THE COORDINATED ACTION OF ABDOMINAL POSTURAL AND SWIMMERET MOTOR SYSTEMS IN RELATION TO BODY TILT IN THE PITCH PLANE IN THE NORWAY LOBSTER *Nephrops norvegicus*

BY PAUL C. KNOX* AND DOUGLAS M. NEIL†

Neurobiology Laboratory, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland

Accepted 18 September 1990

Summary

1. The responses of the abdominal positioning system and the swimmerets of the Norway lobster *Nephrops norvegicus* to tilts in pitch and in other vertical planes have been investigated in intact and semi-intact preparations.

2. Tilt of the intact animal in the pitch plane evoked abdominal flexion with the head up and extension with the head down. The response amplitudes were largely independent of tilt angle, and the null point for switching between flexion and extension responses was at the 10° head-up position, which corresponds to the normal posture of the animal. Intersegmental joint angles in the abdomen were significantly different for head-up and head-down tilts. These pitch responses were dependent upon the integrity of the statocysts.

3. Tilts in different vertical planes demonstrated that the abdominal flexion/extension response was restricted to a range of tilts within ±5° of true pitch. Outside this range, tilts in both directions elicited abdominal extension, which was accompanied by asymmetrical movements of the uropods and swimmerets.

4. In semi-intact preparations, recordings from the motor supply to the abdominal superficial flexor muscles demonstrated a modulation of activity in response to tilt in the pitch plane: several small excitatory axons increased their discharge in the head-up position, while the inhibitory axon f5 fired when the head was down. With tilts in different vertical planes this pattern of firing persisted from pitch almost to roll.

5. The effects of tilt in the pitch and roll planes on the temporal and spatial parameters of swimmeret beating were studied in intact animals. Swimmeret beating was bilaterally symmetrical in pitch: vigorous in the head-down position, when the powerstrokes were directed about 25° to the side, and weak in the head-up position, when the powerstrokes were directed to the rear. Responses in roll

*Present address: Department of Pharmacology, University of Edinburgh, 1 George Square, Edinburgh EH8 9JZ.

†To whom reprint requests should be addressed.

Key words: equilibrium, abdominal posture, swimmerets, Norway lobster, *Nephrops norvegicus*.
were asymmetrical, with the powerstroke of the upper swimmerets directed at about 41° to the side.

6. Recordings of the tonic returnstroke motor neurone of the swimmeret demonstrated that its activity was modulated by tilt in the pitch plane: increasing and becoming rhythmic in the head-down position in active preparations, with the activity phase-locked to the tilt stimulus. With tilts in different vertical planes this unit showed a phase shift at intermediate angles between pitch and roll.

7. Simultaneous recordings of motor activity to the abdominal superficial flexor muscles and the swimmeret tonic returnstroke unit demonstrate closely similar, but not completely coupled, patterns of firing.

8. These results are discussed in terms of the nature of statocyst control of postural and rhythmic abdominal motor systems, the different relationships of motor activities and behavioural responses to tilts in pitch and other vertical planes, and possible neuronal mechanisms that control the interaction of the two abdominal motor systems.

Introduction

Investigations of the control of equilibrium in decapod crustaceans have contributed greatly to our understanding of the nervous control of stereotyped behavioural acts (reviewed by Neil, 1985, 1991). However, these studies of both compensatory responses (e.g. of eyes and antennae) and righting reactions (e.g. of the paired thoracic and abdominal appendages) have been made almost exclusively by imparting tilt stimuli about the animal's longitudinal axis (i.e. body roll). In response to these stimuli, the uropods and swimmerets display bilaterally reciprocal movements which are effective in producing laterally directed righting torques (uropods: Davis, 1968; Yoshino et al. 1980; swimmerets: Davis, 1968; Neil and Miyan, 1986), while the legs produce characteristic asymmetrical cycling movements (Knox and Neil, 1990). These movements are rarely, if ever, expressed when the animal is in the upright position (uropods: Takahata et al. 1984; swimmerets and legs: Cattaert and Clarac, 1983, 1987).

