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The tail flip of the Norway lobster, *Nephrops norvegicus.*

I. Giant fibre activation in relation to swimming trajectories

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Summary. 1. In response to abrupt mechanical stimuli delivered to the rostrum or telson, the Norway lobster, *Nephrops norvegicus*, performs short-latency tail flips (Fig. 2) which are preceded by giant fibre activity in the abdominal nerve cord (Fig. 1).

2. High speed cinematography of freely moving animals demonstrates that two distinct categories of giant fibre mediated tail flip are elicited by stimuli to the rostrum or telson (Fig. 3), and that these have flat or elevated rearward trajectories, respectively (Fig. 4). By analogy with the crayfish these have been identified as MG and LG flips. A third, more variable form of swimming tail flip follows these initial giant fibre flips.

3. Analysis of tail flip flexion in terms of the velocities of abdominal segments relative to the centre of mass (Fig. 5) and of intersegmental angles (Fig. 6) reveals gradients in the order of flexion according to the site of stimulation: caudo-rostrally for the MG flip and rostro-caudally for the LG flip.

4. The timings of flexion movements have been studied in tethered animals using a combination of movement monitors, a force transducer, and electromyographical recordings (Figs. 7–10). These confirm that differences exist in both the form of abdominal flexion and the order of activation of the segments in MG and LG flips (Figs. 7, 8). They also demonstrate that, in contrast to the crayfish, all segments flex during the LG flip (Fig. 9). These features are also expressed when the tail flip is induced by direct electrical stimulation of the giant fibres (Fig. 10).

5. The differences observed between *Nephrops* and crayfish in the tail flip trajectories and the contribution of caudal flexion to the LG flip are discussed in terms of the underlying neuronal circuitry.

Key words: Norway lobster, Tail flip, Giant fibres

Introduction

Many decapod crustaceans evade capture by predators by executing an escape response composed of a series of precisely co-ordinated rapid flexions and extensions of the abdomen (i.e. tail flips). The neuronal basis of tail flip production has been extensively studied in the crayfish (reviewed by Wine and Krasne 1972, 1982; Wine 1984; Krasne and Wine 1988), and it represents one of the best known examples of a stereotyped motor act. Two pairs of giant axons in the ventral cord, the medial giants (MGs) and the segmental series of lateral giants (LGs) command the short-latency initial tail flips, the form of which depends upon the particular giant fibres activated (Wiersma 1947; Wine and Krasne 1972). When the animal receives a mechanical stimulus to the anterior region of the body the MGs are activated and the resulting tail flip carries the animal backwards with a low trajectory. A similar stimulus to the abdomen selectively recruits the LGs and the resulting tail flip, which involves flexion of the rostral abdominal segments alone, has an upward, forward-pitching trajectory.

The neuronal circuitry which underlies LG flips has been shown to contain features of surprising complexity, with segmental differences in connectivity (Miller et al. 1985) and convergence of inhibitory inputs and excitatory inputs onto caudal segments (Kramer et al. 1981; Dumont and Wine 1987a–c). On the basis of these findings alone it is difficult to provide a functional explanation for the existence of pathways with contradictory effects on LG flips. Indeed Dumont and Wine (1987c) favour

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Abbreviations: *CDI* corollary discharge interneuron; *COM* centre of mass; *FF* fast flexor motoneuron; *f.p.s.* frames per second; *GF* giant fibre; *LG* lateral giant, *MG* medial giant interneuron; *MoG* motor giant; *SG* segmental giant neuron

an alternative explanation in terms of the evolutionary constraints and selective forces acting on this highly specialized behavioural act. Comparative studies of tail flip control in different decapod crustaceans now seem essential to provide an insight into the phylogeny of the LG circuitry. The potential variety that might exist in neuronal configurations controlling tail flips has recently been demonstrated by the finding that only non-giant pathways are involved in the control of tail flips in an anomuran decapod, the squat lobster (Sillar and Heitler 1985).

Although nephropid decapod crustaceans, notably *Homarus*, have been extensively used in studies of motor control (reviewed by Ache and Macmillan 1980) virtually nothing is known about their escape behaviour (Lang et al. 1977). The flexor motor system and the giant fibres appear to be homologous with those of the crayfish, although no detailed study has been made of their physiology. For these reasons we have carried out an investigation of tail flips in the commercially important nephropid, the Norway lobster *Nephrops norvegicus*. In this species the occurrence of tail flips is an important factor in their capture by trawls (Main and Sangster 1985; Newland and Chapman 1989), and we have quantified this escape swimming under both natural and laboratory conditions (Newland et al. 1988). In this paper we report a combined kinematic and neurophysiological analysis which identifies 3 categories of tail flip in *Nephrops*, establishes the involvement of giant fibres in two of these categories and reveals different spatio-temporal patterns of activation of the abdominal segments in MG and LG flips. While these results suggest general similarities between crayfish and nephropid tail flips, they highlight important differences of detail in the motor patterns, most notably the involvement of caudal segments in the *Nephrops* LG flip. These findings suggest that there are significant functional differences in the LG circuitry of these two groups of decapod crustaceans.

Materials and methods

Experiments were conducted on *Nephrops norvegicus* (L.) of both sexes, ranging in carapace length from 34–64 mm (112–202 mm from tip of rostrum to end of telson). Animals were caught by trawl off the Isle of Cumbrae on the West coast of Scotland. During capture the eyes of the animals were exposed to daytime levels of light, which caused permanent retinal damage (Shelton et al. 1985). Animals were maintained in running seawater tanks at 10–12 °C until required, and were fed weekly on chopped heart meat.

To study unrestrained tail flips, animals were placed in an experimental aquarium (0.6 × 0.3 × 0.4 m) and allowed to acclimatize for 30 min. Tail flips were induced by tactile stimuli applied with a plastic rod to the rostrum or to the telson of the animal. Tail flips were filmed from the side using a Photosonic 1 LP high speed (200 frames/s) and a Bolex SLR (64 frames/s) cine camera using Kodak 16 mm Eastman 4X negative film (400 ASA). To aid film analysis the edges of each abdominal segment were highlighted with black paint. The centre of mass (COM) of the body was determined by suspending the animal from two fixed points, and was marked by paint. After development, the films were projected frame-by-frame onto a digitizing tablet (Summagraphics MM1201) for analysis. The co-ordinates of the COM and each abdominal segment were entered to a Tuscan S-100 microcomputer, which was programmed to calculate the distances travelled, the velocity and acceleration of the COM and the relative movements of the abdominal segments.

To study tail flips in restrained animals, they were attached to a holding bar through a block cemented to the carapace. Tail flips were induced both by the mechanical stimuli described above, and by direct electrical stimulation (single 10 V, 0.1 s pulses) of the giant fibres delivered through pairs of wire implanted in the cephalothorax in contact with the circumoesophageal commissures and in the abdomen in contact with the abdominal connectives between the 5th and 6th abdominal ganglia. Forces produced by the tail flip were monitored using a strain gauge assembly placed between the block and the bar (Newland 1985). Movements of the abdomen were monitored using the transducer system described by Cattaert et al. (1988). A high frequency (40 kHz, 0.5 V) signal was passed through the experimental tank between two plates. A thin wire attached to the telson received a signal which was proportional to its position in the electric field. This was conveyed to a detector circuit for conversion to an analogue voltage. By placing the detector plates either at the front and back of the animal, or above and below the abdomen, the horizontal and vertical components of abdominal movement could be separately measured.

