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NEURONAL MECHANISMS UNDERLYING CRAYFISH STEERING BEHAVIOUR AS AN EQUILIBRIUM RESPONSE

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SUMMARY

1. When the crayfish *Procambarus* is rolled with legs not upon a substratum, uropod opener muscles on the lifted side are activated in co-contraction whereas antagonistic closer muscles on the same side are all relaxed simultaneously. The closers are activated and the openers are relaxed on the lowered side.

2. This reciprocal pattern is also observed in the motor neurone activity: the contraction of opener muscles on the lifted side and closer muscles on the lowered side is caused by an increase in the activity of excitatory motor neurones innervating these muscles, whereas the relaxation of their antagonists on each side is caused by a decrease in the activity of excitatory motor neurones innervating them. Deafferentation by cutting all roots of the terminal ganglion has no significant effect on the steering pattern.

3. The decrease in the excitatory motor neurone activity during steering was found to be due to an increase in the inhibitory input to the motor neurones.

4. During body rolling, the statocyst receptors on the lifted side increase their activity while those on the lowered side decrease it (Takahata & Hisada, 1979). We conclude that the opener motor neurones receive excitation and inhibition respectively from the ipsilateral and the contralateral statocyst, whereas the closer motor neurones receive excitation and inhibition respectively from the contralateral and ipsilateral statocyst. From these results, the connections between the motor neurones and the identified statocyst interneurones were deduced.

5. The normal, bilaterally organized steering pattern of the uropod muscle activity seems to be produced by the statocysts of both sides, whose information is mediated by a bilateral set of interneurones having different connections to individual motor neurones.

INTRODUCTION

Postural control of positional orientation (Schöne, 1981) based on the equilibrium sense organ in decapod crustaceans has long been a subject of sensory physiology and 'Verhaltensphysiologie' (e.g. Kühn, 1914; von Buddenbrock, 1914; Schöne,

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1951). The relationship between the sensory input and the motor output has been well quantified for a variety of equilibrium responses in many species (e.g. Schöne, 1954; Davis, 1968; Neil, 1982). The mode of interaction of the equilibrium sense with sensory inputs of other modalities has also been intensively studied at the behavioural level using the whole-animal preparation (e.g. Alverdes, 1926; Stein & Schöne, 1975; Schöne, Neil, Scapini & Dreissmann, 1983). Although much quantitative data have thus been accumulated, neurophysiological mechanisms underlying positional orientation remain to be studied.

Neurophysiologically, the most intensively studied crustacean equilibrium response is the compensatory eyestalk movement (e.g. Hisada & Higuchi, 1973; Mellon & Lorton, 1977). In the crab *Scylla serrata*, Silvey & Sandeman (1976) showed that the neuronal pathway subserving eye movements is organized into a parallel system with both monosynaptic and polysynaptic connections between the statocyst sensory neurones and the eyestalk motor neurones. The polysynaptic connection is thought to be mediated by multimodal interneurones which modulate the operation of the monosynaptic pathway according to other inputs.

However, the neural mechanisms underlying 'righting reactions' (Davis, 1968), which are directly responsible for restoring the original upright body position from the tilted one, have been little studied. It is mainly these righting reactions of walking legs, swimmerets and uropods that interact with other motor systems to perform a variety of behavioural acts (Takahata, Komatsu & Hisada, 1984).

In this study, we used unilateral statocystectomy combined with cord hemisection experiments to investigate, in the crayfish *Procambarus clarkii* Girard, how the uropod steering response is controlled by a set of previously identified descending statocyst interneurones (Takahata & Hisada, 1982). We have found that each statocyst interneurone has different connections with individual motor neurones. This provides a neuronal explanation for our previous observation with the whole-animal preparation (Yoshino, Takahata & Hisada, 1980) that each statocyst could produce the normal bilateral steering response of uropods only in a limited range of roll angles.

MATERIALS AND METHODS

Animals and preparation

Experiments were carried out on adult crayfish *Procambarus clarkii* Girard (7–12 cm body length) of either sex. They were obtained commercially and kept in laboratory tanks before use. The animal was fixed to a rotation apparatus in the air with a metal rod which was cemented onto the dorsal anterior region of the cephalothorax (Yoshino *et al.* 1980). No substrate was provided for the legs.

