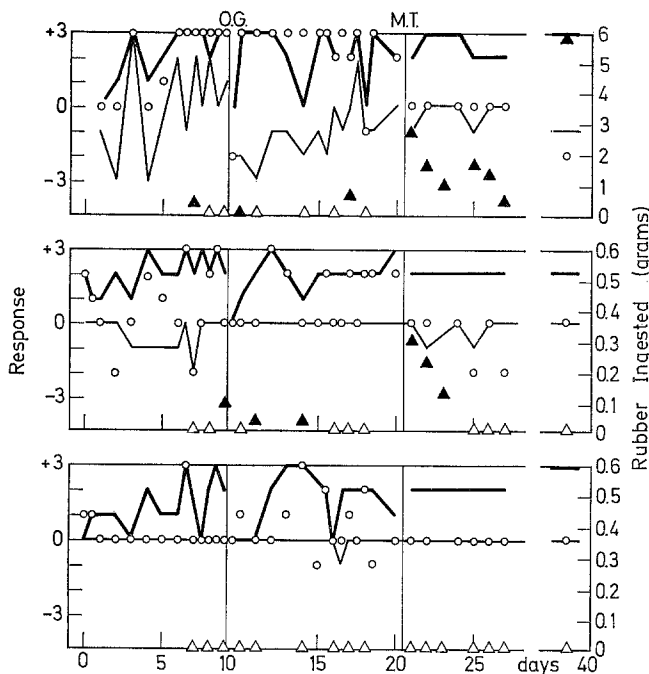
Fig. 1. Plots of feeding responses to varying stimuli in three lobsters. Left ordinate, intensity and sign of response (see text), right ordinate, grams of rubber stopper or tubing ingested overnight. thin line, ——, responses to tactile stimulation of antennules only; ○ responses to chemo-tactile stimulation of antennules; thick line, ——, responses to chemo-tactile stimulation of dactyls. △ nights during which rubber stopper or tubing was presented in aquarium, but was not chewed; ▲ nights during which rubber stopper or tubing was chewed, amount devoured indicated by height above abscissa. After eight or nine days, the optic ganglia were removed bilaterally in all lobsters (O.G.); after 19 or 20 days the entire eyestalks were removed (M.T.). The three lobsters were selected to demonstrate the range of variation encountered

Change in Individual Behavior. In ten lobsters, individual behavior could be determined both before and following operations. In seven, the complete series — optic ganglia ablation followed by eyestalk ablation — was used. In two, only eyestalks were removed, and in one, only optic ganglia. Fig. 1 graphs pre- through post-operative behavior for three lobsters selected to encompass the range of responsiveness encountered in preoperative, intact lobsters. The nature of the change in the relative number of positive responses — decrease, increase, or no change compared to the normal state — was measured for each lobster after optic ganglia were removed and then after eyestalks were severed. The results are not statistically significant, but all were again in the direction indi-

cated by Table 2: a reduction in responsiveness to antennular stimulation and an increase in responsiveness to dactyl stimulation in most lobsters after loss of the medulla terminalis. There was no indication in these experiments that progressive ablation, e.g. removal of first one and then the other eyestalk, or removal of optic ganglia and then the entire eyestalk, led to behavior different from that following immediate complete eyestalk ablation.

Feeding and Ingestion

Maynard and Dingle (1963) and Maynard and Yager (1968) did not observe augmentation of dactyl responsiveness following unilateral eyestalk ablation. Its presence following bilateral ablations supports the suggestion that the medullae terminales may be involved in more than initiation of feeding following olfactory antennular stimulation, perhaps in the organization and maintenance of the feeding and ingestion acts themselves. This possibility is supported by two further observations.

1. Usually normal lobsters do not accept inedible objects. Cleaned rubber stoppers (size 2) or short lengths of black vacuum tubing were left overnight with 12 lobsters for a total of 132 lobster-nights. Fig. 1 and Table 3 illustrate the results. Normal lobsters occasionally chewed and ingested portions of the rubber stoppers. An insignificant reduction in the extent and amount of chewing and ingestion followed removal of the outer optic ganglia. Total eyestalk removal in contrast produced a significant increase in both the instances in which chewing occured, and in the amount chewed. From direct observation and analysis of movie film we noted that normal animals rarely grasped or held the stopper or tubing when first presented to their dactyls. Eyestalkless individuals, however, usually grasped the object and often began chewing immediately.

