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SENSORY CONTROL MECHANISMS OF THE UROPOD EQUILIBRIUM REFLEX DURING WALKING IN THE CRAYFISH *PROCAMBARUS CLARKII*

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Summary

The temporal characteristics of statocyst and leg proprioceptive inputs to the uropod motor system were investigated in crayfish using behavioural and electromyographic analyses to elucidate their functional roles in the control of the uropod steering response under natural conditions. When the animal, which was suspended in the air without a footboard, was actively extending its abdomen, prolonged stimulation of the statocysts by body rolling elicited a maintained asymmetrical configuration of the bilateral uropods. Prolonged stimulation of the walking legs by footboard tilting with the animal body held in the upright position elicited a transient uropod response. When the treadmill was tilted while the animal was walking on it in the upright position, the uropods showed the same transient response. However, when the animal body was rolled, together with the treadmill, while the animal was walking on it, the uropods showed a transient response which was reversed in direction compared with that observed during body rolling without a footboard. This transient response was abolished by the removal of the statoliths. The results show that the statocysts and leg proprioceptors exert sustained and transient control effects, respectively, on the uropod motor system during walking. It is also suggested that the uropod response to body rolling during walking is controlled primarily by leg proprioceptor signals which result from statocyst-induced changes in the leg position.

Key words: crayfish, *Procambarus clarkii*, walking, locomotion, equilibrium reflex, uropod motor system.

Introduction

The upright body posture of crustaceans is maintained by equilibrium responses which are guided by sensory information from the statocysts, leg proprioceptors and eyes (Kühn, 1914; Alverdes, 1926). The contributions of each of these sense organs to the control of the equilibrium responses displayed by various appendages, including the eyestalks, walking legs, swimmerets and uropods, have been extensively studied (Schöne, 1954, 1971; Davis, 1968, 1971; Neil, 1975*a*,*b*,*c*, 1982; Hisada and Neil, 1985; Newland, 1989). Different sense organs are activated in combination under natural conditions, and how their nerve signals interact with each other to elicit and control the equilibrium responses has also been well studied (Schöne and Neil, 1977; Schöne *et al.* 1983; Neil, 1985, 1993). In previous studies, however, the functional roles of sense organs were mainly investigated in tethered animals by analyzing their motor output in response to controlled stimulation of a particular sense organ or of various combinations of sense organs, even though under natural conditions the control of body posture by equilibrium responses becomes more important during locomotor behaviour, such as during landing behaviour following tail-flips in the water (Newland and Neil, 1987), than at rest.

The uropod steering behaviour of the crayfish *Procambarus clarkii* is one of the equilibrium responses elicited by a change in body posture (Yoshino *et al.* 1980, 1982). This behaviour is controlled by the statocyst input and is expressed as bilaterally asymmetrical configurations of the uropods provided that the roll stimulus is given when the animal, which is fixed by its cephalothorax in the air without a footboard, is actively extending its abdomen (Takahata *et al.* 1981). When the animal is provided with a footboard and rolled together with it, the response is reversed in direction (Takahata *et al.* 1984). It has also been reported that the uropods show bilaterally asymmetrical configurations when the walking legs are stimulated by footboard tilting while the animal body is kept upright (Newland, 1989).

Behavioural and electromyographic analyses of crayfish walking freely on a tilted substratum with the abdomen actively extended have revealed, however, that the bilateral uropods showed not only the reversed configuration, which was dominant as expected, but also the normal configuration as well as the bilaterally symmetrical configuration in response to the same stimulus conditions (Takahata *et al.* 1984). This variability in the uropod response cannot be explained by the results obtained using tethered animals. Since both statocysts and leg proprioceptors are stimulated continuously during walking on a tilted substratum, the temporal characteristics of the sensory inputs from these organs during prolonged stimulation should be analyzed in detail under controlled experimental conditions.