In the first systematic study of equilibrium responses to tilts in other vertical planes, Newland and Neil (1987) have shown that, in the Norway lobster Nephrops norvegicus (L.), the bilaterally asymmetrical responses of the uropods to body roll persist through intermediate planes. On approaching the true pitch plane, however, the response switches abruptly to one in which the uropods adopt a symmetrically open posture, which is appropriate to induce righting movements within this plane. Such a discontinuity in the reflex coupling between the statocysts, acting as the major detectors of body tilt, and the uropods has not previously been reported. If the equilibrium responses of other paired appendages also show this feature then it would seem probable that it represents a property of the descending reflex pathway and not of the individual motor systems themselves. It therefore becomes important to know if the other major abdominal equilibrium system, the swimmerets, displays these same abrupt transitions between an
asymmetrical roll reaction and a symmetrical pitch reaction and, if so, whether the latter actively contributes to pitch stability.

Previous studies of the corrective roll reactions of macrurous decapods have concentrated on the role of the bilaterally paired abdominal appendages, since their asymmetrical responses produce the appropriate differential righting effects. However, when pitch correction is being considered, an important contribution might be expected from the axial skeleto-motor system of the abdomen, since, except for its articulation with the thorax, it consists of a series of joints which act in the sagittal (i.e. pitch) plane of the body. We have investigated this possibility in *N. norvegicus* by recording both the movements of the abdomen and the activity of the motor supply to the postural flexor muscles during imposed tilts in pitch.

There is accumulating evidence for a specific interaction between abdominal posture and the equilibrium reactions of abdominal appendages to roll tilts. Asymmetrical uropod responses are expressed only during the active abdominal movements induced by substratum removal (Yoshino et al. 1980; Takahata et al. 1984, 1985; Takahata and Hisada, 1985). This so-called ‘postural facilitation’ may be mediated by specific non-spiaking local interneurones that receive input from abdominal interneurones and provide subthreshold depolarisation to the uropod motor neurones (Takahata and Hisada, 1986). Recordings of the responses of both the swimmerets and abdomen to tilts in the pitch plane provide an opportunity to study this relationship at the level of their individual motor neurones and in the context of their equilibrium reactions. Under these conditions we can be more certain that the relationship between the two systems is functionally significant.

**Materials and methods**

Adult male *N. norvegicus* of carapace length 50–90 mm were obtained from the Universities Marine Biological Station, Millport, Isle of Cumbrae. All animals were visually impaired, having been exposed to daytime light levels during capture (Shelton et al. 1985). They were maintained in communal aquarium tanks with filtered, circulated sea water until required.

The responses of both the swimmerets and the abdomen to body tilt were recorded using a closed-circuit video system (Panasonic 8050). Animals were attached to a tilting frame by a stainless-steel rod glued to the cephalothorax with dental cement. The frame was submerged in a seawater aquarium and was tilted by hand. The position of the animal in the frame could be altered to deliver tilts in different vertical planes. A detailed description of this apparatus is given by Newland and Neil (1987). To record swimmeret movements the camera was held perpendicular to the ventral surface of the abdomen. In most cases particular pairs of swimmerets (normally the final pair) and the spines on the ventral segmental ribs were painted black to improve visualization. To record postural movements of the abdomen the animal was viewed from the side. A timing signal, accurate to 10 ms, was mixed with the recorded images.
Video recordings were analysed frame by frame (representing time intervals of 20 ms) from the replayed video tapes. For temporal analyses of swimmeret beating, the timing of the end points of successive powerstrokes in the most posterior pair of swimmerets was measured over at least 20 cycles. For spatial analyses, moveable cross-hairs generated by an HVS VP110 image analysis system were overlaid with the video image. The $x,y$ coordinates of chosen points on a single frame, or on successive frames, were then sent automatically to a microcomputer. Pairs of points were used to define the orientation on the screen of the midline of the animal, the blade of a swimmeret or a segment of the abdomen, and from these values the relative angle between chosen body parts could be calculated (see Fig. 7). The angle of body tilt is expressed as the angle between the horizontal and a line projected from the tip of the rostrum to the posterior–dorsal edge of the carapace (i.e. the thorax) (Fig. 1). For a swimmeret, measurements of the angle between the bisector of the rami and the longitudinal body axis at the beginning and end of the powerstroke have been used to define its line of action (see Fig. 7B). For the abdomen, the angles of segments 1–6 and of the telson are expressed relative to the thorax (Fig. 1C). Since, in many cases, the first abdominal segment could not be resolved clearly, all data for segments 1 and 2 have been combined (1/2 in Fig. 1C). Total flexion or extension of the abdomen is expressed as the cumulative total of the movements of the individual segments.