2. In several lobsters loss of eyestalks was followed by abnormalities in feeding behavior. Pieces of fish were accepted and brought to the mouthparts in a normal manner when presented to the dactyls. Chewing and ingestion began, but often ceased after a short period, or continued in irregular spurts between prolonged periods of quiescence. This kind of behavior was not ordinarily observed in normal animals, or in these particular individuals before eyestalk ablation. Moreover, some lobsters retained pieces of fish in parieopods and maxillipeds but without feeding for remarkably long times, up to 90 minutes in some instances. Again this behavior is abnormal. The movements and coordination of appendages during actual manipulation and ingestion of food also appeared disturbed and less efficient in many lobsters following eyestalk removal.

We must emphasize, however, that feeding abnormalities were not obvious in all eyestalkless lobsters. Feeding behavior is complex and it

Table 3. *Response to rubber stopper or tubing left in aquarium overnight, under normal and experimental conditions*

Measure	Normal	Opt. gang. removed	Med. term. removed
Percent total instances in which object was chewed	26% (n = 31)	21% (n = 34)	52% [a] (n = 67)
Average amount removed from chewed objects	0.39 ± 0.45 gm (n = 8)	0.16 ± 0.20 gm (n = 7)	0.90 ± 1.32 gm[b] (n = 35)
Median amount removed from chewed objects	0.08—0.20 gm	0.02 gm	0.48 gm

[a] p = less than 0.01 for Normal and Opt. gang. removed *vs* Med. term. removed.
[b] p = less than 0.05 for Normal and Opt. gang. removed *vs* Med. term. removed. When tested against Normal *or* Opt. gang. removed alone, significance was marginal or absent.

is entirely possible that certain abnormalities though present were below the resolution of our current observations. Alternatively, the appearance of feeding abnormalities following eyestalk removal may require specific combinations of other factors which are not yet recognized. There is no doubt, however, that in some lobsters feeding becomes much less efficient following eyestalk removal.

Histological Controls

Since we suggest that the medulla terminalis is the critical structure in the eyestalk associated with feeding and olfaction, it is necessary to verify the extent of the destruction of eyestalk ganglia in the initial operations. Serial sections were made of eyestalks of six of the eight experimental lobsters (Table 1). In all, the outermost optic ganglion, the lamina ganglionaris, was removed by the operation, and ommatidia were absent or degenerating. Visual input was completely interrupted. Conversely, the medulla terminalis was apparently intact in all six lobsters examined. The operation left in addition to the medulla terminalis, varying amounts of the two medial optic ganglia. The remnants ranged from small portions of the medulla interna in two lobsters up to intact medulla interna and medulla externa in one lobster. There was, however, no correlation between the amount of optic ganglion tissue remaining and the general responsiveness of the lobster after the operation. As concluded in an earlier study (Maynard and Yager, 1968), removal or partial destruction of the optic ganglia does not affect the feeding response initiated by antennular stimulation.

Interaction of Behavioral Sets with Antennular-Dactyl Stimulus Configurations

Thus far responses to antennular or dactyl stimulation have been treated as individual, isolated events. It is also possible to consider them in relation to the total test configuration. In each test series two stimuli, chemotactile and tactile, were applied to two receptor loci, the antennules and the dactyls of the first 1—3 pairs of parieopods. The response of the lobster to each of these stimuli was recorded as approach or grasp (positive response), no movement (neutral response), or retreat (negative response). Accordingly there are theoretically 81 possible stimulus-response combinations. Only 29 of these were found in normal animals and only 9 in lobsters lacking medullae terminales (Table 4). The distributions of response sequences departed significantly from those expected from independent combination of response distributions following single stimulus configurations. We may infer that an additional factor, or *behavioral set*, helps determine the nature of a lobster's response during a given testing session.

Since under normal circumstances antennular stimulation may be expected to precede dactyl stimulation, it is instructive to examine the response pattern to dactyl stimulation as a function of the associated antennular stimulus and its behavioral response. Table 5 gives the distrubution of positive, neutral, and negative response percentages for a number of conditions. Twenty three tests in which no response to any stimulus was obtained were omitted from the data, leaving an initial n of 178 tests for nomal lobsters, and 90 for eyestalkless animals. Summed response distributions are given for single stimulus configurations and for combination configurations in which tactile and chemotactile dactyl stimulation are associated with each class of response to antennular tactile and chemotactile stimulation. The response distributions for the various stimulus configurations may be compared statistically. Thus we may ask whether the distribution of responses — positive, neutral and negative — evoked by a given dactyl stimulus differ significantly from one another according to the nature of the associated antennular *response*, or according to the antennular *stimulus* and so on. Table 6 diagrams the results of such comparisons using the Chi-square test.

