STATOCYST CONTROL OF UROPOD RIGHTING REACTIONS IN DIFFERENT PLANES OF BODY TILT IN THE NORWAY LOBSTER, *NEPHROPS NORVEGICUS*

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SUMMARY

1. The righting reactions of the uropod exopodites of the Norway lobster, *Nephrops norvegicus*, induced by stimulation of the statocysts, were studied during both imposed body tilts in different vertical planes and freely expressed manoeuvres.

2. The opening and closing movements of the uropod exopodite were brought about by the reciprocal activity of the dorsal abductor muscles and the reductor muscles, respectively.

3. The uropods were held symmetrically open when the animal was upright, but adopted an asymmetrical pattern, with the downward uropod open and the upward uropod closed, during imposed body roll.

4. In an imposed pitch of the body, the uropods closed symmetrically on head-down movement and opened symmetrically on head-up movement. The response pattern which occured in roll persisted through intermediate vertical planes to within 10° of true pitch.

5. Removal of the statolith from a single statocyst caused the zone of symmetrical uropod responses to shift towards the operated side, but did not alter its angular dimensions. Bilateral statolith removal abolished the uropod reaction to tilt.

6. Animals released in mid-water exactly in the pitch plane recovered their upright posture by a pitching movement, using symmetrical motor reactions of the abdomen and its appendages. Animals released at all other possible orientations used an initial rolling movement, involving an asymmetrical disposition of the appendages. The chelipeds did not contribute significantly to righting in roll, but both the lateral beating of the swimmerets and the asymmetrical disposition of the uropods produced righting torques as the animal descended through the water.

7. These results are discussed in terms of the hydromechanical effect of asymmetrical uropod postures, and the functional significance of the distinct switching between symmetrical and asymmetrical patterns. Implications for the mechanisms of statocyst control of uropod righting reactions, in terms of both the magnitude and the direction of body tilt, are also considered.

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INTRODUCTION

In decapod crustaceans changes in the postural attitude of the uropods produce righting reactions which actively restore the whole body to its preferred orientation (Davis, 1968; Yoshino, Takahata & Hisada, 1980). The flattened uropod blades act as passive drag-based elements to redirect externally applied forces, such as those produced by water currents impinging on the body, to produce righting torque. These uropod righting movements are essentially tonic in nature, and we now know much about the neuronal pathways which control their asymmetrical positioning in response to lateral tilts (Takahata, Yoshino & Hisada, 1985). However, other aspects of their function have received virtually no attention. Thus tilt experiments have been performed exclusively in roll, but we know nothing about the nature of the response in pitch, or in other planes of tilt. Also, nothing has been reported about the normal occurrence of righting reactions in freely moving animals.

Results of a field study of the escape behaviour of *Nephrops* (Newland & Chapman, 1985) suggest one context in which the uropod righting responses are clearly adaptive. Following a sequence of escape swimming initiated by a stimulus to the abdomen, an animal may achieve a height of up to 1 m from the sea bed, and from this point it descends passively to the bottom using movements of the chelae, swimmerets and uropods to correct deviations from an upright attitude. Such mid-water righting manoeuvres will ensure that the lobster lands in an upright posture, ready for further evasive locomotory behaviour. In this clear example of righting behaviour there appears to be close control of body position about all horizontal axes, and this raises the question of whether the uropods can contribute to stabilization in planes other than roll. The necessity for omnidirectional control is also suggested by the finding that *Nephrops* orientate their bodies parallel to the flowing water current (Newland & Chapman, 1985). While the animal moves towards this preferred downstream orientation water flow must act on its body from all possible directions, but subsequently stability in the pitch plane must assume primary importance.

Detection of a deviation from a particular body position in decapod crustaceans is mediated by leg proprioception, vision and primarily through the action of the balance organs, the statocysts (see review by Neil, 1985). The organization of statocyst sensory hairs confers sensitivity to both the direction and the magnitude of imposed tilt (Stein, 1975; Schöne, 1975), and we now have much information for the crayfish about the projection of statocyst sensory receptors onto interneurones (Takahata & Hisada, 1982a,b), and the connections from some of these onto the uropod motoneurones (Takahata *et al.* 1985). However, these data provide no information about the behaviour of the reflex system in response to tilts about other horizontal axes. In particular, it remains to be determined how an omnidirectionally sensitive statocyst controls the attitude of the uropods, which move predominantly in only one plane.

Therefore, in this study we have examined the contribution of various append ages, and particularly the uropods, to righting behaviour of *Nephrops* both during imposed tilts about different horizontal body axes and in free-fall through the water

column. More specifically, we have addressed the question of how the direction of imposed body tilt, as encoded by the pattern of stimulation of statocyst hairs, is transformed into symmetrical and asymmetrical uropod movements observed with the changing magnitude, plane and direction of body tilt.

MATERIALS AND METHODS

Experiments were carried out on *Nephrops* of 30–50 mm carapace length. These were maintained in running seawater tanks at 13–15°C until required. All animals were visually impaired, due to exposure to daytime light levels during capture (Shelton, Gaten & Chapman, 1985).

Animals were fixed to a tilt apparatus which was submerged in a large (1·0×0·5×0·45 m) seawater aquarium. They were provided with a platform on which to stand before and after each test. The tilt apparatus allowed rotation in yaw, pitch and roll (Fig. 1A) so that animals could be rotated through a full circle along particular planes of tilt. Fig. 1B shows the coordinate system used to define these tilts within a spatial frame of reference (Schöne, 1984).

Since uropod steering movements occurred only when animals were actively extending or flexing their abdomens, a standard procedure was adopted to induce
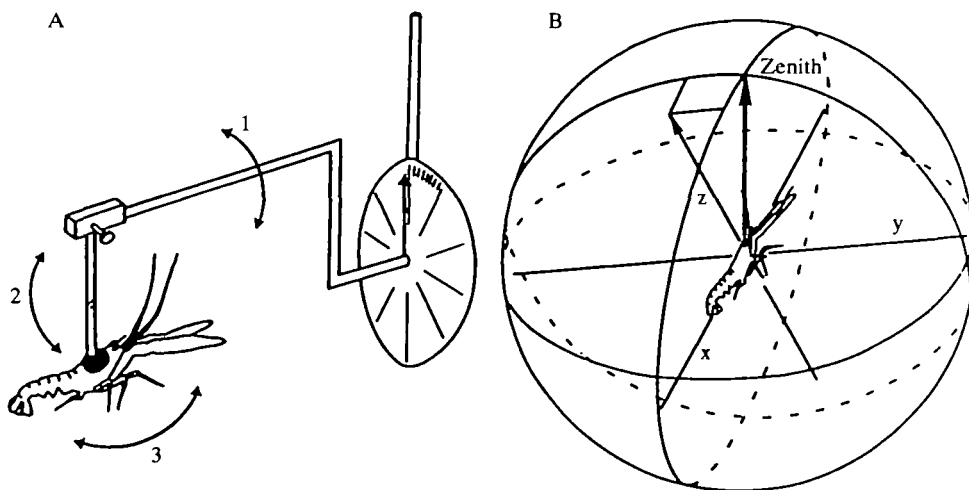