In the present study, we used behavioural observations and electromyogram recordings to investigate the temporal nature of the sensory inputs from the statocysts and leg proprioceptors to the uropod motor system in the tethered condition and during walking driven by a treadmill. The results showed that the statocysts control the uropod response in a sustained way, whereas the leg proprioceptors affect it transiently in tethered animals. When the animal body was tilted together with the treadmill during walking, the uropods showed the reversed response, which soon disappeared as the animal continued to walk in the same stimulus condition. The results suggest that sustained signals from the statocysts to the uropod motor system are overridden by transient signals from the leg proprioceptors to reverse the uropod response, but only during the early phase of prolonged stimulation.

Materials and methods

Experimental animals and apparatus

Experiments were performed on crayfish, *Procambarus clarkii* Girard, of both sexes ranging from 8 to 12 cm in body length. No significant differences were observed between the results for both sexes. They were obtained commercially and kept in laboratory tanks. They were fed weekly on a diet of raw potato and liver pieces. Animals that were to be used in experiments were given extra food on the day before the experiment to make them as responsive as possible to external stimuli. Results of behavioural observation were obtained from 20 animals for each experimental protocol, except one case in which 11 animals were used. Electromyographic recordings were obtained from 44 animals.

A steel nut was glued to the dorso-anterior region of the cephalothorax of an experimental animal, which was then fixed by the nut to the tiltable holder of the experimental apparatus. Depending on the experiment, the animal was either suspended from the holder without a footboard or placed on a treadmill which was also tiltable. The velocity and direction of the treadmill were controlled by a d.c. motor (Mabuchi Motor, RE-280) with a gearbox. The velocity was adjusted to 1.7–2.1 $\mathrm{cm\,s^{-1}}$ to be comparable with that of the walking animal. When the sensory input to the uropod motor system during walking was to be studied, the treadmill was tilted, either by itself or together with the animal body, while the motor was running. When the sensory input during the stance phase was to be investigated, the treadmill was tilted with the motor turned off. In this case, the stationary treadmill simply acted as a footboard on which the animal actively performed abdominal extension. The tiltable animal holder and the treadmill were driven by a stepping motor (Nippon Pulse Motor, PJ55-B1) controlled by a personal computer (NEC PC-8801). The rotation axis of the whole apparatus was rigidly coupled to a variable potentiometer, through which the position of the animal's body was monitored during experiments. Tilting of the animal body and the treadmill could therefore be controlled separately. In order to stimulate the walking legs alone, only the treadmill was tilted while the animal body was kept in the upright (0 °) position. When the statocysts were to be stimulated selectively, the treadmill was uncoupled from the apparatus. All experiments were conducted in air. The animal was kept moist by occasionally spraying it with water.

Behavioural observation

In the behavioural study, uropod movements were observed directly or recorded using a video camera and replayed later for analysis. Although we attempted to keep the condition of the experimental animals as uniform as possible by controlling feeding and the environment, there remained a certain amount of variability in the behavioural data. Therefore, the behavioural response of an individual animal is given in this paper as the most dominant response from ten stimulation trials with at least 1 min between trials. The results were analyzed statistically using the *G*-test and Model II contingency tables (Sokal and Rohlf, 1995). Since the uropod steering movement is elicited only while the animal is performing abdominal extension (Takahata *et al.* 1981), the nature of the sensory input to the uropod motor system was examined only when the animal was actively extending its abdomen or was engaged in driven walking with the abdomen actively extended. Although abdominal extension could occur spontaneously or in response to various stimuli, such as intense light or pricking of the abdomen, we used leg stimulation (Larimer and Eggleston, 1971) to evoke consistent abdominal extension in this study. The uropods typically showed a symmetrical configuration during abdominal posture movements.

When the treadmill motor was turned on with the experimental animal fixed to the holder and resting on the treadmill, the animal usually began to show walking behaviour characterized by alternating rhythmical leg movements. In rare cases, when the animal was simply inactive or became arrested following the fixing procedure, all legs were passively retracted in response to the treadmill movement. In such cases, the experiment was interrupted and postponed until the animal began to walk actively on the treadmill.