Electrophysiological recordings of the swimmeret and tonic abdominal flexor motor activity were obtained using semi-intact preparations mounted in a tilting

---

Fig. 1. Postures adopted by *Nephrops norvegicus*. Tracings from still video frames showing the postures (A) during forward walking, (B) while standing and (D) when suspended in midwater from a tilting bar. Points on the body outline were digitized as indicated in C, to allow measurements to be made of the attitude of the thorax and of intersegmental angles in the abdomen (see Materials and methods).
stereotaxic frame (Neil and Miyan, 1986). The frame was moved through an angle of ±10° about the horizontal by an eccentric connection from a galvanometric drive (General Scanning Inc.) fed with a trapezoidal or sinusoidal driving signal from a function generator. Small windows were made in the ventral cuticle on the right side of the third abdominal segment to expose branches of the first root (R1) supplying the swimmeret and/or the third superficial root (R3s) to the tonic flexor muscle. En passant extracellular recordings were made from these nerves using polyethylene suction electrodes mounted on the stereotaxic frame. The signals were amplified, filtered and stored, together with the position signal from the galvanometric drive, on an FM tape recorder (Racal Store 4) for later filming or analysis.

For analysis, spikes were separated on the basis of size by a window discriminator and fed, together with reference pulses produced on each cycle by the function generator, to a microcomputer (Tuscan S-100). To produce an average phase histogram, spikes were allocated to histogram bins according to their time of occurrence within the period between successive reference pulses. Correlation analyses were performed between discriminated spike trains using the CED 1401 interface and SPIKE2 software package (Cambridge Electronic Design).

To reveal the central anatomy of the motor neurones supplying the tonic abdominal flexor muscles, the whole R3s root was sealed in situ in a Vaseline cup filled with 50 mmol l⁻¹ cobalt chloride. After a period of at least 24 h at 5°C, the abdominal nerve chain was dissected out, washed and treated according to the intensification method of Davis (1982), after which whole mounts were prepared.

For histological sectioning of the abdominal third superficial root, material was fixed with 4% glutaraldehyde in phosphate-buffered saline, post-fixed with 1% osmium tetroxide, dehydrated in ethanol and embedded in Araldite resin. Sections were cut at 1 μm, stained with Methylene Blue and viewed by light microscopy.

**Results**

Abdominal postural responses to body tilt

The abdomen of *N. norvegicus* is constructed on the standard decapod crustacean plan, with six jointed segments and the post-segmental telson. Segments 2–5 bear paired swimmerets, and segment 6 bears the paired uropods.

The normal posture of animals was observed while they were standing or walking freely in an open aquarium. When animals were standing, the cephalothorax was held with a slightly head-up attitude (up to 10° above the horizontal) and the abdomen was usually partially flexed (Fig. 1B). During forward locomotion, the cephalothorax maintained its head-up orientation, but the abdomen became more extended (Fig. 1A). Animals held in midwater with the cephalothorax in its natural head-up attitude, but with the legs out of contact with the
substratum, most often adopted a semi-flexed abdominal posture (Fig. 1D). It was from this position that the responses to tilt were initiated.

Imposed tilts of the animal in the pitch plane produced clear and repeatable alterations in abdominal posture: flexion when the head was up and extension when the head was down. The total extent of these movements was measured over a range of tilt amplitudes up to 60° in the head-up position and 30° in the head-down position (Fig. 2). Although there was a degree of variability in the responses observed, the posture adopted was found to be largely independent of the magnitude of tilt. The switch between these two postures was found to occur around the normally adopted attitude (i.e. 10° head up) rather than at the horizontal. Thus, at less than 10° above the horizontal an extension response, rather than a flexion, occurred. Subsequent references to 'head-up' tilts imply tilts beyond the normally adopted attitude (i.e. greater than 10° above the horizontal).

The responses of the abdomen, as well as those of its appendages, were shown to be dependent upon the integrity of the statocyst organs. Removal of the statoliths abolished all tilt-dependent movements, and the abdomen adopted an intermediate posture, with the anterior segments extended and the posterior segments flexed (Fig. 2, open circles).

To characterize abdominal posture in a more detailed way the relative extents of flexion or extension of segments 1/2, 3, 4, 5, 6 and the telson were measured separately (Fig. 3). Data from a number of different animals tilted either head up

![Fig. 2. Effect of tilting the body in the pitch plane on the posture of the abdomen. Measurements of flexion and extension in each case represent the sum of the intersegmental angles relative to the thorax. Closed circles: data obtained from three normal animals. Open circles: data obtained from an animal after removal of the statoliths from the statocysts.](image-url)
Abdominal righting reactions in lobsters

Fig. 3. Effect of body pitch on the intersegmental angles in the abdomen. Mean values for six tilts of (A) 20° head down, (B) 5° head up and (C) 20° head up. Segment numbers refer to Fig. 1C. Data were obtained from three animals.

