

THE FUNCTION OF CHEMO- AND MECHANORECEPTORS IN LOBSTER (*HOMARUS AMERICANUS*) FEEDING BEHAVIOUR

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SUMMARY

The behaviour of lobsters preying on live mussels (*Mytilus edulis*) was observed before and after chemosensory or chemosensory-mechanosensory deafferentation of different sensory appendages. Deafferentation of the antennules, leg tips, or maxillipeds (but not the carapace or proximal leg segments) interfered with feeding performance by causing an increase in the time necessary to crush a mussel after search initiation. In addition, deafferentation of the leg tips or the maxillipeds caused a decline in number of mussels crushed but for different reasons: leg-treated lobsters walked over the mussels without picking them up, whereas maxilliped-treated lobsters grasped the mussels as usual but either did not crush or did not eat them as readily as did normal lobsters. Deafferentation of leg chemoreceptors resulted in the same behavioural deficiencies as deafferentation of leg chemo- and mechanoreceptors, demonstrating that it is the leg chemoreceptors that are essential in releasing this grasping response. Chemoreceptors on different appendages of lobsters therefore fulfill different functional roles in their feeding behaviour.

INTRODUCTION

Ethologists concerned with determining the location of chemoreceptors in crustaceans have usually either selectively ablated or selectively stimulated the sensory appendages in question. Through such experiments, chemoreceptors have been found on most parts of crustaceans (Fig. 1), including antennae (Bell, 1906; Holmes & Homuth, 1910; Matthews, 1955; Hindley, 1975; Bauer, 1979), antennules (Bell, 1906; Copeland, 1923; Spiegel, 1927; Brock, 1930; Hazlett, 1968; McLeese, 1973, 1974; Ache, 1975; Derby & Atema, 1980), mouthparts and walking legs (Bell, 1906; Luther, 1930; Shelton & Laverack, 1970), branchial chamber (Zimmer, Cook & Case, 1979), foregut (Robertson & Laverack, 1979), and general body surface (Bell, 1906; Hindley, 1975). Although some of these studies (especially the older ones) are little more than anecdotal observations and many of the procedures are questionable, the picture emerges that there are chemoreceptors on virtually all appendages (Fig. 1).

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Neurophysiological experiments also support the conclusion that antennules, antennae, all mouthparts, all pereopods, and gills of aquatic arthropods are chemoreceptive (Shelton & Laverack, 1970; Crabtree & Page, 1974; Tazaki & Shigenaga, 1974; Derby, 1982). Behavioural observations further suggest that the different chemoreceptor systems serve different functions (Copeland, 1923; Luther, 1930; Eder & Atema, 1978).

The function of the antennules has been studied (primarily through ablation experiments) more thoroughly than that of the other chemosensory systems. In some species, chemical stimulation of antennules is necessary to initiate searching behaviour (Hazlett, 1971 *a, b*; Ache, 1975; Derby & Atema, 1980); in others, it may not (Hodgson, 1958; Hazlett, 1971 *a*; Ameyaw-Akumfi, 1977). The lateral antennular flagella appear to be involved in initiating search and in determining the direction of odour sources (McLeese, 1973, 1974; Reeder & Ache, 1980); this is due largely to the presence of the specialized aesthetasc hairs on this appendage (Devine, 1981).

The precise role of receptors on the legs during feeding behaviour is poorly understood due to the obvious problem of performing behavioural studies on leg-ablated animals. Leg receptors are often considered to be high threshold contact receptors, whereas antennules are considered to be low threshold distance receptors (Shelton & Laverack, 1970; Shephard, 1974). However, the leg chemoreceptors of some crustaceans have low thresholds (responses to nanomolar or even picomolar concentrations of certain stimuli) (Fuzessery & Childress, 1975; Derby & Atema, 1982), and lobsters without antennules can be excited by food odours, although they may not initiate searching behaviour (McLeese, 1973, 1974) and they may be less efficient in following the direct search path leading to the odour source (Devine, 1981). Leg chemoreceptors are important in initiating reflexive feeding movements, such as shovelling and grasping food (Maynard & Dingle, 1963; Hazlett, 1971 *b*; Ameyaw-Akumfi, 1977). By simultaneously applying either tactile or chemotactile stimuli to the antennules and dactyls, Maynard & Sallee (1970) concluded that chemotactile stimulation of dactyls overrides any antennular stimulation, be it tactile or chemotactile, by initiating the 'dactyl grasp reflex'. Ameyaw-Akumfi (1977) deafferented various appendages of crayfish by either ablating them or by coating them with glue ('Duco cement'). He found that coating the cuticular receptors on the tips of the first two pairs of walking legs did not change the latency of response to food, but it did negatively affect location and ingestion of the food. Since this procedure not only blocks cuticular chemoreceptors but also mechanoreceptors, the importance of each is uncertain from this experiment.

