

## STEERING REACTIONS AS ADAPTIVE COMPONENTS OF THE TAIL-FLIP IN THE SPINY LOBSTER *JASUS LALANDII*

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### Summary

Steering movements of the abdomen and the terminal appendages, the uropods, of the rock lobster *Jasus lalandii* have been examined during slow postural responses and during tail-flips using a combination of movement and force measurements and by monitoring muscle activity. Gentle mechanical stimulation on one side of the animal elicits a postural steering response of the uropods. The activities of the individual uropod muscles that underlie these movements have been determined.

Progressively intense mechanical stimuli initiate tail-flips, which may incorporate steering responses dependent upon the position of the stimulus. Symmetrical stimuli cause both uropods to open and close symmetrically and only a longitudinally directed force to be produced. However, stimuli delivered to only one side elicit asymmetrical movements of the uropods and rotation of the abdomen to the stimulated side during the preflexion phase of the tail-flip. The pattern of activity in the uropod muscles during this preflexion phase is the same as that in the postural steering response. During flexion itself, the uropods open to their full extent while the abdomen rotates further to the stimulated side. As a result of these movements, appropriate steering forces are produced to take the animal away from the point of stimulation. During re-extension, the uropods close and the abdomen re-extends.

These results are discussed in terms of the relationship between postural reactions and the preflexion phase of the tail-flip, the relative contribution of the different abdominal motor systems to tail-flip steering and the occurrence of steering in different forms of the tail-flip.

### Introduction

Studies of decapod crustaceans under natural conditions demonstrate a great

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variability in their locomotor behaviour (Herrnkind, 1983). Lobsters and crayfish are essentially slow-walking animals, but when threatened by predators or noxious stimuli they can perform escape swimming, comprising a series of rapid flexions and extensions of the abdomen (tail-flips).

The stereotyped movements of the abdomen during tail-flip swimming have been extensively studied at the neuronal level in crayfish (Kramer and Krasne, 1984; Krasne and Wine, 1988; Wine, 1984; Wine and Krasne, 1982). Two pairs of giant axons in the ventral nerve cord, the medial giants (MGs) and lateral giants (LGs), mediate short-latency rapid flexions of the abdomen. Stimuli to the rostrum excite the medial giants, producing a tail-flip with a flat backward trajectory, whereas stimuli to the abdomen excite the lateral giants, producing a tail-flip that pitches the animal forward. All other tail-flips in a swimming sequence do not involve the giant fibres, the so-called non-giant (NG) tail-flips. Moreover, the initial tail-flips of a sequence can also be of an NG type, depending upon the stimulus.

Although we know much about tail-flip production, we know little about how entire swimming sequences are maintained and controlled. Steering has been observed in crayfish tail-flips, with animals turning away from the point of stimulation during a swimming sequence (Cooke and MacMillan, 1985; Reichert and Wine, 1983). The Norway lobster *Nephrops norvegicus* can swim over considerable distances (up to 12 m) in single swimming sequences (Newland *et al.* 1988; Newland and Chapman, 1989). Cycle-by-cycle adjustments occur in body attitude during these sequences of tail-flips, suggesting that control is being exerted over equilibrium (Newland and Neil, 1990*b*). Moreover, an element of steering is often involved in these tail-flips: lobsters escape away from a stimulus delivered to one side (Newland and Neil, 1987*b*), and can apply course correction during a swimming sequence (Newland *et al.* 1988). Since the Norway lobster is one of only a few species that is caught using fishing trawl nets rather than lobster pots, these findings are relevant to the development of fishing techniques for this animal.

For effective steering forces to be produced during limb-based locomotion, precise movements of the appendages must be incorporated at the correct phases of the power and recovery strokes of the propulsive cycle. For example, during insect flight, righting and steering responses are produced by a variety of mechanisms, including rudder-like movements of the abdomen and legs (Arbas, 1986; Camhi, 1970; Camhi and Hinkle, 1974) and changes in the wingstrokes (Möhl and Zarnach, 1977; Thüning, 1986; Zarnach and Möhl, 1977). Almost nothing is known about how steering occurs during swimming in decapods, and what appendages and mechanisms are involved.

Part of the problem in examining such behaviour in decapods lies in the extremely rapid movements of the abdomen during tail-flips. The power stroke of the tail-flip is completed within 50–100 ms in both crayfish (Webb, 1979) and lobsters (Newland and Neil, 1990*a*). The movements of the terminal appendages

are difficult to resolve, even when ciné film rates up to 500 frames  $s^{-1}$  are employed (Cooke and MacMillan 1985).

In this study we have attempted to overcome this problem by using a combination of monitoring techniques: myographic recording from the uropod muscles, simultaneous electronic detection of the unimpeded movements of a number of appendages and recording of the resultant steering forces produced during the tail-flip. The rock lobster is particularly appropriate for this study because of its large size and its sensitivity to a range of mechanosensory stimuli (Schöne *et al.* 1976, 1983). The results we have obtained identify significant contributions by movements of the uropods and rotation of the abdomen to the development of steering forces.

### Materials and methods

Experiments were performed on male specimens of the South African spiny lobster *Jasus lalandii* (H. Milne-Edwards) weighing around 500 g. Animals were maintained in a filtered running seawater system and were fed regularly with *Mytilus*. During the experiments the eyes of the lobsters were covered with heat-shrink tubing to eliminate visual input. Under these conditions mechanical stimulation of the legs, produced by elevating or depressing the legs of either or both sides, was used to elicit tail-flips.

All experiments were conducted in a glass-walled seawater aquarium measuring 90 cm × 60 cm × 50 cm. Forces produced in the longitudinal and transverse body planes during escape movements were monitored using a strain gauge assembly (Fig. 1). The assembly consisted of two Perspex plates fixed at right angles, upon which copper–nickel foil strain gauges (type 308–102, RS Ltd) were mounted in pairs. The whole assembly was coated in silicone rubber for waterproofing. Each pair of gauges was connected in a half-bridge arrangement to an amplifier (SGA 700, CIL Ltd) which had linear characteristics up to 20 kHz. In tests with a vibrator driven by a precision oscillator (Derritron Ltd), the frequency response of the gauges was found to be linear up to 80 Hz. The animal was attached to the gauge system through a plate glued to its dorsal carapace, and was then submerged in the aquarium. Between tests, a platform was raised so that the animal was able to stand. Control tests demonstrated that reflected water movements did not contaminate the strain gauge measurements during tail-flips. This was due both to the large size of the tank and to the stiffness of the gauge assemblies.

