

ROLE OF PROPRIOCEPTIVE FEEDBACK FROM NONSPIKING MECHANOSENSORY CELLS IN THE SAND CRAB, *EMERITA ANALOGA*

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SUMMARY

The two programmes underlying uropod beating in *Emerita* ('swimming' and 'treading water') are distinguished by a difference in timing of the power stroke within the interval between return strokes (cycle). While 'swimming' (cycles approx. 80-400 ms) the *phase* and while 'treading water' (cycles approx. 100-700 ms) the *latency* of the power stroke are relatively invariant. Analyses of electromyograms of unrestrained *Emerita*, before and after bilateral surgical ablation of the four nonspiking mechanoreceptive cells associated with each uropod, established that power strokes in 'treading water' are dependent upon proprioceptive feedback from the nonspiking cells. As cycle duration increases from 80 to 700 ms, the function of the reafference changes from reinforcement of the centrally generated 'swimming' pattern to production of the 'treading water' pattern.

INTRODUCTION

Rhythmic behaviours in a variety of animals result from endogenous properties of the central nervous system, even though precise sensory feedback is ostensibly available for pattern generation. The existence of an array of rhythmic behaviours based on a gradation "from the most purely reflex to the most purely central mechanisms of pattern formation" (Wilson, 1966, p. 199) may have been tacitly assumed, but it has been the concept of central motor programmes for repetitive motor activities which has received extensive experimental support (Kennedy, 1973). Four categories of rhythmic activities can be distinguished: (1) Rhythms reflecting central motor programmes which maintain much of the fine structure, although not necessarily the frequency, of the normal motor output in the complete absence of sensory information (e.g. Dorsett, Willows & Hoyle, 1969; Hartline & Maynard, 1975; Ikeda & Wiersma, 1964; Kovac, 1974; Maynard, 1972; Wilson, 1961). Sensory feedback which reinforces centrally-generated motor output may, nevertheless, be considered to constitute an integral part of such motor systems (e.g. Burrows, 1975; Davis, 1969*b*; Kater & Rowell, 1973; Paul, 1971*c*). (2) Rhythms whose central programmes constitute a basic framework upon which sensory feedback from the periphery elaborates the fully adaptive motor behaviour; walking in vertebrates and arthropods exemplifies

this category (Evoy & Fournier, 1973; Grillner, 1975; Pearson, Fournier & Wong 1973; Pearson & Fournier, 1975). (3) Rhythms of composite origin, one phase initiated by a central driver but sensory feedback required for completion of the cycle (Snow, 1975; Paul, 1975, and this study). (4) Motor patterns the rhythmicity of which depend upon phasic sensory input, the only apparent example being escape swimming in the scallop (Mellon, 1969).

Until more examples of sensory cueing in motor pattern formation are known, its possible adaptive significance will remain obscure. Snow's analysis of antennular flicking in hermit crabs (1975) suggests one category of behaviour in which reflex control might be of general importance, that is, when alterations in posture change the motor pattern required for fulfilment of function. However, such a situation obviously does not apply to the requirement for proprioceptive feedback in one motor pattern underlying uropod beating in *Emerita* (this study). Thrust of the swimming appendage (uropod) in this sand crab is controlled by varying stroke amplitude and, therefore, by the velocity of the power stroke since the duration of the latter is not related to frequency (Paul, 1971*a*); this means that power is supplied in ballistic fashion during only a small portion of the stroke cycle. In this respect uropod beating differs from many rhythmic behaviours, including those of segmental appendages in other members of the same suborder (Reptantia), in which the power stroke occupies approximately half of the movement cycle (Davis, 1969*a*; Hartnoll, 1970; Wilson, 1968). Appreciation of the significance of reflex control in this case probably should be sought in considerations of efficiency at varying frequency of such ballistic locomotion.

Observation of the behaviour of *Emerita* combined with analyses of electromyograms, recorded from return-stroke and power-stroke muscles of the uropods during periods of unrestrained activity, revealed two different behavioural and motor patterns best described as 'swimming' and 'treading water' (Paul, 1971*a*). The essential differences between the motor patterns associated with 'swimming' and with 'treading water' are illustrated in Fig. 2B, C (see also fig. 14, Paul, 1971*a*). In both behaviours the basic cycle of uropod movement is: return stroke, power stroke, pause, return stroke, etc. (Figs. 2A, 3). But, although power-stroke latency is positively correlated with cycle duration during 'swimming' (resulting in an approximately constant power-stroke phase of 0.5–0.6) the correlation is at most very weak during 'treading water' (Paul, 1971*a*; Fig. 2B, C).

The hypothesis which dictated this study was that the power stroke in 'treading water' is driven by a negative feedback reflex from each preceding return stroke, a reflex which is mediated by the nonspiking mechanoreceptors previously described (Paul, 1971*c*; 1972). The series of return strokes are centrally produced. This would explain the lack of correlation of power-stroke latency and cycle duration during 'treading water', for the timing of the power stroke would be determined by a peripheral (sensory) rather than a central mechanism. In contrast, the 'swimming' motor pattern (in which the power-stroke latency is positively correlated with cycle duration) is apparently generated by the central nervous system and independent of sensory feedback from the nonspiking mechanoreceptors (Paul, 1971*c*; this study). One prediction from this hypothesis was that electromyograms of *Emerita* from which the receptor strands had been ablated would contain only values of power-stroke phase of around 0.5. Early phases, characteristic of 'treading water', should be absent.

This prediction has been exactly fulfilled. A second prediction was that post-ablation electromyograms would include sequences of return-stroke bursts alone, with no power-stroke muscle activity. This prediction has not been unambiguously fulfilled because it was based on the apparently erroneous supposition that motor bursts to the return-stroke muscle in the two behaviours originated from different sources.

The main conclusion from this study is that reafference from the nonspiking mechanoreceptors plays a formative role in part of the total repertoire of motor patterns underlying uropod beating in *Emerita*.