Electromyographic recordings were made in both restrained and unrestrained animals by implanting pairs of Teflon-coated silver wires (0.76 mm diameter) into the flexor or extensor muscles of each abdominal segment. The electrodes were held in place using cyanoacrylate glue. The muscle potentials were amplified (Isleworth A101 preamplifiers), displayed on a storage oscilloscope (Tektronix 5515) and recorded on a 4-channel FM tape recorder (Racal). Neurograms of giant fibre activity were obtained in unrestrained animals by inserting twisted silver wires through the pleural plate of the second segment, leading them ventral to the flexor muscles and dorsal to the abdominal connectives, and out to an attachment point on the pleural plate of the third segment. The wires were insulated except for the central section which contacted the dorsal surface of the nerve cord.

Results

The involvement of giant fibres in tail flips

The tail flips of *Nephrops* show a general resemblance to those of crayfish (Wine and Krasne 1972) since they comprise rapid flexions and extensions of the abdomen which propel the animal backwards through the water, and produce swimming trajectories which are dependent upon the site of stimulation (Newland et al. 1988). However, in order to establish that, as in crayfish, the initial flips result from giant fibre activation a number of more critical tests have been applied.

Since it is well established for crayfish that giant fibre activation is consequent upon abrupt mechanosensory stimulation (Wine and Krasne 1972), the standard mechanical stimuli used in our experiments were sharp taps to the rostrum or telson. Evidence for the activation of giant fibres by these stimuli was obtained by chronic neurographic recordings in the abdominal 2–3 connective (Fig. 1). These showed that in response to sharp taps to either the rostrum or telson large, short time course compound potentials preceded the flexor muscle activity of the first evoked flip by approximately 5 ms.

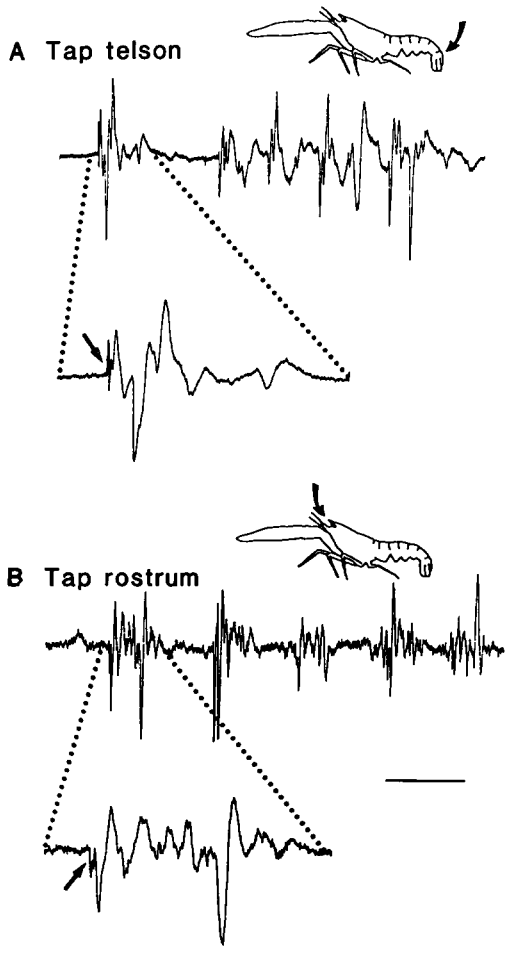

Fig. 1A, B. Giant fibre activity preceding tail flips. Recordings obtained from electrodes implanted dorsal to the ventral nerve cord in the third abdominal segment during sequences of tail flips. Giant fibre activity can only be observed preceding the initial tail flip of each sequence. **A** Tap to telson. **B** Tap to rostrum. The initial tail flips are shown on expanded time scales with giant fibre activity indicated by arrows. The compound muscle action potentials of the deep abdominal flexor muscles are preceded by a discrete compound nerve potential. Scales: 300 ms and 75 ms

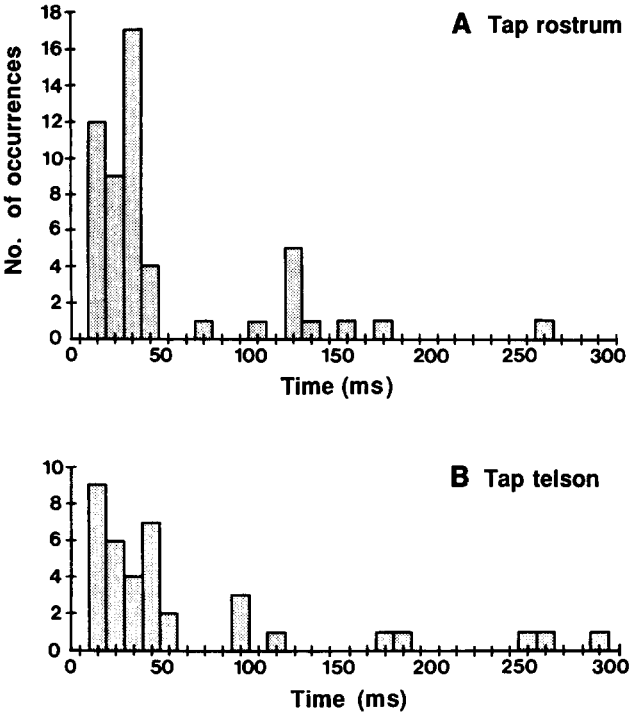

Fig. 2A, B. Response latency of tail flips. Histograms of the delay between the time of contact of the probe with the body and the first observable movement of the tip of the telson. **A** Tap rostrum. **B** Tap telson. Data obtained from cine film taken at 200 f.p.s.

When subsequent tail flips ensued, they did so without the occurrence of these potentials.

Another clear characteristic of giant-fibre mediated flips in crayfish is their short latency (3–10 ms to flexor muscle activation, with a further 10 ms to the first flexion movement) compared with that of swimming flips (mean 200 ms) (Wine and Krasne 1982; Reichert and Wine 1983). In our experiments on *Nephrops*, measurements were taken of the latency from the stimulus (taken as contact of the rod with the animal) to the response (taken as the initiation of flexion in the first tail flip) (Fig. 2). These results show that the mean latency of flips to rostral and caudal taps was 38.8 ms and 57.9 ms, respectively (modal latencies of 35 ms and 15 ms, respectively), although a small number of flips occurred with greater latencies, up to 300 ms. Allowing for there being a greater conduction time in the final motor pathways of the larger species, *Nephrops*, which can be 2–3 times larger than crayfish, these latency measurements suggest that the majority of flips occur within the period expected for a fast-conducting giant fibre pathway, but are far too early to be accounted for by non-giant pathways.

When taken together with other data obtained from direct electrical stimulation of sensory pathways, and myographic recordings in the abdominal muscles (see below) these results strongly indicate that the initial tail flips of *Nephrops* to abrupt mechanical stimuli are mediated by giant fibres.