Electromyography

Electromyogram (EMG) recordings were obtained from the slow opener muscles of the uropod (abductor exopodite ventral muscle; Larimer and Kennedy, 1969) on both sides, the abdominal slow extensor muscle (Kennedy *et al.* 1966; Page, 1982) and the depressor muscle of the third walking leg (Ayers and Davis, 1977*a*) on either side. Recordings were made using pairs of Teflon-coated stainless-steel wires (127 μm in diameter) insulated except at their tips. Signals were amplified (Nihon-Kohden MEG-1100, MEG-2100) and stored on magnetic tapes using a Biologic DTR-1801 DAT data recorder. After experiments, the recorded EMG data were replayed with the body/treadmill position monitor signal and printed using a Gould TA240S EasyGraf recorder.

Results

Sustained control by statocysts

When the statocyst receptors were selectively stimulated by body rolling without a footboard while the animal was actively engaged in abdominal extension, the uropod on the lifted side was spread open, whereas that on the lowered side was closed, as reported previously (Yoshino *et al.* 1980). This response was extremely reliable in these experimental conditions: all 20 animals showed this response immediately following the body roll stimulus. However, when the animal was first rolled by 60 ° and kept in that position for approximately 1 min, the animal became quiescent and the uropods no longer showed any specific configuration. When the animal was again activated to elicit abdominal extension, the uropods showed the same, bilaterally asymmetrical configuration as before (black bar in Fig. 1A).

In the experiment illustrated in Fig. 2, an animal with EMG electrodes inserted was suspended without a footboard. When

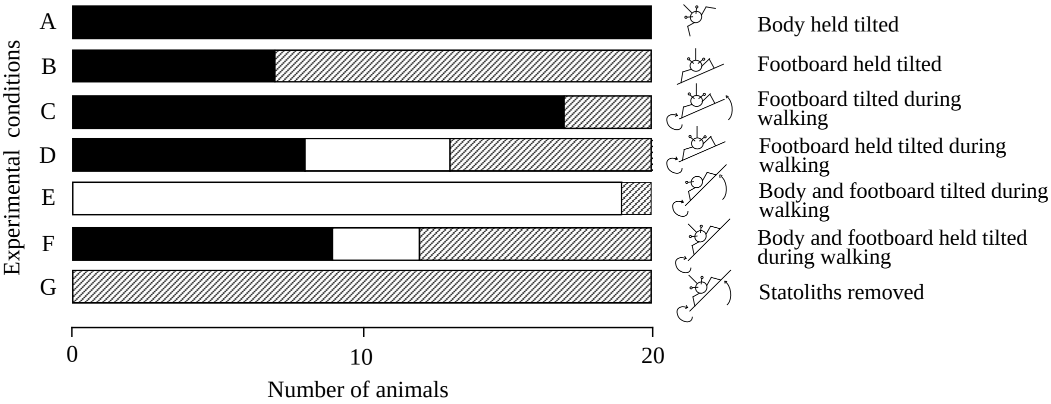

Fig. 1. Uropod responses to stimulation of the statocysts and leg proprioceptors. The numbers of crayfish which displayed each specific configuration of bilateral uropods in 10 different stimulus conditions are shown. (A) The animal body was held in the tilted position without a footboard. The animal was reactivated by leg stimulation after it had become quiescent in the tilted position. (B) The footboard was held in a tilted position while the animal was held in the upright position. The animal was reactivated as above after it had become quiescent. (C) The animal was held in the upright position when the treadmill was tilted sideways while the animal was walking on it. (D) The treadmill was held in a tilted position while the animal was held in the upright position and walking on it. (E) The animal body was rolled from the horizontal position together with the treadmill while the animal was walking on it. (F) The animal body was rolled together with the treadmill and held in a tilted position while the animal was walking on it. (G) An animal whose statoliths had been removed was rolled together with the treadmill from the horizontal position. The black and white bars indicate different bilaterally asymmetrical configurations depending on the stimulus condition. See text for details. The hatched bars indicate the bilaterally symmetrical configuration of the uropods.