For extracellular recording from the uropod motor neurone, a small portion of the sixth pleuron was removed to expose the terminal abdominal ganglion and its roots. The exposed ganglion was repeatedly perfused with crayfish saline (Van Harreveld, 1936). Small holes were drilled in the pleura of the fourth and the sixth abdominal segments for electrode insertion (see below).

To remove the statolith, hairs covering the statocyst aperture were pulled out by forceps. The statolith was then washed away with a water jet generated with a

pipette. The animal was used for experiment after several minutes' resting period following the operation.

Stimulation

To give the natural stimulus, the whole animal was tilted manually around its longitudinal axis using the rotation apparatus. The tilt angle was monitored through a variable potentiometer which was connected to the rotation axis of the apparatus. Position was monitored by a d.c. signal on which the transient upward deflections were superimposed at intervals of 15° (Takahata & Hisada, 1982), although the rotation itself was performed smoothly.

EMG and motor neurone activity recording

A fine pair of needle electrodes (No. 00) were inserted into the target muscle through tiny holes on the exoskeleton of the uropods, and connected to an a.c. amplifier through thin enamel-coated copper wires (50–100 μm in diameter) of about 40 cm length. Recordings were displayed on a storage oscilloscope. To discriminate the activity of one muscle from that of adjacent muscles, simultaneous recordings were made from these muscles.

To record the motor neurone activity during body rolling, an electrode holder was attached to the rotation apparatus so that the recording electrode could move with the animal as a unit. The animal was first placed ventral side up on the rotation apparatus. A cut end or *en passant* recording was made from the ganglionic root with a suction electrode made of polyethylene tubing. The diameter of the electrode tip was almost the same as that of the ganglionic root. The electrode, 10–15 cm long, was inserted into the abdomen through the hole on the sixth segment (see above). The electrode was passed under the ventral rotator muscle to immobilize it in the abdomen. After the recording had been established, the electrode was fixed to the pleuron surface by a drop of adhesive. An indifferent electrode was inserted into the abdomen through the hole on the fourth pleuron. The animal was moved back to the normal (0°) body position and kept there for several minutes before the experiment. Motor neurone spike data were stored on magnetic tapes together with the position-monitor signal, and later played back and photographed. When counting spike numbers, the recorded activity was passed through a window discriminator and the unit spike numbers were counted for a 4- or 8-s period from the onset of rotation by a digital counter.

RESULTS

Muscle activity pattern in steering

Uropod musculature and innervation in *Procambarus clarkii* Girard was first examined by Larimer & Kennedy (1969*a*). A semidiagrammatic drawing of nerve trunks and branches over the uropod musculature based on our observation is shown in Fig. 1. The uropods are movable about three axes (rotation, extension/flexion, promotion/remotion). The muscles are classified into five groups according to which of these five movements each muscle produced (Larimer & Kennedy, 1969*a*). To study which muscle group participates in the steering response to body rolling,

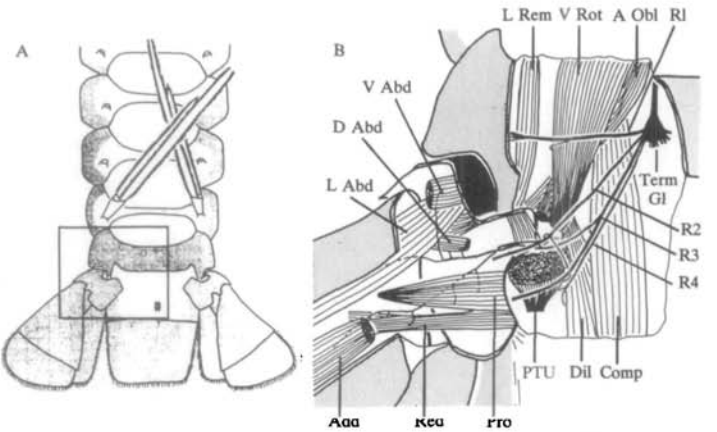


Fig. 1. Ventral view of the crayfish abdomen (A) and uropod innervation (B). Three promotor muscles (L Abd, lateral abductor exopodite; V Abd, ventral abductor exopodite; D Abd, dorsal abductor exopodite) are innervated by the third root motor bundle of the terminal abdominal ganglion (Term Gl) whereas three remotor muscles (Add, adductor exopodite; Pro, productor exopodite; Red, reductor exopodite) are innervated by the second root motor bundle. The sensory bundles of roots 2 and 3 are omitted in this diagram except at the site of their branching from the motor bundle. The ventral cuticle of the protopodite to which the adductor and the dorsal abductor attached and that of the exopodite to which the productor and the ventral abductor attached have been removed to show the musculature. The nomenclature of muscles follows Schmidt (1915). Dil, anal dilator; Comp, anal compressor; A Obl, anterior oblique; PTU, posterior telson uropodalis; L Rem, lateral remotor; V Rot, ventral rotator.

