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THE ANTENNULAR ACTIVITIES OF THE HERMIT CRAB, *PAGURUS ALASKENSIS* (BENEDICT)

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INTRODUCTION

A large amount of behavioural, electrophysiological and ultrastructural evidence has accumulated to suggest that in many crustaceans the antennules are of primary importance to the chemoreceptive process (Bell, 1906; Cowles, 1908; Holmes & Homuth, 1910; Copeland, 1923; Hodgson, 1958; Maynard & Dingle, 1963; Laverack, 1964; Laverack & Ardill, 1965; van Weel & Christofferson, 1966; Ghiradella, Cronshaw & Case, 1968; Ghiradella, Case & Cronshaw, 1968*a*, *b*; Hazlett, 1968; Ache & Case, 1969; Hazlett, 1971*a*, *b*). The antennule chemoreceptors are considered to be distance chemoreceptors which possibly operate in conjunction with the maxillipeds to give an animal the capacity for directional chemosensitivity (Brock, 1926; Hazlett, 1968).

The receptors responsible for chemoreception are generally considered to be the aesthetasc hairs which occur in closely spaced rows on the outer antennular flagellum (Laverack, 1964; van Weel & Christofferson, 1966; Ache & Case, 1969). In addition to chemoreceptors the antennule has mechanoreceptive sensilla, osmotically sensitive receptors and internal joint receptors (Krijgsman & Krijgsman, 1954; Hodgson, 1958; Sandeman, 1963; Laverack, 1964; Wyse & Maynard, 1965; van Weel & Christofferson, 1966). The basal segment also contains the statocyst.

Despite the mass of work on the sensory aspects of the antennule there exists only one detailed description of the antennular activities in a crustacean (Maynard & Dingle, 1963). This description is based solely on the lobster, *Panulirus argus*, and is directed towards describing and classifying these activities rather than determining their function.

In the lobster four types of antennular activities may be recognized: flicking, pointing, wiping and withdrawal (Maynard & Dingle, 1963). Although reports of antennular activities in other crustaceans are incomplete, these four types of activity can be easily recognized in a wide variety of decapods. Between different species, however, there is considerable variation in the form and frequency of antennular activities and in the morphology of the antennules. In these respects there is more similarity between hermit crabs and brachyurans than there is between brachyurans and macrurans (personal observation).

The antennules of hermit crabs are usually larger than those of brachyurans of similar body size. The hermit-crab antennule is thus more accessible to neurophysiological studies (Snow, 1973) and in addition may provide an interesting comparison with behavioural studies on the lobster antennule (Maynard & Dingle, 1963).

The objective of the present study is to provide a detailed qualitative and quantitative description of the antennular activities of a hermit crab. It is hoped that such data may yield strong inferences regarding the functions of these activities and thus be useful in a subsequent study of the factors determining the underlying motoneuronal activity (see Snow, 1973).

The present study has shown that most movements of the hermit-crab antennule represent one of four activities: flicking, rotation, wiping and withdrawal. Flicking occurs almost continuously but in a non-rhythmical fashion. The morphology of the antennules and the form of antennular flicking may be interpreted as facilitating the circulation of water around the aesthetasc hairs and thus facilitating the chemoreceptive process. The function of antennular rotation is less clear, but it may be important in pointing the aesthetasc hairs into water currents, thus facilitating the exchange of water around these hairs during flicking. Antennular wiping appears to be important in removing material trapped amongst the aesthetasc hairs, while antennular withdrawal probably represents a simple protective mechanism against potentially noxious stimuli.

MATERIALS AND METHODS

Specimens of *Pagurus alaskensis* (Benedict) were dredged from 20 to 30 fathoms off Waldron Island, San Juan Archipelago, Washington. For high-speed filming animals were flown to Edmonton, Alberta, where they were maintained successfully in 'Instant Ocean' at 12 °C. Normal-speed filming was carried out at the Friday Harbor Laboratories, San Juan Island, where animals were maintained in circulating sea water. Only large (body length $\simeq 8$ cm) intermoult animals were used in these experiments.

Close-up motion pictures were made of the antennular activities using a Milliken DBM 54, 16 mm, cine camera. Flicking was filmed at 400 frames/sec while other activities were filmed at 200 frames/sec. In the presence of water currents the antennules are frequently flicked without additional stimulation. A variety of stimuli, all of which were applied to animals immersed in sea water, were used to elicit other antennular activities. These stimuli will be mentioned as the other activities are described.

For each crab the right antenna was removed at its base several days before filming. Just prior to filming an animal was removed from its shell and the medial sides of its left eyestalk and antenna were blackened to contrast the outline of the antennules. During filming the crab was placed in a small Perspex tank of 'Instant Ocean' which was continually aerated and maintained at 12 °C. This tank was small enough to prevent a large crab from turning so that all films could be shot from the right-hand side of an animal.

High-speed films were analysed using an L.W. Photo Optical Data Analyser fitted with a frame counter. For all antennular activities measurements were made of the duration, temporal relationship and total angle change of the movements about the medial segment–distal segment (MS–DS) and distal segment–outer flagellum (DS–OF) joints. The OF undergoes considerable distortion during flicking and thus the border of its large basal segment was selected as a reference for measuring angular

lisplacements. For a more critical examination of antennular movements drawings were made from single frames.

To simplify descriptions of antennular movements flexion is considered to be an angle change at a joint, which moves the more distal part of the limb in the direction towards which the aesthetasc hairs point.

In order to establish whether flicking occurred in any easily recognizable temporal pattern, unmolested animals were filmed in circulating sea water (10 °C) at 50 frames/sec, using a Bolex 16 mm cine camera. The number of frames between flicks of antennules, both ipsilateral and contralateral, was measured and these numbers were converted to time (1 frame = 20 msec).

Of primary interest in all the data is the amount of variation within a set of measurements. Calculations of the standard deviations and coefficients of variation are thus based on the equation S.D. = $\sqrt{(S.S./N)}$ rather than the equation S.D. = $\sqrt{(S.S./N-1)}$ (Sokal & Rohlf, 1969).

Qualitative data on antennular activities were derived from repeated examination of many film sequences and from direct observations. Morphological descriptions were based on examination of freshly excised antennules using the light microscope.

RESULTS

(1) *Morphology of the outer flagellum*

The antennules arise below and slightly medial to the eyestalks. They consist of three segments, the most distal bearing the inner and outer flagella. Neither the outer nor the inner flagellum contains muscles, and only the outer flagellum (OF) can be moved independently of the distal segment (DS) (see fig. 1, Snow, 1973).