Movements of the different body parts were monitored using a multichannel transducer system (Crüse and Müller, 1984). A high-frequency (40 kHz, 0.5 V) signal was passed through the experimental tank between two stainless-steel plates placed to monitor either longitudinal components of the movements along the long axis of the animal ( $x-x'$  in Fig. 1) or lateral components of the movements to each side of the animal ( $y-y'$  in Fig. 1). Teflon-coated silver wires (50  $\mu$ m diameter), passed through a flame to produce a ball of silver, were attached to the

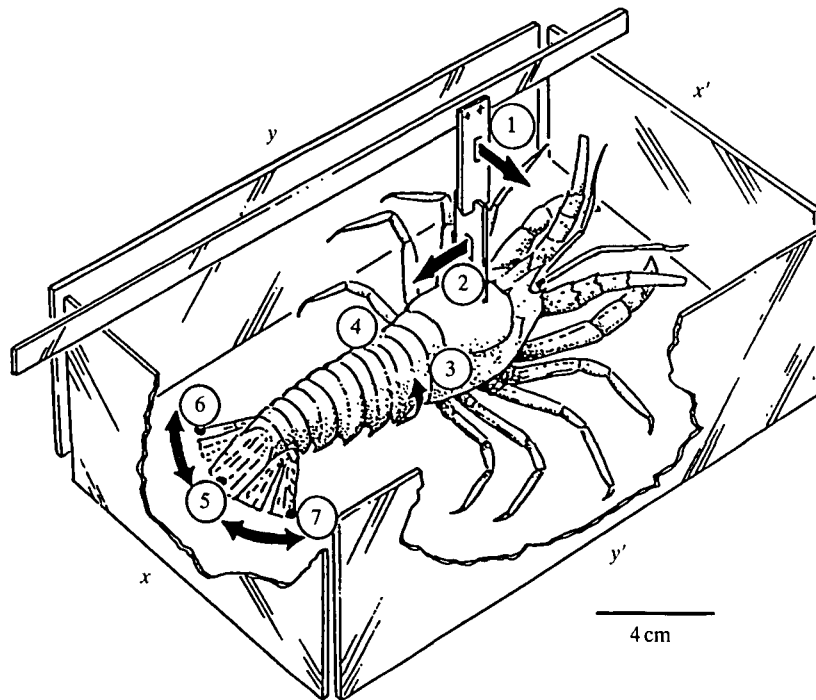


Fig. 1. Movement and force transducers. Swimming forces were measured in the transverse (1) and longitudinal (2) planes using foil strain gauges. The animal and strain gauge assembly was fixed to a rod above the aquarium between two electrodes generating an electric field across the aquarium. The plates were positioned either in the  $x-x'$  plane (2) to record longitudinal movements, or in  $y-y'$  plane (1) to record lateral movements. Electrodes glued on the telson (5) and the extremities of the uropods (6 and 7) allowed the monitoring of the movement of these appendages relative to the telson, while electrodes glued on the ventral thorax (3) and abdomen (4) gave a measure of the relative movement of the abdomen.

uropods, telson, ventral body wall and thorax (Fig. 1). They received signals that were proportional to their positions within the electric field, and detector circuits converted these signals to analogue voltages. To provide a measure of the movement of body parts relative to each other, rather than to a spatial reference, the appropriate outputs were subtracted using high-precision summing circuits.

Electromyographic and neurographic recordings were made using pairs of Teflon-coated silver wire electrodes ( $50\ \mu\text{m}$  diameter) inserted through small holes drilled in the cuticle and fixed in place with cyanoacrylate glue. The nerve and muscle activities obtained were amplified, displayed on a storage oscilloscope and stored on an eight-channel FM tape recorder (Euromag). Permanent records were obtained by replaying the signals through a Gould electrostatic (ES1000) pen recorder.

## Results

### *Musculature and movements*

Unlike the uropods of crayfish and nephropid lobsters, the muscles of the uropod of spiny lobsters insert onto restricted regions of calcified cuticle at the base of the appendages (Fig. 2A). Paterson (1968) provided a detailed morphological description of the skeleton and musculature of *Jasus lalandii*, including that of the uropods and telson. Our anatomical observations were concerned only with the intrinsic uropod muscles involved in opening and closing the exopodite and the extrinsic muscles that promote and remote the protopodite (Fig. 2B). They agree in general with the description made by Paterson (1968), although she failed to

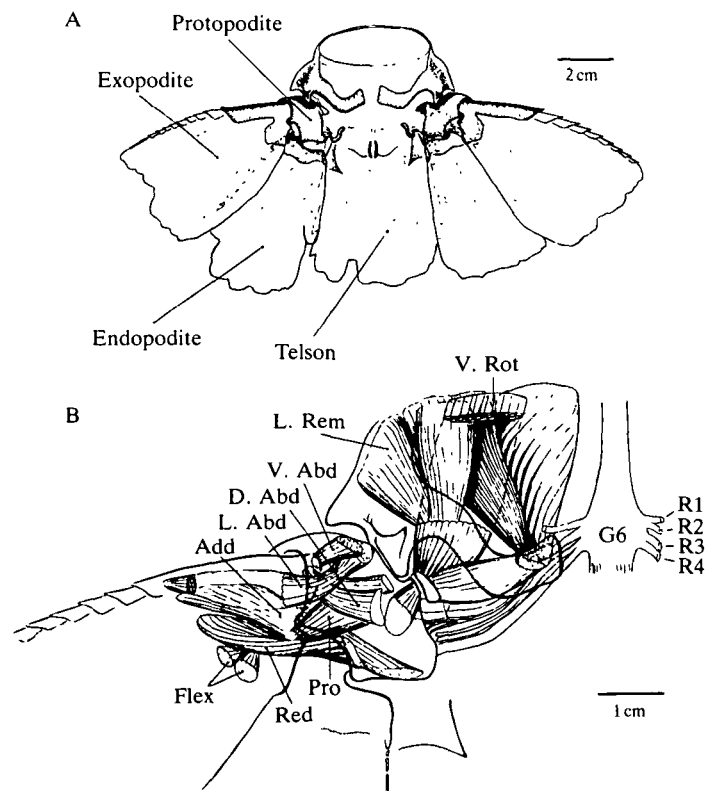


Fig. 2. Organisation of the uropod musculature of *Jasus lalandii*. (A) Ventral view of the uropods. Stippled regions indicate areas of calcified exoskeleton to which the muscles are restricted. (B) Detailed ventral view of the right uropod showing the main muscles involved in protopodite and exopodite movements. V. Rot, ventral rotator; L. Rem, lateral remotor; V. Abd, ventral abductor; D. Abd, dorsal abductor; L. Abd, lateral abductor; Add, adductor; Flex, exopodite flexor muscle; Red, reductor; Pro, producter; G6, sixth abdominal ganglion; R1, R2, R3, R4, nerve roots. The ventral insertions of muscle bundles are indicated by stippled areas.

describe both a second joint on the exopodite (called here the distal joint), about which flexion of the blade can occur, and the exopodite flexor muscle, which lies entirely within the exopodite. Some of the fibres of this muscle originate on the cuticular sclerite proximal to the distal articulation, but other fibres lie entirely beyond the distal joint. Thus, by its action it has the potential to influence movement about the distal joint.

The movements of the abdomen–protopodite joint are complex since it has no condyle. Among the extrinsic muscles responsible for the movement of the protopodite are the ventral rotator, which rotates and protracts the protopodite, and the lateral remotor, which extends it (Fig. 2B and Fig. 3A). These muscles act mainly antagonistically and in both dorso-ventral and medio-lateral planes (Fig. 3A).

The protopodite–exopodite joint has a single condyle on the dorsal surface of the appendage (Fig. 3B,C). The muscles of the exopodite form three distinct categories according to their role in exopodite movements (Figs 2B, 3B,C). The three abductor muscles, which insert in the exopodite ventrally, dorsally and laterally, open the exopodite in the horizontal plane, while the adductor muscle closes the exopodite. The productor muscle, which inserts ventrally on the medial edge of the exopodite, and the reductor muscle, which inserts dorsally on the lateral edge of the exopodite, have three different actions due to their insertions (Fig. 3C). First, an extension of the exopodite brought about by the contraction of the productor muscle alone. Second, a flexion of the exopodite brought about by the contraction of the reductor muscle alone, and third, a rotation in the perpendicular plane (about the condyle) brought about by their combined actions. Since the origins of the productor and reductor muscles lie medially in the protopodite, their contractions also result in a closing of the exopodite, which may be counteracted by the activity of the abductor muscles.