METHODS

Emerita analoga (carapace length of 1.5–3 cm) from Monterey Bay, California, were held at the University of Victoria in aquaria through which 12 °C sea water continually circulated.

Electromyography

Electromyograms were recorded *via* two wire electrodes implanted in the power-stroke and return-stroke muscles controlling one uropod (see Paul, 1971 *a* for details of method, 1971 *b* for morphological details). Cycle duration and power-stroke latency were measured to the nearest millisecond as illustrated in Fig. 2A. The graphs were prepared from correlation tables of power-stroke latency and power-stroke phase as a function of cycle duration. I used probability paper to plot cumulative percent of power-stroke phase in order to analyse the nature of the phase distribution in electromyograms of pre-ablation and post-ablation animals (Harding, 1949). The probability scale is contracted in the centre and expanded at the ends such that cumulative percentage of a normal distribution falls on a straight line. Any deviation from normality of experimental data, such as skewness or bimodality, is immediately apparent from the nature of the deviation from a straight line of the cumulative percentage plot.

The source of electromyographic activity was verified in two ways: by recording activity from the implanted electrodes in response to electrical stimulation of the nerve innervating each muscle to ascertain that it mimicked in sign and general wave form the natural electromyogram; by determining the exact position of each electrode by dissection at the end of an experiment.

Surgery

Following anaesthesia on ice, the crab was pinned ventral side up to a waxed dish containing chilled sea water; the abdomen and telson were partially extended to allow access to the anterior ventral surface of the telson (Fig. 1). A small slit through the thin, ventral cuticular membrane allowed introduction of the tip of microdissecting scissors with which the receptor nerve and strands on each side were cut. The muscular strand was often visible through the membrane and aided in orienting the scissors toward the receptor strand (hidden by the ventromedial and dorsomedial muscles); unavoidably it was cut along with the receptor nerve in experimental animals. Therefore, in control animals the muscular strands alone were ablated bilaterally. At the conclusion of each experiment the extent of the ablations was

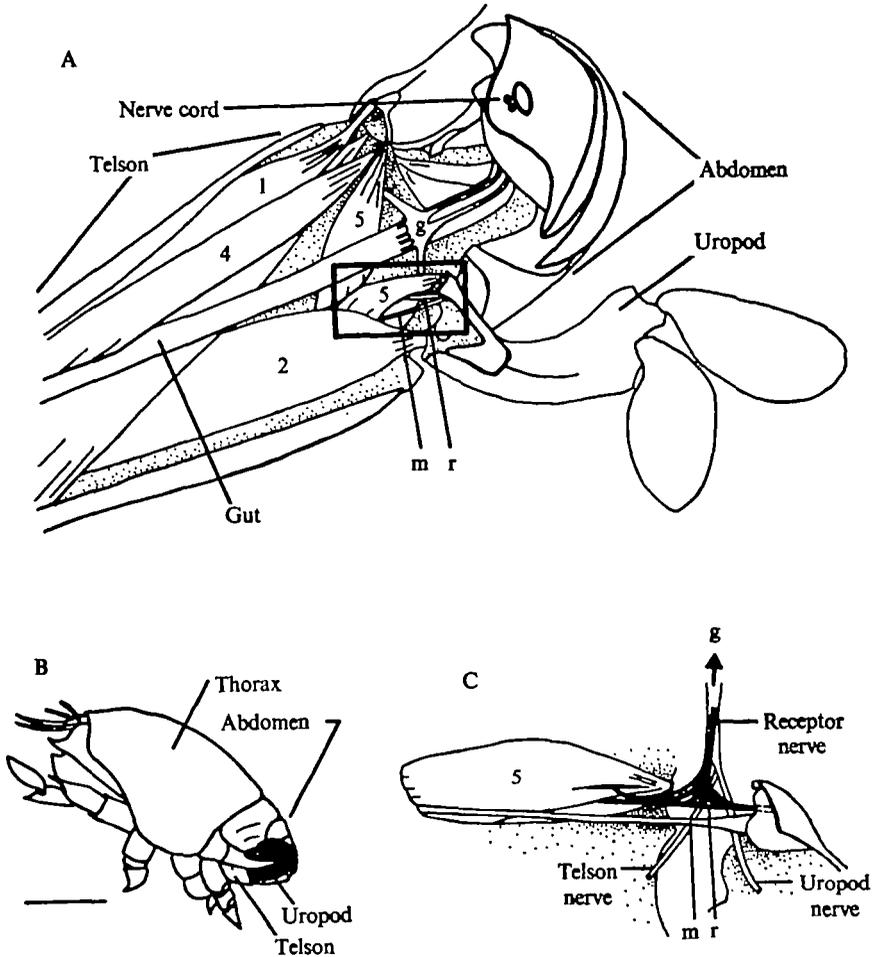


Fig. 1. (A) Camera lucida drawing of oblique view from ventral side of posterior abdominal segments and anterior two-thirds of telson. 1, power-stroke muscle (removed from left (near) side); 2, return-stroke muscle; 4, ventromedial muscle (removed from left side); 5, dorso-medial muscle; g, last abdominal ganglion; m, muscular strand, r, receptor strand. (B) Side view of an *Emerita* with uropod in position at end of power stroke (= at rest). (C) Detail of area outlined in (A). The receptor nerve (black), a ventral branch of the main root of the last abdominal ganglion, contains both the peripheral processes of the four nonspiking mechanoreceptors which insert along the receptor strand and the motoneurons which innervate muscle 5 and the muscular strand. (Innervation of muscular strand not shown.) The telson nerve includes motor fibres innervating the power-stroke and return-stroke muscles. Scale: (A) 2.5 mm; (B) 1 cm; (C) 1 mm.

checked by dissection, sometimes aided by methylene blue staining. Twelve of a total of 22 experimental and control animals provided useful information.