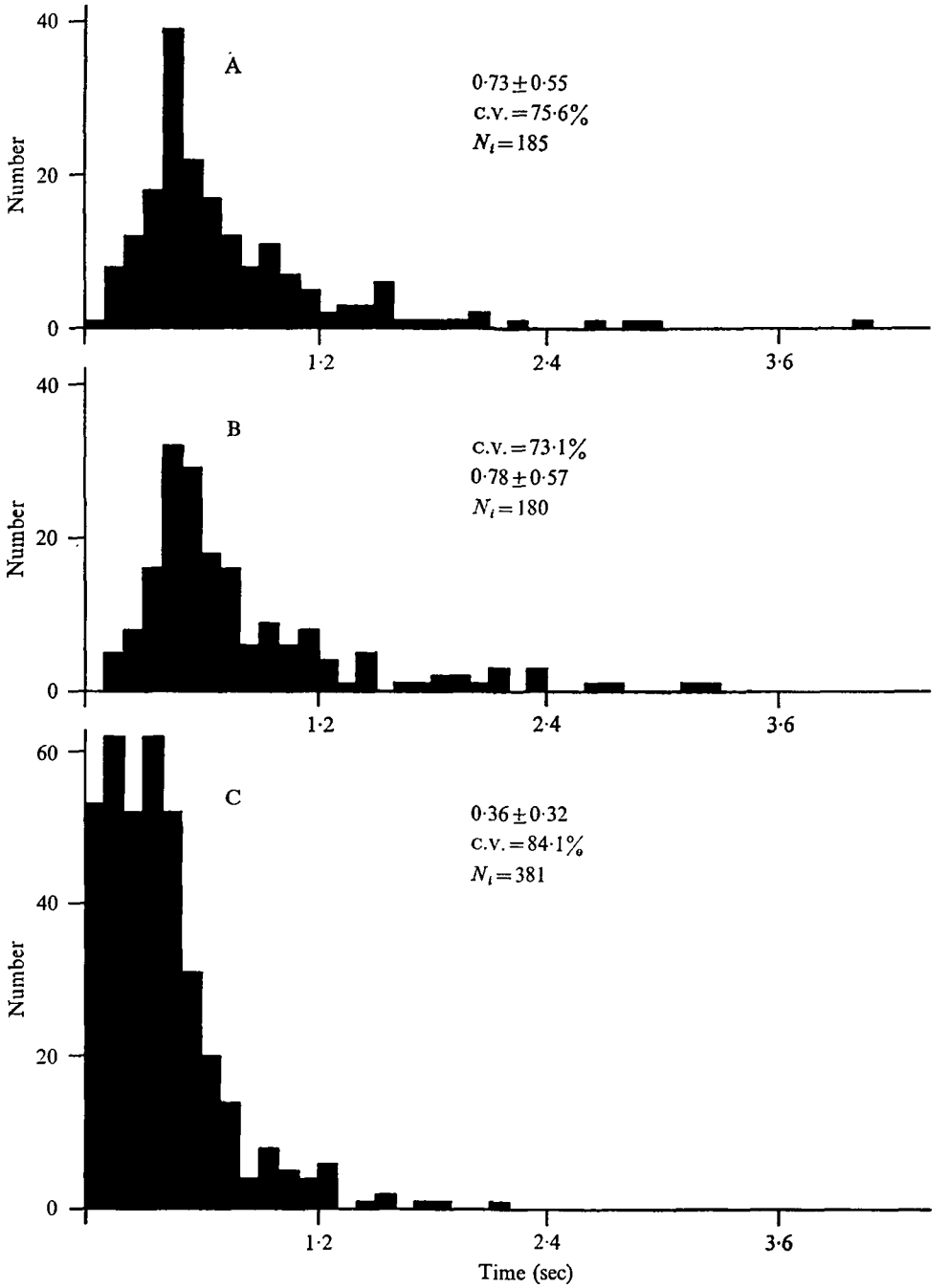
The OF is tapered and has a relatively large basal segment and many shorter (approx. 80 μm) segments which give it considerable mechanical flexibility. The more proximal short segments are partially fused. The distal 1/4 of the OF consists of six or seven long thin segments and is relatively inflexible in comparison with the many-segmented regions (Pl. 1 A).

On the side nearest to the inner flagellum (IF) the shorter segments bear the rows of partially recumbent aesthetasc hairs. Although the rows of aesthetascs are separated by about 80 μm near the base of the hairs, spacing between the hairs of a single row appears to be considerably less. Distally the aesthetascs within a single row are spread slightly laterally, but in this region the rows appear to bunch together so that the inter-row space is considerably reduced.

Each aesthetasc arises from a socket on what is considered here to be the ventral side of the shorter OF segments (Pl. 1 C). In large animals the aesthetascs are between 800 and 1400 μm in length and have a basal diameter of approximately 26 μm. They are tapered towards the tip and have a segmented appearance due to annular bulges in the hair wall which occur every 45–50 μm (Pl. 1 B).

(2) *Antennular movements*

Most movements at the joints of the antennule constitute components of four basic activities: flicking, rotation, wiping and withdrawal. Throughout these experiments, however, slow flexions and extensions at the proximal segment–medial segment



Text-Fig. 1. Histogram of the inter-flick interval of the left (A), the right (B) and the interval between the flick of one antennule and the next flick, whether by the ipsilateral or the contralateral antennule (C). Also shown are the mean inter-flick intervals ± standard deviations (sec), the coefficient of variation (C.V.) and the number of intervals (N_t) over a total filming period of 2·5 min. Note the high coefficients of variation. Bin size equals 0·1 sec.

PS–MS), MS–DS or the DS–OF joints were frequently observed. These movements were not associated with the basic activities, and their frequency, extent and speed were highly variable within and between animals. An accurate description of such movements would require a highly statistical approach based on a large number of observations, and for this reason more attention was directed towards the other more stereotyped antennular activities.

A. Antennular flicking

(1) *Frequency, asymmetry and arrhythmia.* In the holding tanks crabs flick their antennules almost continuously. Even when a crab is withdrawn into its shell flicking usually resumes long before the crab emerges.

The mean frequency of flicking appears to be influenced by the physiological condition of a crab as well as by many sensory parameters such as chemicals, light, osmotic and mechanical stimuli. Although the effects of single modalities on the mean flicking frequency have not been exhaustively tested, the following stimuli have been noted to influence the flicking frequency:

(i) *Inhibitory.* A brief interruption of flicking resulted from: light mechanical stimulation of the antennules, eyestalks or antennae; the application of distilled water to the OF; firm taps to the body or shell. Tonic decreases in the frequency of flicking resulted from: repeated application of the above stimuli; raising the water temperature above 18 °C; cutting off water currents.

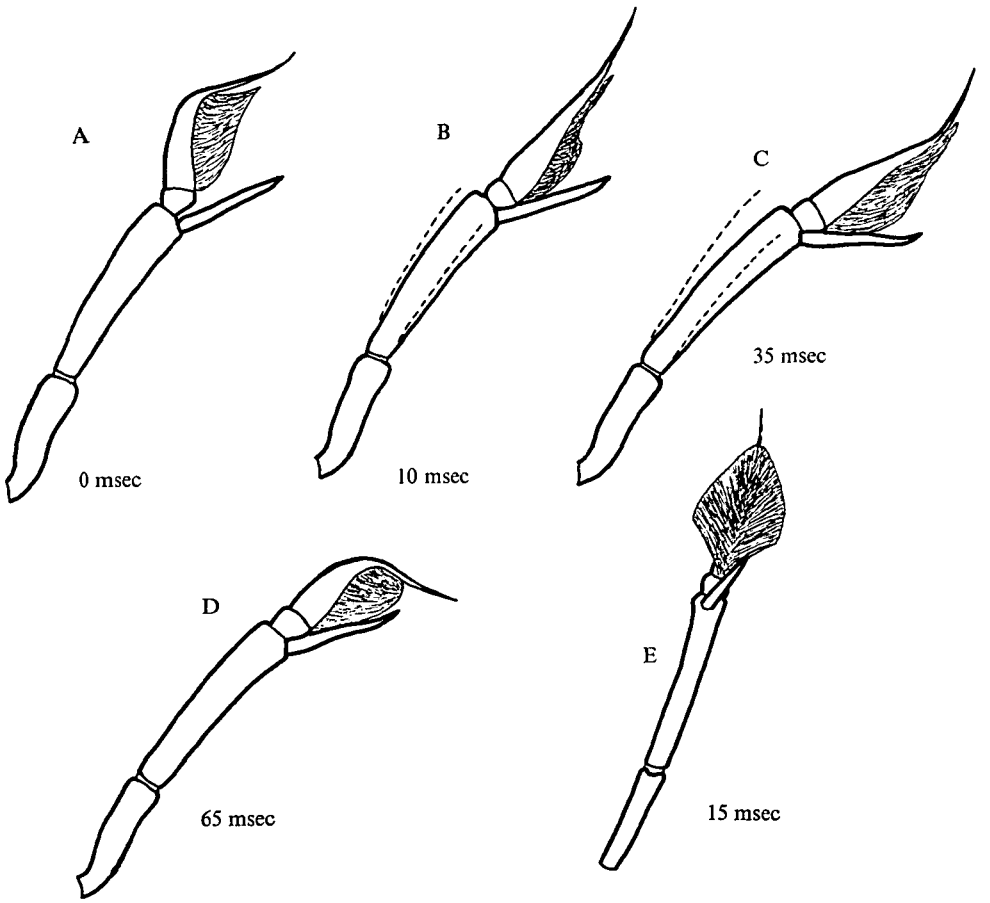
(ii) *Excitatory.* An increased frequency of flicking resulted from: faster water currents (used in high-speed filming); placing crabs in new surroundings; placing fish juice or pieces of fish near a starved animal.