In normal animals, the Chi-square values permit the following conclusions: 1. response distributions to antennular stimuli differ according to the nature of the stimulus; 2. response distributions to dactyl stimuli associated with common antennular stimulus-response configurations differ according to the nature of the dactyl stimulus; 3. within any one stimulus configuration, the response to dactyl stimulation differs according to the associated antennular response, i.e. the internal behavioral

Table 4. *Distributions of stimulus response configurations*

Stimulus locus	Tactile ant	Tactile dct	Chem-tact. ant	Chem-tact. dct	Number of normals observed	Number of normals expected	Number of eyestalkless observed	Number of eyestalkless expected
A.	+	+	+	+	11	2		
	0	0	0	0	23	7	5	2
	0	+	+	+	38	27		
	0	0	+	+	33	39		
	0	−	+	+	1	9		
	0	+	0	+	15	22	56	56
	0	0	0	+	31	32	15	18
	0	−	0	+	1	7		
	0	+	−	+	3	5	4	7
	0	0	−	+	3	6	2	3
	0	−	−	+	1	2		
	0	0	+	0	3	9		
	0	0	−	0	1	2	1	0
	0	0	0	−	1	1		
	0	−	0	−	1	0		
	0	0	−	−	3	0		
	−	+	+	+	5	5		
	−	0	+	+	2	8		
	−	−	+	+	7	2		
	−	+	0	+	1	5	7	8
	−	0	0	+	1	6		
	−	−	0	+	3	1		
	−	+	−	+	0	1	4	1
	−	−	−	+	1			
	−	−	+	0	1			
	−	0	0	0	1			
	−	−	0	0	5	3	1	0
	−	0	−	0	2			
	−	−	−	0	1			
	−	−	−	−	2			
					$\chi^2 = 165$		$\chi^2 = 43$	
					$N = 19$		$N = 6$	
B.	+				11	0		
		+			73	71		
			+		101	0		
				+	157	88		
	0				158	83		
		0			104	23		
			0		83	84		
				0	37	7		
	−				32	12		
		−			24	1		
			−		17	11		
				−	7	0		

Table 5. *Distribution of responses to dactyl stimulation as a function of associated responses to antennular stimulation*

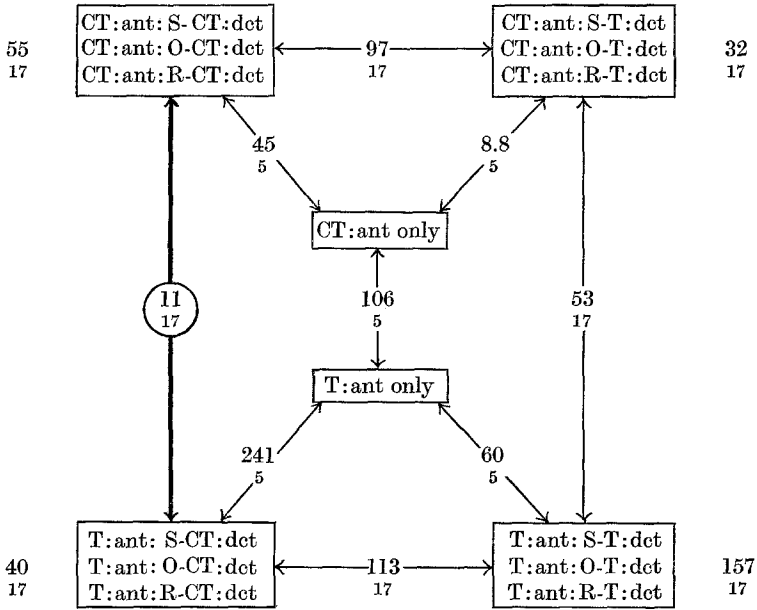| Stimulus-response configuration	Normals % responses			Number	Eyestalkless % responses			Number
	S	O	R		S	O	R	
CT:ant:S-CT:dct	96	4	0	101	0	0	0	0
CT:ant:0-CT:dct	87	10	3	60	99	1	0	79
CT:ant:R-CT:dct	47	24	29	17	91	9	0	11
CT:ant:S-T:dct	54	37	9	101	0	0	0	0
CT:ant:O-T:dct	27	56	17	60	80	19	1	79
CT:ant:R-T:dct	18	53	29	17	73	27	0	11
T:ant:S-CT:dct	100	0	0	11	0	0	0	0
T:ant:O-CT:dct	93	3	4	135	99	1	0	78
T:ant:R-CT:dct	63	31	6	32	92	8	0	12
T:ant:S-T:dct	100	0	0	11	0	0	0	0
T:ant:O-T:dct	41	56	3	135	77	23	0	78
T:ant:R-T:dct	19	19	62	32	92	0	8	12
CT:ant only	57	34	9	178	0	88	12	90
T:ant only	6	76	18	178	0	87	13	90
CT:dct only	88	8	4	178	88	2	0	90
T:dct only	41	46	13	178	79	20	1	90