RESULTS

I. Role of reafference from the nonspiking mechanoreceptors

Representative electromyograms are shown in Figs. 3 and 4. The results of analyses of pre-ablation and post-ablation electromyograms for a representative experimental

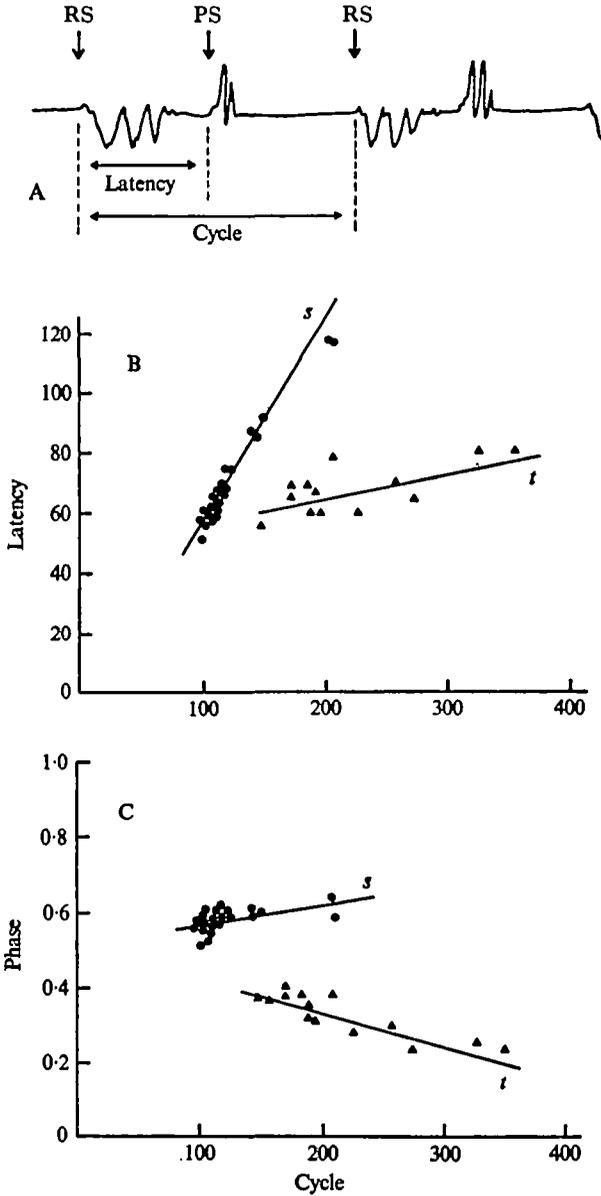


Fig. 2. (A) Typical electromyogram. Definitions: cycle duration = time between beginning of successive bursts of activity in return-stroke muscle (RS); latency of power stroke = time between beginning of RS and beginning of activity in power-stroke muscle (PS); phase of power stroke = latency/cycle duration. (B) Power-stroke latency and (C) power-stroke phase as functions of cycle duration for a single period of 'swimming' (*s*) and of 'treading water' (*t*).

animal are shown in Fig. 5. In the pre-ablation electromyogram, power-stroke latencies fall within a wedge-shaped area of the correlation diagram, the lower boundary (slope < 0.1) corresponding to 'treading water', the upper boundary with a slope of about 0.6, corresponding to 'swimming' (see also Fig. 2). In addition, there is a scatter of intermediate latencies. Note that unlike the original report of the two

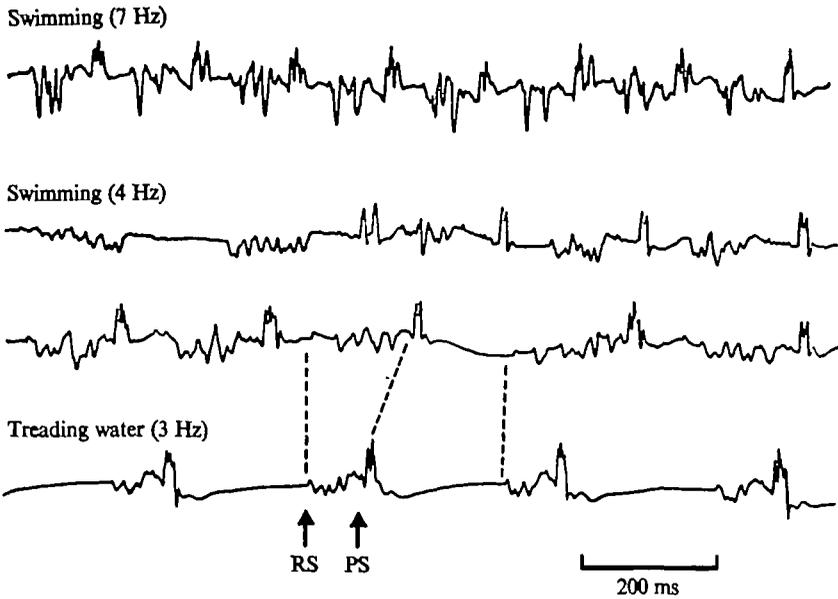


Fig. 3. Representative electromyograms: the upper three traces are from two periods of 'swimming' (middle two traces continuous), the lowest trace from a period of 'treading water' (crab no. 10). The average frequency of uropod strokes for each record is in brackets. The dotted lines connecting RS bursts and PS bursts in the two lower traces assist in comparing the two motor patterns. Note that in cycles of the same duration PS occurred earlier in 'treading water' than in 'swimming'. Traces retouched for photographic reproduction.