The mechanical use of the six pairs of mouthparts during ingestion has been described in detail for the lobster *Homarus gammarus* (Barker & Gibson, 1977), but the role of chemoreceptors in such feeding behaviour has never been rigorously analysed. That chemoreceptors associated with the mouth control the ingestion of food has not been demonstrated for crustaceans as it has been for phylogenetically-related terrestrial arthropods (insects: Dethier, 1976) or ecologically-related aquatic vertebrates (fish: Atema, 1971).

This paper examines more precisely the function of crustacean leg and mouthpart chemo- and mechanosensory receptors during feeding by describing changes in the

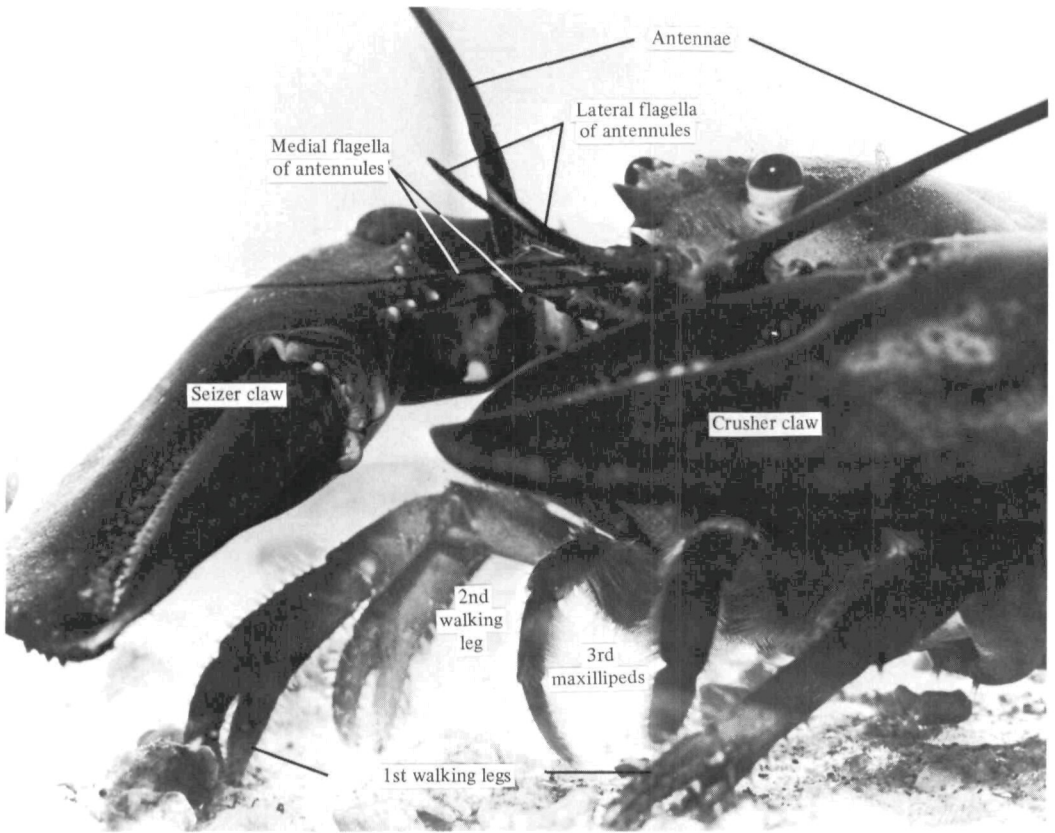


Fig. 1. The lobster (*Homarus americanus*). Note biramous antennules, long antennae, dimorphic claws, walking legs, and mouthparts of which the third maxillipeds are outermost and largest. Also note the abundance of sensory hairs on each appendage.

feeding behaviour of the lobster *Homarus americanus* following deafferentation of chemoreceptors or combinations of chemoreceptors and mechanoreceptors in different appendages.