we recorded the electrical activity of nine representative muscles from the five groups during the steering movement: ventral rotator (rotator), lateral remotor (extensor), anal dilator (flexor), three abductors (promotors) and adductor, productor and reductor (remotors).

Promotors and remotors were most consistently activated when the steering movement occurred, whereas rotators, extensors and flexors were sometimes activated and sometimes not. Typical EMGs from three promotors and three remotors during steering are shown in Fig. 2. Steering, under the present experimental condition, consisted of opening of the uropod on the lifted side and closing on the lowered side (Yoshino *et al.* 1980). The EMG study showed that the opening was performed by co-contraction of three promotors and the closing by co-contraction of three remotors. The remotors on the lifted side and promotors on the lowered side are both relaxed. As an example of an atypical pattern, the adductor muscle could be contracting in one case and not in another case even in the same animal. In Fig. 3 the spikes of adductor motor neurones, which can be identified by their large extracellular spike amplitude (Nagayama, Takahata & Hisada, 1983), are absent during steering. The functional difference among muscles in the promotor and remotor groups was not investigated. Three promotors and remotors will be simply referred to as openers (Op1, Op2 and Op3) and closers (Cl1, Cl2 and Cl3)

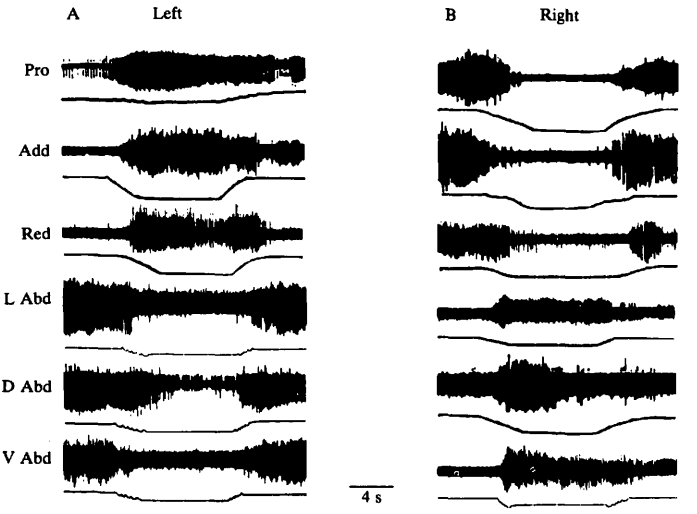


Fig. 2. Activity of uropod muscles on the left side (A) and on the right side (B) during the steering movement. The animal was tilted from 0° to 90° body position in the left-side-down direction and returned to 0° body position. The trace under each record indicates the body position. Although small deflections are superimposed on the d.c. signal from the potentiometer, the tilting itself was performed smoothly (see Materials and Methods). The figure was compiled from recordings of each muscle activity in several animals.

respectively in this paper. The relationship of the old to the new naming systems is summarized in Table 1.

Motor neurone activity pattern in steering

Larimer & Kennedy (1969*a*) reported that all the three openers and one closer muscle (Cl3) are innervated by separate inhibitory motor neurones. Hence relaxation of uropod muscles during steering can result from decreasing activity in excitatory motor neurones, increasing activity in inhibitory motor neurones, or both. To test these possibilities, spike activity of motor neurones during the steering movement was recorded *en passant* from the ganglionic root.