Swimming trajectories produced by the different categories of tail flip

A typical series of frames from a cine sequence at 64 f.p.s. illustrates the patterns of abdominal movement which occur in the different categories of tail flip (Fig. 3). The direction of the powerstroke which results from these movements can be represented by plotting the position in space of the body outline and the centre of mass of the animal (Fig. 4). The tail flip is directed almost directly backwards following rostral stimulation (Figs. 3A, 4A), but has an elevated trajectory when annotated by a caudal stimulus (Figs. 3B, 4B). These differences were consistent between rostral- and caudal-mediated tail flips in all animals tested (Fig. 4D), the mean trajectories being $15.3° \pm 10.4°$ ($N=12$) and $71.0° \pm 11.9°$ ($N=7$), respectively. By analogy with the two distinct cate-

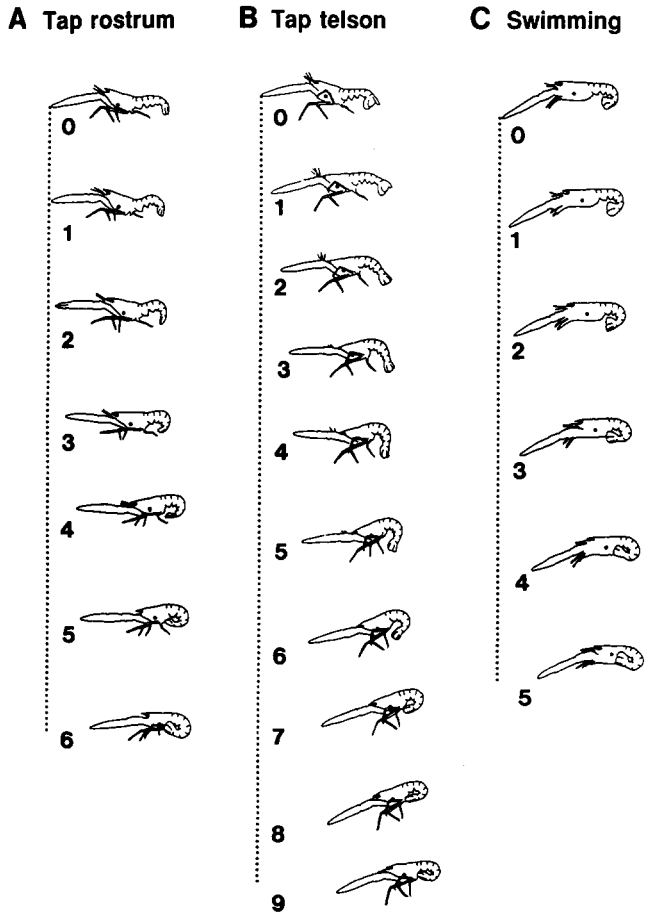

Fig. 3A–C. Body outlines during different categories of tail flip. **A** Tap rostrum. **B** Tap telson. **C** Swimming tail flip. Tracings obtained from cine film taken at 64 f.p.s.. Frame 0 represents the first frame on which contact of the probe with the body was observed. Dotted lines indicate the point in space of the tip of the claw relative to frame 0. Scale: 4 cm

gories of tail flip in the crayfish (Wine and Krasne 1972), and having established their giant-fibre mediation (Figs. 1, 2) it seems appropriate to identify these flips as MG and LG types, respectively.

The swimming tail flips following either type of the initial flips were more variable in nature, but always occurred from a half-flexed position (Fig. 3C) and had a relatively flat trajectory (Fig. 4C). Following an LG flip this caused the initial upward movement to become less elevated (Fig. 4E), although if a number of subsequent swimming tail flips were executed the animals could achieve a height of up to 0.9 m from the substrate (Newland et al. 1988).

Contribution of the abdominal segments to propulsive thrust

In order to assess the contributions of different segments to the propulsive force development in the tail flip it was necessary to measure their velocities of movement relative to that of the centre of mass (COM), for only those segments with a greater velocity than the COM contribute to propulsive thrust. The greatest velocities were achieved by the posterior segments, as a result of the cumulative contributions of flexion at their own and all anterior joints (Fig. 5). In a MG flip only the posterior segments reached velocities much greater than the COM, and they peaked before the anterior segments (Fig. 5A). In a LG flip segments 1–5 reached an early peak of velocity which was greater than that of the COM, while the terminal segment showed a delayed peak (Fig. 5B). In a swimming tail flip only the posterior segments achieved velocities greater than the COM, but their peak values were reached much later than for the MG flip (Fig. 5C). A common feature of all flips was

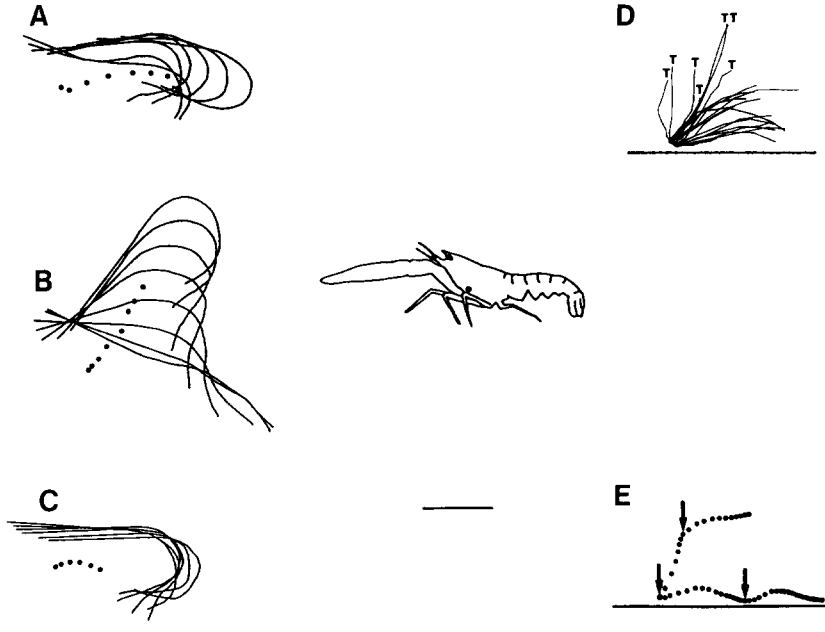

Fig. 4A–E. Tail flip flexions. **A–C** Superimposed outlines of body positions showing flexion movement and displacement of centre of mass in the 3 categories of tail flip. **D** Trajectories of different animals given mechanical stimuli to the rostrum (unmarked) and telson (*T*). **E** Movement of the centre of mass over two tail flips following a mechanical stimulus to the rostrum (lower path) and the telson (upper path). The beginning of each flexion phase is marked with an arrow. The inset shows the initial orientation of the animal in each case. Scale: 4 cm (**A–D**, and inset), 8 cm (**E**)