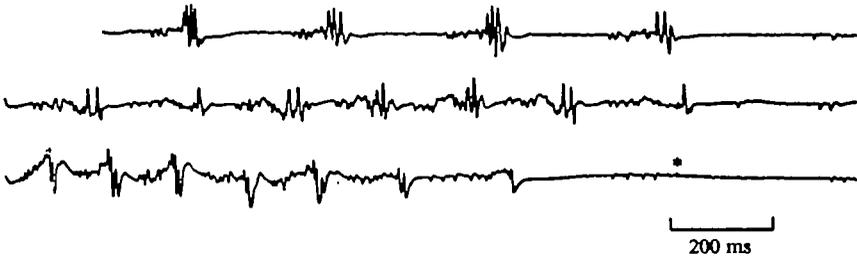


Fig. 4. Pre-ablation (top two traces) and post-ablation (bottom trace) electromyograms of an experimental animal (no. 22). Each trace shows the end of a sequence of uropod strokes which, in each case, terminated with a brief RS burst. Top: pre-ablation 'treading water'. Middle: pre-ablation 'swimming'. Bottom: post-ablation 'swimming'. *, single PS potential. The source of the small deflexions between bursts was not identified. Traces retouched for photographic reproduction.

patterns of coordination (Paul, 1971*a*), 'treading water' may occur in short as well as long cycles, resulting in considerable overlap of the range of cycle durations in which either motor pattern may be observed. Power-stroke phases cluster around mid-cycle, but there is a wide scatter of smaller phases associated with long duration cycles.

Following bilateral ablation of the receptor strands and associated nonspiking cells, correlation diagrams of power-stroke latency and phase as functions of cycle duration are simplified (Fig. 5). Power-stroke latencies are positively correlated with

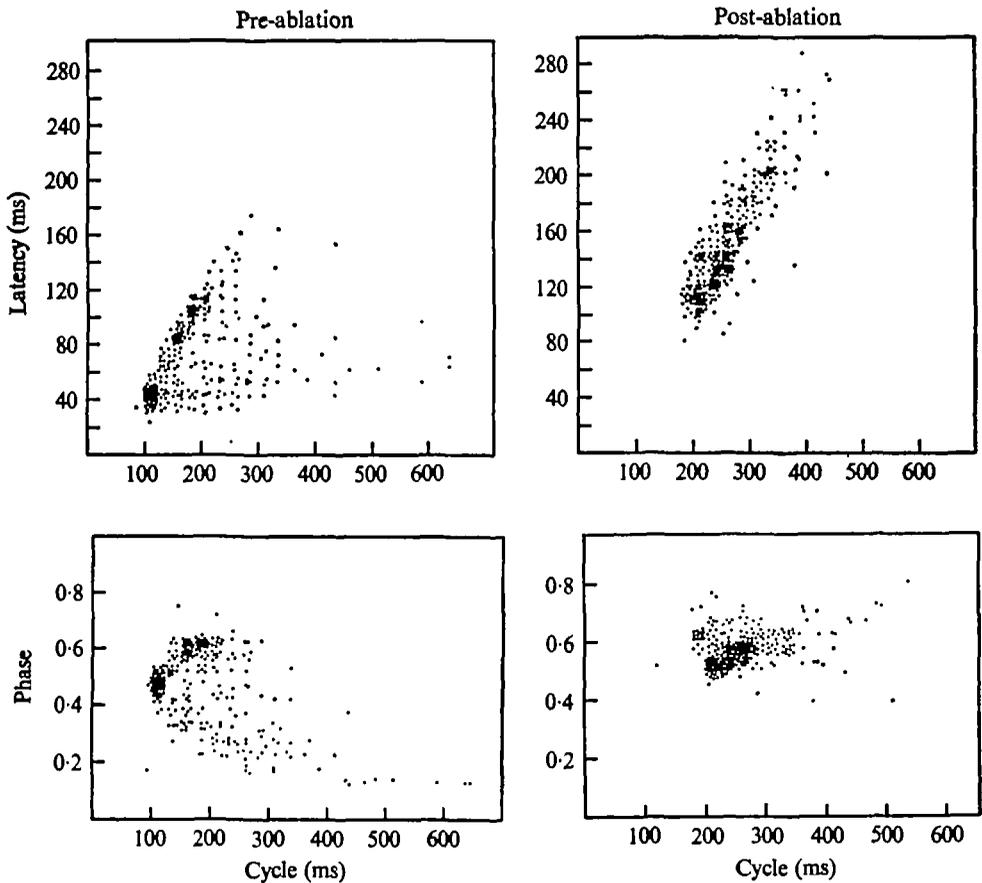


Fig. 5. Latency (above) and phase (below) of power-stroke bursts as functions of cycle duration for an experimental animal (no. 10). Pre-ablation data on the left and post-ablation data on the right.

cycle duration and, correspondingly, values of power-stroke phase cluster between 0.5–0.6. By contrast, following ablation of only the muscular strands (control) correlation diagrams were practically indistinguishable from the pre-ablation pattern.

A more concise comparison of these data from experimental and control animals is shown in Fig. 6. Although the pre-ablation phase distributions are continuous from about 0.1 to 0.8, they are actually bimodal as revealed by the sigmoidal nature of the cumulative percentage curves. The important observation is that the cumulative percentage plot of post-ablation phases for this experimental animal, as for two others analysed in this way, falls on a qualitatively differently shaped curve than for the pre-ablation and post-ablation control data; its deviation from a straight line indicates a skewness toward longer values, but it is not sigmoidal. The cumulative percentage plot of post-ablation data from the control, on the other hand, is distinctly sigmoidal. The simplification of the post-ablation motor patterns in experimental animals is apparently due, therefore, to loss of the nonspiking cells. The conclusion from these experiments is that without proprioceptive feedback from the nonspiking mechano-