Motor neurones supplying the opener muscles travel in root 3 of the terminal abdominal ganglion and those supplying the closer muscles travel in root 2 (Larimer & Kennedy, 1969*a*). This segregation facilitated the selective recording from either opener or closer motor neurones. The target muscle of the motor neurone was detected by successively impaling the putative muscle fibres until PSPs synchronized with the extracellular spikes of the motor neurone were recorded. The two motor neurones shown in Fig. 3 were identified as excitatory ones innervating Cl3 on each side because the spikes of inhibitory motor neurones evoke hyperpolarizing potentials (Yoshino, Masuda & Hisada, 1984).

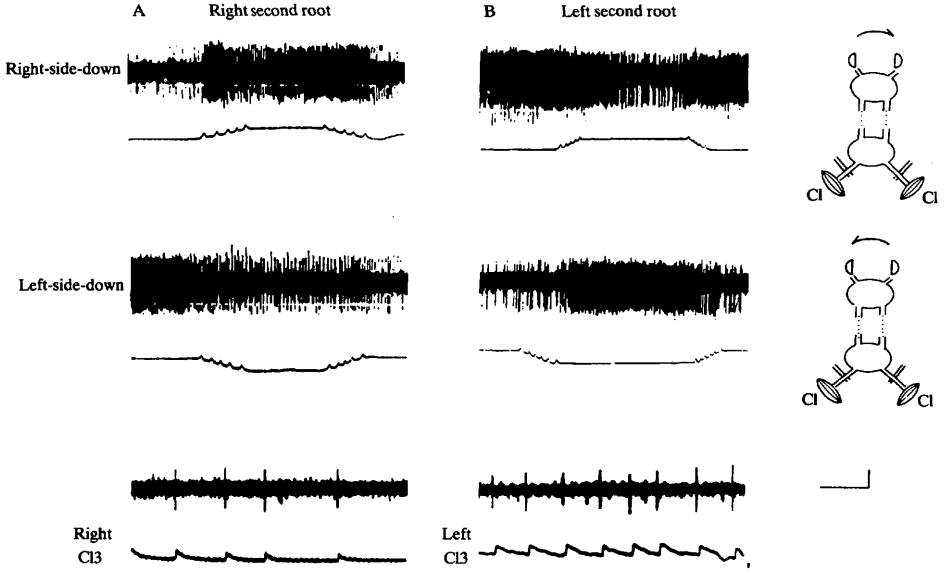


Fig. 3. Activity of uropod motor neurones during the steering movement. The animal was tilted from 0° to 90° body position in the right-side-down (top panels), or the left-side-down (middle panels) direction, and returned to the initial body position. The activity of the right second root (A) and the left second root (B) was recorded *en passant* in the same animal. The units in A and B were identified respectively as the excitatory motor neurones innervating Cl3 on each side by comparison with the intracellular activity in these muscles (bottom panels). Calibration: 2 s for top and middle panels, 100 ms for bottom panels; 10 mV for bottom panels.

Table 1. *Nomenclature of uropod muscles used for steering*

Schmidt (1915)	Larimer & Kennedy (1969*a*)	Present study
	Promotors	Openers
Abductor exopodite lateral	Lateral promotor	Op1
Abductor exopodite dorsal	Dorsal promotor	Op2
Abductor exopodite ventral	Slow promotor	Op3
	Remotors	Closers
Adductor exopodite	Lateral remotor	Cl1
Productor exopodite	Dorsal remotor	Cl2
Reductor exopodite	Slow remotor	Cl3

The results indicate that relaxation of uropod muscles during steering was carried out by decreasing the activity of excitatory motor neurones. Since no increase in any motor neurone activity was observed in the second root (closer, Figs 3, 4) during the same-side-up rolling, it appears that the peripheral inhibitors (Larimer & Kennedy, 1969*a*) did not participate in generating the steering pattern of uropod muscle activity.

We examined the contribution of joint receptor input to this reciprocal pattern formation by cutting all ganglionic roots which contained sensory fibres innervating the exopodite and endopodite, and found that the activity pattern of the motor neurones was not disturbed (Fig. 4). Thus, the reciprocal pattern of antagonistic motor neurone activation seems to be generated principally by central connections.

Inhibitory circuit involved in steering

The excitatory motor neurones innervating the closer muscles on the lifted side and those innervating the opener muscles on the lowered side showed a decrease in their spike activity during the steering (Fig. 3). The body roll causes not only an excitation of statocyst sensory neurones on the lifted side but a depression of those on the lowered side (Takahata & Hisada, 1979). Hence the decrease in the motor neurone activity could be due either to a decrease in the excitatory input or to an increase in the inhibitory input to the motor neurone pool, or to both of them.