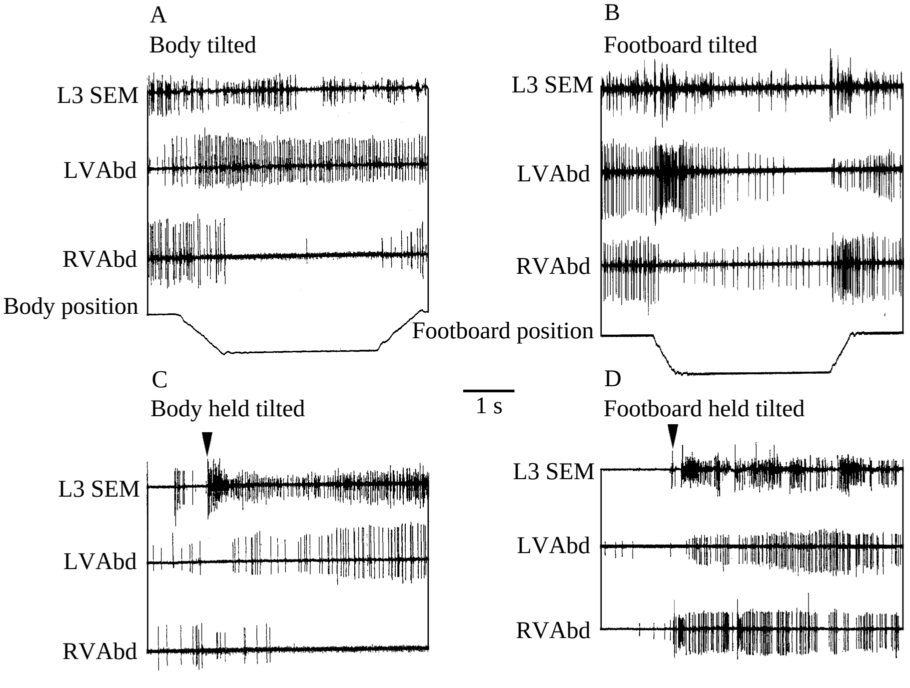

Fig. 2. (A) Responses of bilateral uropods observed when the crayfish body was rolled while the animal was actively engaged in abdominal extension. Electromyographic recordings were obtained from the left (LVAbd) and right (RVAbd) abductor exopodite ventral muscles and the left slow, superficial abdominal extensor muscle under the third tergum (L3 SEM). The experimental animal with EMG electrodes inserted was suspended without a footboard. The animal was rolled from 0 to 30 ° in the left-side-up direction. The lowest trace shows the body position. (B) Responses observed when the footboard was tilted while the animal was actively engaged in abdominal extension. The footboard was tilted sideways, from 0 to 15 °, in the left-side-up direction. The lowest trace shows the footboard position. (C) Responses observed when the crayfish was activated by leg stimulation to initiate abdominal movements after it had been held in a rolled (30 °) body position for 1 min. The arrowhead indicates the beginning of abdominal extension. (D) Responses observed when the animal was activated by leg stimulation to initiate abdominal movements after the footboard had been held in a tilted (15 °) position for 1 min. The arrowhead indicates the beginning of abdominal extension.

the animal was rolled while it was engaged in abdominal extension (Fig. 2A), abductor muscle activity increased on the lifted side and decreased on the opposite side. This reciprocal activation of bilaterally homologous muscles has been reported previously (Takahata *et al.* 1981), but how the prolonged stimulation of statocysts affected the uropod response was not understood. When the animal was kept in the tilted position and became quiescent, the muscle activity level became low on both sides. When abdominal extension was again induced in this tilted position, the reciprocal activity pattern reappeared (Fig. 2C). This pattern was identical to that observed upon tilting from the upright position (Fig. 2A).

Transient control by leg proprioceptors

When the footboard was tilted sideways by 15 ° in either direction along the longitudinal axis of the animal body, while the animal was kept in the upright position, 19 out of 20 animals tested responded by opening the uropod on the lifted side and closing the opposite uropod, as reported previously (Newland, 1989). One animal did not show any distinct asymmetrical uropod configuration. When the footboard was tilted by 15 ° and kept in the tilted position for about 1 min while the animal's body was maintained upright (quiescent animals activated to elicit abdominal extension), seven out of 20 animals were found to show the same asymmetrical configuration of bilateral uropods as before (black bar in Fig. 1B), whereas the remaining 13 animals showed no distinct asymmetrical configuration (hatched bar in Fig. 1B).