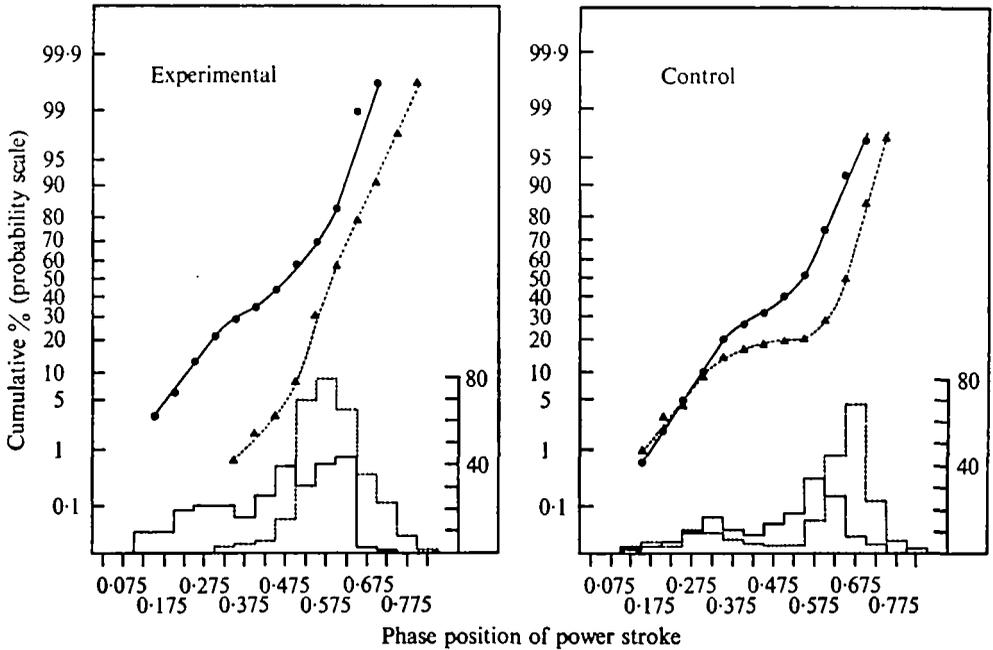


Fig. 6. Comparison of data from an experimental animal (no. 10) and a control animal (no. 5). Frequency histograms along bottom are pre-ablation (solid line) and post-ablation (dashed line) power-stroke phase. The cumulative percentage of each distribution is plotted above on the probability scale. The point of inflexion of each sigmoid curve indicates the relative sizes of the two subpopulations of power-stroke phase making up each bimodal distribution. Mean phase values for pre-ablation and post-ablation 'swimming', estimated graphically (see Harding, 1949 for method), were not significantly different. ●—●, pre-ablation; ▲—▲, post-ablation.

receptors only the 'swimming' motor pattern can occur. Reafference from the non-spiking cells appears to be essential for generation of the power stroke in 'treading water'.

II. Tonic effects of receptor and muscular strand afferents

Mean cycle duration increased slightly following the ablations in experimental and control animals, suggesting that both nonspiking sensory cells and muscular-strand afferents supply tonic excitation to the central nervous system. (For example, pre-ablation and post-ablation $\bar{x} \pm \text{s.d.}$ of cycle duration were, respectively, for an experimental animal 199 ± 87 and 264 ± 56 , and for a control animal 194 ± 88 and 220 ± 99 .) Sham operations indicated that adverse effects of the surgery alone did not contribute to the post-operative increase in cycle duration. Similar decreases in level of motor output following removal of afferent or refferent input are well known (Cohen, 1965).

Since 'treading water' is normally associated with long cycle duration, whereas 'swimming' is not, an increased incidence of 'treading water' might have been expected to accompany a post-ablation increase in cycle duration. Thus, the absence of this motor pattern with concurrent increase in cycle duration in post-ablation electromyograms of experimental animals reinforces the conclusion that ablation of the non-spiking mechanoreceptors resulted in a qualitative change in motor coordination underlying uropod beating.

Table 1. RS cycles without PS bursts

	First		Mid-sequence		Terminal		Total	
	N	%	N	%	N	%	N	%
Expt no. 7								
Pre-ablation	12	0	226	1	18	56	256	5
Post-ablation	6	50	130	8	15	87	151	18
Expt no. 10								
Pre-ablation	21	24	524	1	30	47	596	5
Post-ablation	18	78	516	20	28	64	582	25
Expt no. 11								
Pre-ablation	8	25	124	2	11	73	143	8
Post-ablation	6	33	107	13	11	64	124	19
Expt no. 15								
Pre-ablation	8	12	127	4	11	36	146	7
Post-ablation	6	17	65	5	9	40	80	10
Expt no. 22								
Pre-ablation	12	0	107	3	14	14	133	4
Post-ablation	12	0	156	1	11	21	182	3
Control no. 5								
Pre-ablation	14	29	212	5	21	57	247	11
Post-muscular strand ablation	14	50	217	6	18	61	249	13

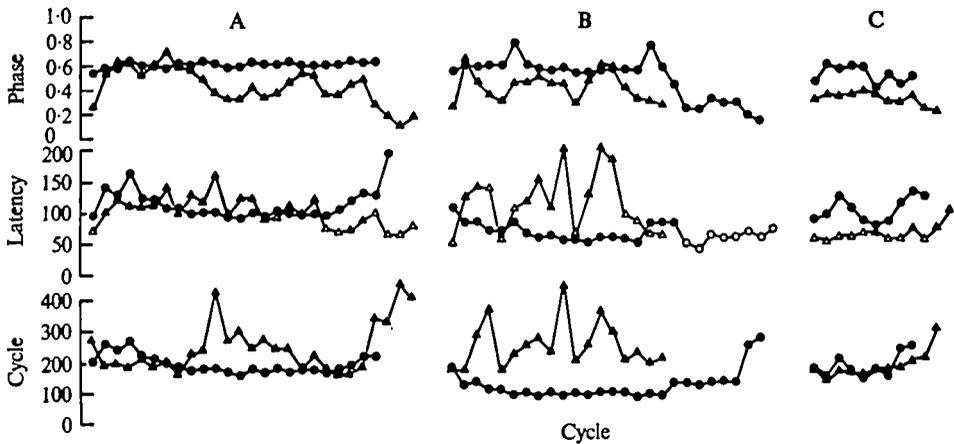


Fig. 7. Cycle duration, PS latency and PS phase for six representative sequences of uropod strokes, grouped in pairs for convenience of comparison of motor patterns. ●—●, sequences in which the 'swimming' motor pattern predominated; but note that in B the crab terminated the sequence by 'treading water', whereas in A and C the mid-cycle phase typical of PSs during 'swimming' continued to the end of the sequence. ▲—▲, sequences in which the 'treading water' motor pattern predominated (C) or alternated with the 'swimming' pattern (A, B). Note that either pattern may typify sequences of cycles of the same duration (C). Open symbols in latency graphs indicate PS bursts which, according to the results shown in Fig. 5, were dependent upon sensory feedback from the nonspiking mechanosensory cells.