(>10°) or head down have been pooled to yield mean values. These demonstrate that, although there was a common trend with both tilts for the anterior segments to be less flexed than the posterior segments, the degree of extension in all segments was greater during head-down tilts (Fig. 3A) than during head-up tilts (Fig. 3C). These differences are statistically significant for segments 1/2, 5 and the telson (P>0.01, Student’s t-test). A similar analysis of data obtained for head-up tilts of less than 10° (Fig. 3B) showed no significant differences from the segmental means for head-down tilts, but significant differences from values obtained on head-up tilts greater than 10° for segments 1/2, 4, 6 and the telson (P>0.01).

By tilting animals in a series of different vertical planes it was established that the response pattern described above occurred in only a very restricted range of tilt planes up to 5° either side of true pitch (Fig. 4A,C). Outside this range, imposed tilts in either direction away from the upright caused the abdomen to extend (Fig. 4B). The amplitude of this extension showed little variation as the plane of tilt was systematically moved through 90° (i.e. roll) to 175° (i.e. to be again within 5° of pitch). These extension movements were associated with bilaterally asymmetrical movements of the abdominal appendages: beating of the swimmerets on the up side (Neil and Miyan, 1986) and opening of the uropod on the down side (Newland and Neil, 1987) (Fig. 4B).

Recordings from the motor supply to the abdominal postural muscles

Since the motor supply to the flexor division of abdominal postural muscles
Fig. 4. Schematic summary of the effect of body tilt in different vertical planes on abdominal posture. In the circle, the position of the animal relative to the axis of the tilting bar is indicated for the initial pitch plane (0°). (A) Sinusoidal oscillation of ±10° at 0.25 Hz in this plane produced flexion in the head-up position and extension in the head-down position (inset figures). Outer arrows around circle indicate the range of this response (±5° around pitch). (B) In the range 5°–175° the abdomen extended on both phases of body tilt (upper inset figures) and was accompanied by asymmetrical responses of the swimmerets and uropods (lower inset figure). (C) The pitch response became re-established within ±5° of the true pitch plane (180°). The inner arrow around the circle indicates the range in which excitatory motor discharge to the superficial flexor muscles occurred with the phase relationship seen in pitch (i.e. activated in the head-up position). The solid line indicates a strong response, the broken line a weaker response (data in Fig. 6).

passes separately from the abdominal ganglia via the third superficial root (R3s), this nerve provides a most convenient point at which to monitor motor traffic concerned with postural movements. Cross-sections of fixed material revealed six
Abdominal righting reactions in lobsters

Fig. 5. (A) Transverse section of the third superficial root (R3s) of the third abdominal ganglion of *Nephrops norvegicus*, showing the profiles of its six motor axons. (B) Extracellular recording from R3s showing spontaneous activity of five motor axons. One axon, f4, is silent in this trace. (C) Extracellular recording from R3s on the right of the third segment during sinusoidal pitch of the animal through ±10° at 0.25 Hz. Upward deflection of the trace represents head down. One small and one large axon fire in the head-down position, while an axon identified as f5 (the inhibitor) fires in the head-up position.

Axons in R3s of *N. norvegicus* (Fig. 5A), and cobalt backfills (not shown) showed five axons travelling anteriorly in the dorsal region of the ipsilateral connective to ventral cell bodies in the ganglion and one axon travelling posteriorly to the next ganglion. This anatomy corresponds closely to that of the homologous nerve in both the lobster *Homarus americanus* (Thomson and Page, 1982) and the crayfish *Procambarus clarkii* (Wine et al. 1974).

Extracellular recordings from R3s in the semi-intact preparation invariably contained a number of spontaneously active units (Fig. 5B). When the preparation was tilted in the pitch plane this activity was clearly modulated: one or more of the smaller units increased their firing rate in the head-up position and decreased it in the head-down position, while a larger unit could often be seen to respond with the opposite polarity (Figs 5C and 11). A unit of the same relative size and firing characteristics as this latter type has been shown by simultaneous intracellular recordings to produce inhibitory postsynaptic potentials (IPSPs) in fibres of the superficial flexor muscles (Fowler and Neil, 1989). The activity shown in Fig. 5C, therefore, most probably includes the peripheral inhibitory motor axon firing reciprocally to the other excitatory axons.