Analysis of 50 frame/sec motion pictures has shown that flicking is a non-rhythmical, asymmetrical activity. The inter-flick interval of a single antennule shows large variations between successive flicks (Text-fig. 1 A, B) and these variations do not appear to follow any simple temporal pattern. The mean frequency of flicking (1/mean inter-flick interval [min]) of a single antennule was about 75/min, under the filming conditions.

A flick of one antennule did not influence the occurrence of a flick in the other antennule. When flicks of the left and right antennules are considered together the inter-flick interval is also highly variable (Text-fig. 1 C). The mean flicking frequency was then about 150/min under the filming conditions. Frequently animals would flick a single antennule several times without flicking the other antennule, but over the 2·5 min filming periods the numbers of flicks of each antennule were approximately the same (Text-fig. 1 A, B). Although at 50 frames/sec flicks of the left and right antennules sometimes appeared to occur synchronously, at 400 frames/sec a flick of one antennule was never exactly synchronized with a flick of the other antennule.

Flicking was not inhibited by removal of one antennule, and even after cutting an antennule off just distal to the MS–DS joint the stump of the DS was still occasionally flicked down.

(2) *Movements of the joints and aesthetasc hairs.* Antennular flicking consists of a phasic depression of the OF and DS. Analysis of high-speed motion pictures has shown that a single flick usually lasts 100–160 msec. Table 1 and Text-fig. 2 show the timing of movements at the MS–DS and DS–OF joints. Some error in these



Text-fig. 2. Movements of the MS–DS and DS–OF joints during an antennular flick. (A) shows the antennule following the small initial flexion of the MS–DS joint. During the next 10 msec the DS–OF joint is fully flexed (B). No flexion of the MS–DS joint occurs during the first 5 msec of a flick and once re-initiated lasts 30 msec (C). The dotted lines in B and C represent the position of the DS at the beginning of a flick (A). After a pause, the MS–DS and DS–OF joints are extended (D) returning the antennule to its initial posture. During the first 15 msec the aesthetasc hairs are splayed apart (E).

measurements results from the minimum inter-frame interval of 2·5 msec (400 frames/sec) being large in comparison with some of the durations being measured.

The first evidence of a flick is a very small flexion at the MS–DS joint which usually occupies the time between two consecutive frames (2·5 msec). The second frame is considered to mark the zero time of a flick (Text-figs. 2A and 3A). During the second to sixth frames (10 msec) the DS–OF joint is flexed through an angle of 30–45° (Text-fig. 2A, B). From the second to fourth frame (5 msec) no further angle change occurs at the MS–DS joint, but over the next four to six frames (20–30 msec) this joint is flexed through 5 to 15° (Text-fig. 2B, C). Towards the end of MS–DS flexion there is a slight outward movement of the antennule around the PS–MS joint. The DS–OF and MS–DS joints are usually retained in their flexed positions for 20–35 and 5–11 msec, respectively. Extension at the DS–OF joint begins 30–45 msec after the beginning of a flick (Table 1).

Table 1. *Timing of joint movements during antennular flicking*

Row no.	Whole flick, $\bar{X}\pm$S.D./C.V.	DS–OF joint: Flexion, $\bar{X}\pm$S.D./C.V.	DS–OF joint: Maintained flexed, $\bar{X}\pm$S.D./C.V.	DS–OF joint: Extension, $\bar{X}\pm$S.D./C.V.	MS–DS joint: Flexion, $\bar{X}\pm$S.D./C.V.	MS–DS joint: Maintained flexed, $\bar{X}\pm$S.D./C.V.	MS–DS joint: Extension, $\bar{X}\pm$S.D./C.V.	Initial movement of MS–DS joint to movement of DS–OF joint, $\bar{X}\pm$S.D./C.V.	Pause in flexion of MS–DS joint, $\bar{X}\pm$S.D./C.V.	*N*
1	157·5±9·0 5·7%	10·0±0·0 0·0%	24·3±5·6 23·2%	123·2±9·7 7·9%	30·4±4·3 14·2%	7·9±1·6 20·4%	95·4±4·9 5·1%	2·5±0·0 0·0%	4·3±1·1 26·4%	7
2	124·0±6·7 5·3%	10·0±0·0 0·0%	22·1±1·7 7·7%	92·5±6·3 6·8%	21·7±2·6 19·9%	6·3±1·3 20·6%	77·1±11·0 14·3%	2·5±0·0 0·0%	5·4±1·9 18·9%	6
3	156·8±6·6 4·2%	10·4±0·9 8·4%	25·0±7·9 31·6%	122·5±11·8 9·6%	31·8±5·0 15·6%	8·2±3·9 48·0%	91·2±7·5 8·2%	2·5±0·0 0·0%	6·1±1·2 20·4%	7
4	155	10	20	125	27·5	10	112·5	2·5	5·0	1
5	125·0±9·0 7·1%	10·8±1·2 10·9%	15·8±2·4 15·0%	21·7±4·3 20·0%	30·9±1·2 3·8%	4·2±1·2 28·3%	90·8±7·8 8·5%	2·5±0·0 0·0%	0·0*	3
6	204·0±24·1 11·8%	10·5±1·0 9·5%	26·0±2·0 7·7%	176·0±27·7 15·7%	34·5±4·3 12·5%	7·0±2·5 35·0%	139·5±27·4 19·7%	119·0±63·3 57·4%	0·0†	5

Table shows the mean times (msec) ± standard deviations ($\bar{X}\pm$S.D.) and the coefficients of variation (C.V.), of the duration and patterning of antennular joint movements. Rows 1–3: normal flicks of the left antennule of three animals. Row 4: flick of the right antennule of animal featured in row 3. Row 5: flicks of the left antennule following removal of all but the basal segment of the OF. Row 6: flicks of the left antennule of an animal in which flicks usually followed a smooth, slow, prolonged flexion at the MS–DS joint.

* In the absence of most of the OF there is no pause in the flexion at the MS–DS joint during flexion at the DS–OF joint.

† When prolonged flexion at the MS–DS joint precedes flexion at the DS–OF joint there is no pause in the flexion of the MS–DS joint during flexion of the DS–OF joint.

A feature of most movements during antennular flicking is their variability. Within any individual, however, the time required for flexion of the DS–OF joint is fairly constant (Table 1). In addition, the time between initial movement of the MS–DS and DS–OF joints appears constant at 2·5 msec, but it must be emphasized that a film speed of 400 frames/sec does not allow measurements of variability of less than 2·5 msec.

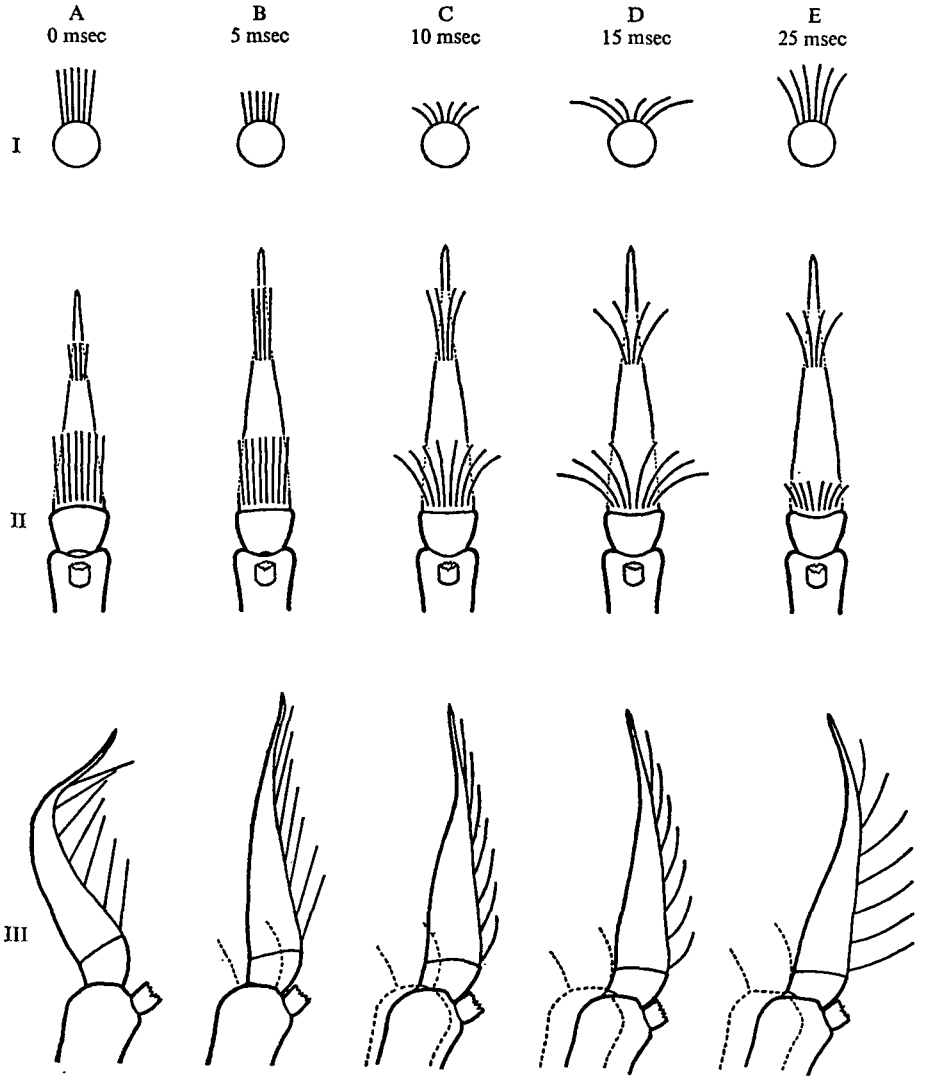
Although flicking usually occurs while the antennule is in its extended position shown in Text-fig. 2A, it may also occur during tonic flexion at the MS–DS joint. Under these circumstances there is little or no movement at the MS–DS joint but flexion at the DS–OF joint is unaffected. This form of flicking was frequently observed in animals which had withdrawn into their shells when extension of the antennule would result in the outer flagellum hitting the inside of the shell.