Fig. 1. (A) Tilting apparatus used to examine the tonic righting reactions of *Nephrops*. Tilts were produced by rotation of the cranked bar (1). The vertical plane of tilt was dictated by the yaw position of the animal (2) which could be altered by rotating the vertical bar in the angle block. The animal was moved through oblique planes of tilt by changing the angle of the lower part of the vertical bar about its central pivot (3). (B) The coordinate system used to define the tilt of the animal. The sphere represents the spatial frame of reference, based on gravity and the horizontal plane, with the zenith indicated by the wide arrow. The primary axes of the animal (x = longitudinal, y = transverse, z = dorsoventral) are projected onto the surface of the sphere. The projection of the z axis (narrow arrow) gives a composite measure of the degree of tilt about both x and y axes (in the illustration a combination of head-up and left-side down). In Fig. 7 data are plotted in this manner on a polar orthographic projection of the sphere, i.e. viewed from the zenith.

this state of activity prior to each imposed tilt. A series of gentle taps to the tilt apparatus was found to induce abdominal movement, such that the uropod response to a subsequent tilt was reliably elicited. Body and uropod positions were recorded using a closed-circuit video system (Panasonic 8050), and measured from the replayed video signal either directly through the monitor, or by using an automatic image-analysing unit (HVS VP110) interfaced to a microcomputer (Tuscan S-100). The positions of uropods were determined 20 s after arrival at a given angle of tilt.

To remove a statolith from the statocyst, a small opening was made on the dorsal surface of the basal antennular segment directly above the statocyst sac. A fine jet of water was injected into the sac to wash out the statolith. This procedure was repeated until all sediment particles were removed. Animals were allowed to recover for at least 30 min before being used in experiments.

To record uropod muscle activities, sinusoidal body oscillations of ±30° were imparted using a motorized drive linked eccentrically to the tilting bar, as used by Schöne, Neil, Stein & Carlstead (1976). Angular position was monitored using a drive to a variable potentiometer. Myographic recordings were made from the uropod muscles by implanting pairs of Teflon-coated silver wire electrodes (0·075 mm in diameter), and fixing them in place with cyanoacrylate glue. Myographic and angular position signals were amplified, displayed on an oscilloscope and stored on a four-channel FM tape recorder (Racal Store 4).

Free-fall behaviour was studied by releasing animals at various positions, including completely inverted, just below the water surface. The animals' reactions were recorded on video tape, and righting times were determined from the replayed sequences. To determine the contribution to righting made by different appendages, some animals were induced to autotomize their claws. Some of these and other intact animals also had their uropods fixed to the telson in the closed position.

<div align="center">RESULTS</div>

<div align="center">*Uropod muscles and their action*</div>

The most obvious components of the uropod righting reactions in roll are the opening and closing movements of the exopodites which occur about their proximal, major articulations (Fig. 2). Various names have been given by different authors to the muscles of the uropods, namely: abductors/adductors (Schmidt, 1915), promotors/remoters (Larimer & Kennedy, 1969) and openers/closers (Takahata *et al.* 1985). A full description of these, and of other muscles which act about a distal articulation of the exopodite in nephropid lobsters, is given by D. M. Neil, W. S. Fowler & P. L. Newland (in preparation). The present study has been concerned only with the tonic members of the antagonist muscle groups, since it has been found that the righting reactions of the uropods are produced by the actions of these muscles alone.

The reductor muscle, which closes the exopodite, originates on the proximal edge of the protopodite and inserts on the dorsal surface of the exopodite, just beyond the distal articulation (Fig. 2). Two dorsal abductor muscles, which open the exopodite,
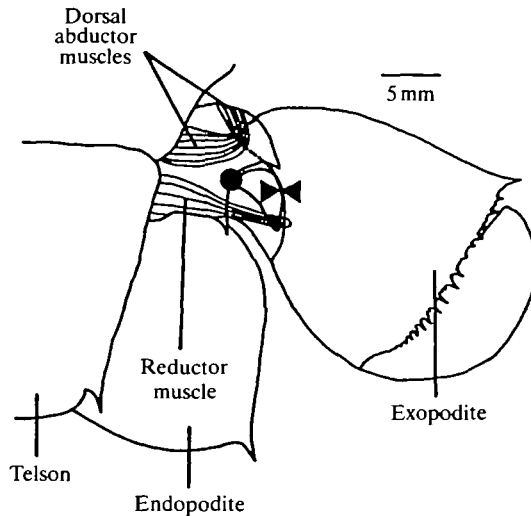
Fig. 2. Disposition of the muscles involved in the tonic righting reaction about the primary, dorsoventral articulation (●) and the secondary horizontal articulation (▶◀) of the uropod exopodite.

originate ventrally in the protopodite and insert on the dorsal, anterior tip of the exopodite.

As an upright animal extends its abdomen, in response to removal of the platform beneath the legs, the uropods of both sides are expanded symmetrically. This involves the opening of the exopodites relative to the endopodites, which is brought about by activity of the dorsal abductor muscles alone. However, a body tilt in roll evokes an asymmetrical response of the uropods, the exopodite on the down-side opening and the exopodite on the up-side closing. During these body tilts, only the dorsal abductor and reductor muscles are involved in generating the uropod movements. Activity recorded from the homologous muscles of the two uropods during ±30° body tilts around the upright position demonstrates their reciprocal action. A tilt to one side up is accompanied by activity in the ipsilateral reductor muscle, and in the contralateral dorsal abductor muscles (Fig. 3).

Uropod response to gravity input

To determine how the bilateral pattern of coordinated uropod movement changes with the direction of imposed tilt, animals were subjected to a series of full-circle tilts in various vertical and oblique planes. The experimental procedure was standardized by activating the animals prior to tilt (see Materials and Methods).

Reactions in roll

Both uropods were held open at the 0° body position. Body roll to the right-side down resulted in the left uropod closing while the right uropod remained open. This asymmetrical pattern was maintained through all angles up to the inverted (180°), where the left uropod opened once again. On continued body roll away from the

Right
dorsal
abductor
muscle

Left
dorsal
abductor
muscle

Body
roll

Left
reductor
muscle
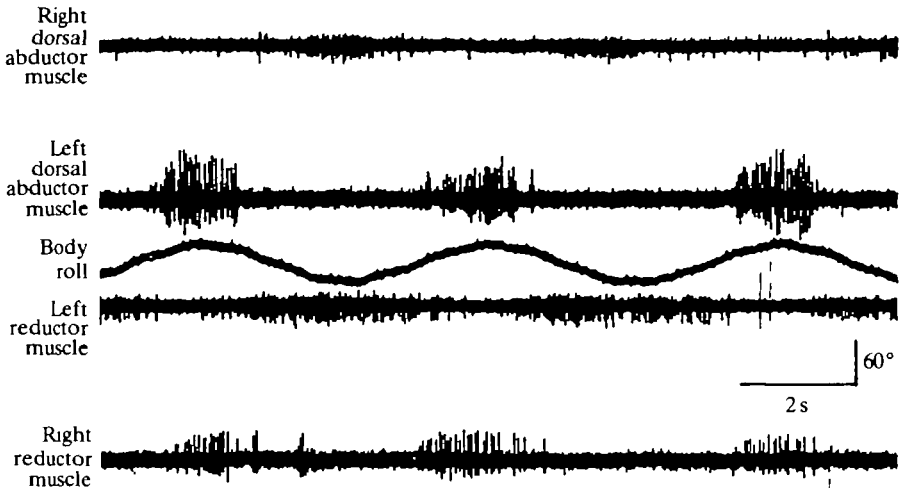
Right
reductor
muscle

|60°

2 s

Fig. 3. Electromyograms of the dorsal abductor muscles and the reductor muscles of the left and right uropod exopodites during a sinusoidal body tilt in roll through ±30°. Upward movement of the body trace represents right-side up roll.

inverted, the right uropod closed and this reversed asymmetrical pattern was maintained until close to the upright, where the original symmetrically open uropod pattern was resumed. Therefore, three possible uropod positions were displayed: (1) asymmetrical right-side fully open, left-side fully closed; (2) asymmetrical left-side fully open, right-side fully closed; (3) both uropods symmetrically open. However, at no position were the uropods symmetrically closed, and with the animals alerted as described, no intermediate uropod positions were consistently maintained.