EMG recordings revealed that the bilaterally reciprocal muscle activities elicited by the footboard tilt became unclear when the animal was kept in the tilted position for 1 min, although the abdominal posture system remained active (Fig. 2B). When the crayfish was returned to the original horizontal position, the reversed reciprocal pattern of bilateral uropod muscle activities was always observed. When the footboard was kept in a tilted position and the abdominal posture system was then activated, no reciprocal activation pattern of bilateral uropod muscles was observed, even when the animal was activated to elicit abdominal extension (Fig. 2D). These results indicate that sensory signals from the leg proprioceptors do not exert sustained control over the uropod motor system, but activate it dynamically following displacement of the leg position.

Effects of leg proprioceptive input during walking

When the animal was kept upright and engaged in forward walking driven by the treadmill, it responded to treadmill tilting by opening the uropod on the lifted side and closing the opposite uropod in 17 out of 20 cases (black bar in Fig. 1C). However, when the animal was forced to walk on the tilted treadmill for 1 min, the uropod configuration showed more variability than that observed immediately after the tilt stimulus ($P<0.05$): eight out of 20 animals tended to open the uropod on the lifted side and close the opposite uropod (black bar in Fig. 1D). Another five animals showed the reversed configuration: the uropod on the lifted side tended to be closed, whereas the opposite uropod tended to be opened (Fig. 1D, white bar). The remaining seven animals did not show any distinct tendency (hatched bar).

In response to treadmill tilting during driven walking, the activity of the abductor muscle on the lifted side increased while that on the opposite side decreased (Fig. 3). This is the same as the pattern observed when the footboard is tilted while the animal is in the stance phase (Newland, 1989). The activity of the leg depressor muscle was also affected by treadmill tilting: it was reduced on the lowered side and enhanced on the raised side. Fig. 3 also shows that the reciprocal pattern of bilateral uropod muscle activities in response to prolonged tilting of the treadmill during walking was more persistent than that observed in response to prolonged tilting of the footboard (Fig. 2B). This difference could be accounted for, at least partly, by the fact that the right and left leg proprioceptor systems are activated alternately by the rhythmical movement of the legs during walking so that they can exert a relatively sustained effect on the uropod motor system. However, the result of the behavioural experiment (Fig. 1D) indicates that such alternate activation of leg proprioceptors during walking cannot completely override the phasic nature of leg inputs to the uropod motor system.

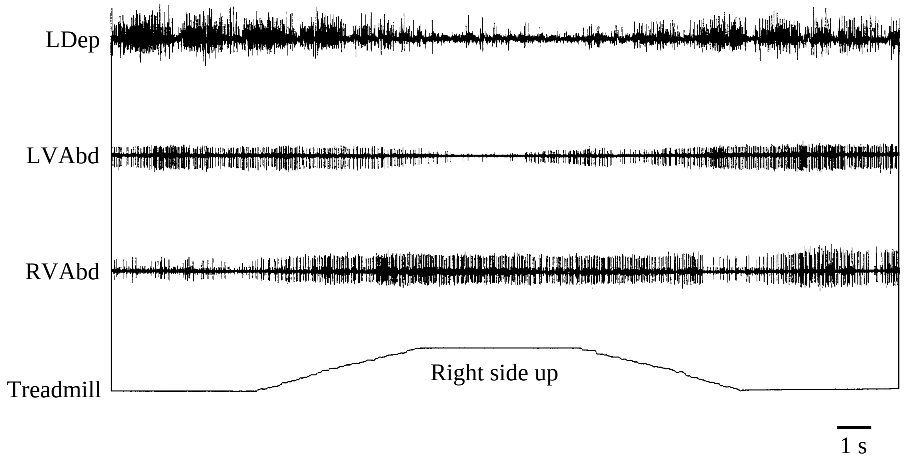

Fig. 3. Responses of the bilateral uropods of the crayfish observed when the treadmill was tilted while the animal was walking on it. Electromyographic recordings were obtained from the left (LVAbd) and right (RVAbd) abductor exopodite ventral muscles and the anterior basipodite depressor muscle of the third walking leg on the left side (LDep). The animal with EMG electrodes inserted was placed on a treadmill which was tilted sideways, from 0 to 15 °, in the right-side-up direction, while the animal was engaged in driven walking. The lowest trace monitors the treadmill position.