Sometimes animals were encountered in which a flick was frequently preceded by a prolonged, slow flexion of the MS–DS joint. In analysing this activity a flick was considered to begin at the first sign of depression of the OF. The initial flexion at the MS–DS joint may take up to 240 msec during which time the angle of the MS–DS joint may change up to 35°. When the flick begins there is no pause in MS–DS flexion. A flick of this type takes a longer total time (e.g. 200 msec) and examination of the various phases of a flick show that this is due to increase in the extension times of the MS–DS and DS–OF joints (Table 1).

During antennular flicking there is considerable bending of the OF and movement of the densely packed aesthetasc hairs (Text-fig. 2). When animals flicked towards the camera the aesthetasc hairs could be seen to splay out laterally (Text-fig. 2E). Although the resolution on single frames was insufficient to plot the movements of single hairs, observations of many flicks, slowed down about 100 times, furnished the following description. During the first 5 msec of DS–OF joint flexion the aesthetascs are depressed into a more recumbent position (Text-fig. 3A, B). Over the next 10–15 msec there is flexion at the MS–DS joint and the aesthetascs are splayed laterally. In the resting antennule the aesthetascs are slightly splayed laterally so that during a flick the water resistance forces generated by flexion at the DS–OF and MS–DS joints are probably sufficient to cause full splaying of the hairs. Maximal splaying occurs 15–20 msec after the beginning of a flick (Text-fig. 3C, D) and is followed by movement of the hairs back to their resting position over the next 30–40 msec (Text-fig. 2C). Amongst the proximal rows of hairs this movement consists of a lateral swing of the hairs around the OF which initially results in them returning to a less recumbent position than they adopt in the resting antennule (Text-fig. 3E).

Over the first 25 msec of a flick the OF is arched back by water resistance forces acting on its long, thin, distal region (Text-figs. 2C and 3E) and does not return to its resting shape until 45–50 msec after the beginning of a flick. Bending of the OF is maximal across the more distal shorter segments (Pl. 1A) and this increases the distance between the more distal rows of aesthetascs (Text-fig. 3E). Lateral splaying of the aesthetascs is maximal amongst the more proximal rows of hairs and it thus seems that bending of the OF facilitates a uniform separation between adjacent aesthetascs irrespective of their position on the OF (Text-fig. 3D, E).

During flicking, deflection of the aesthetasc hairs occurs both by movement around



Text-fig. 3. Diagrammatic representation of the movements of the aesthetasc hairs and OF during the first 25 msec of an antennular flick. Line III shows a lateral view of the movements of the end hair in each of 7 rows of aesthetascs. The dotted lines represent the initial position (0 msec) of the DS and OF. Note the greater separation between the more distal rows of aesthetascs and the concurrent bending of the OF (EIII). Line II shows a frontal view of the movements of the hairs in row 1 and row 6 (CII). Line I shows the movements of the hairs in row 2 as they might appear in a cross-sectional view of the OF. See text for further explanation.

their basal attachment with the OF and also by some bending along the shank of the hairs (Text-fig. 3). These observations suggest that the sockets in which each aesthetasc is borne and the periodic annular bulges may constitute structural adaptations to antennular flicking.

The marked influence of water resistance on the OF raised the question of how much this factor was involved in the timing of movements during a normal flick. To test this, flicking was filmed in animals from which all but the basal segment of

the OF had been removed. Two marked modifications were observed. First, there was no pause in the flexion of the MS–DS joint. This movement usually led flexion of the DS–OF joint by 2·5 msec (Table 1). Secondly, there was a marked reduction in the rise time of the OF (Table 1).

Both these modifications can be interpreted in terms of water resistance affecting the movements of the DS–OF joint during flicking in normal animals. At the initiation of a flick the pause in the flexion of the MS–DS joint probably results from an upward force generated by water resistance to the rapid flexion at the DS–OF joint. Movement at the MS–DS joint prior to this pause is so small that it was initially concluded that a flick is initiated by contraction of the muscle responsible for flexion at the DS–OF joint. The above experiment suggests that a flick is initiated by contraction in the muscle responsible for flexion at the MS–DS joint. The assumption is made that any changes in the patterning of activity in these muscles caused by removal of the outer flagellum cannot explain the above observations.

It is further concluded that, in operated animals, the duration of extension at the DS–OF joint is increased by the effects of water resistance. This factor would be enhanced by extension at the MS–DS joint during extension at the DS–OF joint. It seems unlikely that alteration in motor output due to OF removal could account for the decreased duration of the DS–OF joint extension. This joint is extended by elastic elements and thus the only muscular influence on the duration of the extension phase is the relaxation rate of the fast muscle probably responsible for DS–OF flexion during flicking (muscle 32F). The duration of a single twitch of this muscle is only 20 msec (Snow, 1973), whereas the duration of DS–OF joint extension, even following OF excision, is about 20 msec (Table 1). It is therefore improbable that the relaxation rate of the underlying musculature influences the duration of this movement.