The uropod response curve to a full-circle roll, obtained from measurements at 30° increments, approximates to a square wave (Fig. 4A). To determine with more accuracy the true sensitivity of the system, animals were rolled in 3° increments about the upright. The transition between the open and closed positions (or vice-versa) was achieved within a single 3° shift from the upright (0° body position) (Fig. 4B). Similar results were obtained about the inverted position. The uropod response curve therefore almost exactly follows a square wave.

Reactions in pitch

Uropod responses to body tilts in the pitch plane differed markedly from those in roll (Fig. 5). From an initial open posture at the upright, the uropods closed symmetrically during head-down tilting, then switched to be symmetrically open at 180°, and remained open until they both closed again at 330°. The transition point between one uropod pattern and another therefore shifted from 30° (i.e. during the initial head-down movement) to 330° (i.e. during the final phase of head-up movement). This new transition point persisted over subsequent cycles of tilt. In roll, no such effects were obtained.
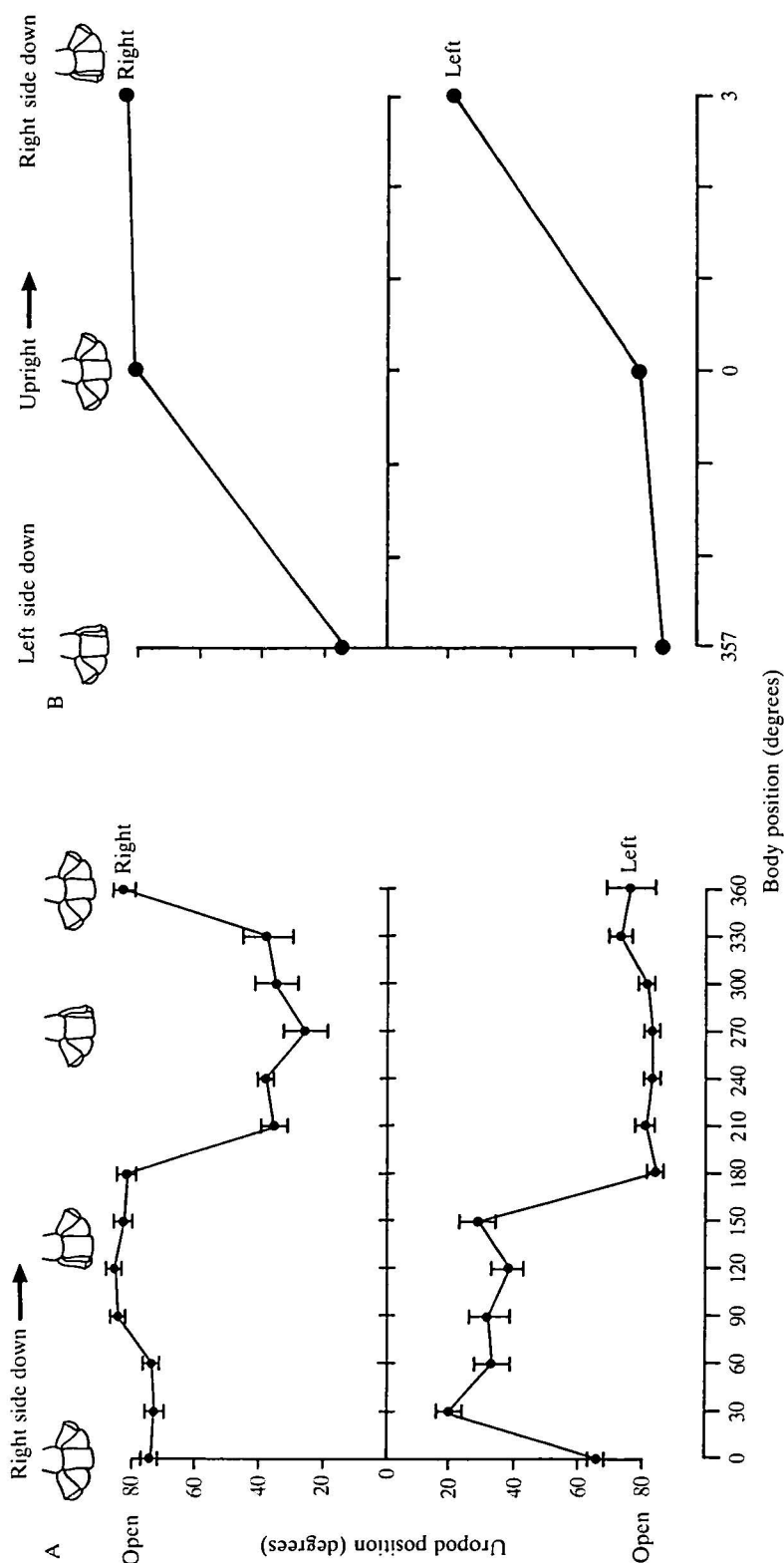
Fig. 4. (A) Responses of the right (upper curve) and left (lower curve) uropod exopodites of an intact animal to a full circle tilt in roll, executed in 30° increments and beginning with rotation to the right-side down. Measurements were taken of the angle between the lateral edge of the exopodite and the midline of the body. Each point represents the mean value of measurements from 14 animals. Vertical bars indicate ±2 s.D. The insets show the uropod postures adopted. (B) A more accurate determination of the transition between the symmetrical and asymmetrical uropod postures adopted on rolling away from the upright position. Representative data from one animal. Transitions occur within a 3° interval.
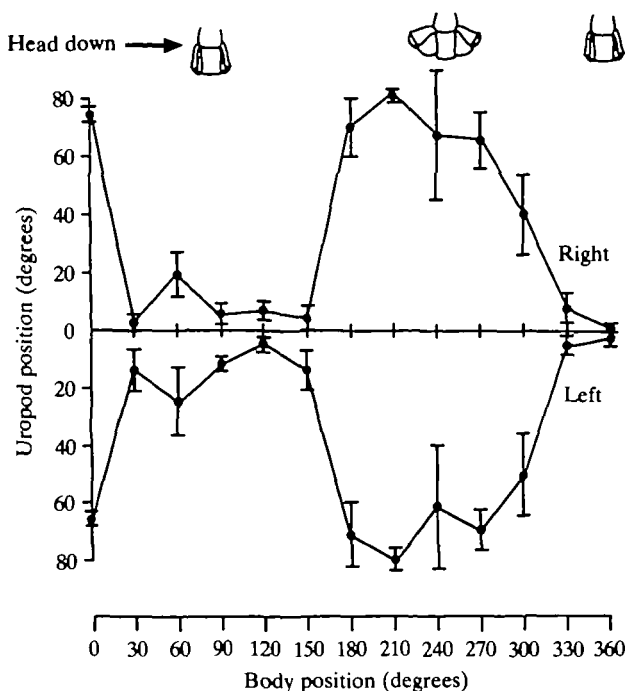
Fig. 5. Responses of the right (upper curve) and left (lower curve) uropod exopodites of an intact animal to a full circle tilt in pitch, beginning with rotation to head-down. Each point represents the mean value of measurements from eight animals. Vertical bars represent ±2 S.D.