CT = chemotactile stimulus; T = tactile stimulus; ant = antennules; dct = dactyls; S = search response, positive; O = no observed response, neutral; R = retreat, negative. In combination, for an example, CT:ant:S-CT:dct refers to that group of lobsters which responded with positive, search activity to chemotactile antennular stimulation and received chemotactile stimulation of the dactyls. The response percentages then give the distribution of responses, positive, neutral, or negative to the chemotactile dactyl stimulus. The number of tests in each group are listed in the number column.
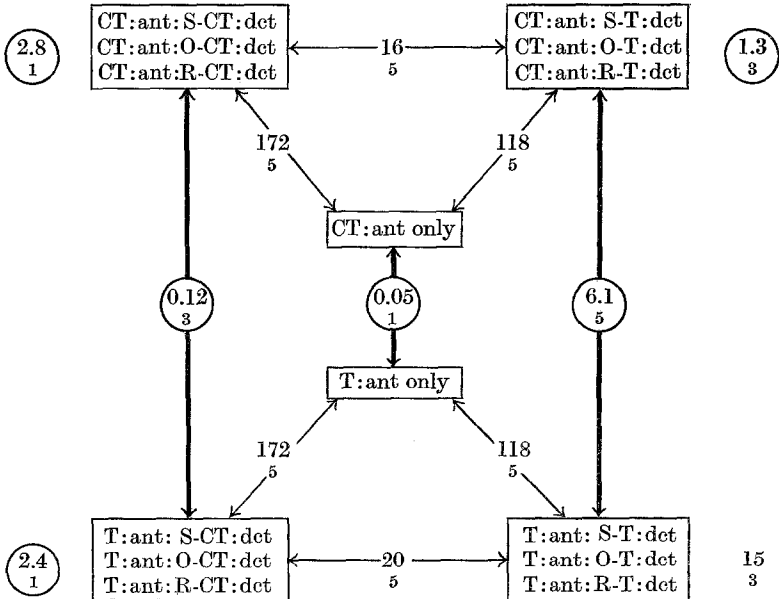
Declaration to Table 4

A. Stimulus-response configurations are to the left of the Table; + indicates an approach or grasping response, 0 indicates no response, and — indicates retreat. Thus in the 5th line, $0 - + +$, there was no response to tactile antennular stimulation, retreat with tactile dactyl stimulation, and approach and grasp with chemo-tactile stimulation of both antennules and dactyls. Only one normal animal responded once in this configuration. The number of expected incidences of each configuration was calculated on the basis of random combination of responses using the values of Table 4 B for individual stimulus-response frequencies. Chi-square values for comparisons of observed and expected distributions show differences significant beyond the 0.01 level for both normal and eyestalkless animals. The degrees of freedom are indicated, *N*. B. The numbers of each kind of response to each kind of stimulus are tabulated.

Table 6. *Comparison of response distributions under varying stimulus-response configurations*