The motor responses of R3s to tilts in different vertical planes between pitch and roll was also examined. In contrast to the changing pattern of abdominal movement observed within 5° of the pitch plane, the strong modulation of the response of motor units observed in pitch persisted up to at least 45° away from this plane, and disappeared completely only at angles close to roll, where the firing
of units was reduced below the spontaneous resting level (inner arrow in Fig. 4). This was illustrated most clearly by constructing phase histograms of unit activity over a number of cycles of sinusoidal stimulation (Fig. 6). As the plane of tilt changed from pitch to roll the motor response became less sharply defined, until in roll it was completely tonic. Thus, there was a wide region in which the flexor motor activity was modulated, yet only a persistent extension was observed (Fig. 4).
Table 1. *Spatial and temporal parameters of swimmeret beating during body tilt*

<table>
<thead>
<tr>
<th>Tilt</th>
<th>Type of beat</th>
<th>Angle of powerstroke (degrees)</th>
<th>Period of beat (s)</th>
<th>State of abdomen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upright</td>
<td>Bilateral</td>
<td>25±7 (N=12)</td>
<td>0.36±0.06 (N=125)</td>
<td>Extended</td>
</tr>
<tr>
<td>Roll</td>
<td>Unilateral on up side</td>
<td>41±6 (N=12)</td>
<td>0.36±0.04 (N=126)</td>
<td>Extended</td>
</tr>
<tr>
<td>Pitch head down</td>
<td>Bilateral</td>
<td>25±8 (N=12)</td>
<td>0.37±0.05 (N=119)</td>
<td>Extended</td>
</tr>
<tr>
<td>Pitch head up</td>
<td>Bilateral</td>
<td>3±8 (N=12)</td>
<td>0.36±0.07 (N=84)</td>
<td>Flexed</td>
</tr>
</tbody>
</table>

*Responses of the swimmerets to body tilt*

During experiments on the abdominal postural responses to tilts in pitch it became clear that the swimmerets also exhibited responses in this plane which were distinct from those previously observed in other situations (Cattaert and Clarac, 1983, 1987; Neil and Miyan, 1986). The patterns of swimmeret beating in the upright animal and during responses to roll and to pitch, both head up and head down, were therefore examined in terms of both a temporal parameter, the period of the beat, and a spatial parameter, the line of action of the powerstroke (Table 1 and Fig. 7).

Swimmeret beating in the unrestrained animal occurred with a period dependent on the behavioural context. However, in the tethered animal held in its normal posture out of contact with the substratum, the period of beat had a consistent mean value of 0.36 s. Under these circumstances swimmeret beating was usually associated with an abdominal extension. The line of action of the swimmeret powerstrokes was not directly rearwards, but made an angle of approximately 25° with the longitudinal body axis, thus producing a lateral force component. The swimmerets of the two sides were bilaterally symmetrical in this respect.

In response to roll, only the swimmerets on the raised side exhibited consistent and strong beating, while those on the downward side would beat weakly if at all. Although the period of beating was little different from that occurring in the upright position (Table 1), the line of action of the upward swimmerets was directed more laterally, making an angle of around 41° with the longitudinal body axis (Fig. 7D).

In response to pitch of the body, swimmeret beating was also induced but was always bilaterally symmetrical. During head-down tilt, beating was vigorous, with a mean period of 0.37 s, and continued as long as the animal remained in this position. The powerstroke angle was around 25° to the body axis (Fig. 7A). During head-up tilts, beating was weak and irregular, although with a similar
period. When it occurred, the powerstroke of each beat was directed almost exactly to the rear (mean value $3^\circ$), unlike the case in the other postures (Fig. 7C).

**Recordings from the motor supply to the swimmeret muscles**

The motor supply to the swimmeret is carried by the first abdominal root, which branches to form a posterior trunk supplying the powerstroke (PS) muscles and
steering muscles, and an anterior branch trunk, which supplies the returnstroke (RS) muscles as well as sending branches to the abdominal musculature and sensory hairs on the lateral abdominal wall (Neil and Miyan, 1986). No units showing responsiveness to water movements were encountered in branch a12, and so this recording site was chosen in order to select RS units alone, in the absence of sensory fibres (Fig. 8A). Of particular interest was a tonic RS unit which was found by Neil and Miyan (1986) to exhibit modulated activity in response to body roll.