#### *Postural steering movements of the uropods*

In contacts between conspecifics held in aquaria, the uropods of *Jasus* are moved in a number of ways. However, it is a consistent observation that, when touched by another animal on one side of the body, the uropod on the stimulated side opens while the contralateral uropod closes. These steering responses were examined in detail by recording from the muscles that move the uropods.

Stimulation of the legs on one side alone elicited an opening of the ipsilateral uropod and a closing of the contralateral one. On the stimulated side, the lateral remotor muscle was excited while the ventral rotator muscle remained silent and, as a result, this uropod opened horizontally (Fig. 4A). The adductor and abductor muscles were also involved in the response (Fig. 4B) showing a strict antagonism, with the three abductors on the stimulated side excited while the adductor was silent. A reversed response was elicited in the uropod contralateral to the stimulus, with the lateral remotor and abductors silent and the ventral rotator and adductor excited. Thus, the contralateral uropod partially closed and rotated.

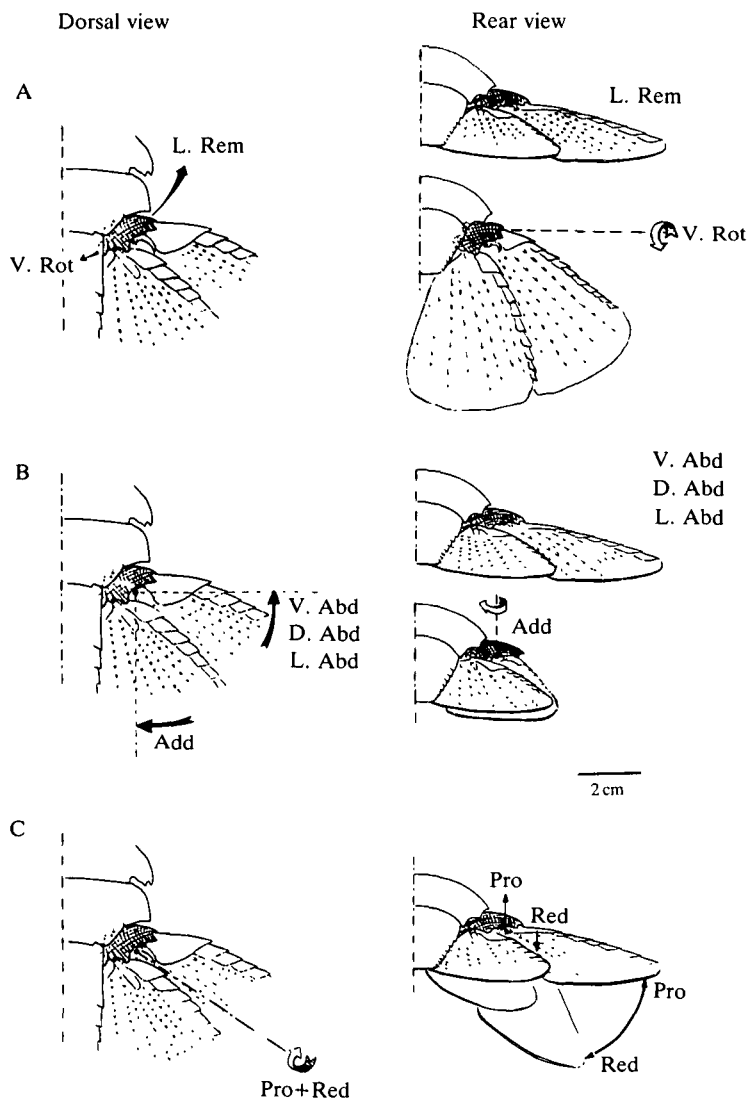


Fig. 3. The contributions of different muscle groups to uropod movements. (A) Contribution of the lateral remotor (L. Rem) and the ventral rotator (V. Rot) to the movements of the protopodite. On the right, the two diagrams represent the result of the contraction of the indicated muscles. (B) Contributions of the ventral, dorsal and lateral abductor (V. Abd, D. Abd and L. Abd) and adductor (Add) muscles to the opening and closing of the exopodite. (C) Contribution of the productor (Pro) and reductor (Red) muscles to the rotation of the exopodite. The insertions of these muscles as well as the absence of a ventral condyle are responsible for complex movements. Their simultaneous contraction produces a rotation (represented on the left part of C). During independent contractions, the reductor moves the exopodite forward in a flexion, while the productor extends it.

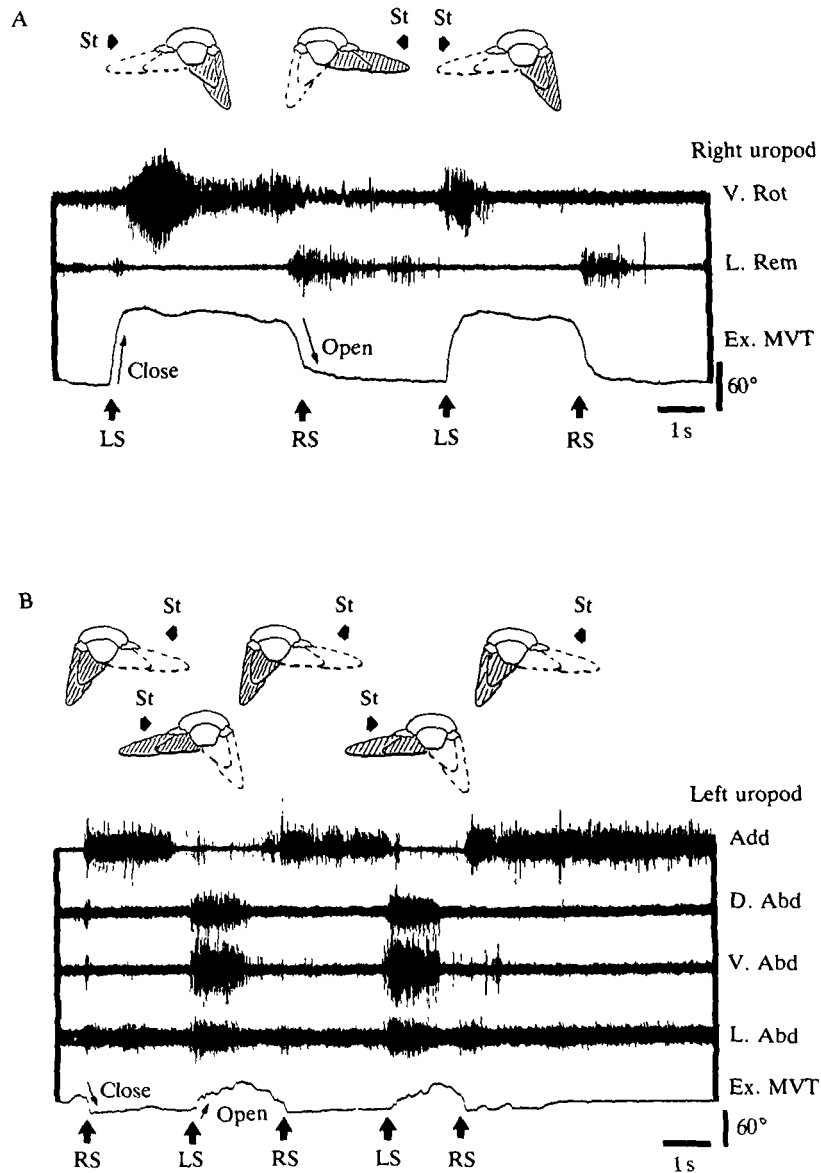


Fig. 4. Responses of uropod muscles during postural steering movements. (A) Recordings of the activity in the right side ventral rotator (V. Rot) and lateral remotor (L. Rem) during gentle stimulation (St) of the left and right sides (LS and RS, respectively). The movement of the exopodite is shown on the lower trace (Ex. MVT). These two muscles are reciprocally activated during stimulation of either side. Hatched areas in the insets indicate the uropod from which the recordings were obtained. (B) Responses of the adductor (Add) and abductor muscles (D. Abd, V. Abd, L. Abd) and exopodite movement (Ex. MVT) of the left uropod during gentle tactile stimulation (St) to the right and left legs. The three abductor muscles are co-activated during ipsilateral stimulation while the adductor is silent. The opposite pattern is elicited in response to contralateral stimulation.