MATERIALS AND METHODS

Predators and prey

Lobsters (6–8 cm carapace length) were collected locally and maintained on a diet of blue mussels (*Mytilus edulis*) prior to use. All behavioural observations were made on lobsters individually held in 100-litre aquaria (0.7 m length × 0.4 m width × 0.3 m depth).

Blue mussels (3–5 cm length) were provided as prey during all of the feeding experiments. Three 'types' of mussels were used: (1) normal live mussels (= real mussels); (2) mussels with the soft tissue removed, filled with an equivalent weight of cement, and sealed shut with cyanoacrylic glue ('Krazy Glue') (= fake mussels); and (3) live mussels with a thin layer of cement and some glue spread over the outer surface of each valve (= cement-control mussels).

Preliminary experiments

Food preferences: (A) Choice between real and fake mussels. In this experiment, nine lobsters were fed real mussels and fake mussels, maintained at a density of three of each type for 5 days; the number of each type crushed was checked several times daily. (B) Choice between real and cement-control mussels. Experiment was as described above, except that cement-control mussels were used instead of fake mussels.

Neurophysiology. Responses to chemical and mechanical stimuli were obtained from legs either covered with cyanoacrylic glue ('Krazy Glue') or exposed for 5 min to distilled water in order to determine if these treatments obliterated chemo- or mechanoreceptor function. The chemical stimulus was a 70 mg/l mussel (*Mytilus edulis*) extract. Mechanical stimuli were: (1) increased rate of sea water flow over the leg from 10 to 40 ml/min; (2) deflexion of individual hairs or application of pressure to the cuticular surface; and (3) deflexion of the segmental joints using a hand-held or micromanipulator-held probe. Details of stimulating and recording techniques are described in Derby & Atema (1982).

Feeding behaviour of normal and deafferented lobsters

The feeding behaviour of 36 lobsters held individually in 100-l aquaria was observed. The lobsters were evenly divided into six groups. Treatments consisted of deafferentation by either coating cuticular hairs on various appendages with 'Krazy Glue' or by exposing the appendages to distilled water for 5 min. The treatment groups included: (1) glue on antennules; (2) glue on the three pairs of maxillipeds; (3) glue on dactylus and propodus of legs and claws; (4) glue on maxillipeds, legs, and claws; (5) distilled water on the legs; and (6) control group, which consisted of treatment with glue on the proximal leg segments (ischium and merus) or glue on the carapace (2 lobsters), with distilled water on the carapace (2 lobsters), or with sea water on the legs (2 lobsters). Data from the six lobsters in the three control treatments were lumped since the feeding behaviour of all was similar.

Each lobster was observed 20 times, 10 before and 10 after treatment. Each observation period lasted for 20 min or until the first mussel was crushed and eaten. At the beginning of each observation period, four mussels (two real and two fake) were introduced into the aquarium. Behaviour recorded included the number of times each type of mussel was touched, picked up, manipulated, dropped, or crushed, as well as the time from initiation of searching until the first mussel was crushed and whether the crushed mussel was eaten. A trial was omitted from the analysis if the lobster did not touch a mussel with any of its walking legs within the 20 min period. These data provided the basis for the construction of an ethogram for the feeding behaviour of normal lobsters and for assessing the importance of different sensory receptors in this behaviour.

RESULTS

Preliminary experiments

Food preferences: (A) Choice between real and fake mussels. All nine lobsters showed a preference for real over fake mussels (chi-square tests: $P < 0.005$ for each lobster; $P < 0.001$ overall). The ability of lobsters to crush fake mussels was not a factor in these observed preferences. In fact, the time necessary for lobsters to crush fake mussels was significantly less than for real mussels ($P < 0.05$; Wilcoxon matched-pairs signed-ranks test). (B) Choice between real and cement-control mussels. All nine lobsters showed no preference for either the real or cement-control mussels (chi-square tests: $P > 0.05$ for each lobster; $P > 0.10$ overall). Thus, the cement or glue in the fake mussels was neither a chemical deterrent nor attractant for the lobsters.