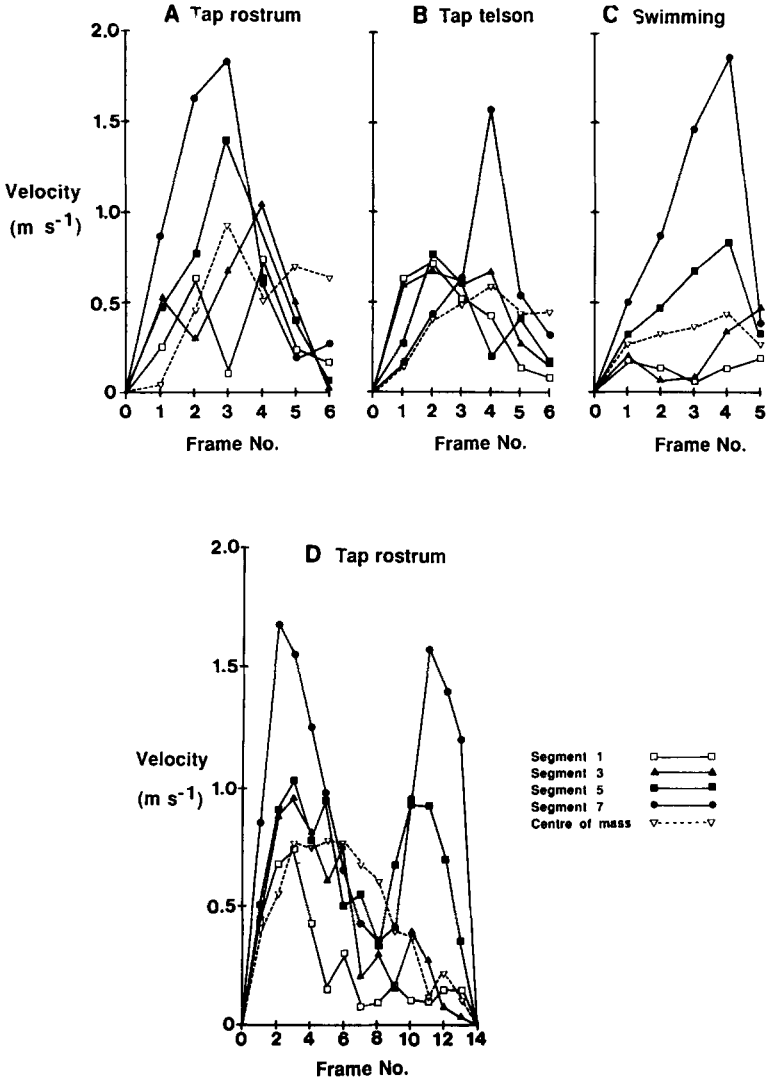

Fig. 5A–D. Velocities of movement of abdominal segments in tail flips. Measurements of the velocities of the individual abdominal segments relative to the centre of mass, and the velocity of the centre of mass in space. Data obtained from cine film taken at 64 f.p.s.. **A** Tap rostrum. **B** Tap telson. **C** Swimming tail flip. **A–C** Flexion phase of tail flip. **D** Flexion and extension phases of tail flip

the correspondence between the times of peak velocity of the COM and of the posterior segments, which indicates the major contribution of these segments to the propulsive thrust.

The velocities of segments during a complete cycle of flexion and extension were measured for a MG flip (Fig. 5D). The velocities of the COM and of all the segments were lower in the extension phase than during flexion, although this was much less marked for the posterior segments. The order in which the segments attained maximum velocity during extension, with a rostro-caudal gradient, was opposite to that which occurred during flexion (Fig. 5D).

Flexion of individual abdominal segments in tail flips

For an analysis of the motor control of tail flips it is more appropriate to consider the movements of individual abdominal segments relative to each other, rather than to an external spatial reference. In Fig. 6 the intersegmental angles at each abdominal joint are plotted during the course of the different GF-mediated tail flips. The data are grouped to clarify the differences between anterior and posterior segments. In the MG flip, flexion was initiated in the caudal segments and progressed rostrally, although segments 1–3 contributed relatively little flexion (Fig. 6A). Conversely the LG flip involved initial flexion of the rostral segments (Fig. 6B), while the caudal segments contributed large flexions in the later stages. These observations lead to the conclusions that all segments flex during the course of both tail flips, but that the order of activation is strictly dependent upon the manner of activation, by either MG or LG pathways.

A more detailed study of the order of activation of flexion in the abdominal segments during tail flips was carried out using chronic recordings of myographic activity. Initial studies were made on freely moving animals, and although these confirmed that differences exist in the order of recruitment of segments in the two categories of GF-mediated flips, the presence of movement artefacts in the records precluded detailed analysis. For this reason, and for later study of the effects of different

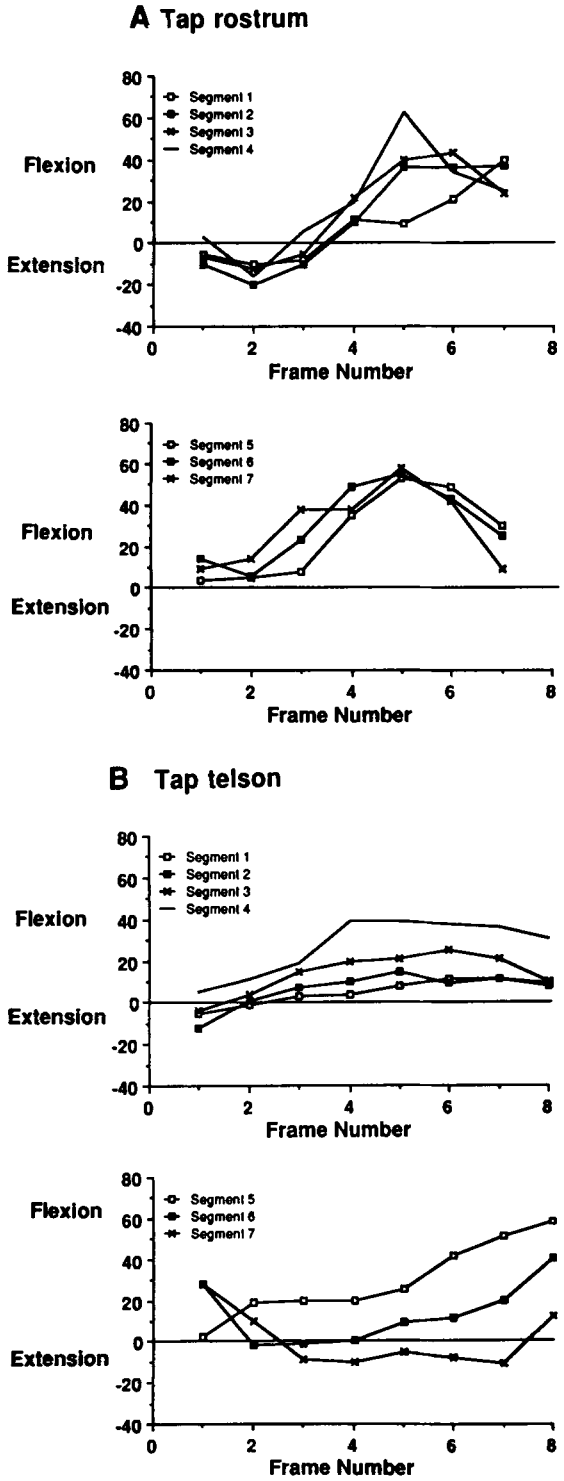

Fig. 6A, B. Angles between abdominal segments in tail flips. Measurements expressed as angle between the projection of the dorsal surface of a segment and that of the anterior adjacent segment (or, for segment 1, the thorax). **A** Tap rostrum. **B** Tap telson. Upper plots show segments 1–4, lower plots segments 5–7