These firing relationships were consistently found in all animals in which the abdomen was held extended.

#### *Uropod movements during tail-flips*

With an animal mounted on the force transducer assembly, a mechanical stimulus was delivered to the legs with increasing intensity until a tail-flip was induced. From the graded nature of the stimulus, and by analogy with the effect of similar stimuli in the crayfish (Wine and Krasne, 1982) and other lobsters (Newland and Neil, 1990*a,b*), it is most probable that the escape responses elicited were of the non-giant type, i.e. not involving the activation of medial giant fibres.

The non-giant nature of the tail-flips was confirmed in a number of tests by recording from electrodes implanted in the abdomen and in contact with the abdominal connectives (Krasne and Glanzman, 1986; Newland and Neil, 1990*a*). These electrodes recorded not only the activity in the connectives but also the activity of the fast flexor muscles when the animal produced a tail-flip. In control tests involving abrupt stimuli to the rostrum, which are known to elicit giant-fibre-mediated flips (Wine and Krasne, 1972), large-amplitude neuronal activity was recorded at the expected time (approximately 5 ms) before the activation of the fast flexor muscles. However, with the progressively applied stimuli described above, on no occasion was giant-fibre activity recorded prior to muscle activity.

The propulsive force produced by the animal in the longitudinal plane provided a convenient monitor of the time of occurrence of the tail-flip. The relationship between this force and the electrical activity in the fast flexor muscles of the third abdominal segment is shown in Fig. 5A. The propulsive thrust of the tail-flip was detectable 20–25 ms after the initiation of flexor activity and reached a peak value some 40–50 ms later, corresponding to the point just prior to mid-flexion (Fig. 5B). At this time, electrical activity in the muscles had subsided, although the flexion movement of the abdomen continued for a further 130–140 ms, during which time the longitudinal force decreased rapidly. The complete flexion phase lasted about 220 ms and was followed by abdominal extension. The entire escape response thus occupied approximately 550 ms in this animal.

The relationships between the rotational movements of the abdomen and the lateral movements of the uropods during different phases of the escape response were determined with the aid of independent movement transducers, while the effect of their movements on the lateral forces produced during the tail-flip was monitored by a lateral force transducer.

Tail-flips induced by symmetrical stimuli to the legs were virtually symmetrical in their output characteristics (Fig. 5C). This was expressed in the movement of the abdomen itself (a very small rotation relative to the thorax), in the movements of the paired uropods (Fig. 5C) and in the mechanical forces produced during the tail-flip (only a small lateral component being registered).

In such tail-flips, three phases of stereotyped uropod movement could be recognised. First, a preflexion phase (Fig. 5B) (PF in Fig. 5C) in which the exopodites opened symmetrically. This phase was also characterised by a tonic

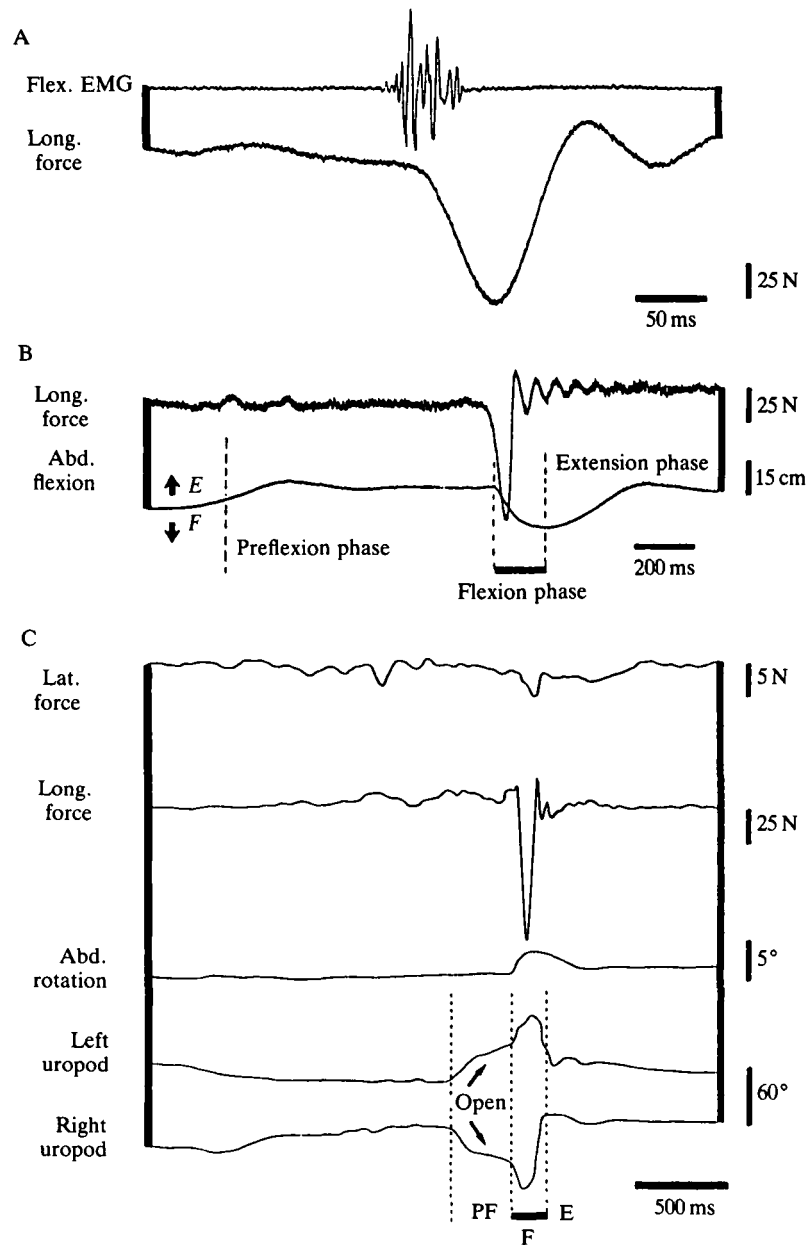


Fig. 5. Tail-flips elicited in response to a symmetrical stimulus. (A) Simultaneous recording of the fast flexor activity in the third abdominal segment (Flex) and the resulting longitudinal force (Long. force). (B) Simultaneous recording of the longitudinal force and the extension (*E*) and flexion (*F*) movements of the abdomen (Abd. flexion). (C) Simultaneous recording of lateral force (Lat. force), longitudinal force, abdominal rotation (Abd. rotation) and uropod movements during the reflexion phase (PF), the flexion phase (F) and the extension phase (E). Symmetrical stimuli result in almost symmetrical movements of the exopodites of both sides, with little laterally directed swimming force produced.

extension of the abdomen (as previously reported in the crayfish: Page and Jones, 1982), an internal rotation and extension of the antennae, a depression of the legs and an opening of the swimmerets (Cattaert *et al.* 1988). Second, a flexion phase (F in Fig. 5C), following the preflexion phase with a variable delay of up to several seconds, which was characterised by a phasic contraction of the abdominal flexor muscles and was accompanied by rapid movements of the exopodites to their fully opened positions. Third, an extension phase in which the abdomen was re-extended while the uropods were held in a closed position (Fig. 5C).