III. *Bursting of return-stroke motoneurones*

The second prediction from the hypothesis that power strokes during 'treading water' are the result of reflex activity was that post-ablation electromyograms should include sequences of return-stroke bursts without power-stroke bursts. This possibility was investigated by tabulating return-stroke bursts which were not followed by power-stroke electromyographic activity. Return strokes were classified as (1) first cycle, (2) midsequence, or (3) terminal (Table 1). In intact animals power-stroke electromyograms rarely failed to occur in mid-sequence; the majority of the few cycles in which there were failures were terminal, although first cycle failures were not unusual (Table 1). This tabulation correlates with the observation that power-stroke phase was often less than 0.3 for the first and particularly for the last of a sequence of uropod strokes regardless of which motor pattern was most characteristic of that sequence (Fig. 7). Together these observations implicate reafference from the non-spiking mechanoreceptors in the generation of many first and terminal power strokes.

In three experimental animals there was an increased incidence of power stroke failures, particularly in mid-sequence, following ablation of the receptor strands (Table 1); but in two other experimental animals post-ablation power stroke failures were as infrequent as in the intact animal. The ambiguity of these data most likely reflects the simplistic nature of the original prediction which implied a separation between the mechanisms generating the motor patterns underlying the two behaviours (cf. Discussion).

DISCUSSION

I. *Role of reafference from the nonspiking mechanoreceptors*

Uropod beating in *Emerita* involves organized motor activity in approximately 50 motoneurones associated with each appendage; the principal movement cycle, however, results from activity in only five neurones, three excitors (E) and two peripheral inhibitors (I) which innervate a pair of antagonistic muscles, the return stroke muscle (2E, 1I) and the power-stroke muscle (1E, 1I) (Paul, 1971*b*). The movement cycle during 'swimming' can be described as a basically sinusoidal oscillation such as is performed by the serially homologous swimmerets, for the power stroke and the return stroke begin 180° out of phase with respect to each other (Fig. 8) (Davis, 1969*a*, 1973; Paul, 1971*a*). In a second pattern ('treading water') the power stroke occurs earlier in the return-stroke cycle, at a rather uniform latency following the preceding return stroke (Paul, 1971*a*). This study has shown that the occurrence of power-stroke bursts in 'treading water' requires proprioceptive feedback from the nonspiking mechanoreceptors. Is the reafference actually generating the power stroke or is it merely summing with a subthreshold central excitation already impinging on the power-stroke motoneurone to depolarize it past threshold? Since the 'swimming' pattern generator drives the power-stroke motoneurone at a phase *ca.* 0.55 with respect to the return-stroke cycle, whereas the reflexly-timed power strokes of the 'treading water' pattern occur much earlier, e.g. phase = 0.2 for cycle durations around 300 ms, the reafferent input is closer to being in antiphase than inphase with the central power-stroke cycle (see Fig. 8). Moreover, the central excitation of the power-stroke motoneurone in mid-cycle can be suprathreshold at lower frequencies than normally

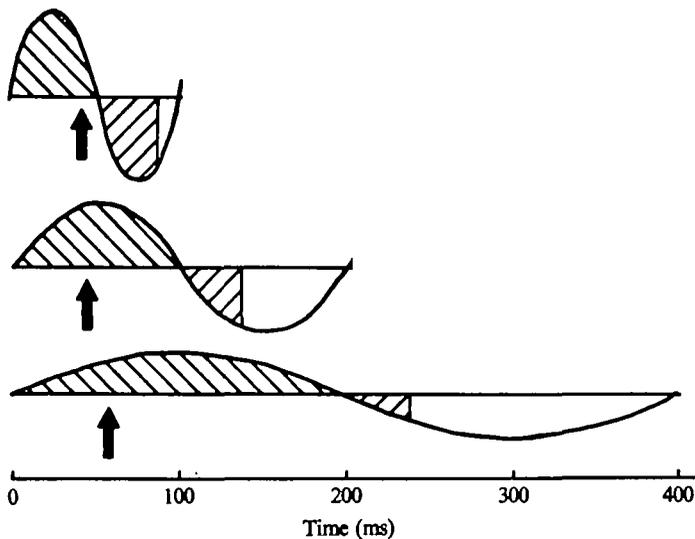


Fig. 8. Diagrammatic summary of temporal relationships of events in uropod beating. Cycle of uropod movement during 'swimming' is represented as sine wave (the product of a hypothetical 'driver' system responsible for generating 'swimming' motor pattern (cf. Fig. 9)). RS part of cycle above and PS part of cycle below the horizontal line. Cross-hatching indicates duration of activity of return-stroke muscle (▨), and of power-stroke muscle (▤) at cycle durations of, from top to bottom, 100, 200 and 400 ms. Arrows mark time of proprioceptive feedback from RS movement mediated by the nonspiking mechanoreceptors. At high output frequencies (top), sensory feedback is approximately concurrent with the initiation of PS by the 'driver'. At intermediate frequencies (middle), sensory feedback occurs in middle of RS (and may or may not generate a PS (for example, cf. Figure 7C)). At low frequencies (bottom), sensory feedback occurs early in RS part of cycle (and regularly generates PS and blocks a (later) centrally driven PS burst to produce the 'treading water' motor pattern).

expressed since 'swimming' continued at lower frequencies of uropod beating than normal in post-ablation experimental animals (Fig. 5; see below). It appears, therefore, that the reafferent input alone is responsible for the generation of power-stroke bursts in the 'treading water' motor pattern. At the same time, this argument does not obviate the possibility that the power-stroke motoneurone may be receiving concurrent central excitatory input since the reafference might also release the power-stroke motoneurone from central inhibition (see Fig. 9). Nevertheless, an arrangement such as this, in which "a feedback loop . . . starts the next cycle of events before some central pacemaker does", is an example of a peripherally cued temporal pattern (Bullock, 1961, p. 49).