Reactions in other planes

The very different nature of the pitch and roll responses indicates that the sensory control is complex, since the reflex system can operate in either an asymmetrical or a symmetrical mode. Transition points must exist between these modes, and knowledge of the positions of these transitions provides essential information for interpreting the organization of the reflex system. A series of experiments was therefore performed in different vertical planes.

The results of these tests at intermediate planes around a full circle (Fig. 6), clearly show that the symmetrical response pattern is limited to a region of ±10° around the true pitch plane. The asymmetrical pattern seen in roll is expressed in all other planes outside this region.

The consistent bistable nature of the uropod response, with the uropods being held either fully open or fully closed, allows us to use a symbolic form of notation to denote uropod responses to tilts in a number of different planes (Figs 1B, 7B).

Experiments were also performed along oblique planes of tilt (Fig. 7C,D) so that a given tilt position was approached from a different direction. The results indicate that the transition points between the two patterns of uropod response occur at the same position when approached along an oblique plane (Fig. 7C,D) as they do when reached by tilting along vertical planes (Fig. 7A,B). These results also confirm the

limited range around the pure pitch plane in which the symmetrical pattern of opening and closing of the uropods was adopted, compared to the wide range over which the uropods were held asymmetrically.

Statocyst influence on uropod movement

Previous studies of the influence of the statocyst organs on equilibrium responses have examined the effect of removing single statoliths, without damaging the sensory hairs (Schöne, 1954; Yoshino *et al.* 1980). Thus, by eliminating the shearing
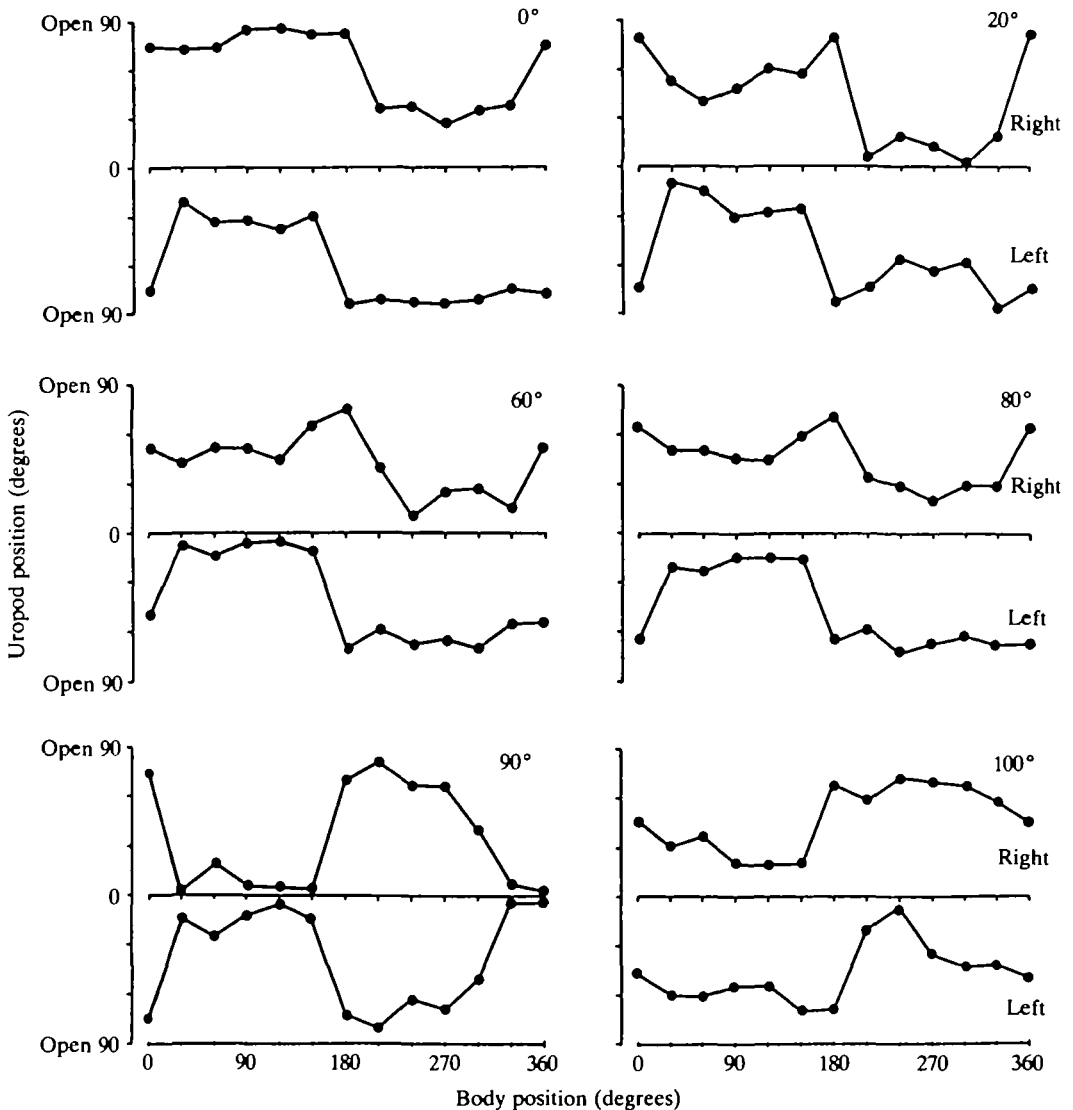