Neurophysiology. Treatment of legs with distilled water for 5 min eliminated the responses of chemoreceptors for up to one day, followed by a period of a week when chemoreceptor sensitivity was slowly regained. The responses of cuticular mechanoreceptors to changes in water-current velocity were unaffected by this treatment. Covering the surface of the legs with glue eliminated all chemoreceptor activity as well as the activity of those mechanoreceptors responsive to water-borne vibrations. Tactile receptors still responded to touch and pressure applied directly to the cuticular surface and proprioceptors still responded to bending of the joints.

Feeding behaviour of normal and deafferented lobsters

An ethogram of the feeding behaviour of normal lobsters is illustrated in Fig. 2. A lobster generally alerts to the introduction of a chemical stimulus or a live mussel by increasing the rate of antennular flicking (= antennule burst), maxilliped exopodite beating, and antennal waving. The lobster may also groom the antennules with the third pair of maxillipeds (= antennule wipe), rub the third maxillipeds together (= maxilliped wipe), slowly sway the third maxillipeds from side to side (= maxilliped wave), wave the walking legs along the rostral-caudal axis (= dactyl wave), or shift the position of the body. The searching phase of feeding behaviour starts when the lobster begins walking. During the search, a lobster often walks high on its legs, with the legs extended to probe the substrate and feel for food. A lobster may occasionally use its antennae to scan the surface of the surrounding substrate. Upon touching a mussel with an antenna, any of the eight walking legs, or sometimes a maxillip

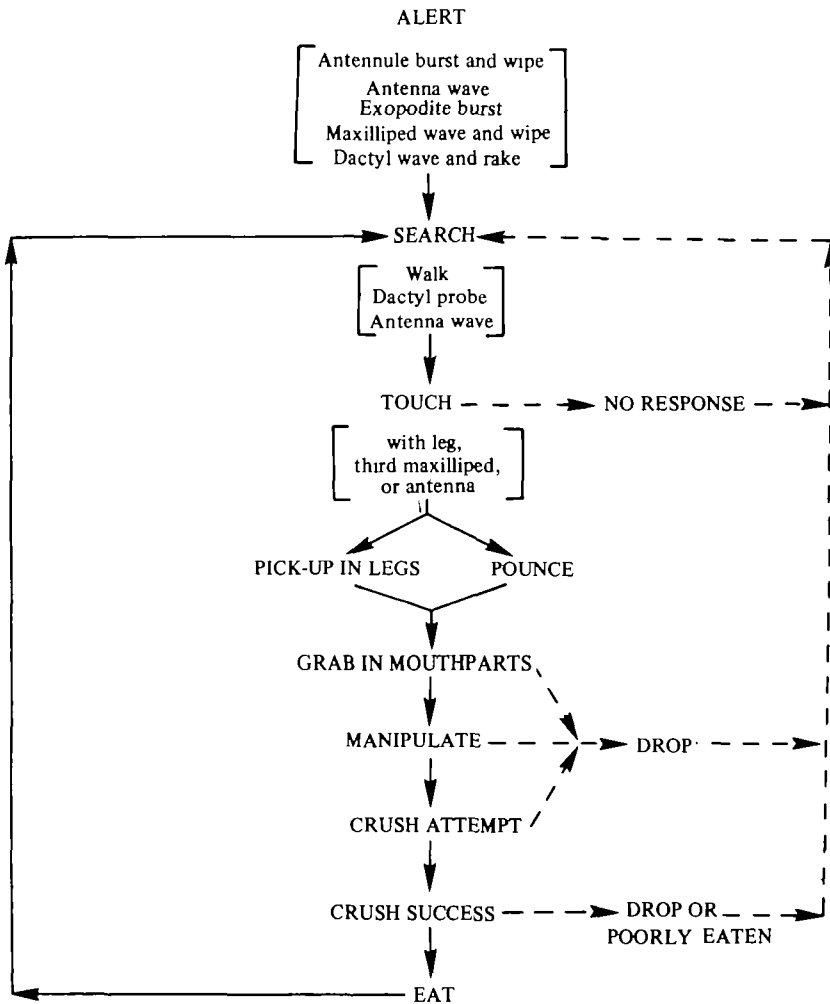


Fig. 2. Behavioural sequence in the predation on mussels by lobsters. Solid arrows indicate sequence for normal lobsters. Dashed arrows represent potential points of departure from normal sequence; these were rarely observed for normal lobsters, but were much more common for deafferented lobsters (see Figs. 3-5).