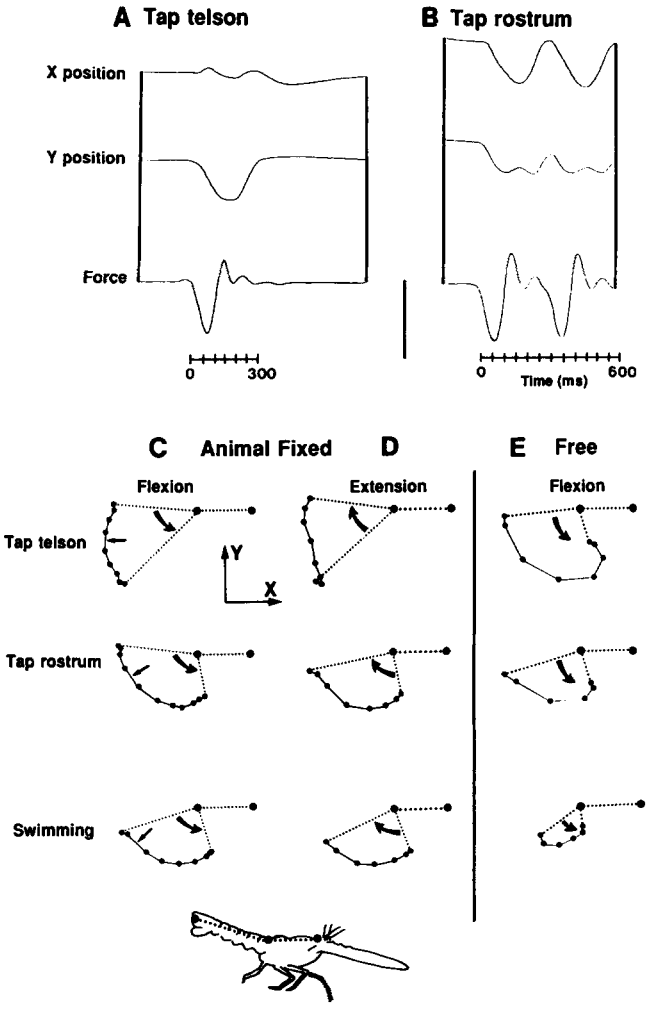

Fig. 7A–E. Combined measures of movement and force in tail flips. **A, B** Composite records of the movement of the telson tip in the horizontal (*X*) and vertical (*Y*) planes, obtained using a movement transducer, and the force produced in the longitudinal plane, obtained using a strain gauge. **A** Tap telson. **B** Tap rostrum. First flip is followed by a swimming tail flip. Scale: 10 N. **C, D** Reconstruction of path of telson tip from X and Y movement data in **A, B** during **C** flexion and **D** extension phases of different categories of tail flip. Inset shows reference lines for thorax and abdomen. Measurements made at intervals of 20 ms, and small arrow indicates point of peak force. **E** Path of tip of telson during tail flip flexions of a free animal measured directly from cine film taken at 64 f.p.s.. Thorax depicted as horizontal, although it actually rotates (see Fig. 4)

initial orientations of the animal on the form of the tail flip (Newland and Neil 1990) a method was developed for studying tail flips with the animal held in a fixed position in midwater.

Simultaneous recordings of abdominal movements and propulsive force

By incorporating strain gauges into the rod which held the animal it was possible to record the longitudinal propulsive thrust produced in the tail flip, thus providing a convenient indication of its time course. In order to relate this force record of the tail flip to the flexion movements observed in the free moving animal it was necessary in a number of control experiments to obtain simultaneous measures of both abdominal movement and the force output. Movements of the tip of the telson

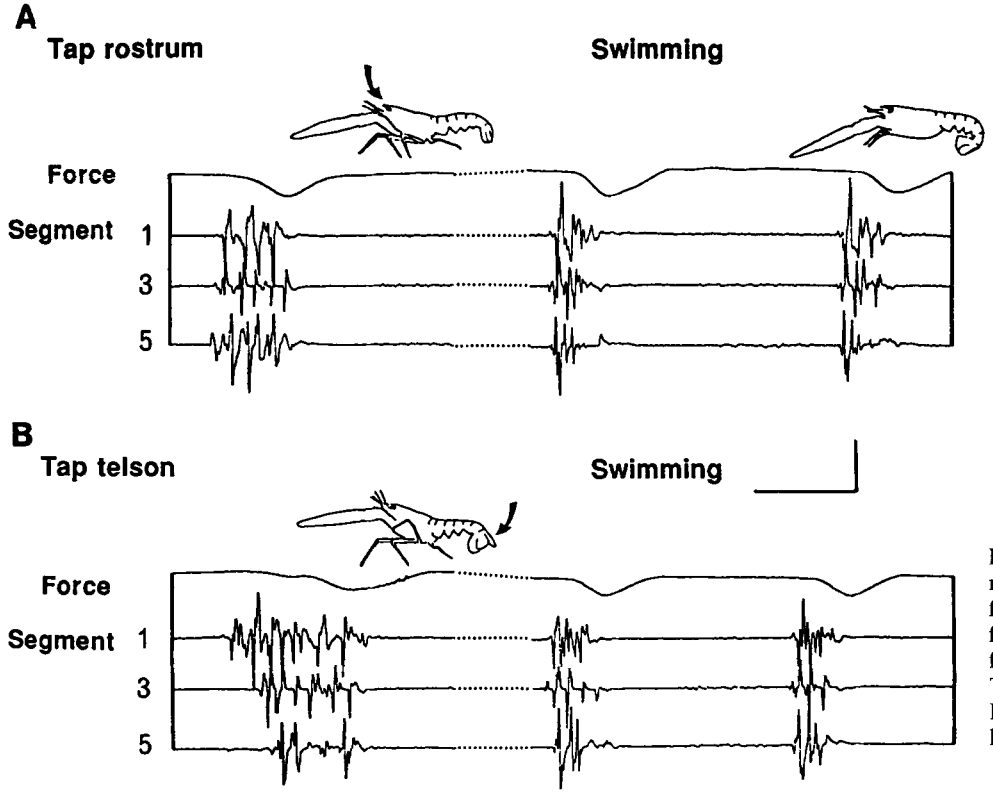

Fig. 8A, B. Segmental gradients in myographic activity of the deep flexor muscles during tail flips. Data from segments 1, 3 and 5. **A** Tail flips induced by tap to rostrum. **B** Tail flips induced by tap to telson. Each sequence is continuous. Scales: horizontal 100 ms, vertical 20 N

were measured in two dimensions using an electronic movement monitor system (Fig. 7A, B), so that its path could be reconstructed (Fig. 7C, D).

The relative horizontal and vertical movements in the different categories of tail flip can be compared with those which occur in the freely moving animal (Fig. 7E). The path described by the tip of the telson in relation to the axis of the thorax was very similar in both the free and tethered MG flips, being directed predominantly forward during the first third of flexion. The telson paths in free and tethered LG flips also resemble each other, showing a predominant downward component in the initial period of flexion, although the tethered path did not show the later forward and upward components.

Comparison of the force and movement records (Fig. 7A, B) shows that the longitudinal force began to develop at the same time as movement of the telson tip was initiated, and the time of peak force shows a consistent relationship to the maximum velocity of flexion of the telson. This provides a point of cross reference for comparing timings of events made in tethered animals with those obtained in free swimming animals.