#### *Dynamic steering movements of the uropods during tail-flips*

Steering upon initiation of the swimming sequence was readily elicited under experimental conditions by applying asymmetrical stimuli to an animal, i.e. stimulating one side only.

If the stimulus used to initiate the tail-flip was asymmetrical, then the preflexion phase of the response was also asymmetrical and involved not only abdominal extension but also a rotation of the abdomen about the thoraco-abdominal joint by 20–50°, such that the ventral surface of the abdomen was presented to the stimulated side. The responses of the uropods were also asymmetrical, so that the exopodite ipsilateral to the stimulated legs opened and the contralateral exopodite closed (Fig. 6A,B). A rotation of the contralateral uropod also occurred (as it did in the postural responses), but in a plane that was not detected by the movement-monitoring system.

In those responses that did not result in a tail-flip, the posture adopted during the preflexion phase persisted for up to 10 s after termination of a stimulus. If a tail-flip ensued, then during the flexion phase the ipsilateral exopodite maintained an open position, the contralateral exopodite also opened briefly (Fig. 6A,B) and the abdomen rotated further in the direction of the stimulated side (Fig. 6A,B). During the extension phase, the abdomen returned to a symmetrical position and the uropod exopodites closed.

During such tail-flips, considerable forces were produced directed to the stimulated side. For example, a stimulus to the right side elicited a tail-flip in which the lateral force was directed to the right (Fig. 6A). Thus, if the animal had been free to move it would have escaped to the left, away from the stimulus. Conversely, a stimulus to the left elicited a tail-flip in which the lateral force was directed to the left. The lateral force record provided a measure of the effectiveness of these asymmetrical corrective movements. A lateral force of up to 4 N, representing 5 % of the longitudinal force, was directed to the stimulated side. Such forces, when free to act in the swimming animal, could generate significant steering effects.

Since a number of different body parts were observed to alter their disposition according to the laterality of the initiating stimulus, a series of selective blocking experiments was performed to determine the contributions made by each of these systems to the lateral force.

Abdominal rotation was prevented by fixing an aluminium bar between the

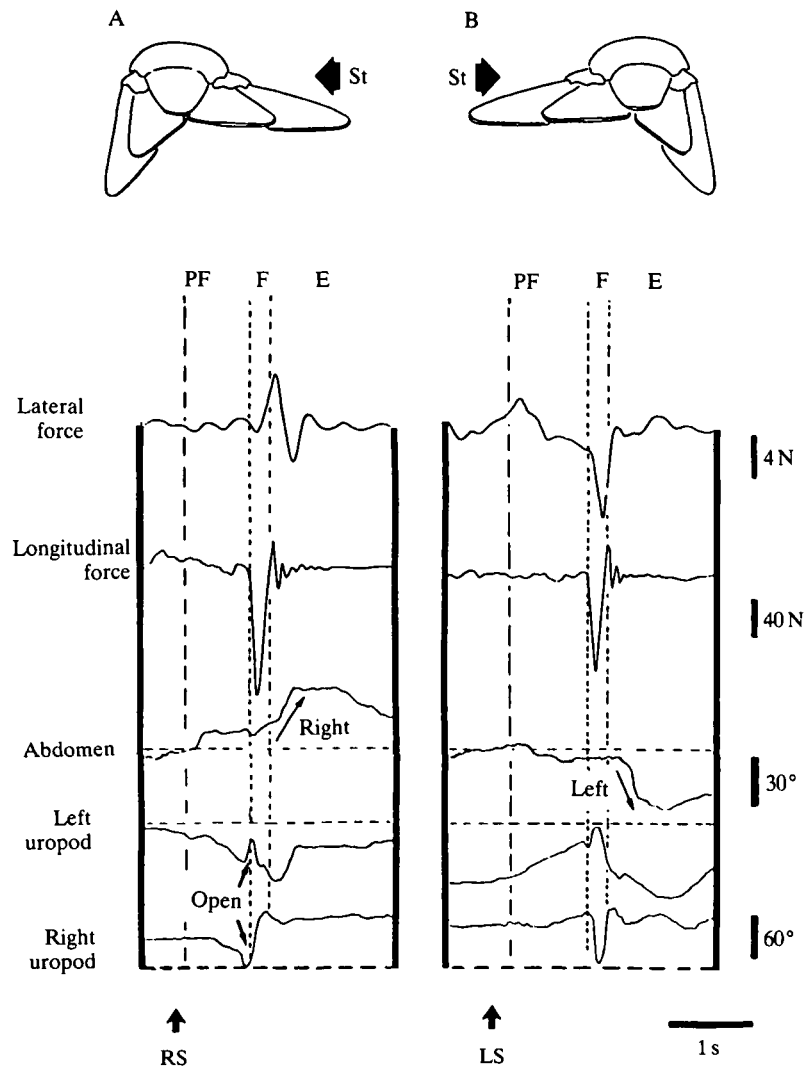


Fig. 6. Tail-flips in response to asymmetrical stimuli. Steering responses elicited by mechanical stimulation of the right legs (A) and the left legs (B). Stimuli to one side only result in tail-flips in which the abdomen rotates to the stimulated side, the uropods both open fully from their preflexion positions and a lateral force is produced directed towards the stimulated side. The drawings above the records represent posterior views of the uropods in the preflexion phases for each situation. PF, preflexion; F, flexion phase; E, extension phase.

thorax and the first abdominal segment with the abdomen in the normal extended position. Stimuli were again delivered to the legs of the animal. Asymmetrical stimuli elicited the same uropod movement as in the normal animal, but the magnitude of the lateral force was reduced to approximately 1.25 % of the longitudinal force (Fig. 7B) compared to 5 % in the control animal (Fig. 7A). This