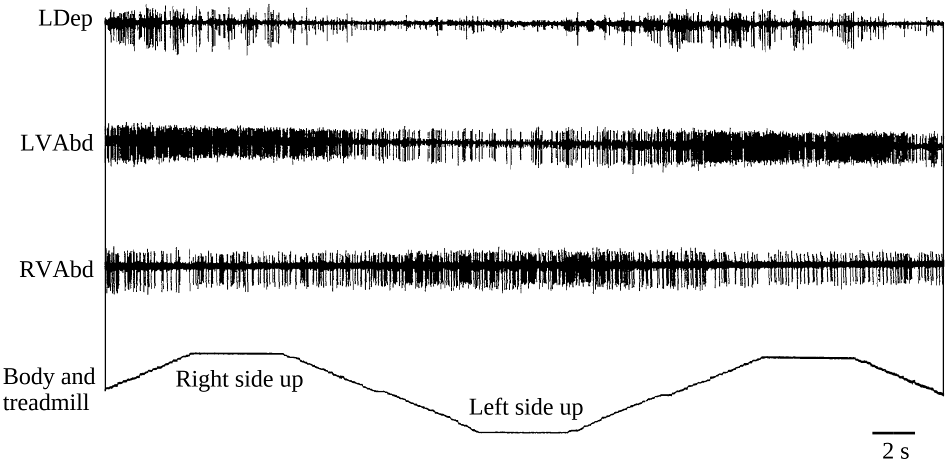

Fig. 4. Responses of the bilateral uropods of the crayfish observed when both the animal's body and the treadmill were rolled together during driven walking. Electromyographic recordings were obtained from the left (LVAbd) and right (RVAbd) abductor exopodite ventral muscles and the anterior basipodite depressor muscle of the third walking leg on the left side (LDep). The animal with EMG electrodes inserted and the treadmill were rolled together from 0 to 15 ° in either direction while the animal was engaged in driven walking. The lowest trace shows the position of the animal's body and the treadmill.

Interactions between the statocyst and leg inputs during walking

In response to rolling of the animal body together with the footboard while the animal was actively extending its abdomen, the uropod on the lifted side was closed whereas that on the lowered side was spread open in 10 out of 11 animals tested, as reported previously (Takahata *et al.* 1984). One animal did not show any distinct asymmetrical configuration. Since the animal was in the stance phase, no systematic stimulation of leg proprioceptors was involved in this experimental condition. When the crayfish and the treadmill were tilted simultaneously while the animal was engaged in driven walking, the uropod on the lifted side was closed whereas that on the opposite side was spread open in 19 out of 20 animals (white bar in Fig. 1E). One crayfish did not show any distinct asymmetrical configuration (hatched bar in Fig. 1E). When both the animal body and the treadmill were kept in a tilted position before the treadmill was turned on, to induce forward walking for 1 min, the uropod configuration showed significantly more variability than immediately after the tilt stimulus ($P<0.025$): nine out of 20 animals tended to open the uropod on the lifted side and to close the opposite uropod (black bar in Fig. 1F). Another three animals showed the reversed configuration (white bar in Fig. 1F) and the remaining eight animals did not show any distinct tendency (hatched bar in Fig. 1F).