In addition to cueing the power stroke in 'treading water', afferent input from the nonspiking cells appears to intercept a central process which otherwise would give rise to a (second) power-stroke burst 180° out of phase with the return-stroke cycle. The indirect evidence for this second function of the reafference is twofold: (a) in post-ablation electromyograms of experimental animals the 'swimming' pattern occurred in longer cycles than it did in the intact crab, that is, in cycles in which normally only 'treading water' would have occurred (Fig. 5). This suggests that the central mechanism for generating the 'swimming' pattern at low frequencies is always present, but normally its expression in long cycles is suppressed by input from

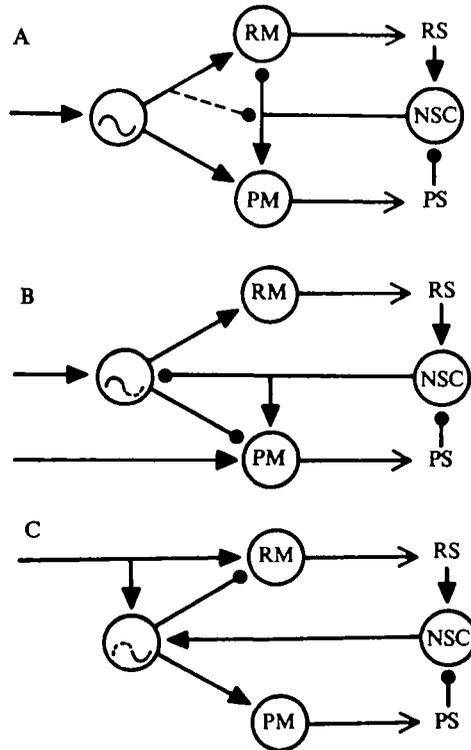


Fig. 9. Models of possible neuronal organization underlying uropod beating. Circles at left of each model represent a driver, which in response to central excitation (arrows from left) generates periodic output during that portion of its cycle which is indicated by the continuous line part of its sine wave (shown within each circle). NSC, nonspiking mechanosensory cells; PM, power-stroke motoneurone; PS, power-stroke movement; RM, return-stroke motoneurone; RS, return-stroke movement; \rightarrow , excitatory connexions; \bullet , inhibitory connexions.

(A) The driver excites RM and PM on opposite phases of its cycle. Sensory feedback from NSC impinges directly on the motoneurons. At high frequencies central and sensory excitation of PM coincide (cf. Fig. 8); 'swimming' at intermediate frequencies of uropod beating entails central suppression of the refference (dashed line) concurrent with the return-stroke phase of the cycle in order to prevent an early PS. At low frequencies the central inhibition of the sensory feedback is too weak to suppress reflexly-generated PSs; but the absence of a later, centrally-driven PS is not accounted for by this model.

(B) The driver simultaneously excites RM and inhibits PM during one half of its cycle. Inhibitory sensory feedback onto the driver mediates both the inhibition of RM and the interruption of the anticipated centrally-generated PM burst during 'treading water'. Direct sensory excitation of PM is required to explain PM reflexes in preparations deafferented except for the receptor nerve in which central excitation is very low (Paul, 1971c). 'Swimming' at intermediate frequencies is accounted for by insensitivity of the driver during the middle of its output phase to resetting by the reafferent input.

(C) One source of central excitation impinges on the driver and directly onto RM. The latter is inhibited concurrently with the periodic excitation of PM. NSC project uniquely to the driver. As in B, the driver must be insensitive to reafferent input in the middle of its output phase to account for 'swimming' at moderate frequencies. The central projections of NSC shown in each model are not obligatory for that particular model (i.e. for example, the NSC projections proposed in B would be equally plausible in A). The brevity typical of PM's bursts, whether they be in response to excitatory input (A, C) or to release from inhibition (B), is attributable to inherent properties of this motoneurone. Release of tension on the receptor strand by PS is shown as (delayed) inhibition of NSC. For simplicity the peripheral inhibitors have not been included in the models; their activity is usually reciprocal with that of their respective excitors (Paul, 1971c). Omitted also are reflexes mediated by sensory setae of the uropod rami which reinforce PS (Paul, 1971c). See text for further discussion.

the nonspiking cells; (b) if reafference from the nonspiking cells were merely giving rise to an early power-stroke burst during 'treading water' without interfering with the central mechanism generating power strokes as well as return strokes ((a), above), one would expect double power-stroke bursts in long cycles, the first reflexly, the second centrally timed (cf. Fig. 8). This has never been observed. The absence of a second power-stroke burst cannot be attributed to refractoriness of the power-stroke excitatory motoneurone following the first burst since the excitor can burst at repetition rates greater than 10 Hz (cycle durations < 100 ms) and the anticipated delay between the two bursts would be longer (e.g. of the order of 200 ms in cycles of 400–500 ms in duration (Fig. 5)). Since reflexly mediated inhibition of the return-stroke muscle accompanies excitation of the power-stroke muscle by the nonspiking mechanoreceptors (Paul, 1971c), the simplest explanation of observations *a* and *b* is that the nonspiking cells provide feedback which resets the central mechanism responsible for 'swimming' (see Fig. 9).