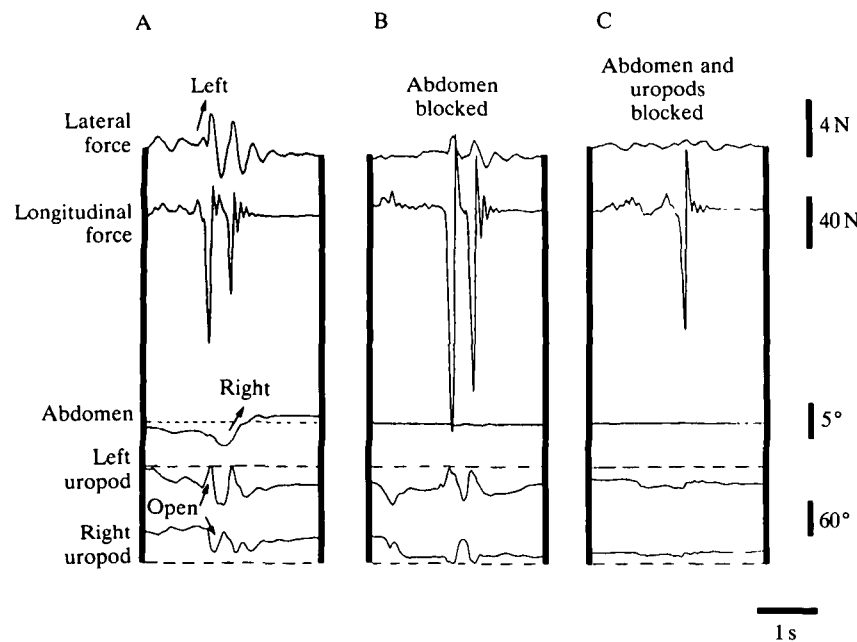


Fig. 7. Estimation of the dynamic participation of the uropods and abdomen in steering reactions. (A) Lateral force produced when all appendages are free to move. (B) Lateral force produced when the first abdominal segment is fixed to the thorax and (C) when the first abdominal segment and the uropods are fixed (same parameters as in Fig. 5C). Responses were elicited by stimuli to the right side. Comparisons of lateral to longitudinal forces indicate that approximately 70 % of the lateral force is produced as a result of abdominal rotation, with the remainder produced mainly by the uropods.

degree of uropod asymmetry represents a contribution of approximately 25 % towards the steering response, the remainder (70 %) being from abdominal rotation. By fixing the uropods of both sides to the telson in a fully closed position, it was possible to eliminate the lateral forces almost entirely (Fig. 7C). The small remaining component, which was often masked by a natural oscillation of the gauge introduced by the mechanical stimulus, was probably produced by asymmetrical movements of the swimmerets (Cattaert *et al.* 1988).

#### *Muscular control of the uropods during tail-flips*

The joint-movement monitoring system provides a detailed picture of the movements of the abdomen and appendages in a single plane during the tail-flip. However, this information is, in itself, insufficient to allow us to understand the way in which the uropods can produce a steering force when they open symmetrically during a steering tail-flip. To resolve this problem it was necessary to make further recordings from the muscles involved in moving the uropods.

During the preflexion phase of tail-flips induced by asymmetrical leg stimu-

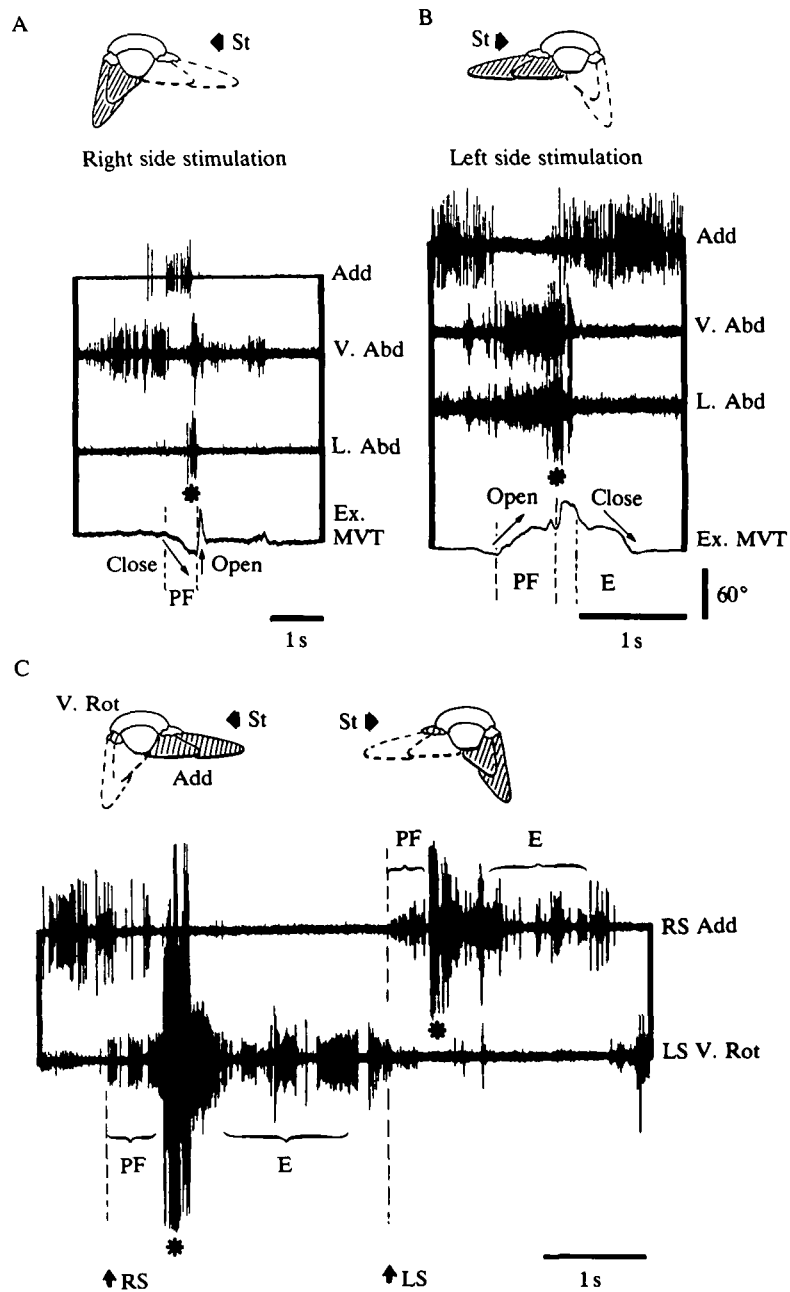


Fig. 8

lation, the abductor muscles on the stimulated side were excited while the adductor muscle was silent (Fig. 8B). At the same time, the adductor muscle of the contralateral side was also excited (Fig. 8A). These muscle responses are similar to those elicited by weaker stimulation (c.f. Fig. 4B). A key observation was that

Fig. 8. Responses of the uropod muscles during asymmetrical tail-flips. Tail-flips induced by strong mechanical stimulation (St) to the right (A) and the left (B) legs. Myograms and exopodite movement (Ex. MVT) have been monitored for the left uropod as indicated by the hatched areas in the insets. The star indicates the flexion phase of the tail-flip. Abbreviations are as in Fig. 2B. (C) Responses of the right side adductor (Add) and left side ventral rotator (V. Rot) muscles during tail-flips initiated by stimuli to the left (LS) and right (RS) sides. During preflexion (PF), the uropod opens on the side ipsilateral to the stimulus and closes and rotates on the contralateral side. During flexion, the abductors are active to open the uropods irrespective of the side stimulated. The adductor muscle is responsible for closing the uropods during the extension phase (E).

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the ventral rotator was also activated differentially during the preflexion phase (Fig. 8C), as was found during postural responses (Fig. 4A). The ventral rotator on the side contralateral to the stimulus was excited, while that on the side ipsilateral to the stimulus was silent.

During the flexion phase of the tail-flip, the posture adopted in the preflexion phase was modified, with both uropods moving rapidly to their fully open positions. Accompanying this opening, there was a phasic activation of the abductor muscles, irrespective of the side stimulated (stars in Fig. 8A,B) and irrespective of their level of activity during the preflexion phase. Moreover, despite this symmetrical opening, the ventral rotator activity on the contralateral side persisted at a high level (Fig. 8C).