EMG recordings from a crayfish tilted together with the treadmill during walking (Fig. 4) confirmed that the abductor muscles on both sides were reciprocally activated to produce the uropod steering movement observed. This was in the opposite direction to that observed in response to body rolling without the footboard (Fig. 2). This reversed reciprocal pattern of bilateral uropod muscle activities was no longer elicited by body rolling after the statoliths had been removed on both sides (hatched bar in Fig. 1G). The activity of the leg depressor muscle on the lowered side was also enhanced, whereas that on the opposite side was reduced. This pattern of leg muscle activity continued as long as the body roll was maintained (Fig. 4), but it remains to be determined whether the walking system also receives sustained control signals from the statocysts, as does the uropod system.

Discussion

In the present study, we have investigated the sensory control mechanisms of equilibrium responses during free walking by examining the sensory effects on the activity of the uropod motor system during driven walking on a treadmill. It has been shown that driven walking on a treadmill differs from free walking in several respects, including the temporal organization of the stepping cycle (MacMillan, 1975; Ayers and Davis, 1977*a*; Clarac and Chasserat, 1983) and the forces developed by the legs in a series of consecutive steps (Clarac and Cruse, 1982). However, detailed analyses of these differences have revealed that driven walking is controlled by a neuronal mechanism that is fundamentally identical to that underlying free walking (Ayers and Davis, 1977*b*; Ayers and Clarac, 1978; Chasserat and Clarac, 1980; Cruse *et al.* 1983; Cruse, 1983, 1990).

It is also noteworthy that crayfish showed a strong tendency to extend the abdomen when driven walking was initiated by the treadmill, as reported for free walking (Ward, 1879; Takahata *et al.* 1984). This tendency of the animal was advantageous for the present study since the behavioural output of the uropod motor system in response to a positional change could be reliably observed only when the tilt stimulus was accompanied by extension of the abdomen (Takahata *et al.* 1981, 1984).

Statocyst and leg proprioceptive inputs to the uropod motor system

It has been reported that uropod steering behaviour is under the strict control of sensory signals from the statocysts (Yoshino *et al.* 1980) and leg proprioceptors (Newland, 1989) as well as central signals from the abdominal posture and walking systems (Takahata *et al.* 1984). However, the temporal characteristics of the sensory signals responsible for controlling uropod motor output have not been investigated and are important to the understanding of control mechanisms during locomotor behaviour under natural conditions. In the present study, we have addressed this problem and showed that the statocyst sensory input exerts tonic control over the uropod motor system, whereas the leg proprioceptive input affects it in a transient way (Figs 1, 2). The finding that the uropods resumed the appropriate steering configuration when the abdominal system was reactivated after the animal had become quiescent during maintained body roll (Fig. 2A,C) is consistent with previous results suggesting that a maintained body posture is detected by tonic-type statocyst receptors and is represented in the spiking activity of a set of interneurones descending to the thoracic and abdominal ganglia (Takahata and Hisada, 1979, 1982), although the synaptic input to the uropod motor system remains subthreshold when the animal is in the quiescent state (Takahata and Murayama, 1992). The results of this study thus confirm our previous conclusion that sensory control signals from the statocyst descend continuously to the uropod motor system irrespective of whether the animal is actively engaged in abdominal posture movements, but that they are effectively transmitted to the motor neurones only when the animal is active (Takahata and Hisada, 1986).

The major leg proprioceptive input to the uropod motor system for the control of steering behaviour comes from the coxo-basipodite joint (Newland, 1989). At present, the type of information that is transmitted from the joint proprioceptor to the central nervous system is unknown. However, the presence of position- and movement-sensitive receptors in the pro-dactylopodite, coxo-basipodite, mero-carpopodite and carpo-propodite joints in the crab *Carcinus maenas* (Burke, 1954; Wiersma and Boettiger, 1959; Bush, 1965*a,b*; Mill, 1976) suggests that a similar receptor system is also present in the coxo-basipodite joint of the crayfish. The present finding, that the bilateral uropods no longer showed the steering configuration when the abdominal system was reactivated after the animal had become quiescent during maintained footboard tilt (Fig. 2D), suggests the possibility that only dynamic information on leg joint displacement is effectively transmitted to the uropod motor system.