We examined whether the statocyst on the lowered side made any contribution to the decrease in the motor neurone activity, by first removing the left statolith, and rolling the animal in the left-side-down direction. A single statocyst can normally control the bilateral uropod movement over a limited range of roll angles (Yoshino *et al.* 1980). The activity of opener and closer muscles on both sides was examined with this operated animal during the roll stimulus. If the decrease in muscle activity of the left opener and right closer under the normal condition were caused solely by a decrease in the excitatory input from the left statocyst, this animal should show no decrease in the muscle activity during steering. This was clearly not the case (Fig. 5).

The responses of the motor neurone to body rolling before and after the unilateral statolith removal were compared (Fig. 6). The opener motor neurone on the right side increased its spike discharge rate during the left-side-down rolling and

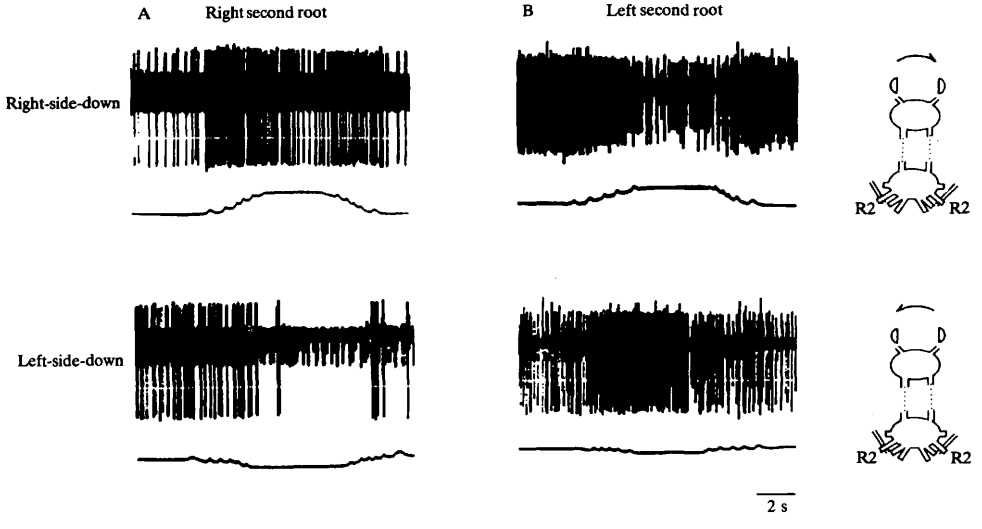


Fig. 4. Activity of closer motor neurones in response to body rolling in the right-side-down (upper panels) and the left-side-down (lower panels) direction in a deafferented animal. All the ganglionic roots were severed but both the connectives remained intact. The animal was tilted from 0° to 90° body position in each experiment and returned to the initial body position. The activity of the right second root (A) and the left second root (B) was recorded from their proximal cut ends. The units in A and B could not be identified but were probably those innervating Cl3.