Myographic activity in tethered tail flips

Using the tethered preparation it proved possible to obtain reliable chronic recordings, free from movement artefacts, from both the phasic flexor and extensor muscles. Figure 8 shows simultaneous recordings from the phasic flexor muscles of segments 1, 3 and 5 during tail flips initiated by taps to the rostrum and telson. In each case the first flip was followed by a series of swimming flips. From a number of such recordings, involving different combinations of segments, a composite picture of the responses of all the abdominal segments was constructed (Fig. 9). It is clear in all these recordings that for each of the categories of tail flip electrical activity occurred in the flexor muscles of all the abdominal segments, that it preceded force development, and that it continued up to or beyond the force peak.

In confirmation of the observations made on free swimming animals, the flexor muscles of different segments were recruited in a strict temporal sequence which was characteristic of the type of tail flip induced (Fig. 9A, B), and which also occurred at short latencies (approximately 40 ms for MG and 55 ms for LG). In MG flips the flexor muscles were activated in a caudo-rostral order, with a delay of approximately 25 ms between the onset of activity in segments 6 and 1. In LG flips the order of activation was reversed, with the flexor muscles of segment 1 firing first, and longer intersegmental delays, amounting to around 50 ms between segment 1 and segment 6. In swimming tail flips muscle activation displayed variable rostro-caudal gradients irrespective of whether they followed MG or LG flips (Figs. 8, 9).

Myograms from the phasic extensor muscles showed that in both MG and LG flips activity began around 35 ms after the force peak, and showed a steep rostro-caudal gradient (Fig. 9A, B).

A comparison between tail flips elicited by mechanical stimulation and by direct electrical stimulation of the giant fibres was made by delivering single brief elec-

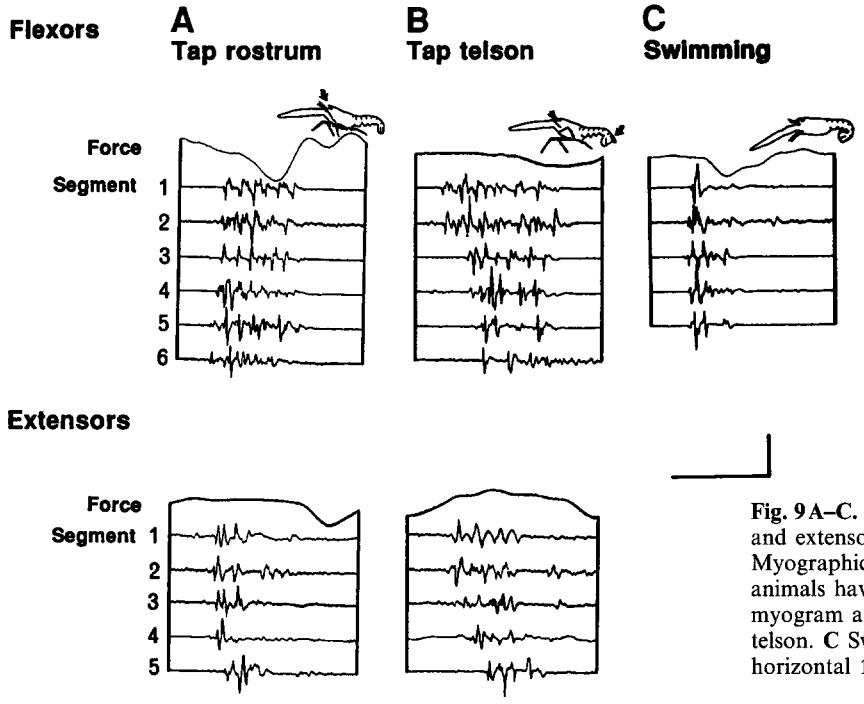

Fig. 9A–C. Composite records of activity in the deep flexor and extensor muscles of the abdomen during tail flips. Myographic records obtained at different times from several animals have been aligned with reference to the segment 1 myogram and the force record. **A** Tap rostrum. **B** Tap telson. **C** Swimming tail flip following rostrum tap. Scales: horizontal 100 ms, vertical 20 N

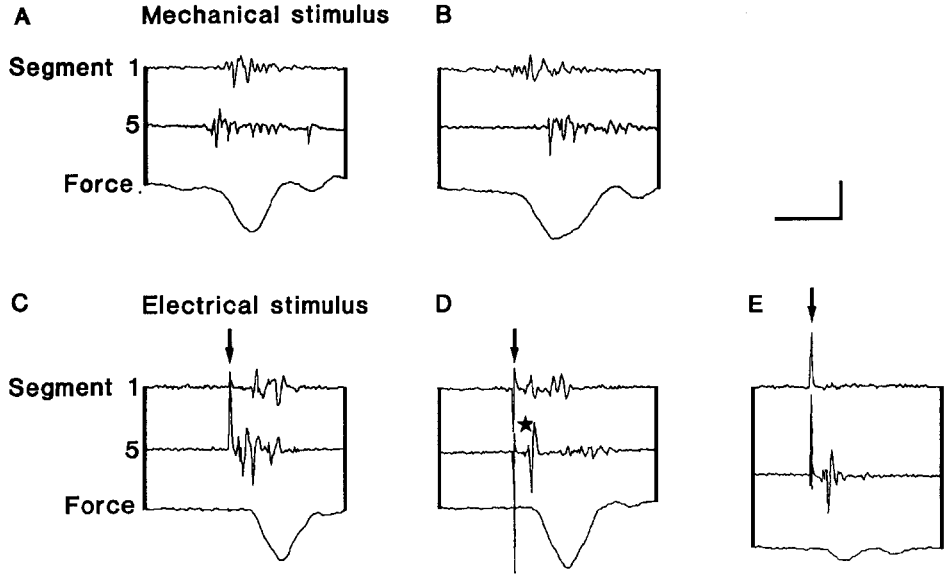

Fig. 10A–E. Comparison of segmental gradients of myographic activity in tail flips induced by mechanical stimuli to the rostrum (**A**) and telson (**B**), and by electrical stimuli (10 V, 0.1 s pulse) to the circumoesophageal commisures (**C**) and abdominal connectives (**D**). **E** Subthreshold stimulation (7 V, 0.1 s pulse) of the abdominal connectives stimulates an unidentified muscle in segment 5. This early muscle potential is also present when stimulation leads to a tail flip (star in **D**), however, muscle potentials mediated by the giant fibre pathway in segment 5 occur with a much longer delay in **D**. Artefact of the stimulus is indicated by the arrow. Scales: horizontal 50 ms, vertical 5 N

trical pulses through implanted wires in contact with the circumoesophageal connectives (MG) and in contact with the abdominal connectives (LG) (Fig. 10). When of appropriate strength (typically 10 V, 0.1 s pulses) these electrical stimuli reliably elicited individual (and occasionally multiple) tail flips. A correspondence was found at each site of stimulation between the effects of the electrical stimulation and that of the standard sharp mechanical tap. This was evident both in the response latency (approximately 10 ms from the electrical stimulus to the first muscle activity) and the characteristic order of recruitment of segmental flexor muscles, caudo-rostral for cephalothoracic stimuli and rostro-caudal for abdominal stimuli (Fig. 10). These results provide further confirmation of the involvement of short latency GF pathways in *Nephrops* tail flips, and emphasize that the segmental gradient of flexor recruitment is a distinguishing characteristic between MG and LG flips.