Attempts to determine whether the basic bursting cycle is reset, by relating cycle duration of a reflexly generated power stroke with the preceding cycle duration, were inconclusive. Such an analysis must await more dependable ways of turning on the behaviour than relying on *Emerita's* 'free will'. As yet no behavioural role has been assigned to the nonspiking thoracico-coxal receptors in other crabs (Ripley, Bush & Roberts, 1968; Bush & Roberts, 1971) which are possibly serial homologues of the nonspiking cells in *Emerita*, although they could be the 'stress' receptors implicated in crustacean walking (Evoy & Fournier, 1973).

II. Interaction between central and peripheral sources of power-stroke excitation

The regression lines of power-stroke phase for 'swimming' and for 'treading water' patterns intercept at a cycle duration $\ll 100$ ms (see Fig. 2C). In cycles ≤ 115 ms, when the anticipated difference in phase between centrally- and reflexly-timed power-stroke bursts would be ≤ 0.15 , a tightening of the phase distribution around intermediate values occurred as a direct consequence of shorter latencies than anticipated for 'swimming' (e.g. Fig. 5, pre-ablation). This suggests that at high frequencies of uropod beating reafferent input slightly advances the power-stroke burst. Thus, in cycles ≤ 100 ms the reflexes mediated by the nonspiking mechanoreceptors appear to function as a positive feedback which reinforces the centrally generated motor programme of return-stroke muscle off and power-stroke on in mid-cycle. However, in cycles of longer duration, and as duration becomes longer, central and peripheral drives onto the power-stroke motoneurone are increasingly out of phase with each other (Fig. 8). During 'swimming' at intermediate frequencies of uropod beating central excitation takes precedence over (earlier) reflex excitation of the power stroke. Is the sensory feedback loop from the nonspiking mechanoreceptors actually opened (as in Fig. 9, model A) or formally opened (as in models B and C)? My experiments have not yet provided an answer to this question. But active suppression of reafference by presynaptic inhibition of the sensory terminals of telson mechanoreceptors occurs as an integral part of a centrally programmed motor pattern in crayfish escape swimming, which involves the 'fast' neuromuscular system of the abdomen (Krasne & Bryan, 1973; Kennedy, Calabrese & Wine, 1974). Swimming in *Emerita* could represent a phylogenetic derivative of such typically crustacean

tail-flipping behaviour (Paul, 1971 *a*), since high frequency uropod beating in *Emerita* is accompanied by extension-flexion cycles of the abdomen which share several temporal characteristics with crayfish escape swimming (Schrammeck, 1970), and since command fibres for repetitive motor output to crayfish uropod muscles exist (Kovac, 1974 *a, b*; Larimer & Kennedy, 1969). An alternative prototype is the cyclical extension and flexion movements of the 'slow' abdominal muscles recently demonstrated in crayfish (Kovac, 1974 *a*).

III. Organization of the motor system

Several separate observations suggest that there is a single source of return-stroke bursting cycle which operates during both 'swimming' and 'treading water' and that the motor pattern elaborated depends on whether the reafferent loop involving the nonspiking mechanoreceptors remains closed (for 'treading water') or is opened (for 'swimming'). These include (1) the occurrence of 'swimming' in post-ablation crabs at low frequencies in which normally only 'treading water' is performed (Fig. 5), (2) the ability to express either pattern at the same frequencies (Fig. 7), (3) the transitions from one to the other pattern within one series of uropod strokes (Fig. 7) and (4) the absence of return-stroke bursting alone (without power-stroke bursting) in some post-ablation crabs (Table 1). This is most easily explained by the assumption that if a reflexly-timed power-stroke burst has not occurred, a centrally-generated one will (cf. Fig. 9). (Since power-stroke failures did increase in some post-ablation animals, this explanation presupposes individual differences in relative excitabilities of return-stroke and power-stroke neuronal systems.)

Fig. 9 presents three possible models of neuronal organization underlying uropod beating. In each, a hypothetical neurone or group of neurones, the driver, cyclically generates an output which determines the frequency of uropod strokes either by initiating return-stroke motoneurone (RM) bursts as in A and B or by periodically suppressing RM activity as in C. In A, the driver excites RM on one phase of its cycle and the power-stroke motoneurone (PM) on the other in a manner conceptually analogous to the oscillator neurone associated with crustacean ventilatory rhythm (Mendelson, 1971). In B and C, output is generated during only one half of the driver's cycle; such asymmetrical models could account for the apparent asymmetry of the motor system (i.e. RM, but not PM, has been observed to burst alone). Any of the models could guarantee that uropod beating begin with RM activity. Each of these schemes seems adequate to explain 'swimming' in post-ablation crabs. Normally, however, the return-stroke movement (RS) stretches the receptor strand which depolarizes the nonspiking sensory cells (NSC) and thereby reflexly excites PM and inhibits RM (Paul, 1971 *c*). This proprioceptive reflex constitutes an integral part of the 'treading water' motor system as well as apparently reinforcing centrally-generated power-strokes (PS) at high frequencies of uropod beating. Monosynaptic excitatory and inhibitory connexions with motoneurones as in A would not be unprecedented in arthropods (Burrows, 1975), but neither the occurrence of post-ablation 'swimming' in longer cycles than normal nor single power-stroke bursts during 'treading water' are readily accounted for by this model. On the other hand, pre-motoneuronal sensory projections (models B and C) could explain the following features of the motor system: (1) the nonspiking sensory cells make reciprocal con-

rections to excitatory and inhibitory motoneurons of antagonistic muscles; (2) during 'treading water' the reflexly-timed power-stroke burst is not followed by a centrally-timed one; (3) post-ablation crabs 'swim' in longer cycles than do intact crabs; (4) most if not all motoneurons associated with the uropods are probably subject to sensory feedback from the non spiking cells (Paul, 1971*c*, 1972) although the details of these reflexes remain to be described.

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