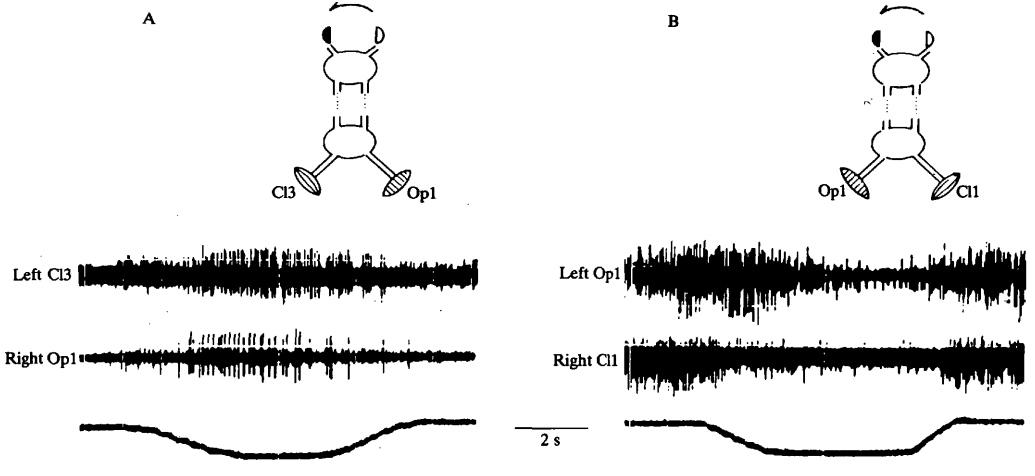


Fig. 5. Simultaneous recordings from the opener and closer muscles on different sides during the steering movement in response to left-side-down rolling. The statolith of the left statocyst had been removed (filled symbol). The animal was tilted from 0° to 90° body position and returned to the initial body position (bottom trace in each panel). In A, both the opener on the lifted side (middle trace, Op1) and the closer on the lowered side (upper trace, Cl3) are activated while in B, both the opener on the lowered side (upper trace, Op1) and the closer on the lifted side (middle trace, Cl1) are suppressed. Under this unilaterally statocystectomized condition, only the activity of the remaining statocyst will increase during body-rolling in this direction.

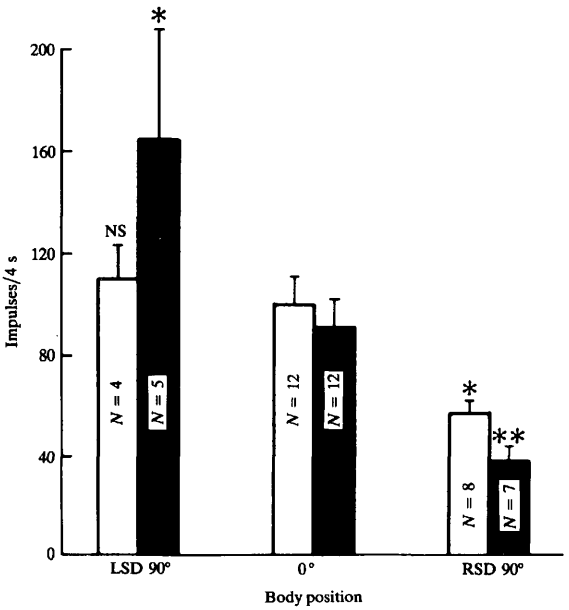


Fig. 6. Comparison of the opener motor neurone response before and after unilateral statolith removal. The activity of an unidentified opener motor neurone was recorded from the proximal cut end of the third root on the right side. When the intact animal was rolled by 90° in the left-side-down direction (LSD), the motor neurone significantly increased its spike discharge rate and decreased it when rolled in the right-side-down direction (RSD) (black bars). After the removal of the right statolith, the same motor neurone showed no significant change in its spike activity when the body was rolled in the left-side-down direction although it showed a significant decrease when rolled in the right-side-down direction (white bars). The bars indicate the means and the standard errors. NS, not significant; $^{*}0{\cdot}01 < P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$ with the two-tailed t-test.

decreased it during the right-side-down rolling. After the removal of the right statolith, the motor neurone showed no significant change in spike activity during the left-side-down rolling. However, there was a significant decrease in the spike activity during the right-side-down rolling. Thus the right statocyst seems to be responsible for the increase in the right opener motor neurone activity during the left-side-down rolling but not for the decrease during the right-side-down rolling.

We conclude that the decreased motor activity is due to increased inhibitory input from the statocyst on the lifted side. This conclusion was further supported by comparing the spike activity of the right closer motor neurone during the right-side-down rolling before and after removal of the right statolith (Fig. 7). The discharge rate of the closer motor neurone at 180° body position was lower than that at 0° body position in the intact animal (Fig. 7A). After statolith removal, the