The results obtained in this study therefore suggest that the different control effects of the statocyst and the leg proprioceptive inputs on the uropod steering response are due not to a lack of either tonic or phasic sensory signals in each receptor system but to different sensori-motor functional connections, although the anatomical bases of these selective connections remain to be investigated. The observations that the leg proprioceptors can exert both a long-lasting tonic effect on the oculomotor system and a phasic effect on the antennal motor system of the spiny lobster (Schöne *et al.* 1976; Neil and Schöne, 1979) also support this possibility.

Control mechanisms of the uropod steering response during walking

When the animal body is rolled together with the treadmill while the animal is walking, the uropods show a bilaterally asymmetrical configuration which is reversed in direction compared with that observed during body rolling without a footboard (Figs 1A,E, 4). It is not known how the presence of a footboard reverses the direction of uropod movement. However, the results of this study seem to provide a clue for further analysis of this mechanism. The leg proprioceptive input during walking is phasic in nature (Fig. 1D), as it is during the stance phase (Fig. 1B), although the phasic nature is less obvious (Fig. 3). When the walking animal is rolled together with the treadmill, the uropods adopt a steering configuration (Fig. 4) which tends to disappear during maintained stimulation (Fig. 1F). Since tonic sensory signals should still descend to the uropod motor system during this maintained stimulation, as seen in Fig. 2C, the absence of the reversed uropod configuration after movements in response to phasic input from leg proprioceptors (Fig. 1F) strongly suggests that the sensory signals from the statocysts and leg proprioceptors summate in a manner that places much greater weight on signals from the leg proprioceptors. An alternative possibility would be that statocyst signals are suppressed by those from leg proprioceptors (Fig. 5).

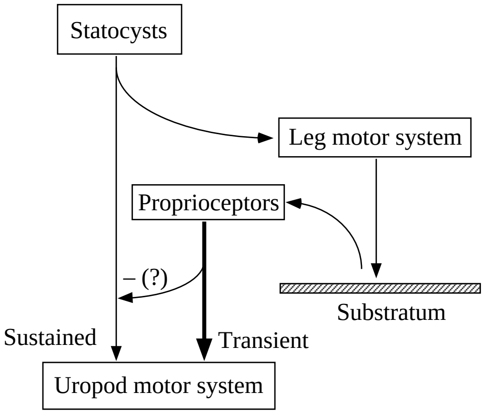

Fig. 5. Hypothetical mechanisms underlying the multisensory control of uropod steering in response to simultaneous body and treadmill rolling during driven walking. It is unclear whether the interaction of the statocyst and leg proprioceptive inputs is based on their weighted summation, as illustrated by the different thicknesses of the arrows marking each pathway, or inhibition of statocyst inputs by the leg proprioceptive pathway, as indicated by a question mark.

The site of interaction of the sensory signals from the statocysts and leg proprioceptors also remains unknown. Newland (1989) suggested that the signals enter the terminal abdominal ganglion *via* separate pathways, although the descending interneurones which selectively carry leg proprioceptive information have not been identified. The presence of independent parallel pathways for the leg and statocyst inputs would indicate that their interaction takes place in the terminal abdominal ganglion. However, the presence of multiple gates in the descending statocyst pathway, including one in the terminal ganglion (Takahata and Hisada, 1986; Takahata and Murayama, 1992), suggests that this interaction may also occur outside the terminal ganglion. Further study is needed to identify the site of interaction and to investigate its synaptic mechanisms at the cellular level.

In an earlier study, behavioural observations of crayfish walking freely on a tilted substratum revealed that the uropods sometimes showed not only the reversed configuration, which was dominant, but also the normal configuration as well as the bilaterally symmetrical configuration (Takahata *et al*. 1984). This variability in the uropod response to the same tilt stimulus during walking can be accounted for, at least partly, by the phasic nature of the leg input: when the animal walks continuously on a tilted substratum, the leg input becomes weaker, making the uropod response more ambiguous. The present study demonstrates experimentally that the uropod configuration shows significant variability when the animal continues to walk on a tilted substratum (Fig. 1D), reflecting the phasic nature of the leg proprioceptive input (Figs 1B, 2D).

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