Fig. 6. Responses of the right (upper curves) and left (lower curves) uropod exopodites of an intact animal to tilts in different vertical planes from roll (0°) through to pitch (90°) and beyond. Each point represents the mean value of measurements from five animals.
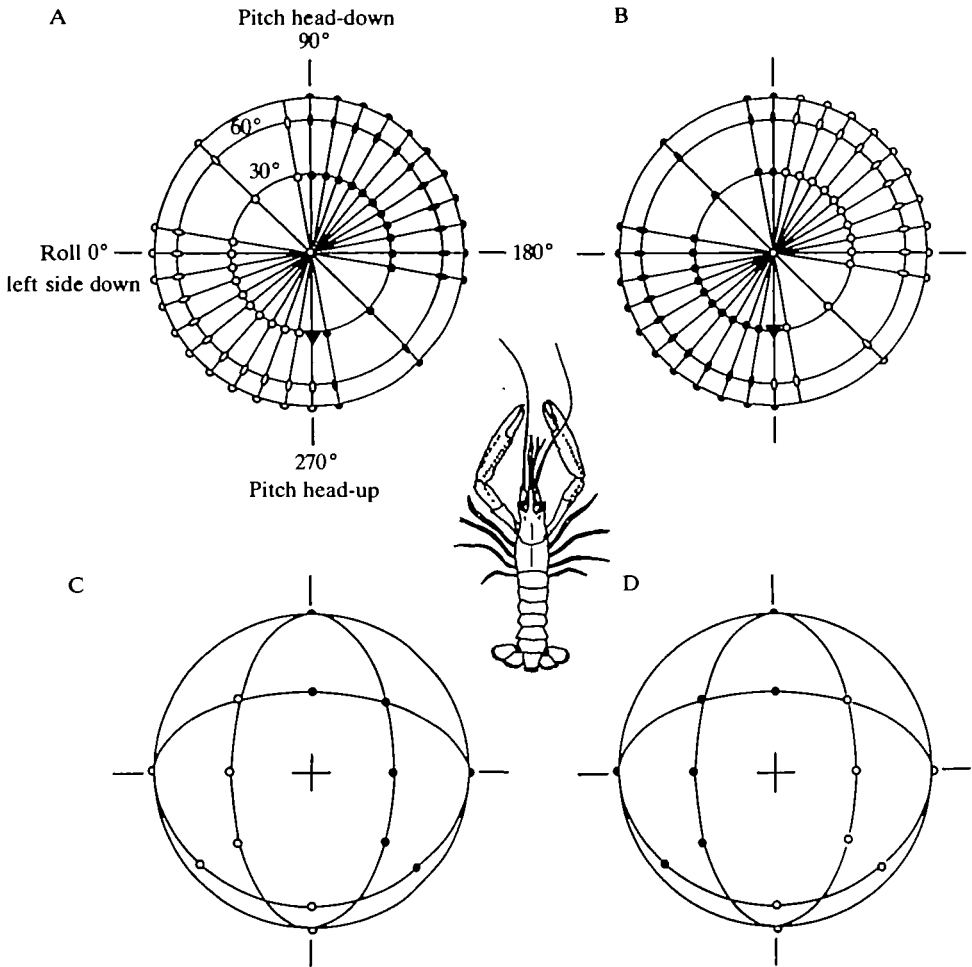
Fig. 7. Polar orthographic projections, viewed from the zenith, of the responses of the left (A,C) and right (B,D) uropod exopodites to tilts in all planes tested. Data points are plotted as projections of the animal's z axis on the upper hemisphere, as described in Fig. 1B. The inset diagram shows the orientation of the animal within the sphere. Open symbols represent an opened uropod, filled symbols a closed uropod. (A,B) Tilts in vertical planes. The 30° latitude lines are marked for reference. The filled triangle at the 330° pitch position indicates the hysteresis of the response (see text). (C,D) Tilts in oblique planes.

stimulus to the sensory hairs, it is possible to determine how these shearing forces ultimately influence uropod movements. A similar series of experiments was carried out in *Nephrops*, but again extending the analysis to three dimensions.

At 0° animals with the left statolith removed closed the uropod on the right side, while the left uropod remained open. When tested in roll, a symmetrical opening of both uropods was only restored when the animal was tilted by 30° to the operated side down (i.e. 330° in Fig. 8A). The transition point around the inverted position was also shifted by 30° (i.e. to 150° in Fig. 8A). Removal of the right statocyst

resulted, at 0°, in closing of the left uropod, while the right uropod remained open. Symmetrical opening was restored at 30° and 210° from the upright and inverted transition points, respectively (Fig. 8B).

By tilting animals in other vertical planes it was possible to demonstrate that the zone of symmetrical uropod posture remained only 20° wide, but shifted by 30° to the operated side from the original upright and inverted body positions (see Fig. 9). However, this displaced symmetrical region intercepted that for the normal animal at 90° and 270°, so that at these angles the operated and normal animals showed the same response.

Bilateral statolith removal resulted in a constant symmetrical opening of both uropods, which remained unaltered with tilt in roll (Fig. 8C) and in any other plane of tilt (Fig. 9).
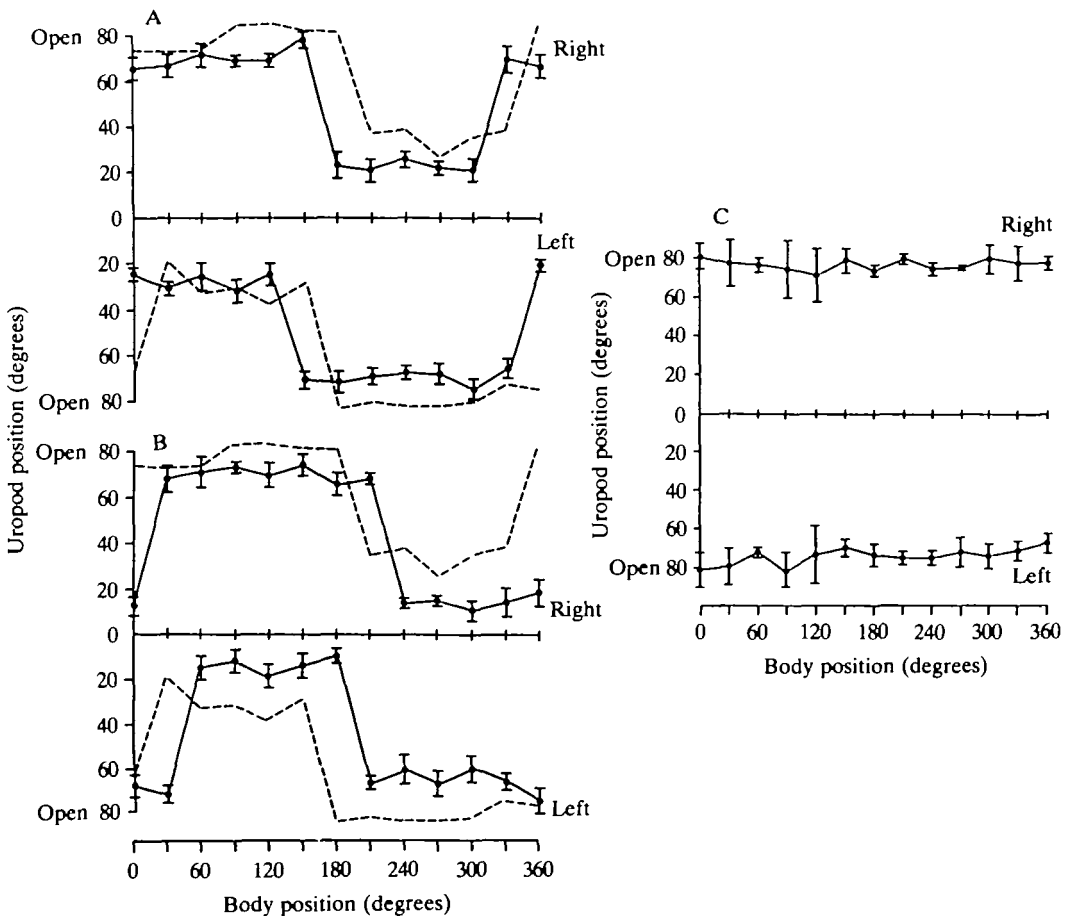