seizer, or crusher, lobsters often push and probe the mussel with their legs, quickly grasp it, and transfer it to the mouth; other lobsters are more excited after touching a mussel, and pounce on it by suddenly lunging and lowering their bodies onto the substrate surface and thereby grabbing the mussel with their legs and maxillipeds. None of these responses were observed when a mussel was touched with the uropods or telson. Once the mussel is grabbed, the first two pairs of walking legs (both of which are chelate) and the third maxillipeds are used to feel and manipulate the mussel. The mussel is usually rotated in the maxillipeds with the third maxillipeds pressed against the two valves of the mussel so that the groove between the valves passes along the inner mouthparts of the lobster. After several rotations, the mussel is then

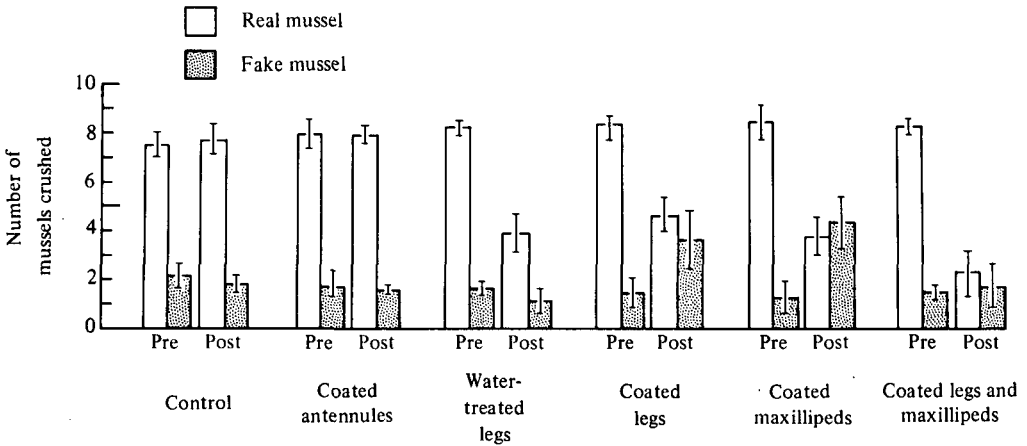


Fig. 3. Crushing behaviour. Untreated lobsters (control and all Pre groups) crushed significantly more real than fake mussels ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Treatment of the legs or maxillipeds with either water or glue caused a loss of this ability to differentiate between real and fake mussels, as well as a significant decrease in the number of real mussels crushed ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Control and antennule Pre-treated groups had no such effect. Pre = pre-treatment observation periods; Post = post-treatment observation periods. Values represent mean \pm standard error. Each treatment group consisted of six lobsters.