B. Antennular rotation

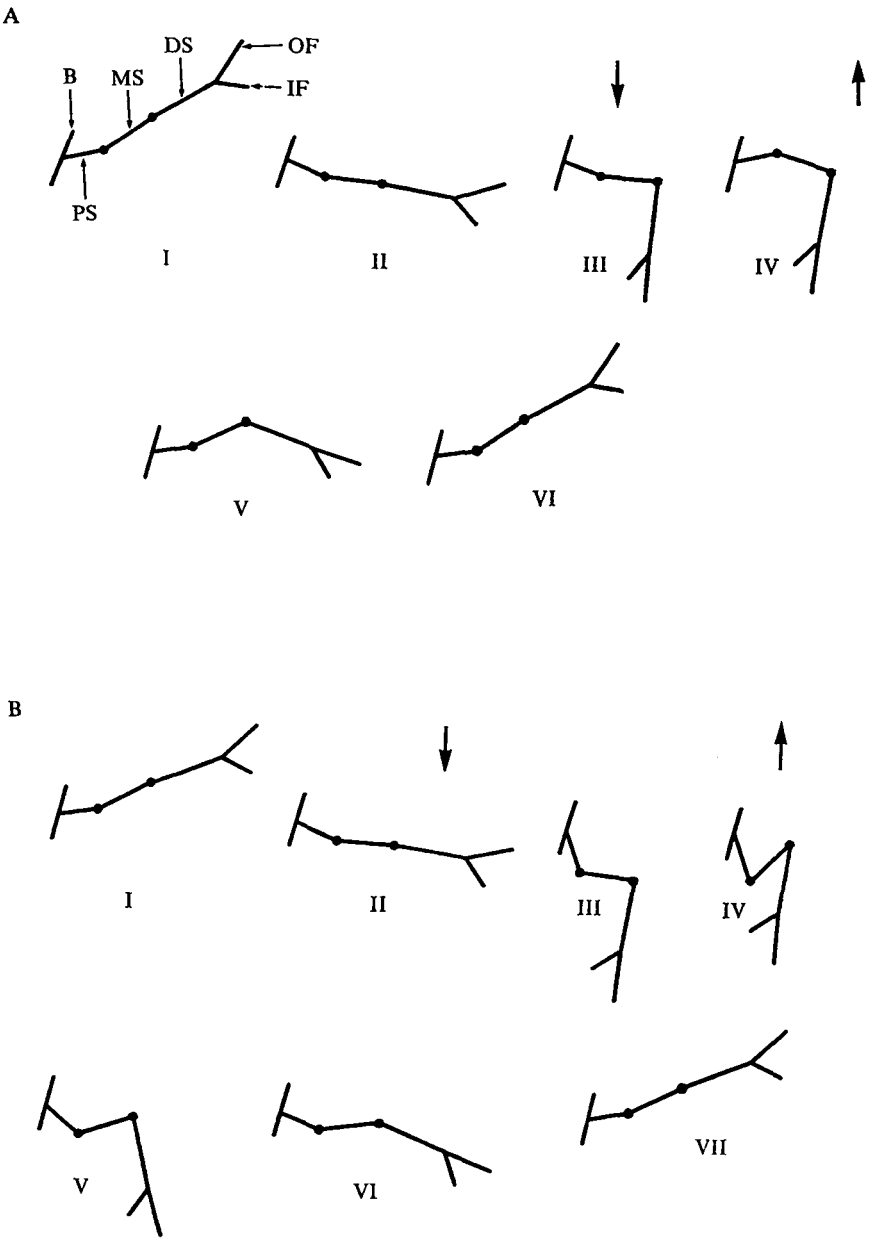
Antennular rotation consists in a twisting of an antennule at the PS–MS joint. The antennule can thus be rotated about its longitudinal axis through approximately 180° so that the aesthetasc hairs may point back over the ipsilateral eyestalk and along the ipsilateral side of the carapace.

Usually both antennules are orientated towards the same side and both are usually re-orientated in approximate unison. When flicking is tonically inhibited (e.g. by removal of water currents) antennular rotation does not occur. The frequency of re-orientation is greatest when locomotory activity and the mean flicking frequency are high, as they are when the crab is placed in new surroundings. One antennule is often flicked immediately on cessation of a re-orientation movement.

C. Antennular wiping

The specific movements employed in wiping vary between animals. The number of wiping sequences recorded from a single animal by means of high-speed filming was insufficient to confirm whether the same variation occurs within a single animal. Two sequences recorded from different animals will be detailed below as examples of this variation (Text-fig. 4A, B).

Sequence 1 involves slow depression of the antennule around the PS–MS joint followed by flexion at the MS–DS joint (Text-fig. 4AI, AII and AIII). When the



Text-fig. 4. Two sequences of antennular movements during wiping. The downward arrows mark the position of the antennule when the endopodites of the 3rd maxillipeds enter a sequence and the upward arrows mark where they leave a sequence. Note the variation in joint movements between sequence 1 (A) and sequence 2 (B). B, body wall; PS, proximal segment; MS, medial segment; DS, distal segment; OF, outer flagellum; IF, inner flagellum. See text for further explanation.

DS is fully depressed the endopodites of the 3rd maxillipeds are raised and brough down along the DS to clasp the OF and IF. The PS is then raised by movements at the PS–MS and MS–DS joints and the OF and IF are thus pulled from between the endopodites (Text-fig. 4AIV, AV). The antennule assumes its initial posture by further extension at the MS–DS joint (Text-fig. 4AV, AVI).

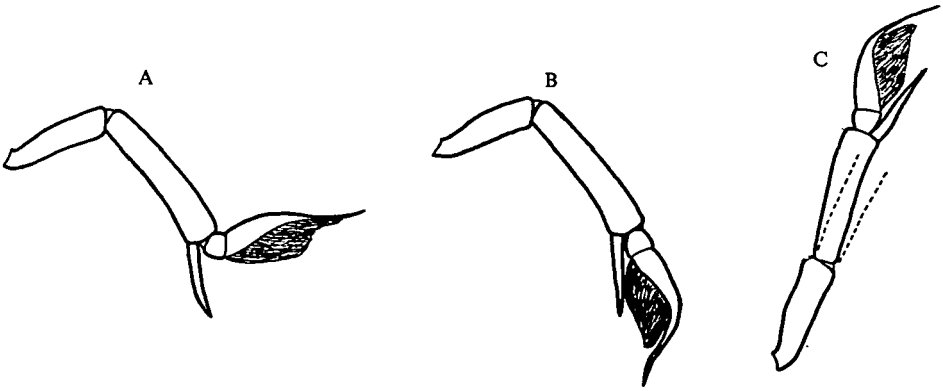
Sequence 2 involves earlier activation of the maxillipeds. Initial depression of the antennule occurs about its basal joint (Text-fig. 4 BI and BII). The endopodites are brought down along the DS and clasp the OF and IF. During this phase the PS and DS are held down while the MS is elevated by angle changes around the PS–MS and MS–DS joints (Text-fig. 4 BIII and BIV). The OF and IF are finally pulled free of the endopodites by this movement of the MS. The PS and DS are then synchronously raised about their basal joints until the antennule resumes its initial position (Text-fig. 4 BV, BVI and BVII).

In both sequences depression of the DS is usually achieved by flexion of the MS–DS joint through 50–100° in 300–1300 msec (Text-fig. 4 AIII and BIII). The angle moved depends on the initial angle of this joint, but the angle attained by this movement is usually between 80 and 95°. The entire wiping sequence may take from 500 to 2000 msec. From direct observations there is a strong suggestion of a slow and maintained flexion at the DS–OF joint during flexion at the MS–DS joint (Text-fig. 4 AII, AIII, BII and BIII). Unfortunately, however, the outer flagellum is usually obscured from lateral view by the maxillipeds during this phase of wiping.

Wiping frequently occurs in the absence of apparent stimuli, although it can be elicited by light mechanical stimulation of the aesthetascs with a clean piece of filter paper. Although the interval between wipes is highly variable within any individual, an increased mean frequency of wiping has been observed in animals that had recently sustained damage to an OF or IF and in animals that had had carbon particles pipetted over their aesthetascs. Pipetting filtered fish juice around the aesthetascs was generally unsuccessful in eliciting wiping.

Usually only the stimulated antennule is wiped although wiping of both antennules occurs in the stimulated and unmolested animal. When one antennule is being wiped the other may continue flicking as if unaffected by the activity of the first. Occasionally the endopodites are used to wipe an eyestalk, antenna or the flagella of the 1st, 2nd and 3rd maxillipeds.

The above observations suggested that antennular wiping was functionally important in cleaning the aesthetasc hairs. Material caught amongst the aesthetascs during flicking could thus be removed by the large 'comb-like' setae on the endopodites of the 3rd maxillipeds. Examination of the aesthetascs of normal animals showed them to be almost free from any debris, but after removal of even one endopodite the aesthetascs became darkened within 48 h owing to the accumulation of diatoms and dirt. Operated animals made repeated attempts to wipe their antennules with the remaining endopodite, and even following bilateral removal of the endopodites the antennules were frequently depressed into the position they adopt during wiping.



Text-fig. 5. Movements of the antennule during the withdrawal reflexes. A fast flexion-withdrawal reflex (A) involves rapid flexion at only the MS–DS joint whereas a slow flexion-withdrawal reflex (B) involves slow flexion at both the MS–DS and DS–OF joints. An extension-withdrawal reflex (C) involves extension at the MS–DS joint during which slight flexion at the DS–OF joint probably results from water resistance forces. The dotted lines in C represent the position of the distal segment prior to extension withdrawal.

D. Antennular withdrawal

Antennular withdrawal is considered as posturing or movement of one or both antennules away from a source of stimulation. Four types of withdrawal have been observed: (1) extension withdrawal; (2) slow flexion withdrawal; (3) fast flexion withdrawal; (4) tonic flexion withdrawal (Text-fig. 5A, B and C; Pl. 1D). The first three types are reflexes while the fourth is a postural modification of the antennule and other appendages.