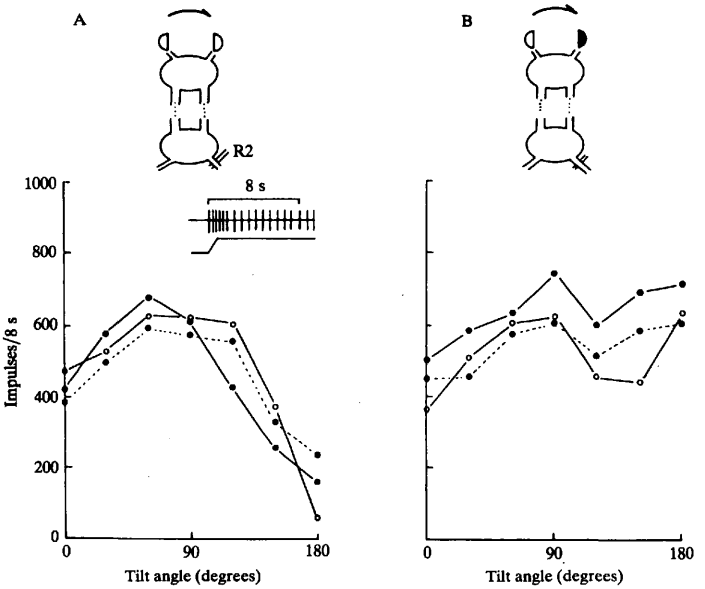


Fig. 7. Response of unidentified closer motor units on the right side to body rolling in the right-side-down direction. Results obtained from three animals are superimposed in each panel. In A, the intact animals were tilted. In B, the right statolith was removed. In either case, the animals were tilted from 0° body position to each measuring body position and returned to the initial body position. The motor neurone activity was recorded *en passant* from the right second root. The number of motor neurone spikes was counted for 8 s beginning from the start of positional change (see the inset in A).

discharge rate at 180° body position became higher than that at 0° body position (Fig. 7B). Input from the right statocyst in the intact animal gradually decreases with the roll angle in the right-side-down direction and reaches a minimal value at 60° body position, then it gradually increases and reaches the same level at 150° body position as that at 0° body position. At 180° body position, the right statocyst input increases to a level higher than that at 0° body position (Yoshino *et al.* 1980). The low activity of the closer motor neurones at 180° body position and the increase in activity after statolith removal can only be explained by postulating an inhibitory pathway from the statocyst to ipsilateral motor neurones.

Role of statocyst interneurones in steering

A single statocyst excites the opener motor neurones on the same side and closer motor neurones on the opposite side (Fig. 5A), and at the same time inhibits the closer motor neurones on the same side and opener motor neurones on the opposite side (Fig. 5B). Each statocyst excites two descending interneurones (C_1, C_2) on the

opposite side, one interneurone (I_2) on the same side, and one interneurone (I_1) bilaterally (Takahata & Hisada, 1982). What is the role of each of these four interneurones in each hemicord in generating the reciprocal pattern of uropod muscle activity during the steering movement?

We have examined the pathway between the statocyst interneurones and uropod motor neurones by nerve cord hemisection in the unilaterally statocystectomized animal. Spike activity of the closer motor neurone on the right side was recorded during the steering response to right-side-down rolling (Fig. 8A). After removal of the right statolith (Fig. 8B), the activity at 150°–180° body position increased due to the deletion of inhibitory input from the right statocyst (see above). When the ventral nerve cord on the left side was severed at the 5–6 abdominal connective (Fig. 8C), the closer motor neurone was still driven almost normally by the left statocyst at any roll angle, though a slight decrease in the overall spike activity was observed. Cutting the remaining right-side hemicord completely abolished the motor neurone response to body rolling (Fig. 8C). The result shows that the closer motor neurones are primarily excited by interneurones C_1 and/or C_2 which are excited by the contralateral statocyst and descend the nerve cord ipsilateral to the motor neurones. We could not discriminate a functional difference between C_1 and C_2 in this study. As discussed previously (Takahata & Hisada, 1982), interneurone I_1 is unlikely to serve the directional response itself.

A similar experiment was performed with the opener motor neurones (Fig. 9). Spike activity of an unidentified opener motor neurone on the left side was recorded during the steering movement elicited by right-side-down rolling (Fig. 9A). Deletion of inhibitory input from the right statocyst due to statolith removal resulted in an increase in the spike activity at 150°–180° body position (Fig. 9B). The response pattern was not affected at all by cutting the right hemicord (Fig. 9C). Further cutting of the left one completely abolished the motor neurone response (Fig. 9C). This result indicates that the opener motor neurones are primarily excited by interneurone I_2 which is excited by the ipsilateral statocyst and descends the nerve cord ipsilateral to the opener motor neurones.