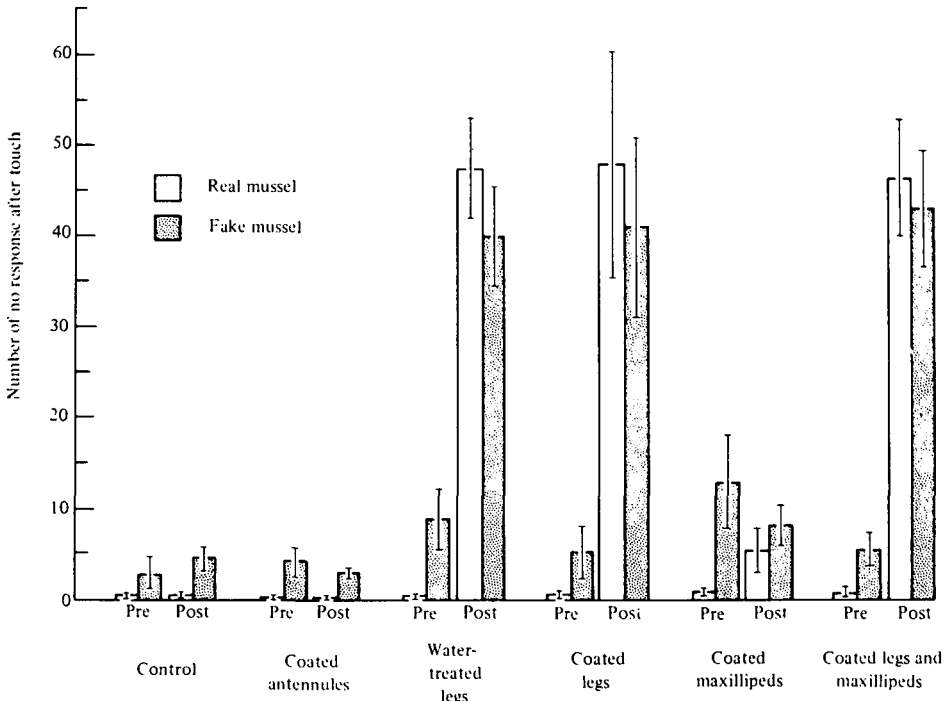


Fig. 4. Behaviour following leg contact with a mussel. Untreated lobsters (control and all Pre groups) were more responsive to real than fake mussels ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Treatment of legs with either water or glue caused lobsters to become more unresponsive to real mussels, with a loss of the ability to differentiate between real and fake mussels ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Control, antennular, and maxilliped treatment had no such effect. Values represent mean \pm standard error. Each treatment group consisted of six lobsters.

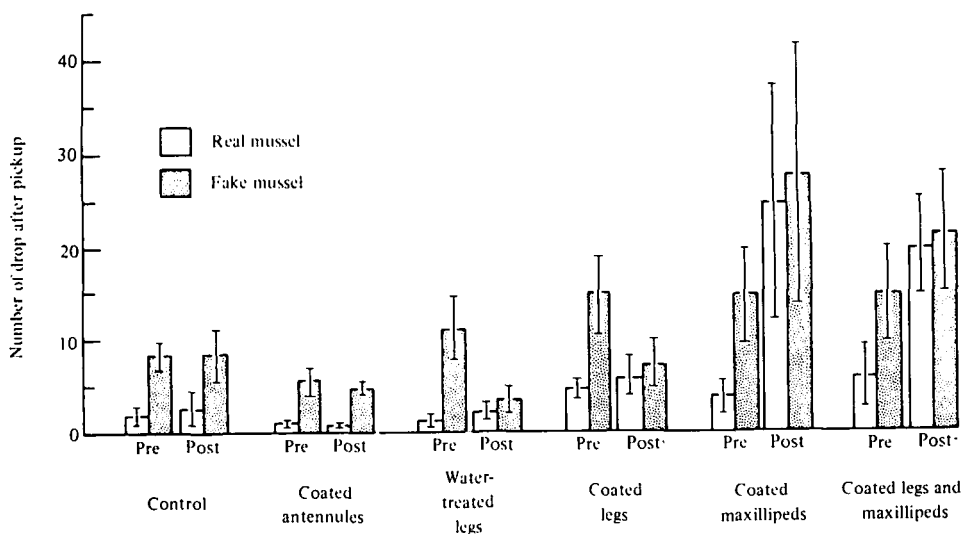


Fig. 5. Behaviour after mussel held in maxillipeds. Untreated lobsters (control and Pre groups) dropped real mussels less frequently than they did fake mussels ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Treatment of maxillipeds with glue caused an increase in the number of real mussels dropped after having been picked up in the mouthparts ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test). Control, antennular, and leg treatments had no such effect. Values represent mean \pm standard error. Each treatment group consisted of six lobsters.