(1) *Extension-withdrawal reflex.* It was difficult to consistently elicit extension-withdrawal reflexes for the purposes of filming and the following description is based mainly on direct observations.

Extension withdrawal may be elicited by mechanical stimulation of the IF. Pipetting distilled water near the aesthetascs for several seconds sometimes elicits extension withdrawal but only after a slow flexion-withdrawal reflex. Extension withdrawal may thus occur when the DS is depressed or when the antennule is in the normal extended position shown in Text-fig. 2A. In the latter case an angle change of 10–20° occurs at the MS–DS joint (Text-fig. 5C).

Stimulation of one antennule usually elicits only an ipsilateral response. Extension withdrawal may occur rapidly and smoothly or in a disjointed manner. During a rapid extension withdrawal the DS–OF joint may be slightly flexed due, probably, to the effects of water resistance.

(2) *Slow flexion-withdrawal reflex.* Touching the sides or dorsal surface of the OF with a glass rod usually causes a slow, smooth flexion at both the MS–DS and DS–OF joints (Text-fig. 5B). Slow pipetting of diluted sea water (20%) around the aesthetascs usually produces similar movements, of one or both antennules. No withdrawal occurred when sea water was substituted in these experiments. Touching an eyestalk, antenna or the carapace with a glass rod elicited slow flexion withdrawal of both antennules, but a larger movement occurred on the stimulated side. The extent and rate of the component movements of slow flexion withdrawal seemed to depend on

the duration or intensity of the stimulus. Very intense stimuli elicited a rapid flexio at the MS–DS joint without flexion at the DS–OF joint, but this is considered to constitute a fast flexion-withdrawal reflex.

Following a slow flexion withdrawal the antennule was normally maintained, for at least half a second, in its flexed condition. Extension from this position occurred at a variable but slow rate. The antennule was not always completely extended before the resumption of antennular flicking, and further stimulation often causes further flexion withdrawal.

(3) *Fast flexion-withdrawal reflex.* The fast flexion-withdrawal reflex is most easily elicited by pipetting distilled water around the aesthetascs, strong taps to the eyestalks or shell, or bending the tip of the OF towards the aesthetascs with a glass rod. It consists of a rapid flexion of the MS–DS joint which is not accompanied by flexion of the DS–OF joint (Text-fig. 5A). Water resistance thus causes the OF to trail through the water in an extremely extended position. The application of these stimuli during a slow flexion withdrawal still elicits a strong flexion at the MS–DS joint characteristic of the fast flexion withdrawal.

The extent and duration of a fast flexion-withdrawal reflex varies and in part depends on the initial angle at the MS–DS joint. Usually this joint angle changes 50–80° in 60–200 msec. Extension of the antennule occurs at a variable rate and the MS–DS joint may remain flexed for several seconds.

Although mechanical stimulation of the OF results in an ipsilateral response, very intense stimuli sometimes produced a bilateral response. Generally tapping on an eyestalk or the shell or stimulation of the aesthetascs with distilled water were more effective in eliciting a response in both antennules.

(4) *Tonic flexion withdrawal.* Animals which have been removed from their shells or animals occupying shells too small to permit their withdrawal, responded to continual tapping of the eyestalks, antennules or antennae or stimulation of the antennules with distilled water or to several hard taps to the shell or legs by adopting a tonic withdrawal posture. During tonic withdrawal the MS–DS and DS–OF joints of both antennules are flexed, the eyestalks are depressed in an anterior direction and the 2nd antennal segments are folded under the eyestalks and antennules (Pl. 1D). The intensity and duration of stimulation required to elicit tonic flexion withdrawal varies; animals which have recently sustained damage to an OF often showed tonic withdrawal in response to very light mechanical stimulation. Tonic withdrawal cannot be properly observed in animals which are able to withdraw completely into their shells.

DISCUSSION

(1) *Antennular flicking*

In seeking the major function of antennular flicking one is led to consider the most obvious result of this activity: the splaying of the aesthetasc hairs. Although the movements during flicking are very rapid, they are also relatively small. Consequently it seems unlikely that they could generate water currents which are of significance to structures other than those on the antennules. In addition, the antennules are usually extended upwards in front of the crab so that antennular flicking is generally away from the body and other appendages. It could be suggested that flicking is important

removing debris caught amongst the aesthetasc hairs but debris rapidly accumulates following the removal of the endopodites of the 3rd maxilliped and this operation does not inhibit flicking. I therefore propose that the function of antennular flicking in aquatic decapods is related to the function of the aesthetasc hairs.

There is considerable behavioural, electrophysiological and ultrastructural evidence that the aesthetasc hairs are of primary importance in distance chemoreception (Laverack, 1964; Laverack & Ardill, 1965; van Weel & Christofferson, 1966; Hazlett, 1968; Ghiradella *et al.* 1968*b*; Ache & Case, 1969). Marine brachyurans and anomurans have long (up to 1700 μm), thin (basal diameter: 10–30 μm) aesthetascs which are crowded into closely spaced rows on the outer antennular flagellum (Balass, 1944; Ghiradella *et al.* 1968*b*). In *Pagurus alaskensis* the maximum separation between the rows of aesthetascs occurs near the hair bases and is only 80 μm. This suggests that there would be little exchange between the water surrounding the aesthetascs and that of the crab's immediate environment. The limitations which this structural organization may place on chemoreception are emphasized when one considers that probably only the distal portions of the aesthetascs of marine decapods are permeable to dissolved materials (Ghiradella *et al.* 1968*b*). Any mechanism which facilitates the circulation of water around the aesthetasc hairs could thus be considered of primary importance to the chemoreceptive process.

In *P. alaskensis* there are two types of specializations which could be important to the circulation of water around the aesthetasc hairs: (*a*) the specialized structure of the outer flagella and the aesthetasc hairs; (*b*) the patterning of movements during antennular flicking.

A. Structure of outer flagella and aesthetasc hairs

The aesthetascs of marine decapods may contain the processes of up to 400 sensory neurons per hair (Ghiradella *et al.* 1968*b*). Water resistance forces during antennular flicking result in bending of the aesthetascs and movement about their basal attachment with the outer flagellum. If the wall of an aesthetasc resembled a uniform cylinder, rigidly fixed to the surface of the outer flagellum, then these water resistance forces might be sufficient to cause distortion of the wall and damage to the densely packed sensory processes. The socket in which each aesthetasc of *P. alaskensis* is borne would allow some movement of each aesthetasc around its basal attachment while the periodic annular bulges along each aesthetasc may act as joints which permit bending of the hairs without distortion of the cylindrical form (Pl. 1 B, C).

Flexibility of the basal attachment of the aesthetascs of *Cancer productus* and *P. hirsutiusculus* is suggested by figures 2 and 3 shown by Ghiradella *et al.* (1968*b*) and such structures have also been observed in *Paragrapsus gaimardii* (personal observation) and in epicarid isopods (Nielsen & Strömberg, 1972). Structures which resemble the periodic annular bulges of the aesthetascs of *Pagurus alaskensis* have been observed in the aesthetascs of the brachyurans, *Paragrapsus gaimardii* (personal observation), *Cancer antennarius* and *C. productus* (Ghiradella, Cronshaw & Case, 1970), in the anomuran, *Pagurus hirsutiusculus* (Ghiradella, Cronshaw & Case, 1968) and in seven families of cryptoniscinid isopods (Nielsen & Strömberg, 1972). Nielsen & Strömberg (1972), however, have suggested that these nodes may be important in retaining the cylindrical form in the resting aesthetasc.

In *P. alaskensis* there is extreme bending of the outer flagellum about 25 msec after the initiation of a flick. This results from water resistance forces acting on the long, thin distal segments of the outer flagellum to cause considerable bending across the distal shorter segments. The result of this bending is a more uniform separation between adjacent aesthetascs irrespective of their position on the outer flagellum. The outer flagella of many marine brachyurans and anomurans are of similar morphology to those of *P. alaskensis* (personal observation). In contrast, however, the outer flagellum of the semi-terrestrial hermit crab, *Coenobita compressus*, lacks the thin distal segments and the conical form of the outer flagellum of *P. alaskensis*. The aesthetascs of *Coenobita* are short pegs and (particularly in a gaseous medium) distortion of outer flagella (if possible) would not greatly increase contact of the aesthetascs with chemical stimulants.