In active preparations, alternating activity could be recorded in the PS and RS motor branches, with the latter clearly involving the tonic unit (Fig. 8B). In the absence of rhythmic bursting, activity was found to persist in the tonic RS unit, but not in any units of the PS branch.
Both these patterns of activity in the tonic RS unit could be modulated by tilt in the pitch plane. In active preparations, head-down tilt induced rhythmic firing (Fig. 8C). Phase histograms of this RS unit activity constructed over several cycles of tilt contain a number of clear peaks, indicative of phase locking (Fig. 9). This suggests that both an activation and a phase resetting of the rhythmic activity occur at specific angles of tilt. In less active preparations, in which no observable beating could be seen, head-down tilt nevertheless induced an elevated level of tonic activity in the tonic RS unit (Fig. 8D).

Head-up tilts had the opposite effect on RS unit activity. In active preparations rhythmic activity became tonic (Fig. 8C), and in less active preparations the level of tonic activity was reduced (Fig. 8D).

Outside the pitch plane the tonic activity of the RS unit continued to be modulated by tilt, but a transition in the phase of its firing occurred within 45° of this plane (i.e. between 270° and 315° for the right-side unit in Fig. 10). This contrasts with the phase shift of the abdominal flexor motor neurones, which occurred close to roll (Figs 4 and 6).

Relationship of activity in swimmeret and superficial flexor muscle motor neurones

Simultaneous recordings from branch a12 of abdominal root 1, supplying the swimmeret RS muscles, and from root R3s, supplying the superficial flexor muscles, during imposed pitch of the preparation confirmed the evidence of the individual recordings that the RS tonic unit was co-activated with the flexor
Abdominal righting reactions in lobsters

Fig. 10. Phase histograms of activity of the tonic returnstroke units to left and right swimmerets of the third abdominal ganglion during sinusoidal tilts of ±10° at 0.25 Hz in different vertical planes. Data were collected over 10 cycles of stimulation and allocated to 100 bins, using downward points on the stimulus trace (i.e. head-down position in pitch, left-side-down position in roll) as reference points for the beginning of the cycle (phase point 0). In the circle, the position of the animal relative to the axis of the tilting bar is indicated for the initial pitch plane (0°). The inset diagrams indicate changes in the position of the animal relative to the tilt bar: A, 0° (pitch); B, 45°; C, 90° (roll); D, 135°; E, 180° (pitch).

inhibitor unit in head-down positions, while the excitatory flexor motor neurones fired in head-up positions (Figs 11 and 12A). Other general mechanosensory stimuli induced a similar form of reciprocal activation. However, in all these cases correlation analysis between spikes in each train indicated that there was no
preferred timing relationship between their discharges (Fig. 12B). This suggests that any coupling between these units is indirect and probably due to common inputs rather than direct synaptic connections.

Discussion

Abdominal postural responses to tilt

Although the control of abdominal posture has been extensively studied in both crayfish (reviewed by Page, 1982) and nephropid lobsters (Jones and Page, 1986a–c), little attention has been paid to the nature of its reflex activation by physiological stimuli. Tatsumi et al. (1985) have studied some aspects of tilt responses in crayfish, but the only reflex action studied in detail is the extension response elicited by removing the substratum from beneath the animal's legs (Larimer and Eggleton, 1971; Sokolove, 1973), which has become a standard experimental protocol (Williams and Larimer, 1981; Takahata and Hisada, 1985). Most emphasis has been placed on the 'command' concept of motor activation in the abdominal positioning system. Studies involving the electrical stimulation of connective nerve bundles in isolated abdomens (Evoy and Kennedy, 1967; Bowerman and Larimer, 1974; Williams and Larimer, 1981) and the intracellular recording of premotor interneurones involved in abdominal positioning (Larimer and Moore, 1984; Jellies and Larimer, 1986) have concluded that a large number
Abdominal righting reactions in lobsters

Fig. 12. (A) Simultaneous extracellular recordings from the swimmeret tonic return-stroke unit in branch a12 of the first root (upper trace) and the superficial flexor motor neurones in R3s root (lower trace) of the third right abdominal ganglion in response to sinusoidal tilts of the body through ±10° at 0.25 Hz in the pitch plane. (B) Correlation analysis of activities of the tonic returnstroke unit (reference spikes) and the f5 inhibitory axon in R3s (large spikes in lower trace of A). Bin width, 12 ms; number of reference spikes, 246. The origin of the plot represents the times of occurrence of the reference spikes.

of intersegmental interneurones interact with each other by serial and parallel connections to form the motor programmes (Larimer, 1988). By their nature these findings, derived from the isolated nervous system, are difficult to relate to normal motor behaviour. In contrast, the investigation reported here of the contribution of the abdominal postural system to righting in the pitch plane was performed on intact or near-intact preparations, and therefore not only identifies an accessible motor system for more detailed studies of equilibrium reflex pathways but also extends our knowledge of its physiological activation.