manipulated into a position to be crushed. The anterior or posterior end of the mussel is positioned to face away from the lobster; either the ventral or dorsal side of the mussel is held near the dactylus-propodus joint of the crusher claw as pressure is applied laterally to the valves of the mussel (see Elner & Campbell, 1981, for a discussion of the biomechanics of crushing of *Mytilus* by lobsters). The seizer claw is placed in front of the mussel to prevent the mussel from slipping out of the grasp of the crusher claw; in addition, the third maxillipeds and the first two pairs of walking legs are used to hold, support, and position the mussel from behind. The lobster is often unsuccessful on its first crushing attempt. Following each unsuccessful attempt, the mussel is rotated and manipulated and finally repositioned for the next crushing attempt. After the mussel is cracked, the mandibles hold the crushed mussel while the third maxillipeds and first two pairs of walking legs pull the mussel away from the mandibles and body. The other maxillipeds and maxillae tear and then manoeuvre the pieces of shell and flesh. The use of mouthparts during feeding is similar to that pattern described for *Homarus gammarus* by Barker & Gibson (1977). The crusher claw is used to crush the mussel several more times between bouts of tearing and eating. The chelate walking legs are also used for picking up pieces of shell and flesh and transferring them to the mouthparts. The lobster will normally eat the entire mussel before searching for another one, or if it already has captured another mussel, before attempting to crush it.

In the behavioural assay, normal lobsters (pre-treatment and control lobsters) readily found and crushed mussels, and demonstrated a preference for real over fake mussels (Fig. 3), as was shown in the preliminary experiments. Treatment of legs or maxillipeds with glue or of legs with distilled water affected the ultimate feeding

success by decreasing the number of mussels crushed, whereas control and antennule-treated lobsters suffered no such effect (Fig. 3). The point of interruption of the normal behavioural sequence was different for leg- and for maxilliped-treated lobsters. Treatment of legs with either glue or distilled water caused a significant increase in the number of times a real or fake mussel was touched with the legs or maxillipeds without giving rise to any further behavioural response (Fig. 4). Lobsters in the maxilliped-treated group, on the other hand, picked up the mussels as usual but frequently dropped them without crushing them (Fig. 5); if these lobsters eventually did crush a mussel, they did not eat it as would a normal lobster (for five of the six maxilliped-treated lobsters). Control or leg-treated lobsters did not show such behavioural patterns. Antennular treatment did not affect the number of mussels crushed, nor the responsiveness after touching mussels, nor the number of times mussels were dropped after having been picked up. However, antennular treatment as well as leg or maxilliped treatment did increase the time necessary for the lobsters to crush the first mussel ($P < 0.05$, Wilcoxon matched-pairs signed-ranks test); control treatment had no such effect ($P < 0.05$).

DISCUSSION

Based on these findings, the sensory basis of feeding behaviour in crustaceans can now be described more completely than by Maynard & Dingle (1963) and Shelton & Laverack (1970). Although the antennules, antennae, six pairs of mouthparts, and five pairs of pereopods of lobsters are all chemosensory (Derby, 1982), they appear to mediate different behavioural functions. The lateral flagella of the antennules are probably responsible for initiating and initially directing the search (McLeese, 1973, 1974; Reeder & Ache, 1980; Devine, 1981), although other chemoreceptors may be involved, possibly depending on the concentration of the chemical stimulus (Zimmerfaust, 1980; Devine, 1981). The shift from searching to grasping is dependent on stimulation of chemoreceptors on the dactylus and propodus of the walking legs. If the receptors on the mouthparts are subsequently stimulated, further manipulation (e.g. crushing) and ingestion occur. Chemoreceptors in the foregut may then stimulate gut movements and, possibly in consort with gut proprioceptors, prevent overfeeding (Robertson & Laverack, 1979).

Division of functions within the chemical senses has been demonstrated for such phylogenetically diverse species as insects and fish. Dethier (1976) has identified the chemoreceptors that control feeding behaviour of blowflies. Stimulation of olfactory receptors (sense of smell) may attract or repel the blowflies from the odour source, but it has little effect on actual ingestion of food. Ingestion is sequentially controlled by the following taste receptors: tarsal hairs, labellar hairs, interseudotracheal hairs, and perhaps also pharyngeal receptors. Catfish have not only an olfactory sense but also two neuroanatomically distinct taste systems (Atema, 1971). The external taste system is innervated by cranial nerve VII (facial) and controls the food pick-up reflex; internal taste, innervated by cranial nerves IX/X (vagal and glossopharyngeal) triggers the swallow reflex. The roles of pereopod and mouthpart chemoreceptors of lobsters during feeding behaviour therefore parallel those of the external and internal taste receptors of catfish. Such behavioural evidence from flies, catfish, and

Lobsters illustrates that the senses of smell and taste (and in some cases subsystems within the sense of taste) can be distinguished on the basis of functional differences.