During the extension phase, the rapid closing of the uropod was brought about by the action of the ventral rotator muscle about the proximal joint (Fig. 8C) and by the activation of the reductor (Fig. 9A) and adductor (Fig. 8B) muscles about the distal protopodite–exopodite joint. During a swimming sequence in which several tail-flips were produced, alternating bursts of activity in the dorsal abductor muscle and reductor muscle occurred during abdominal flexion and extension, respectively (Fig. 9A). The adductor muscle, therefore, appears to be involved in slow closing movements during postural movements (Fig. 4B), during the preflexion phase on the side contralateral to the stimulus (Fig. 8A) and during the extension phase of the tail-flip (Fig. 8B,C).

The productor muscle, however, was never active during postural and preflexion movements, but was strongly activated during the later part of the flexion phase of the tail-flip, whether this was asymmetrical (Fig. 9B) or symmetrical. However, the exopodite flexor muscle, which displayed a varying level of tonic activity at all times in the absence of specific stimulation, was differentially activated during the preflexion phase of asymmetrical tail-flips (Fig. 9B). In the exopodite flexor muscle ipsilateral to the stimulus, existing tonic activity was suppressed throughout both the preflexion and flexion phases, but resumed during the extension phase. In contrast, the activity of the exopodite flexor contralateral to the stimulus was increased during the preflexion phase, but was suppressed during flexion itself.

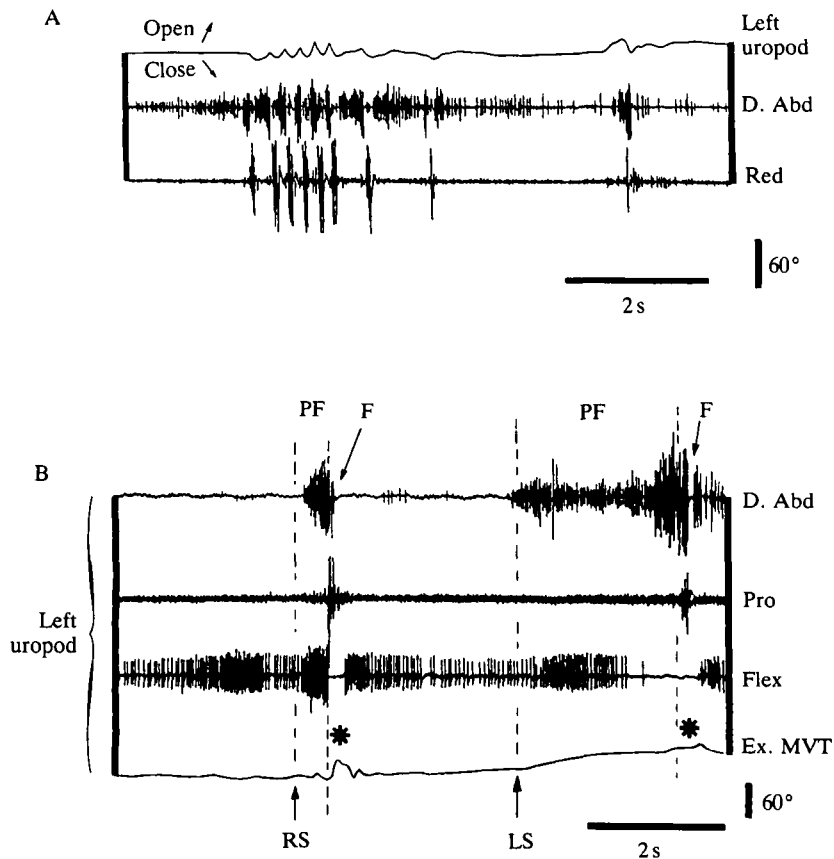


Fig. 9. Responses of the uropod muscles during tail-flips. (A) A series of tail-flips produced in response to a symmetrical stimulus to both sides. The reductor (Red) muscle is involved in closing the uropods during the extension phase. An opening of the uropod blade is brought about by the action of the abductor muscles (D. Abd). (B) The producter muscle (Pro) is only active during the flexion phase (F), whereas the exopodite flexor (Flex) is always silent during flexion, irrespective of its tonic level of activity during the preflexion phase (PF). Responses initiated by stimuli to the right (RS) and to the left (LS) sides are shown. Same abbreviations as in Fig. 2B. The star indicates the flexion phase of the tail-flip. In B an upward deflection of the Ex. MVT trace represents an opening of the left uropod.

### Discussion

The results of this study demonstrate that mechanical stimuli to the legs not only produce postural steering movements of the uropods but, when applied progressively to a sufficient intensity, are also capable of both initiating NG tail-flips and, by their site of application, inducing associated steering forces. Unlike previous studies on crayfish and lobsters, we have been able to identify the mechanisms that



underlie this steering behaviour and course control during tail-flip escape swimming.

#### *Postural steering responses of the uropods*

A gentle stimulation of the legs on one side elicits a steering response in which the ipsilateral uropod opens and the contralateral uropod closes, protracts and rotates. These uropod movements on their own are unlikely to produce a significant propulsive force to move the animal away from the source of stimulation. However, when expressed in conjunction with locomotion, water flow over uropods disposed in this way will induce appropriate hydrodynamic steering forces. Our results, therefore, suggest that uropod asymmetries are part of a larger, hierarchically arranged motor programme and that the uropod posture has a functional meaning only within a whole assembly of motor acts.

Similar relationships exist between different components of motor behaviour in the avoidance reflexes of crayfish to tactile stimuli (Nagayama *et al.* 1986) and of lobsters to acoustic stimuli (Goodall *et al.* 1991). They also occur extensively in equilibrium reflexes, where they involve both the postural and rhythmic motor systems of the abdomen and thorax (Neil and Miyan, 1986; Newland and Neil, 1987a; Knox and Neil, 1991; Neil, 1991). Another well-studied example in crayfish is the platform withdrawal response, in which removal of leg contact with the substratum induces both abdominal extension and associated movements of the uropods (Larimer and Eggleston, 1971; Jellies and Larimer, 1986). In this case, the extension of the abdomen seems to be a pre-requisite for any postural movements of the uropods, a relationship that has been termed 'postural facilitation' (Takahata *et al.* 1981). It is mediated by non-spiking interneurons postsynaptic to abdominal interneurons and presynaptic to uropod motor neurones (Takahata and Hisada, 1985, 1986).

The association of motor patterns can show interesting variations, as between different crayfish species in terms of the direction of the uropod righting reflex (Yoshino *et al.* 1982) or with age in the case of the crayfish tactile avoidance reflex (Nagayama *et al.* 1986). In small crayfish the uropod reflex is accompanied by forward locomotion which moves the animal away from the point of stimulation, whereas in larger crayfish defence is preferred to escape and animals simply turn towards the point of stimulation while maintaining an asymmetrical uropod posture.

#### *Prelexion and the steering of the tail-flip*

The steering response in the *Jasus* tail-flip also involves the coordination of a number of motor systems, but in this case there is a more critical need for them to be precisely timed in order to produce an effective output during the short time course of the tail-flip.