An example of the importance of this approach is the finding that in its normal posture N. norvegicus adopts a head-up attitude (Fig. 2), and that this acts as the physiological null point between head-up and head-down righting reactions.
A similar feature exists in the equilibrium responses of crabs (Janse and Sandeman, 1979; Neil, 1982). This has important consequences for interpreting experiments in which platform release was used to induce abdominal extension (Jellies and Larimer, 1986), since it was assumed that the effective stimulus for this reaction was loss of leg contact. However, our results suggest that, although this might act to trigger the response, the form of abdominal movement that occurs will be dictated by the position of the animal in the pitch plane. In at least some of the crayfish experiments the animal appears to have been held with its carapace horizontal (Page, 1975), and so, if crayfish react as does *N. norvegicus*, it may be appropriate to regard this abdominal extension as a head-down righting reaction. Moreover, it should be possible to elicit a flexion response to platform release by holding the animal in a head-up posture. This may be an exploitable finding for investigating the neuronal circuitry which controls not only the extension (Larimer, 1990) but also the flexion component of abdominal positioning.

*Types of swimmeret beat*

Our results demonstrate that for imposed tilts about the major body axes the patterns of swimmeret beating that are evoked in each case represent appropriate corrective reactions. Thus, following an imposed roll of the body the asymmetrical lateral beating of the upward swimmerets produces a righting torque in the same transverse plane. In a similar way, the pitch responses, being bilaterally symmetrical and operating in concert with the abdominal position, produce righting reactions that act in the sagittal plane of the body. Responses to head-up and head-down positioning are distinguishable by the degree of ipsilateral rotation that occurs.

These various tilt-related forms of swimmeret beating must be added to the accumulating catalogue of different swimmeret behaviours observed in lobsters. Distinct patterns of swimmeret beating occur in walking locomotion, midwater swimming, the defensive 'startle' response and in gravid females (Cattaert and Clarac, 1983, 1987). These patterns in upright animals differ from each other in terms of the period and amplitude of swimmeret movement and the metachronal delay between segments, but they all appear to share the common feature of a tight bilateral coupling of swimmeret movements. In this respect some of the tilt-related forms of swimmeret beating are exceptional, since they display degrees of redirection of the swimmeret powerstroke on one or both sides, and in some cases a complete bilateral uncoupling of the rhythmic activity.

The possible neuronal basis for such bilateral disconnection has been discussed by Paul and Mulloney (1985a, b), who found that coupling between hemiganglionic swimmeret oscillators in crayfish is based on a number of weak connections acting in parallel, rather than a single strong link. It is possible that their effect is sufficient to maintain bilateral coupling under most conditions, while being susceptible to suppression by inhibitory inputs. To test this prediction it will be necessary to determine whether descending statocyst interneurones make appropriate inhibitory connections onto bilaterally projecting swimmeret interneurones.
Another feature of the swimmeret neuronal circuitry revealed in our recordings is the entrainment of even the more tonic motor neurones to the rhythm produced by the central pattern generator (CPG). Thus, the tonic RS unit shows a weak but distinct coupling to the swimmeret CPG when the animal is tilted in the pitch plane (Fig. 9). In this respect there may be differences depending on the plane of tilt, since we have previously reported on the basis of experiments performed only in roll that this motor neurone shows no evidence of input from the CPG (Neil and Miyan, 1986). We now conclude that, despite such differences in sensitivity to different planes of tilt, none of the swimmeret motor neurones appears to be totally isolated from the influence of the CPG. The tonic RS unit behaves in a similar way to the basipodite steering muscles M9 and medial M10 (Neil and Miyan, 1986), responding tonically to the drive from descending statocyst input in the absence of swimmeret beating, but becoming entrained to particular phases of the swimmeret rhythm when it occurs (M9 and M10 to the powerstroke, the tonic RS unit to the returnstroke).