Fig. 8. Responses of the right (upper curves) and the left (lower curves) uropod exopodite to full circle tilts in roll, beginning with rotation to right-side down, in animals with the right statolith removed (A), the left statolith removed (B) and with both statoliths removed (C). Each point represents the mean value ±2 s.D. of measurements from six animals. Dashed lines in A and B indicate the responses of intact animals.
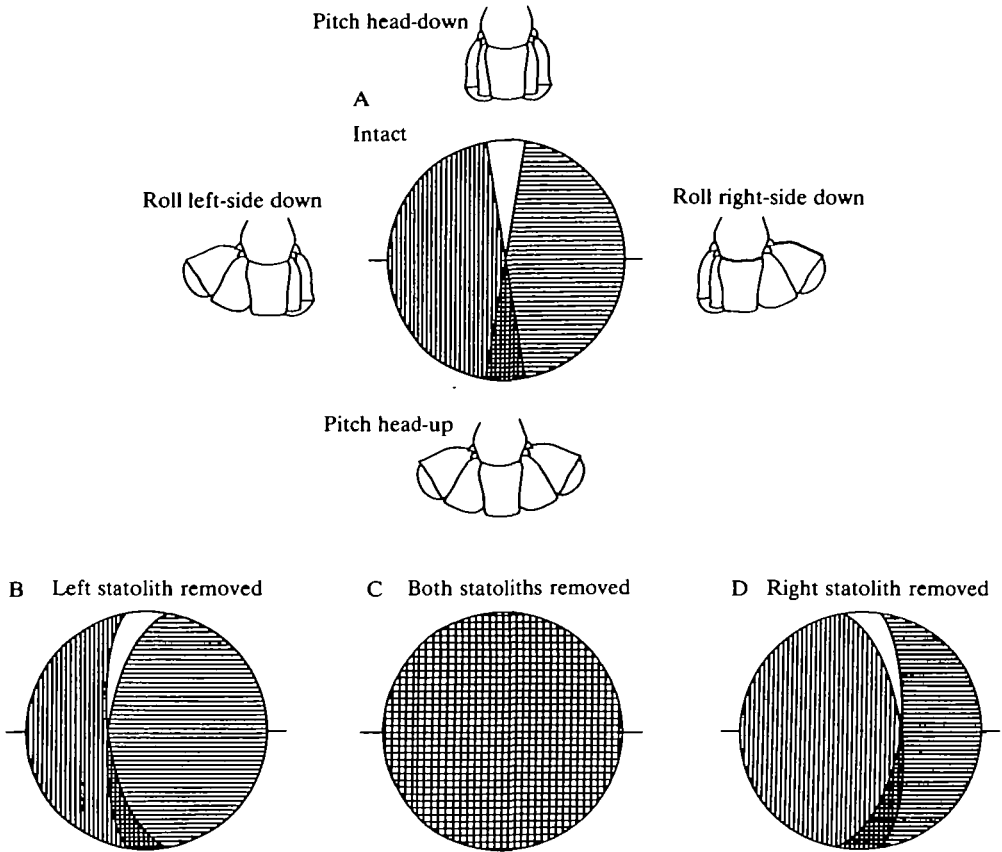
Fig. 9. Diagrammatic summary of the uropod postures adopted under different experimental conditions, presented as orthographic projections. Insets in A depict the uropod postures adopted during tilts in the major planes. Horizontal hatching indicates an open right uropod and vertical hatching an open left uropod. Thus cross hatching represents both uropods open, and the unshaded area represents both uropods closed. (A) Intact animal; (B) animal with the left statolith removed; (C) animal with both statoliths removed; (D) animal with the right statolith removed. Note in A,B and D the narrow ranges in which symmetrical uropod postures are adopted.

Righting reactions of freely moving animals

Despite numerous studies of righting responses in lobsters and crayfish under fixed, open-loop conditions (Davis, 1968; Yoshino et al. 1980), nothing is known about how these animals perform during free-fall, closed-loop conditions, or whether the results obtained from tethered preparations reflect the true movements of animals in their natural environment. Righting reactions of *Nephrops* were therefore examined during free-fall in the water column.

Animals which were released from any roll angle away from the upright, and up to within a few degrees either side of the 180° inverted position, simply rolled back to the upright position and then descended to the bottom of the tank (Fig. 10B–D). This roll movement was accompanied by an asymmetrical positioning of the uropods, with the down-side uropod open, and asymmetrical swimmeret beating,

A   Both uropods open,
     swimmerets beat rearwards

B   Forces produced by
     swimmerets and uropods oppose

C

D   Forces produced by
     swimmerets and uropods sum

E   Both uropods open,
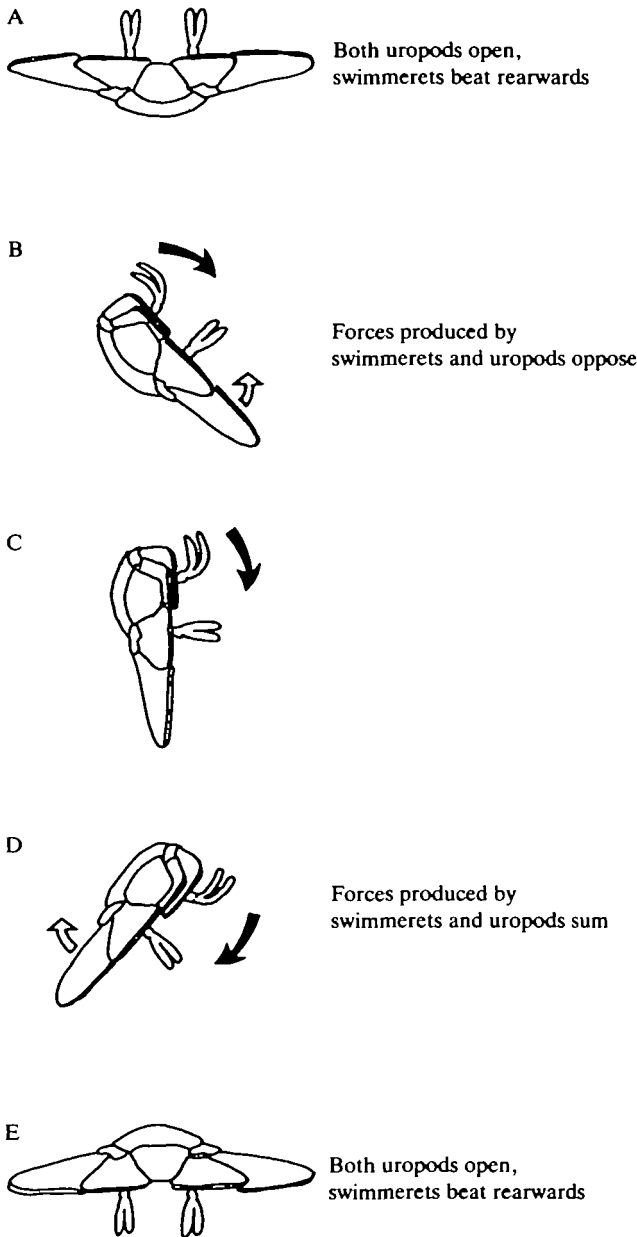   swimmerets beat rearwards

Fig. 10. (A) Symmetrical postures of the uropods and swimmerets in an animal held in an exactly inverted position. From this position righting is accomplished by a pitching response (see Fig. 11). (B–D) Schematic diagrams of the righting torques generated by the swimmerets and the uropods during a recovery roll from close to the inverted. The torque produced by lateral beating of the swimmerets has a constant direction (filled arrows in B–D) while the torque generated by the reaction of the asymmetrical uropod posture (open arrows) will tend to return the animal to the inverted in the first half of the turn (B), but will act to right the animal to its normal orientation during the second half of the turn (D).

Table 1. *Righting times of intact animals*

	First half of turn	Second half of turn
Time (s)	1·3 ± 0·1	0·6 ± 0·1
Vertical distance (cm)	16·1 ± 4·2	8·4 ± 2·1
N	8	8

those on the up-side twisting to produce a laterally directed force. The chelae showed a characteristic twisting movement, with the up-side claw being brought across the midline of the body.