B. Patterning of movements

During flicking in *P. alaskensis* the temporal relationship of movements at the MS–DS and DS–OF joints appears to be important to the spreading of the aesthetasc hairs. A flick is initiated by flexion at the MS–DS joint 2·5 msec before movement of the DS–OF joint. This infers that tension development in muscle 32F which produces fast flexion at the DS–OF joint occurs only after the development of tension in muscle 31F which produces fast flexion at the MS–DS joint (Snow, 1973). Myogram recordings from these muscles in *P. ochotensis* have shown that electrical activity in muscle 31F precedes activity in muscle 32F by 2·3 msec (Snow & Field, unpublished). In *P. alaskensis*, flexion at the MS–DS joint is interrupted for about 5 msec following flexion at the DS–OF joint, but this interruption is not observed following excision of all but the basal segment of the outer flagellum. It is thus possible that the contraction of muscle 31F before muscle 32F may be important in preventing extension at the MS–DS joint resulting from water resistance forces generated by flexion at the DS–OF joint. Such a mechanism would ensure that the outer flagellum is moved through sufficient water to spread the aesthetasc hairs.

Unfortunately the timing of movements within a single flick have not been precisely described in other crustaceans. Preliminary observations suggest that the morphology of the antennules of most aquatic decapods either resembles that described in *P. alaskensis* or that described in lobsters and shrimps (Maynard & Dingle, 1963; Ache & Case, 1969). The outer flagellum of the latter type of antennule is long and thin and bears little resemblance to the short, conical outer flagella of *P. alaskensis*. Decapods with antennules similar to those of *P. alaskensis* show relatively high frequency of vigorous flicks but, in contrast, in species with antennules resembling those of shrimps and lobsters antennule flicks occur less frequently and are less vigorous (personal observation). Maynard & Dingle (1963) report that single flicks of the lobster antennule may involve movement of the outer flagellum only. More frequently, however, they observed a series of flicks of the outer flagellum which were accompanied by a tonic flexion of the MS–DS joint which lasted for the duration of the series. In lobsters the rows of aesthetascs are borne on the distal portion of a long (about 20 cm), flexible outer flagellum and are separated by approximately 250 μm (Laverack, 1964). A series of flicks of the outer flagellum might thus be

hfficient to exchange the water around the aesthetascs despite the length and flexibility of the outer flagellum.

A comparative study of the structure and activity of the antennules of various aquatic decapods may reveal a strong correlation between the vigour and frequency of antennular flicking, the density of the aesthetasc hairs and the size and morphology of the outer flagellum. Experimentally, however, the most conclusive test of whether flicking is important to chemoreception may come from attempts to record gross activity from the aesthetasc sensory nerve (nerve 1, Snow, 1973) during antennular flicking in a chemically changing environment.

If flicking is essential for the circulation of water around the aesthetasc hairs then it could be considered that a crab only senses changes in dissolved chemicals upon flicking an antennule. Although the inter-flick interval is highly variable in a constant environment, the mean inter-flick interval may be decreased by increasing the water currents or fish odour in the crab's surroundings. In addition, certain stimuli result in an interruption of flicking. These observations suggest that the inter-flick interval may be determined by the selective advantage of flicking, firstly in relation to recent sensory conditions and secondly under the immediate sensory conditions. Assuming that flicking does provide a means of phasically sampling the dissolved chemicals in a crab's immediate environment, the plasticity of the inter-flick interval might thus provide a means of directing attention towards or away from chemical stimuli. It is difficult, however, to see why a central neuronal circuit would not be a more economical means of achieving the same ends.

(2) *Antennular rotation*

In the lobster the antennules are frequently pointed towards the source of chemical stimuli. These pointing movements frequently form part of more complex 'exploring-feeding' sequences (Maynard & Dingle, 1963). Similarly, antennular rotation in the hermit crab, *P. alaskensis*, was most frequent when crabs appeared to be exploring new surroundings or when there was a high mean frequency of flicking.

In the aquatic environment the movement of chemical stimulants would be heavily dependent on water currents. In general, the antennules are considered to be important to distance chemoreception (Hazlett, 1968, 1971*b*). Furthermore, it has been argued above that flicking facilitates the circulation of water around the aesthetasc hairs which are probably the major sites of antennular chemoreception (Laverack, 1964; Ghiradella *et al.* 1968*b*). The splaying of the aesthetasc hairs would be maximal when flicking is directed into existing water currents. Antennular rotation might thus be important to chemoreception by ensuring that flicking is usually against water currents. It would be interesting to test whether the antennules are generally orientated into water currents and, if so, what receptors are involved in this response (see Brock, 1930; Luther, 1930; Laverack, 1962). A second important question is whether the rotation of the antennules is important to orientation of the whole animal towards a food source in the presence and absence of water currents (see Brock, 1926; Hazlett, 1968; Burrows & Willows, 1969; Charlton, 1971).

(3) *Antennular wiping*

The function of wiping is probably to remove debris caught amongst the aesthetasc hairs. In high densities such materials would greatly impede the exchange of water around the aesthetascs which is suggested above to be of importance to the chemoreceptive process. During wiping in *Pagurus alaskensis* the long comb-like setae on the endopodites of the third maxillipeds probably pass through the rows of aesthetasc hairs removing any trapped material. In contrast, in the sand crab *Emerita*, the antennules are cleaned with a group of setae on the fifth antennal segment (Efford, 1971). The flexibility of the aesthetascs around their basal joints may be important in preventing the endopodites or antennae from damaging the hairs.

In attempting to determine the function of an activity it is important to consider the modality of the triggering stimulus. In the hermit crab wiping may be elicited by light mechanical stimulation of the aesthetasc hairs, but pure chemical stimuli were ineffective. Effort (1971) has noted that the sand crab *Emerita* wipes its antennules when graphite particles become caught amongst the aesthetascs. In contrast, Maynard & Dingle (1963) report that wiping in the lobster was best elicited by chemical or chemotactile stimuli and only occasionally followed mechanical stimulation. Stimulation of mechanoreceptors situated near the aesthetasc hairs may be sufficient to elicit wiping in the hermit crab, but in lobsters the increased responsiveness to chemotactile stimuli means that specific chemotactile sensilla cannot be ruled out (see Laverack, 1964; Hazlett, 1971*a*). The observations that wiping in the sand crab, hermit crab and lobster occur in the absence of apparent stimulation and that in the lobster chemical stimulation alone appears to be a sufficient stimulus, possibly means that only very small particles are necessary to elicit this activity. Any facilitation of wiping by chemical stimuli would be selectively advantageous, as soluble materials trapped among the aesthetasc hairs could result in an invalid interpretation of the chemical environment.

(4) *Antennular withdrawal*

Although no attempt has been made to elicit antennular withdrawal by stimulating specific receptors, both mechanical and osmotic stimulation of the antennules have been used successfully. The electrophysiological experiments of Krijgsman & Krijgsman (1954), Laverack (1964) and van Weel & Christofferson (1966) have demonstrated the presence of mechanoreceptors and osmotically sensitive receptors on the antennules of various decapods, and the evidence of Maynard & Cohen (1965) has suggested that some fast-conducting antennular mechanoreceptors have a monosynaptic, excitatory influence on an antennular motoneuron in the lobster.

In both the lobster (Maynard & Dingle, 1963) and the hermit crab an extension reflex could be elicited by mechanical stimulation of the inner flagellum while a flexion reflex resulted from stimulation of the outer flagellum. Both the extension and flexion reflexes thus move the antennule away from the stimulus. Similarly, prolonged osmotic stimulation of the antennules in the hermit crab sometimes resulted in flexion and then extension of the antennule in what appears to be an attempt to remove the antennule from the stimulus. Mechanical or osmotic stimulation could be interpreted as being potentially noxious to the aesthetasc hairs and other antennular

tructures and thus antennular withdrawal may be regarded as a purely protective response.