The association of swimmeret movements with abdominal postures

An association exists in *N. norvegicus* between the different swimmeret righting responses and particular abdominal postures. Asymmetrical responses of swimmerets to both left-up and right-up roll tilts occur with abdominal extension, while the symmetrical pitch responses occur with either flexion or extension, depending on whether it is a head-up or head-down tilt. In all cases there is a clear functional utility in the relationship. The abdominal extension in roll allows lateral swimmeret beats to generate the appropriate rotational righting torque. The directly rearward swimmeret beating in the head-up position takes place in association with partial flexion of the abdomen, so that the powerstrokes are directed downwards. This redirected propulsion, although weak, will create a turning moment about the centre of mass of the animal to correct the head-up attitude. In a head-down position the strong symmetrical half-lateral beating of all swimmerets will contribute a propulsive force that has both ipsilateral and rearward components. The overall effect of this response will be to correct and maintain the orientation of the animal in the pitch plane and provide thrust along the line of the abdomen. Since the animal adopts an extended posture, a righting torque will be induced about its centre of mass to correct the head-down attitude. These interpretations have been confirmed by a series of free-fall experiments in which animals were released in midwater with different body orientations (Newland and Neil, 1987).

The movements of the swimmerets and abdomen during tilts in different vertical planes show the same abrupt phase transitions adjacent to true pitch plane as have been described for the uropods (Newland and Neil, 1987). This suggests that a common basis exists for these motor patterns at a premotor level. However, we have insufficient knowledge at present about the response characteristics of either the descending interneurones or the final motor pathways to make more than preliminary suggestions about the source of the patterning. The movements of the
uropods in different planes of tilt have been analysed, but not the underlying motor activities (Newland and Neil, 1987). In the swimmerets the motor activities of the steering muscles have been recorded in roll, but not in other planes (Neil and Miyan, 1986). There is a suggestion from the present study that the phase transitions of the tonic RS unit do not correspond to those of the lateral swimmeret beat, but this result is difficult to interpret since the action the RS unit in steering has not been established. The most relevant data obtained so far are for the abdominal flexor system, which clearly contributes in a direct way to righting. Even in this case, however, the picture remains incomplete since no data are available for the behaviour of the extensor system during righting.

A large discrepancy exists between the narrow range of expression of the abdominal flexion response (in the head-down position close to pitch) and the much wider range over which flexor motor activity occurs (Fig. 4). However, this pattern of motor activity corresponds closely to the wide acceptance angles of the statocyst pitch interneurones in *N. norvegicus* (Knox et al. 1987). This suggests that there may be a relatively direct drive from these interneurones onto the flexor motor neurones, and that the discrepancy between flexor muscle activity and abdominal movement might be resolved peripherally. One way in which this could occur is through the co-contraction of the extensor muscles with the flexor muscles over part of the range, so that the observed movements result from a mechanical integration of opposing forces. The occurrence of co-contraction in antagonist muscle sets is well-established in the reflex responses of both the oculomotor and antennal motor systems (Mellon and Lorton, 1977; Neil et al. 1982) and may be a more widespread feature of neuromuscular integration in crustaceans than has previously been recognised (Neil, 1985). This must now be examined in the abdominal postural motor system.

Our results show a clear relationship between the firing of motor units in the abdominal and swimmeret systems (Figs 11 and 12A), which does not appear to be due to a direct connectivity between them (Fig. 12B), but may reflect coupling in the drive from some premotor source. The nature of this drive is not known, but two main possibilities exist. Descending statocyst interneurones may project in parallel onto the motor system for abdominal posture as well as onto those of the swimmerets (and uropods). Indeed, interneurones with synaptic connections onto both swimmeret motor neurones and abdominal extensor motor neurones do exist in *Homarus gammarus* (Barthe et al. 1988) and crayfish *Procambarus clarkii* (Murchison and Larimer, 1990). However, since the abdominal flexor motor neurones and swimmeret tonic RS unit are modulated differently as the angle of tilt changes (Figs 6 and 10), such common interneuronal inputs cannot alone control these motor systems.

A second possibility, not necessarily mutually exclusive to the first, is that these relationships represent the expression of 'postural facilitation' (Takahata and Hisada, 1985, 1986), whereby activation of the abdominal postural system is necessary to gate the righting reactions of abdominal appendages such as the swimmerets. Our results complicate this concept since they demonstrate that the
Abdominal postural response is itself a righting reaction, capable of being driven to flexion or extension according to the imposed tilt stimulus. The neuronal control of ‘postural facilitation’ during body tilt must, therefore, incorporate an interneuronal drive from the statocysts onto the abdominal flexors and extensors, in addition to any serial connections such as those proposed by Takahata and Hisada (1986) between the motor systems of the abdomen and its appendages.

We would like to acknowledge the assistance of Mr G. Tobasnick with video image capture. PK was supported by a Studentship from the SERC.

References