Measurements of the times taken to complete the first and second halves of the turn (Table 1) demonstrate that the second half was completed in approximately half the time of the first. A possible reason for the large discrepancy between these two measurements is that although the righting torque produced by the swimmerets has a constant direction, relative to the animal, throughout the turn, the righting torque produced by the uropods changes as the dorsoventral body axis changes relative to the line of descent (Fig. 10) (see Discussion). In some instances it was observed that the asymmetrical uropod posture was not expressed during the first part of the tilt from close to the vertical position.

A comparison of righting times in roll was made in animals in which particular appendages, potentially involved in righting, were impaired or removed (Table 2). Results show that the movements of the chelae do not significantly decrease the righting times and, therefore, play no major part in righting reactions in roll in the water column. However, preventing uropod movement increased the effective righting time by as much as 63%. Animals with no chelae and with uropod movement prevented were still able to right themselves using asymmetrical swimmeret beating alone. The characteristic twisting and crossing-over movements of the chelae therefore seem to be passively generated, with the chelae lagging behind the active body rotation caused by the uropods and swimmerets.

When animals were released in an exactly inverted position (Fig. 10A, Fig. 11) a different pattern of movement was consistently observed. Instead of rolling around to the upright, they showed a characteristic head-down pitching with the chelae held out symmetrically in front of the animal, the abdomen curved in a partial or full extension, the uropods symmetrically closed and the swimmerets beating bilaterally to each side. Maintaining this posture, the animals turned in the pitch plane until they were in the upright position (Fig. 11). From this point they then descended to

Table 2. *Righting times of experimental animals*

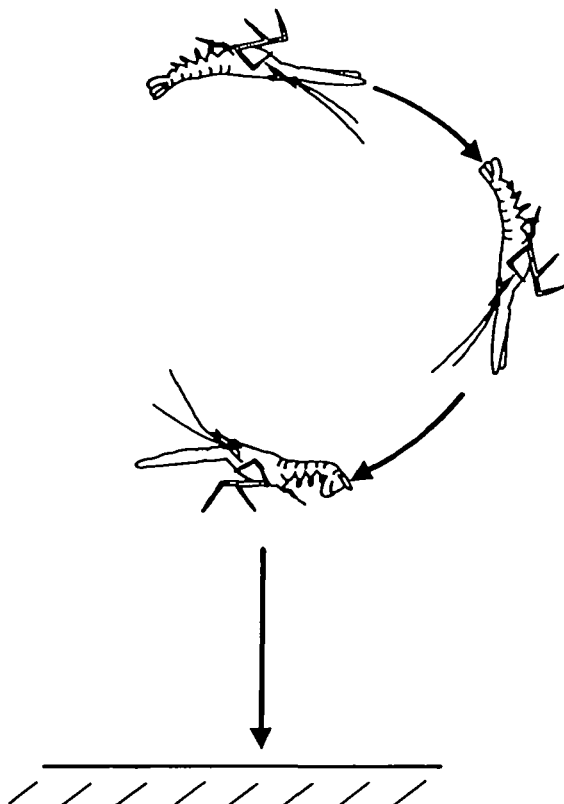|	Time (s)	*N*
Intact	1·9 ± 0·1	6
Claws removed	1·7 ± 0·1	9
Uropods fixed	2·6 ± 0·2	7

Fig. 11. Diagrammatic representation of the pitching righting response of an animal released from an exactly inverted position in the water column. It turns head-down through a full half-circle before descending to the bottom in an upright position.

the bottom of the tank in an upright position, using asymmetrical movements of the swimmerets and uropods to maintain this posture.

DISCUSSION

The results of both the controlled tilts and the free-fall experiments demonstrate that, under both closed-loop and open-loop conditions, *Nephrops* produce movements of the abdominal segments and of the appendages which contribute to righting for imposed directions of tilt about all horizontal axes. The importance of the uropods has been established, and the experiments described provide insights into the mechanisms of statocyst control for the uropod righting reactions.

Uropod righting reactions in roll

We have performed rotation experiments through the whole circle of roll tilt, and find that the uropods of *Nephrops* show an asymmetrical response pattern to one side of the upright which persists through to the inverted position. The reversal points of the response are thus at 0° and 180°. However, for an animal falling freely in the

water column, the hydromechanical effect of an asymmetrical uropod posture depends on the geometrical relationship between the expanded surface and a constant direction of water flow (Fig. 10). In the upper half of a roll from the inverted, the dorsal surfaces of the uropods are presented to the water flow, and since the downward uropod is open, a force driving the animal back to the inverted is produced. In the lower half of the roll, the water flow is intercepted by the lower surfaces of the uropods, and a righting torque driving the animal round to the upright is then produced. The direction of the rotational force produced will therefore reverse at angles of 90° and 270°. The lateral thrusts produced by twisted swimmeret beating do not suffer such reversals, since they are directly produced, and act with reference to the body itself. Therefore, during the first 90° of roll from the inverted position the righting torque produced by the uropods actually opposes that of the swimmerets. Since the observed resultant torque is in the righting direction, it must therefore be dominated by the swimmerets. These discrepancies between the positions at which changes occur in the uropod posture and in its hydromechanical effects probably account for the finding that the second half of a recovery roll from the inverted is completed in approximately half the time of the first (Table 1).

These results highlight the fact, not stated explicitly by previous workers (Schöne, 1984), that an inherent anomaly exists in the behaviour of equilibrium systems around the inverted. These systems include not only those for righting, such as the uropods which act with reference to external forces, but also compensatory eye movements which also occur relative to a spatial reference. Thus, eye movements become inappropriate as compensatory responses in the range of tilt around the inverted, even though they are classical examples of equilibrium responses around the upright (Neil, 1982). An explanation for these discrepancies may be that they reflect the action of a strictly 'hard-wired' system: in the inverted range of tilt, responses are evoked which continue to reflect in a strict manner the directionality of the forces acting on the statocyst sensory hairs.

It is unlikely that such systems will be required to operate far from the upright position under normal behavioural conditions. Most often animals will be displaced by water currents by only a few degrees from the upright position, and under closed-loop conditions these small disturbances of body posture will be corrected before they become significant. Inverted positions in the water column may only be achieved when animals are released by predators, or complete a sequence of upwardly directed tail flicks. Therefore, righting reactions might be expected to be adapted for small tilts, which are apparently the most common in the natural environment, and indeed the uropods and swimmerets coordinate to produce maximum righting forces at these angles.

Righting reactions in pitch and other vertical planes

It has been suggested that stability in the roll plane of long-bodied macruran decapods is particularly prone to water-induced disturbance (Alexander, 1971). Although this is undoubtedly true, pitch stability will also be threatened by mass water movements if animals align themselves with the water flow. It has been shown

that many decapods, including *Nephrops* (Newland & Chapman, 1985), and many species of crayfish (Maude & Williams, 1983), do indeed orientate either upstream or downstream in flowing water, and actively change body position in the pitch plane to counteract water movements.

In accordance with these observations, animals tilted in a true pitch plane produce symmetrical movements of the uropods which are effective righting responses, but represent patterns of movement never seen in roll (Fig. 9). Observations of free fall confirm the adaptive nature of these movements.

In the righting reactions which occur about intermediate horizontal axes of tilt, asymmetrical uropod postures predominate and are adopted through wide ranges up to 10° to either side of pitch. As a consequence of this, and of the fact that the uropods adopt one of only four distinct postures in response to tilt (Fig. 9), it may be concluded that the correction of an imposed tilt about an intermediate axis is accomplished in a sequential manner. Thus for an intermediate left-side down/head-up tilt the asymmetrical posture initially adopted will correct the roll component of the deviation, bringing the left side up. The animal will then lie exactly head-up in the pitch plane, and this head-up deviation will subsequently be corrected by a symmetrical opening of both uropods.