The different functional roles of the chemoreceptive appendages of crustaceans are not necessarily due to different characteristics of their primary chemosensory neurones. Neurophysiological experiments have demonstrated that the leg and antennular chemoreceptors of *H. americanus* are stimulated by many of the same compounds (Shepherd, 1974; Derby & Atema, 1982). This indicates that their response spectra may be broadly similar; however, because the compounds tested are biased toward amino acids and amines and these by no means represent the total chemosensory capabilities of lobsters, differential responsiveness could lie in other compounds. Concerning thresholds of peripheral receptor cells, some of the leg chemoreceptors of *H. americanus* are excited by nanomolar or picomolar concentrations of several stimulants (Derby & Atema, 1982) and therefore seem to be more sensitive than most of the other crustacean chemoreceptors previously studied. However, as discussed by Thompson & Ache (1980) and Derby & Atema (1982), comparisons of thresholds determined from different studies that have used different methodologies are of limited value. Therefore, although leg chemoreceptors of *H. americanus* are very sensitive, differences in thresholds of the peripheral receptor cells associated with gustation (legs and mouthparts) and olfaction (antennules) are at present uncertain.

There is evidence in crustaceans that a hierarchy of behaviours can be evoked by different stimulus concentrations, with the grasping response occurring only at higher concentrations (Pearson & Olla, 1977; Pearson *et al.* 1979). Several explanations for these observations exist in addition to the possibility of differences in responsiveness of primary sensory cells, as discussed above. One explanation is that there is differential access of the stimulus molecules to the receptor sites, which may effectively lower both physiological and behavioural thresholds. In support of this idea, Schmitt & Ache (1979) and Reeder & Ache (1980) have demonstrated in *Panulirus argus* that periodic flicking of the antennules (which have their chemosensory cells packaged into tufts of aesthetasc hairs) results in improved spatial and temporal chemosensory resolution. An analogous phenomenon may operate with legs where the chemoreceptors are packaged into dense rows and tufts of hairs (Shelton & Laverack, 1968, 1970; Derby, 1982) and where leg waving is a behaviour commonly elicited by chemical stimulation (Hazlett, 1971a; Derby & Atema, 1981). However, experimental evidence for this enhancement effect in leg chemoreceptors is not available.

Another possible explanation is that sensory information from organs of smell and taste is processed differently in the central nervous system (Atema, 1977). The neural circuitry in the central nervous system responsible for the generation of the motor programme controlling the grasping response might be elicited only with higher concentrations of chemical stimuli, even though the peripheral receptors mediating this response have relatively low thresholds. Similarly, it is possible that the central nervous system compares the input from the legs and the antennules. According to this hypothesis, the grasping response would be elicited only when activity of the leg receptors reaches some critical value above that of the antennular receptors, thus indicating that the source of chemical stimulus is near. In addition, even though chemical stimulation alone of either the legs or the whole animal causes grasping reflexes (Maynard & Dingle, 1963; Hazlett, 1968), a concomitant tactile stimulus may

effectively lower the threshold of the behavioural response to a chemical stimulus (Symons, 1964; Hazlett, 1971*b*). The two taste systems of catfish provide a clear example that functional differences in chemosensory organs can be due to central rather than peripheral nervous system mechanisms: the facial and glossopharyngeal second-order taste cells have strikingly similar response spectra and thresholds (Kanwal & Caprio, 1981), yet the facial system alone controls the food pick-up reflex while the glossopharyngeal system controls the food-swallowing reflex (Atema, 1971).

In summary, experimental elimination of chemoreceptors on the various sensory organs of lobsters demonstrates that each organ controls different subsets of behaviour in the sequence of actions leading to food acquisition and ingestion.

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