Discussion

The involvement of giant fibres in Nephrops tail flips

Several lines of evidence indicate that activation of the tail flip in *Nephrops* following abrupt mechanical stimu-

lation is mediated by giant fibres. The very distinct character and highly stereotyped nature of the tail flips produced by the stimuli to rostrum and telson correspond in many respects to the patterns of flexion and extension observed in crayfish following stimulation at these same two sites. The occurrence of subsequent swimming tail flips following the initial flip is a further feature of correspondence in the two species. Since it is well established that the different categories of initial flip in crayfish are produced by giant fibres (Wiersma 1947; Wine and Krasne 1972) our observations on *Nephrops* are entirely consistent with a GF origin for these initial flips. Lang et al. (1977) have presented similar evidence for *Homarus*.

This strong evidence is reinforced by the fact that medial and lateral GFs occur in the ventral nerve cord of nephropid lobsters (Otsuka et al. 1967; Govind and Lang 1976), and that chronic recordings show GF activity preceding the initial tail flips (Fig. 1). The measures of response latency (Fig. 2) provide quantitative confirmation that the majority of initial flips to abrupt taps are mediated by extremely rapidly conducting pathways, almost certainly the GFs. The possibility that these measures underestimate the true latency due to the stimulus being a visual rather than a mechanical one is remote, since the animals were effectively blinded by exposure to daylight (Shelton et al. 1985) and indeed showed no detectable eyeshine. The fact that direct electrical stimulation of the commissures and connectives also induces a short latency response (Fig. 10) provides an independent confirmation of the involvement of rapid conducting pathways. It may be assumed that the minority of flips which showed substantially longer delays to activation represent flips of the swimming type, and are activated by slower conducting non-giant pathways.

Differences between Nephrops and crayfish

Although our results demonstrate general similarities in the mode of activation of tail flips by GFs in lobsters and crayfish, there are clear differences of detail. Kinematic measurements of tail flip trajectories of *Nephrops* indicate that, as in crayfish, a distinction exists between MG flips induced by rostral stimuli and LG flips induced by caudal stimuli. The backward trajectory of the *Nephrops* MG flip is similar to that of the crayfish, although somewhat flatter. However, a much larger difference exists between the trajectories of the LG flips of the two species. In crayfish the LG flip is actually a pitching movement which carries the animal forward by a small amount from the point of stimulation. This is typically followed by a swimming flip which rotates the animal further about its centre of mass to an inverted position. A subsequent series of twisting flips completes the somersaulting manoeuvre by rotating the animal back to the upright (Cooke and Macmillan 1985). In *Nephrops* the LG flip is a backward movement elevated at an angle of approximately 70°, and is followed by swimming flips which continue to carry the animal backwards away from the point of stimulation (Newland et al. 1988). Such a movement enables the animal both to evade the immediate threat from the rear and to remove itself to a distance from the threatening stimulus. The escape paths of *Nephrops* were never observed to be directed forwards, as in crayfish.

We have demonstrated that the neuromuscular basis of the lower trajectory of the *Nephrops* LG flip lies in the contribution of the caudal segments to abdominal flexion (Figs. 8, 9). These segments, and particularly the expanded tail fan will, therefore, as in the MG flip, make the major contribution to the production of thrust in the powerstroke (Webb 1979). This contrasts with the well-established finding that segments 4–6 contribute virtually no flexion to the LG flip in crayfish (Larimer et al. 1971; Mittenthal and Wine 1973; Wine and Krasne 1982) (although in some experimental conditions caudal flexion can, in fact, occur – J.J. Wine, personal communication).

We have also revealed that there are distinct temporal patterns of activation of the fast flexor muscles in *Nephrops* related to the MG and LG flips (Figs. 8, 9). Both the caudo-rostral gradient of the MG flip and the rostrocaudal gradient of the LG flip are appropriate hydromechanical adaptations to produce the different observed trajectories. The order of flexion dictates the path travelled by the caudal segments, and therefore the relative horizontal and vertical displacements which contribute to force production. In the MG flip this ratio is small, so that the tip of the telson covers a large horizontal distance and contributes substantially to thrust along the major axis of the body. The largest horizontal displacements of the body are achieved in this type of flip (Fig. 4). In the LG flip the early flexion of rostral segments generates a rotation of the animal about its centre of mass and redirects the long axis of the body with respect to the substrate. The subsequent serial flexions of the caudal segments produce thrust along this new line of action, which interrupts the rotation and directs the animal backwards and upwards. It can thus be seen that a precise temporal as well as spatial co-ordination of the initial tail flip underlies the ability of *Nephrops* to redirect an essentially unidirectional escape movement away from threatening stimuli approaching from either in front or the rear.

Surprisingly, little is known about the temporal patterning of crayfish tail flips. A caudo-rostral gradient has been noted, but not quantified, in MG flips (J.J. Wine, personal communication), and when examined in LG flips no consistent order of activation was observed (Uyama and Matsuyama 1980). More attention has been paid to the potential for differential activation of abdominal segments according to the exact location of the stimulus along the abdomen. Although a neuronal substrate exists for such effects (Dumont and Wine 1987b; Takahata and Wine 1987), behavioural observations have failed to detect any variation in trajectory (Dumont and Wine 1987c).

Consequences for tail flip circuitry in Nephrops

The fact that the LG flip of *Nephrops* has a lower trajectory than that of crayfish, and that this is due to the involvement of the caudal segments has particular significance for a consideration of the possible underlying neuronal circuitry. The mechanism whereby caudal flexion is suppressed in the crayfish LG flip has been the subject of extensive investigation. LG appears to act through 3 parallel pathways: monosynaptically via the motor giants (MoG) (Mittenthal and Wine 1973), disynaptically via the segmental giants (SG) and fast flexor motoneurones (FF) (Roberts et al. 1982) and by an intersegmental route (CDIs) (Kramer et al. 1981). The differential activation of the rostral abdominal segments, which is the basis of the elevated trajectory, is achieved by an absence of LG-MoG synaptic contact in the caudal segments (Wine 1984). The disynaptic pathway is actually activated in all segments, only for its effect to be selectively cancelled in the caudal segments by at least 3 feed-forward inhibitory mechanisms which are triggered from the sensory side of the circuit (Dumont and Wine 1987b, c; Takahata and Wine 1987).

In discussing the functional 'sense' of such duplicated circuitry in which motor neurones are simultaneously excited and inhibited by parallel pathways activated by the same stimulus, Krasne and Wine (1988) consider that the detailed knowledge of the crayfish tail flip circuitry allows alternative suggestions to be made with some confidence. They favour the idea that the LG flip has evolved from a condition essentially similar to that of the MG flip by the successive overlaying of inhibitory effects. Having reached this state it may be that no selective pressures have operated to change the arrangement (Dumont and Wine 1987c). Similar explanations have also been put forward for apparently vestigial features of the tail flip and other motor circuits (Krasne and Wine 1988; Dumont and Robertson 1986), and on this view many features of contemporary circuitry may only be explicable in the context of their phylogeny or development.

An obvious way in which to resolve questions of phylogeny is to apply the comparative approach, and the results we have obtained for *Nephrops* suggest that this group of lobsters will provide a rich source of relevant information. In view of the low trajectory of its tail flip, a neurophysiological study of *Nephrops* tail flip circuitry should aim to determine:

1) The occurrence and involvement of MoGs in abdominal flexion. Since these giant cells are known to be present in both the crayfish and the anomuran *Galathea* (Sillar and Heitler 1985) it is a reasonable expectation that they also occur in lobsters. If so, is caudal flexion due to the formation of functional connections between LG and the MoGs of all abdominal segments?