The form of extension withdrawal in the lobster is similar to that described in the hermit crab and involves extension at the MS–DS joint (Maynard & Dingle, 1963). In the hermit crab both fast and slow flexion-withdrawal reflexes are recognizable. A slow withdrawal reflex involves a smooth, slow flexion at both the MS–DS and DS–OF joints while a fast withdrawal reflex involves a rapid flexion at only the MS–DS joint. Although flexion-withdrawal reflexes in the lobster usually involve flexion at both the MS–DS and DS–OF joints it is not clear that what have been defined as fast and slow flexion-withdrawal reflexes in the hermit crab are not both involved in flexion withdrawal as described in the lobster (see Maynard & Dingle, 1963).

In the hermit crab, fast flexion-withdrawal reflexes could be elicited by strong taps to the eyestalks or shell or by bending the tip of the outer flagellum towards the aesthetasc hairs. In contrast, however, slow flexion-withdrawal reflexes could be elicited by touching the eyestalks, antenna, carapace or sides or dorsal surface of the outer flagellum. These observations suggest that the fast flexion-withdrawal reflex serves to rapidly remove the antennules from a stimulus which may cause immediate damage to the antennules while the slow flexion-withdrawal reflex serves to temporarily adjust the posture of the antennules so as to avoid repetition of a less severe stimulus.

In the hermit crab repeated mechanical stimulation of the antennules, eyestalks, antennae, legs or body, or continual stimulation of the antennules with distilled water, results in tonic flexion of both antennules as well as in postural modifications of the eyestalks and antennae. This response appears to be an avoidance which provides maximum protection of the antennules from the possibly noxious effects of these stimuli. In the natural state this tonic withdrawal posture would provide protection of the antennules in animals occupying shells too small to permit their complete withdrawal or in animals disturbed in the process of changing shells.

It is interesting to note that many brachyurans withdraw their antennules by folding them into a groove in the ventral side of the cephalic sternum (personal observation). This folding involves movement at the MS–DS joint which is in the opposite direction to flexion at this joint in the hermit crab antennule. Although such differences may be purely the result of differences in the anatomy of the antennular musculature (cf. Schmidt, 1915; Cochran, 1935; Snow, 1973), a comparative behavioural and neuromuscular study of the brachyuran and macruran antennules may provide interesting examples of the adaptations of a neuromuscular system.

SUMMARY

1. The antennular activities of the hermit crab, *Pagurus alaskensis*, were studied with the aid of motion pictures taken at speeds of 50, 200 and 400 frames/sec.

2. Most movements of the antennule represent one of four types of antennular activity: flicking, rotation, wiping and withdrawal. These activities are described in detail.

3. Water resistance forces contribute to the timing and duration of some antennular movements.

4. Flicking occurs non-rhythmically and flicks of the left and right antennules are never synchronized. The factors which influence the mean frequency of flicking are discussed.

5. The timing of joint movements during a flick, and the morphology of the outer flagellum and the aesthetasc hairs, appear to be adapted to facilitate splaying of the aesthetascs. It is proposed that this splaying might facilitate the chemoreceptive process by circulating water around the aesthetasc hairs.

6. During antennular wiping the endopodites of the 3rd maxillipeds are used to remove debris caught amongst the aesthetasc hairs. Light mechanical stimulation of the aesthetascs is sufficient to elicit wiping.

7. The antennules are reflexively withdrawn from certain stimuli either by extension or by slow or fast flexion. The functional significance of the withdrawal reflexes are discussed in relation to the stimuli involved and the form of the reflexes.

8. Continued application of certain stimuli to the antennules, eyestalks, antennae or body results in tonic flexion withdrawal which involves postural modifications of the antennules, eyestalks and antennae.

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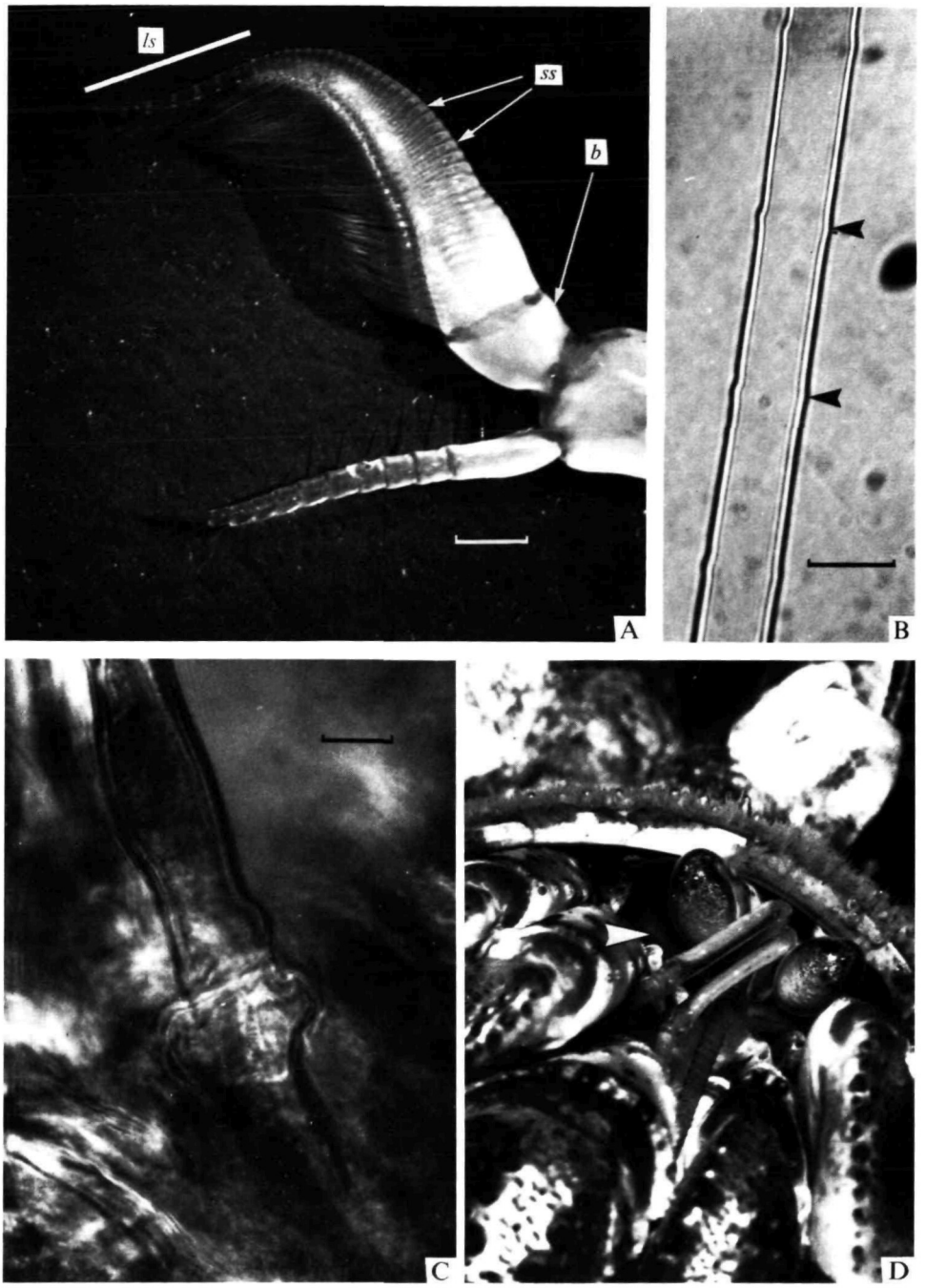
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EXPLANATION OF PLATE

(A) A medial view of the right outer and inner flagella, showing the extent of the long, thin, distal segments (*ls*) (white line), the shorter segments (*ss*) bearing the aesthetasc hairs and the large basal segment (*b*) of the outer flagellum. Note the fusion of the more proximal short segments and the distal bunching of the rows of aesthetascs. Scale 500 μm. (B) Light micrograph of an aesthetasc hair showing the periodic annular bulges (arrows). Scale: 25 μm. (C) Light micrograph of a socket at the base of a single aesthetasc. Scale: 24 μm. (D) Tonic withdrawal of the antennules in a crab occupying a shell too small to permit its full withdrawal. Note the flexion of the antennules at the MS–DS and DS–OF joint, the anteriorly depressed eyestalks and the folding of the 2nd antennal segment (arrow) beneath the eyestalks and antennules.