A symmetrical stimulus to the legs of both sides elicits a tail-flip in which there is virtually no abdominal rotation, the uropods and swimmerets open and close symmetrically and laterally directed forces are virtually absent. The swimming

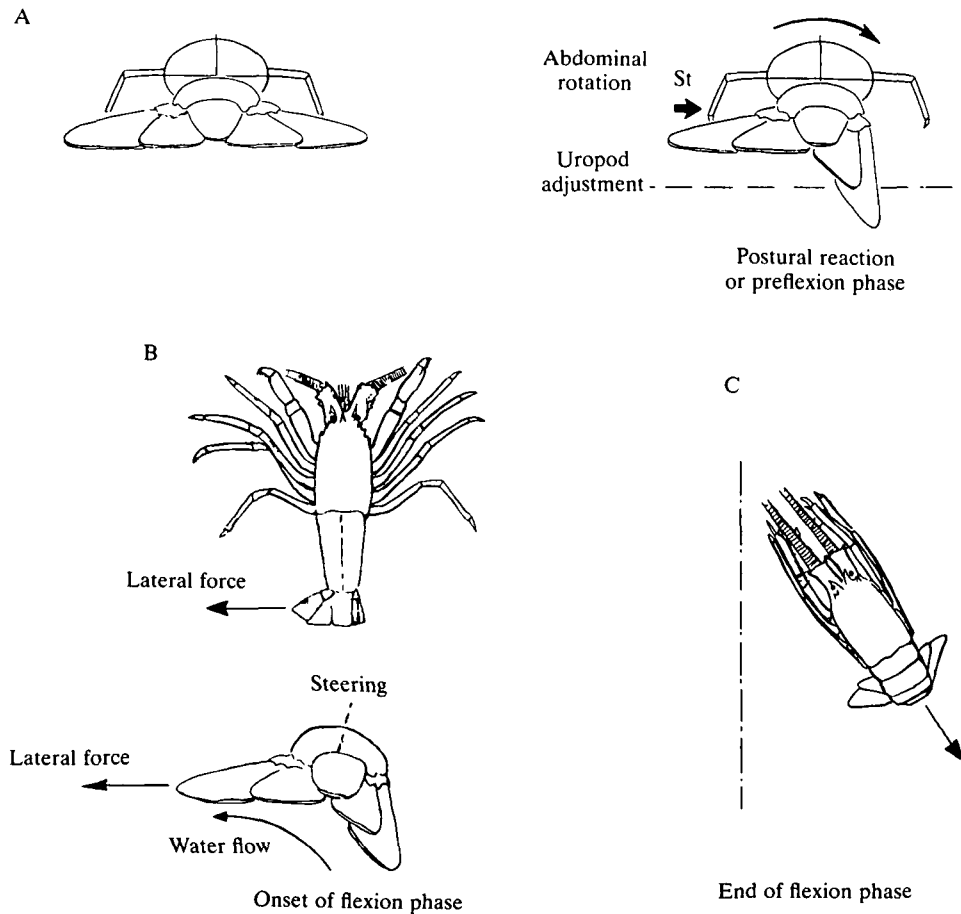


Fig. 10. Summary diagram of the steering movements of the uropods during the postural and preflexion phases (A) and the flexion phase (B) of a tail-flip of *Jasus lalandii* that results from an asymmetrical stimulus (St) to the left side. The steering force moves the animal away from the stimulated side (C). As a result of the asymmetrical position of the uropods during the preflexion phase, a lateral force is produced during early flexion which orientates the escape of the animal. Towards the end of the flexion phase, both uropods are fully opened to maximise the longitudinal force developed for escape.

forces developed during the tail-flip are, therefore, directed almost entirely forward, causing the animal to escape directly backwards and away from the stimulus.

When the stimulus is delivered to the legs of one side alone, this is not only sufficient to bring the tail-flip system to threshold, but in addition induces a rotation of the abdomen and an asymmetrical positioning of the uropods (open on the stimulated side and closed, protracted and rotated on the contralateral side) (Fig. 10). From these movements, which occur during the preflexion phase and

persist through the early stages of flexion, it is possible to predict what the resultant steering force will be.

Our results indicate that the patterns of uropod muscle activation in the preflexion phase of the tail-flip are identical to those expressed during postural adjustments. Indeed, on occasions when tail-flips could not be elicited in response to strong stimulation, the preflexion uropod motor pattern persisted for many seconds as a postural aftermath.

A preflexion phase has also been observed in crayfish and is accompanied by bursts of activity in interneurons in the dorsal part of the nerve cord that cease firing just before flexion occurs (Kramer and Krasne, 1984). Other interneurons are differentially activated during the flexion phase. In support of our conclusions, it has been suggested that this preflexion phase is also due, in part, to postural adjustments since it continues even if no tail-flip is initiated, and that it determines the form of the motor pattern once flexion is triggered.

The tail-flip trajectory reflects the prebiasing posture adopted during preflexion. Our results indicate that it is the asymmetrical positions of the abdomen and uropods during the transition from the preflexion phase to the early stages of flexion that are the major determinants of the lateral corrective forces. The rotation of the abdomen has a direct effect on steering since it causes the propulsive thrust to be completely redirected. However, changes in the attitude of the uropods produce steering effects more indirectly. Rotation of the contralateral uropod during the early part of the flexion phase will direct water flow to the stimulated side, which will, in turn, produce a turning torque to direct the animal away from the source of stimulation. Although steering forces are produced in this way, both uropods open to their full extent during the later stages of flexion and this, it may be assumed, maximises the propulsive force produced during the tail-flip.

Each of these motor systems can act independently, but their effects combine to produce the overall steering response of the animal. Abdominal flexion and rotation produce 70 % of the corrective force, while the uropods contribute up to 25 % of this force (Fig. 7). In a previous study we have shown that the swimmerets of *Jasus* also contribute to the steering force by adopting a particular asymmetrical posture during both the preflexion phase and the tail-flip itself (Cattaert *et al.* 1988). These swimmeret movements may contribute up to 5 % of the final steering force.

Our results indicate that it is the timing of the geometrical changes of the abdomen and uropods that is crucial in determining the appropriate balance between the steering and propulsive forces produced in the tail-flip. Not only are specific muscles recruited that are otherwise silent in tonic postural reactions, but their activity is incorporated at specific points in the tail-flip motor programme (Fig. 8). In this respect the NG tail-flips we have studied are similar to giant-fibre-mediated flips, in which it is known that precise control is exerted over both the pattern and timing of motor activity in the abdominal and thoracic appendages (Wine and Krasne, 1982; Cooke and Macmillan, 1985).

*Giant and non-giant tail-flips*

Our results are consistent with those obtained by Reichert and Wine (1983) demonstrating that the NG tail-flips in crayfish are steerable according to the site of mechanical stimulation. A distinction has previously been drawn between this relative plasticity of NG tail-flips and the rigid stereotypy of giant-fibre-mediated tail-flips (Wine and Krasne, 1982; Reichert and Wine, 1983). However, this distinction may not be as great as previously thought, since several lines of evidence suggest that crayfish giant-fibre-mediated tail-flips are susceptible to sensory modulation (Wine, 1984; Edwards and Mulloney, 1987). Steering forces have also been measured in lobster giant-fibre-mediated tail-flips (Newland and Neil, 1987*b*; Neil, 1991). A current interpretation of these findings is that giant fibre activity is necessary, but not alone sufficient, to release the complete tail-flip motor programme (Krasne and Wine, 1988).

These findings suggest that giant fibre circuitry may be pre-biased by the activity in parallel feedforward pathways that arise from the sensory side of the circuit. If this proves to be the case in *Jasus lalandii*, the detailed analysis we have made of the steering responses in both postural adjustments and the NG tail-flips will allow us to determine whether these adaptive motor responses are also expressed in the same form in giant-fibre-mediated tail-flips.

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