A. Normal lobsters


```
55        ┌─────────────────┐              ┌─────────────────┐        32
17        │ CT:ant: S- CT:dct│ ←──97──→    │ CT:ant: S-T:dct │        17
          │ CT:ant: O-CT:dct │    17       │ CT:ant: O-T:dct │
          │ CT:ant: R-CT:dct │             │ CT:ant: R-T:dct │
          └─────────────────┘              └─────────────────┘
                      45                        8.8
                       5                          5
                        ┌──────────────┐
                        │ CT:ant only  │
                        └──────────────┘
          11               106                   53
          17                 5                    17
                        ┌──────────────┐
                        │ T:ant only   │
                        └──────────────┘
                  241                         60
                    5                          5
40        ┌─────────────────┐              ┌─────────────────┐        157
17        │ T:ant: S-CT:dct │ ←──113──→    │ T:ant: S-T:dct  │        17
          │ T:ant: O-CT:dct │    17        │ T:ant: O-T:dct  │
          │ T:ant: R-CT:dct │              │ T:ant: R-T:dct  │
          └─────────────────┘              └─────────────────┘
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B. Lobsters with *Medullae terminales* removed


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2.8       ┌─────────────────┐              ┌─────────────────┐        1.3
 1        │ CT:ant: S-CT:dct│ ←──16──→     │ CT:ant: S-T:dct │         3
          │ CT:ant:O-CT:dct │    5         │ CT:ant:O-T:dct  │
          │ CT:ant:R-CT:dct │              │ CT:ant:R-T:dct  │
          └─────────────────┘              └─────────────────┘
                    172                       118
                      5                         5
                        ┌──────────────┐
                        │ CT:ant only  │
                        └──────────────┘
          0.12            0.05                  6.1
           3                1                     5
                        ┌──────────────┐
                        │ T:ant only   │
                        └──────────────┘
                  172                         118
                    5                           5
2.4       ┌─────────────────┐              ┌─────────────────┐        15
 1        │ T:ant: S-CT:dct │ ←──20──→     │ T:ant: S-T:dct  │         3
          │ T:ant:O-CT:dct  │    5         │ T:ant: O-T:dct  │
          │ T:ant:R-CT:dct  │              │ T:ant: R-T:dct  │
          └─────────────────┘              └─────────────────┘
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set of the lobster; 4. the relative importance of a stimulus in determining a given response distribution depends upon its nature and locus, thus chemotactile stimulation of dactyls overrides any antennular stimulus configuration, whereas tactile stimulation of dactyls has relativeley little effect on the response distribution, particularly when associated with chemotactile antennular stimulation. If tactile stimulation is a less effective input, then we might expect that the behavioral set of the animal would have greater influence on its response distribution when both antennular and dactyl inputs were tactile. There is support for this supposition in that the Chi-square of the response distribution within a stimulus configuration is greatest for the tactile-tactile input.

The comparisons in animals lacking medullae terminales are quite different. In general they support the notion that antennular input in operated animals has no significant effect on the behavior elicited by associated dactyl stimulation. This confirms casual observations, and incidentally provides a control for this method of analysis, i.e. significant response distribution differences are lacking in appropriate comparisons. There is greater reason, therefore, to feel that the differences noted in the normal animal can be ascribed to the associated differences in stimulus or response rather than noise or undetected system parameters. Another important result of eyestalk ablation seems to be the loss of effectiveness of the behavioral set as measured by antennular response in determining response distributions within a given stimulus configuration. Perhaps an increase in responsiveness to all dactyl stimuli following medulla terminalis removal (see Table 5) tends to overcome any other intrinsic behavioral bias.

Discussion

In earlier experiments in which only one eyestalk was removed from the lobster (Maynard and Dingle, 1963; Maynard and Yager, 1968), the animal served as its own control and variations in responsiveness with time or among animals could be recognized and compensated. In most of the present experiments in which both eyestalks were removed, such simultaneous internal controls were impossible. Accordingly, the behav-

Declaration to Table 6

Chi-square values for comparison of response distributions are indicated between compared stimulus-response configurations (see Table 5 for actual distributions). The degrees of freedom for each comparison are indicated beneath each Chi-square value. Comparisons which do *not* differ significantly from chance are circled and indicated by heavy arrows.

Abbreviations of stimulus-response configurations are the same as those used in Table 5.

ioral resolution of the present experiments must be considered relatively coarse, and we can be certain only of the most obvious observations. These seem to include the following:

A. Fish-juice stimulation of antennules usually, but not always, initiates a feeding sequence. The incidence of positive responses in normal animals in this study, 55%, compares with 63% in the study by Maynard and Yager (1968) under similar conditions.

B. Dactyl chemo-tactile stimulation is more effective than antennular stimulation. There is even an appreciable incidence of positive responses to a presumably chemically neutral tactile stimulus, e.g. 37%.

C. Lobsters which do not respond positively to chemo-tactile antennular stimulation are more prone to respond negatively to dactyl stimulation; and in general the responses to dactyl stimulation will differ according to the nature of the response to associated antennular stimuli. This is taken as evidence of a behavioral set or bias for a given lobster at any given time.

D. Blinding a lobster by removal of varying portions of the three optic ganglia in the eyestalk produces no significant effect on chemo-tactually initiated feeding acitivity as observed in these experiments.

E. Removal of both eyestalks with their contained medullae terminales completely disrupts the initiation of feeding by antennular stimulation. This was predicted from the earlier results of unilateral operations (Maynard and Dingle, 1963; Maynard and Yager, 1968).

F. Bilateral eyestalk ablation also produces at least three further effects on feeding activity that were not described following unilateral ablations. These effects, like the antennular anosmesis, do not appear if the medullae terminales remain intact. They are similar to those reported by Bethe (1897) following section of both circumsophageal connectives in the crab *Carcinus* and include:

1. An increased incidence of positive responses to dactyl stimulation with either chemically neutral or fish-juice swabs. Significantly, all discrimination is not lost, for fish-juice swabs remain the most effective stimuli.

2. An increased tendency to "mouth" and ingest inedible objects. Perhaps the increased ingestion occurs simply because more inedible objects are likely to be grasped by the dactyls and brought to the mouthparts.

3. An apparent disturbance of normal ingestion of natural food objects. The effects are not evident in all lobsters, and when present are often difficult to quantify. The common result seems to be a reduction in the rate or efficiency of ingestion (see Bethe, 1897). More extensive observations under controlled conditions are necessary to confirm the detailed actions involved.

For the sake of clarity it is also important that certain qualifications and observations *not* made be explicity stated. These are:

A. Observations after eyestalk ablation were continued for a period of weeks at most in these studies. Although there is no indication that the observed effects can or should be considered the result of experimental trauma, and although more extended observations following unilateral eyestalk ablation (Maynard and Dingle, 1963) suggest antennular anosmesis is likely to be permanent, still the possibility that increased responsiveness to dactyl stimulation or disturbances of ingestive behavior are transient has not been excluded.

B. Although some of the observations of increased responsiveness to edible objects and increased tendency to ingest foreign items are consistant with hyperphagia, experiments were not designed to measure total food consumption. Consequently there is no direct evidence relating to the problem of over- or under-eating following eyestalk ablation. It should be noted, however, that Bethe (1897) found that removal of the entire brain produced hyperphagia in crabs.

C. Observations were insufficient to permit statements about discrimination at the level of the mouthparts. Direct application of stimuli to the mouthparts without intervening dactyl stimulation never occurred, and the range of objects presented under such conditions was minimal — pieces of fish, a cloth swab, and a piece of rubber tubing.

In the present experiments ablation of the eyestalks not only removed portions of the brain surmised to be important in the specific behavioral changes noted, but also removed other structures — the visual system and the neurosecretory, sinus gland system — known to have other important effects on behavior (see Waterman, vol. 1, 2, 1960, 1961). The control operations in which varying portions of the eye and associated optic ganglia were removed without obvious effect seem sufficient to exclude the optic ganglia from a major role in feeding behavior initiated by chemotactile antennular or dactyl stimulation. The problem of the sinus gland is more difficult. The immediate loss of appropriate antennular olfaction following unilateral or bilateral ablations and the lack of observed progressive changes argue against the importance of neurosecretory deprival in the origin of antennular anosmesis. These arguments are less compelling when applied to changes in dactyl responsiveness and feeding activity, because the changes were often less striking and could not always be recognized immediately after an operation. It is conceivable that the loss or gain of some blood-borne agent could be responsible for generalized changes in dactyl responsiveness and appitite, but it is difficult to reconcile such a generalized effect with the specific discoordination and delayed ingestion observed in some animals. It is also significant that Bethe (1897) reported similar results in crabs having only
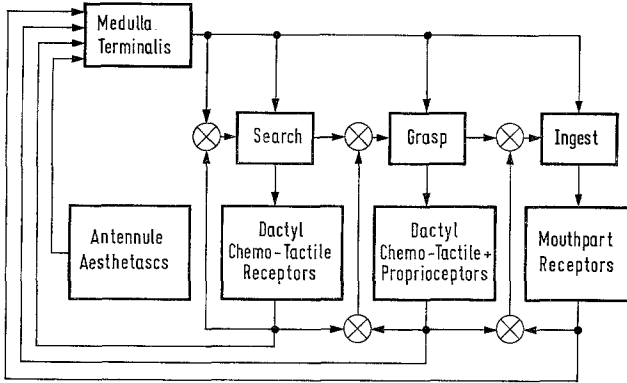
Fig. 2. Hypothetical diagram of functional connections of system controlling feeding