2) The existence of the SG-FF pathway, and the segmental gradient of its strength. If it remains more than the vestigial feature it represents in crayfish caudal segments (Miller et al. 1985) then it may be the source of the greater flexor drive.

3) The sources, if any, of feedforward inhibition and the reasons why these fail to suppress flexion of the caudal segments. It is perhaps significant that crayfish LG flips elicited by direct electrical stimulation have lower trajectories than natural LG flips (Wine 1984), and thus resemble the natural LG flip of *Nephrops*. It is thought that this occurs in crayfish because electrical stimulation causes no activation of the parallel sensory pathways which countermand caudal flexion. Are these pathways naturally less effective in *Nephrops*?

4) The basis of the opposite temporal gradients in segmental flexion during MG and LG flips of *Nephrops*. Since the intersegmental delays are relatively long (Fig. 9), and in each case the first segment activated is the one most distant from the point of stimulation (Fig. 4), it is necessary to invoke some integrating mechanism between the giant fibres and the motor systems. Mechanical integration at the level of the musculo-skeletal system has been suggested to explain the early caudal flexion of crayfish MG flips (F. Krasne, personal communication), but it is difficult to reconcile a single mechanism with the opposite gradients of the two giant fibre flips of *Nephrops*. In crayfish a set of interneurones, the CDIs, which form part of the non-giant circuitry (Kramer et al. 1981) act in parallel to the GFs to produce longer latency effects (Wine and Mistick 1977), and it may be speculated that equivalent integrative pathways may underlie the segmental gradation of tail flip flexion in *Nephrops*.

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References

Ache BW, Macmillan DL (1980) Neurobiology. In: Cobb JS, Phillips BF (eds) The biology and management of lobsters. I. Physiology and behaviour. Academic Press, New York, pp 165–213

Cattaert D, Clarac F, Neil DM (1988) Anatomical and physiological organisation of the swimmeret system of the spiny lobster *Jasus lalandii* as adaptive components of the tail flip. J Comp Physiol A 162:187–200

Cooke IRC, Macmillan DL (1985) Further studies of crayfish escape behaviour. I. The role of the appendages and the stereotyped nature of non-giant escape swimming. J Exp Biol 118:351–365

Dumont JPC, Robertson RM (1986) Neuronal circuits: an evolutionary perspective. Science 233:849–853

Dumont JPC, Wine JJ (1987a) The telson flexor neuromuscular system of the crayfish. I. Homology with the fast flexor system. J Exp Biol 127:249–278

Dumont JPC, Wine JJ (1987b) The telson flexor neuromuscular system of the crayfish. II. Segment-specific differences in connectivity between premotor neurones and the motor giant. J Exp Biol 127:279–294

Dumont JPC, Wine JJ (1987c) The telson flexor neuromuscular system of the crayfish. III. The role of feedforward inhibition in shaping a stereotyped behaviour pattern. J Exp Biol 127:295–311

Govind CK, Lang F (1976) Growth of lobster giant axons: correlation between conduction velocity and axon diameter. J Comp Neurol 170:421–434

Kramer AP, Krasne FB, Wine JJ (1981) Interneurons between giant axons and motoneurons in crayfish escape circuitry. J Neurophysiol 45:550–573

Krasne FB, Wine JJ (1988) Evasion responses of the crayfish. In: Guthrie DM (ed) Aims and methods in neuroethology. Manchester University Press, Manchester, pp 10–45

Lang F, Govind CK, Costello WJ, Greene SI (1977) Developmental neuroethology: changes in escape and defensive behavior during growth of the lobster. Science 197:682–685

Larimer JL, Eggleston AC, Masukawa LM, Kennedy D (1971) The different connections and motor outputs of lateral and medial giant fibres in the crayfish. J Exp Biol 54:391–402

Main J, Sangster GI (1985) The behaviour of the Norway lobster, *Nephrops norvegicus* (L.) during trawling. Scottish Fisheries Research Report 34

Miller LA, Hagiwara G, Wine JJ (1985) Segmental differences in pathways between crayfish giant axons and fast flexor motoneurons. J Neurophysiol 53:253–265

Mittenthal JE, Wine JJ (1973) Connectivity of crayfish giant interneurons: visualisation of synaptic regions with cobalt dye. Science 179:182–184

Newland PL (1985) The control of escape behaviour in the Norway lobster, *Nephrops norvegicus*. Ph.D. Thesis, University of Glasgow

Newland PL, Chapman CJ (1989) The swimming and orientation behaviour of the Norway lobster, *Nephrops norvegicus* (L.) in relation to trawling. Fish Res 8:63–80

Newland PL, Neil DM (1990) The tail flip of the Norway lobster, *Nephrops norvegicus*. II. Dynamic righting reactions induced by body tilt. J Comp Physiol A 166:529–536

Newland PL, Chapman CJ, Neil DM (1988) Swimming performance and endurance in the Norway lobster, *Nephrops norvegicus*. Mar Biol 98:345–350

Otsuka M, Kravitz EA, Potter DD (1967) Physiological and chemical architecture of a lobster ganglion with particular reference to GABA and glutamate. J Neurophysiol 30:725–752

Reichert H, Wine JJ (1983) Co-ordination of lateral giant and non-giant systems in crayfish escape behavior. J Comp Physiol 153:3–15

Roberts AM, Krasne FB, Hagiwara G, Wine JJ, Kramer AP (1982) Segmental giant: evidence for a driver neuron interposed between command and motor neurones in the crayfish escape system. J Neurophysiol 47:761–781

Shelton PMJ, Gaten E, Chapman CJ (1985) Light and retinal damage in *Nephrops norvegicus* (L.) (Crustacea). Proc R Soc Lond B 226:217–263

Sillar KT, Heitler WJ (1985) The neural basis of escape swimming behaviour in the squat lobster *Galathea strigosa*. J Exp Biol 117:251–269

Takahata M, Wine JJ (1987) Feedforward afferent excitation of peripheral inhibitors in the crayfish escape system. J Neurophysiol 58:1452–1467

Uyama C, Matsuyama T (1980) Coordinated excitation of flexor inhibitors in the crayfish. J Exp Biol 86:187–195

Webb PW (1979) Mechanics of escape responses in crayfish (*Orconectes virilis*). J Exp Biol 79:245–263

Wiersma CAG (1947) Giant nerve fiber system of the crayfish. A contribution to the comparative physiology of synapse. J Neurophysiol 10:23–38

Wine JJ (1984) The structural basis of an innate behaviour pattern. J Exp Biol 112:283–319

Wine JJ, Krasne FB (1972) The organisation of escape behaviour in the crayfish. J Exp Biol 56:1–18

Wine JJ, Krasne FB (1982) The cellular organisation of crayfish escape behavior. In: Sandeman DC, Atwood HL (eds) The biology of Crustacea vol 4: Neural integration and behaviour. Academic Press, New York, pp 241–292

Wine JJ, Mistick DC (1977) Temporal organisation of crayfish escape behavior: delayed recruitment of peripheral inhibition. J Neurophysiol 40:905–925