Functional significance of the switches in the righting reaction

The square wave response curves obtained for uropod righting reactions of *Nephrops* in both pitch and roll represent an unusual pattern of motor behaviour, since the uropods move to extreme opened or closed positions rather than showing a proportional response to tilt. These movements are achieved by a strict reciprocity in the action of the antagonist muscles (Fig. 3). In functional terms, such abrupt switching between extreme positions will maximize the hydromechanical effect of the uropod postures, but in control terms it is potentially unstable. However, the sensitivity of the statocyst, which is capable of initiating reflex activity to tilts of as little as 3° from the upright (Fig. 4B), might be expected to damp oscillation of the output. It is interesting that instability, in the form of a rapid oscillation of the uropods between opposite asymmetrical postures, is sometimes expressed when the animal is held in the inverted position. This may serve to initiate righting if an animal finds itself in an exactly inverted position. The swimmeret righting reactions of *Nephrops* incorporate a similar switching in the twisting movements of the basipodite (Neil & Miyan, 1986), and it has been shown that a positive feedback reflex from intrinsic proprioceptors drives the movements to completion (Miyan & Neil, 1986). Similar proprioceptors exist at the base of the uropods in anomurans, and have been shown to exert positive feedback reflex effects on the uropod muscles (Maitland, Laverack & Heitler, 1982). They also occur in the uropods of nephropid lobsters (M. S. Laverack, personal communication), although their reflex properties are not yet known.

The uropod responses obtained both by Davis (1968) for the lobster and by Yoshino *et al.* (1980, 1982) for crayfish differ in a common respect from those descibed in this study. They show an approximate proportionality with the degree of

roll tilt (only tested over a 30° range from the upright in *Homarus* by Davis, 1968), contrasting with the square wave relationship in *Nephrops*. These differences must, to some extent, reflect differing experimental procedures: *Homarus* were tilted by Davis (1968) without prior arousal, and the crayfish experiments of Yoshino *et al.* (1980, 1982) were performed in air. Under normal conditions the animals will be both underwater and aroused (e.g. after a sequence of escape swimming). Our experiments were designed to duplicate these conditions as closely as possible, but the crayfish experiments performed in air may have produced anomalous results. Until data are available for crayfish under more physiological conditions, the reasons for these observed species differences must remain unresolved.

Statocyst control of uropod righting reactions

The statolith hairs within the statocysts of decapod crustaceans form a directionally sensitive raster, since they are arranged in a crescentric array and are sensitive to displacement in one direction within narrow radial polarization planes (Cohen, 1955, 1960; Stein, 1975; Takahata & Hisada, 1979). This allows the system to abstract information separately about the magnitude and direction of a tilt imparted to the body. Its magnitude in a particular direction is proportional to the overall excitation of sensory units, while its direction is embodied in the pattern of excitation around the crescent (Schöne, 1975).

Effects of changes in the magnitude of statocyst hair stimulation

In the crayfish, Takahata & Hisada (1979) have shown that movement of the hairs to the centre of the crescent increases the discharge rate of their receptors, so that hairs in the anterior and posterior regions are responsive to head-up and head-down tilts, respectively, and those in the lateral region code ipsilateral side-down roll. In paired organs, such as statocysts, homologous hairs in the two organs will receive common stimulation in pitch, but opposite stimulation in roll. Since there is only a single row of lateral statolith hairs, the only possible basis for bidirectional sensitivity of one statocyst in roll is if decreases as well as increases in sensory discharge from a resting level produce postsynaptic effects (Cohen, 1960). Although such opposite changes in firing level appear to initiate eye movements in different directions (Cohen & Dijkgraaf, 1962), it has been concluded by Yoshino *et al.* (1980) and Takahata *et al.* (1985) that crayfish uropod reactions are controlled by single statocysts only in the restricted angular ranges where receptor discharges are increased.

In *Nephrops* there are several rows of statolith hairs in the lateral regions of the crescent (Newland, 1985) which, it is now known, have different polarizations (D. M. Neil & B. Cuthbert, unpublished observations). The basis therefore exists in the arrangement of hairs in a single statocyst for responsiveness to opposite directions of tilt in roll. The removal of one statolith results, as in crayfish (Schöne, 1954) and as expected from the geometry of the sac floor (Miyan, 1982), in a shift of the transition points between the symmetrical and asymmetrical patterns by 30° towards the operated side. Despite this shift, however, the uropod response pattern to roll

tilts, with its abrupt switching between extreme postures, still remains. A single statocyst therefore exerts bilateral control over uropod movements at all angles of tilt in the roll plane.

In both crayfish and nephropid lobsters there thus seems to be a good correlation between the morphological arrangement of the hairs in the statocyst and the form of the motor output in the uropod righting reactions. This will need to be confirmed by more direct methods, such as separate stimulation of particular hair groups in the statocyst whilst recording motor activity to the uropods.

Effects of changes in the plane of statocyst hair stimulation

Our experiments on *Nephrops* with one statolith removed, and tilted in intermediate planes from roll through to pitch, not only demonstrate that sensory input from the intact organ is adequate to elicit the full asymmetrical and symmetrical responses seen in the normal animal, but also that the region of expression of the latter, pitch-related, pattern remains limited to a ±10° arc around the displaced reference. These results indicate that the precise angular information available in the output signal of statocyst receptors concerning the plane of imposed tilt is not utilized to produce proportional changes in the motor output to the uropod. Only four distinct motor patterns, with unequal ranges of expression, are produced. This is in marked contrast to the statocyst control of eye movements, which reflect in their movements about all three axes the exact plane of body tilt (Stein, 1975).

Available evidence suggests that the properties of the statocyst interneurones which project to the uropods are, in themselves, insufficient to account for the characteristics of the uropod righting reactions. It has been shown for crayfish that the sensory axons from statolith hairs converge onto only a small number of interneurones (Takahata & Hisada, 1982*a,b*) and, as a consequence, resolution is sacrificed for sensitivity, the interneurones having wider acceptance angles than the individual statocyst hairs. Thus interneurones primarily sensitive to pitch have response ranges from 120° to 180° wide, which also encompass tilts in the roll plane (Takahata & Hisada, 1982*b*). In *Nephrops*, where the uropod pitch response is only expressed over a ±10° arc, one might expect to find pitch-sensitive interneurones with much narrower acceptance angles. However, a survey of statocyst interneurones has failed to locate any with these properties (Knox & Neil, 1987). Different interneurones are predominantly sensitive to either pitch or roll, but they all have wide acceptance angles, as in crayfish. While the asymmetrical uropod motor patterns which occur in roll and about intermediate horizontal axes may be derived in a relatively direct manner from the outputs of interneurones with these wide-field characteristics, the fine tuning of the symmetrical pitch pattern must emerge from a more extensive integration of signals from different statocyst interneurones. This general conclusion about the organization of reflex pathways from statocysts to equilibrium motor systems is similar to that reached by Takahata *et al.* (1985) on the basis of statocystectomy and cord hemisection experiments in crayfish. However, it suggests that the outputs of statocyst interneurones will be integrated in a number of

different ways to produce the distinct patterns of uropod coordination observed in different planes of tilt.

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