in spiny lobster. See text for details.

circumesophageal connectives severed, and thus retaining presumably
intact blood supply to and from sinus glands in the eyestalks. According-
ly we suggest that the simplest interpretation of our findings requires that
the effects described result primarily from the removal of the medulla
terminalis.

Assuming that the medulla terminalis is the critical structure ablated,
the major problem is that of devising an internal neural organization
which could account for our experimental observations. The simplistic
hypothesis that medulla terminalis removal is equivalent to no more than
severence of the afferent olfactory transmission line seems unlikely be-
cause if that were so then changes in the responsiveness to dactyl input
would not be anticipated, nor would the observed discoordination in feed-
ing acitivity be easily explained. It is more attractive to ascribe a com-
plex regulative role to the medulla terminalis, a role that involves inter-
pretation of input in terms of the state of the organism, and appropriate
long-term regulation of more specific control centers governing limited
behavioral acts. Fig. 2 presents a tentative diagram indicating how such
a system might operate in the present context.

The three major feeding acts, search, grasp and hold, ingestion and
mouthpart acitivity, are each presumed controlled by a separate spatial-
temporal construct of neural activity which can be turned on, turned off,
or modulated in intensity. The output of each construct produces pat-
terned motor acitvity and also acts as partial direct input to the next
construct of the sequence. The latter seems necessary because under some
circumstances appropriate behavioral sequences apparently occur with-
out the normally intervening sensory input. The peripheral motor acti-
vity initiated by each construct results in sensory feedback to the same

construct and in feed forward to the next. The sensory messages themselves must be complex, involving chemical, tactile, and proprioceptive information, and according to their nature turn on, turn off, or modulate the construct. According to the schema some component of the sensory input must also pass to the medullae terminales in the eyestalks, and thus form a parallel pathway through higher brain centers from peripheral sense organs to neural constructs. Perhaps the elements involved are similar to those found in the optic tract by Bush, Wiersma, and Waterman (1964) which respond to dactyl and mouthpart stimulation. Olfactory input from the antennules must pass through the medullae terminales if it is to turn on the feeding sequence. And finally, the diagram suggests that output from the medullae terminales not only may turn on the sequence through input to the first construct, but may also set or tune the various constructs to produce the appropriate responses to given inputs.

Obviously much of the diagram is without firm experimental support and it fails to deal satisfactorily with all observations. In particular, although it distinguishes two classes of input to the hypothetical constructs, it does not indicate exactly how the second of these, the "tuning" input from the medullae terminales, might act on the construct. It does form a working schema, however, and many of its assumptions and implications can be tested in more detail. For example, an experiment to determine whether the role of the medullae terminales in feeding requires specific sensory input from mouthparts and dactyls might allow us to decide whether or not the effects on feeding are no more than a partial, nonspecific expression of a more general disturbance in postural and orientational behavior.

Striking similarities exist between the effects of eyestalk removal on feeding activity in lobsters reported here, and certain effects of amygdala and orbital frontal cortex ablation on feeding and oral behavior in mammals (see Gloor, 1960, for review and the recent experiments of Butter, McDonald, and Snyder, 1969). Obviously such cross phyletic comparisons cannot indicate similarities in underlying mechnsisms, but they do raise an interesting question. It is possible to assume from the results of convergent evolution that given the general physical limitations of organisms, optimum morphological configurations often exist for specific environments and functions (see Rosen, 1967, for detailed discussion). Perhaps certain complex behaviors likewise have optimum modes of organization. If so then we may expect to find analogous behavioral subcomponents and analogous pathologies when a complex system is fragmented or disturbed experimentally. The analogy of transistor and vacuum tube radios may illustrate the point. The characteristics of the active components, tubes and transistors, and the associated circuitry differ

markedly between the two classes of instruments, just as the detailed neural characteristics and connectivity patterns of animals from widely divergent phyla might differ. Still if a radio is to function it must perform certain specific tasks and both the kind of subcomponents, e.g. power supply, amplifier, tuner, etc., and the block diagram defining the relations between the various subcomponents are essentially alike for both tube and transistor instruments. Considerably more data is needed, but we may eventually find that common behavioral subcomponents can be recognized in the organization of many complex behavioral acts in widely differing organisms.

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