Inhibition of the closer motor neurones on the lifted side and the opener motor neurones on the lowered side seems to be mediated through both the right and left hemicords, unlike their excitation (Fig. 10). The spike activity of a closer motor neurone on the left side was recorded while the animal with its right statolith removed was rolled (Fig. 10A). The inhibition of the motor neurone was reduced, but not completely abolished, by cutting the ipsilateral hemicord (Fig. 10A). Cutting the contralateral hemicord in another preparation also incompletely abolished the inhibition (Fig. 10B). Although we could not quantify the contribution of each hemicord to the inhibition of the motor neurone activity, the closer motor neurone seems to be inhibited by interneurones C_1 and/or C_2 descending the contralateral hemicord together with interneurone I_2 descending the ipsilateral hemicord, all of which are excited by the statocyst ipsilateral to the motor neurone.

The results of the cord hemisection experiments are summarized in Fig. 11.

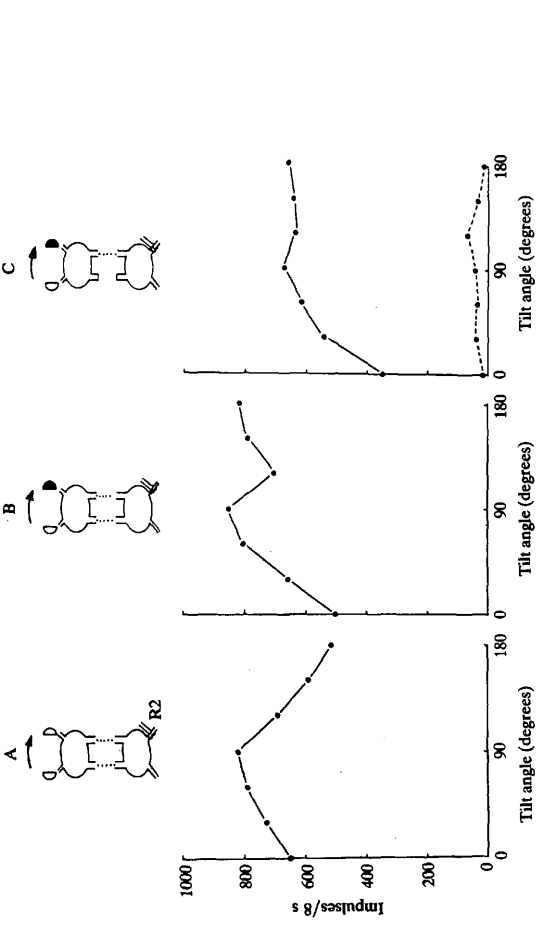


Fig. 8. Response of an excitatory motor neurone innervating the right C13 to body rolling in the right-side-down direction. In A, the intact animal was tilted. In B, the right statolith was removed. In C, the left abdominal connective was cut between the 5th and the terminal abdominal ganglia (solid line). Finally the right connective was also cut (broken line). All measurements were obtained from the same animal. The motor neurone activity was recorded *en passant* from the right second root.

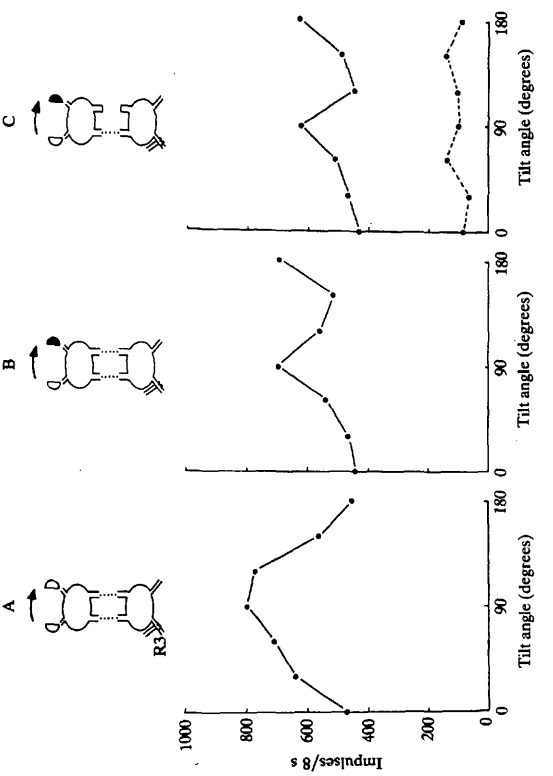
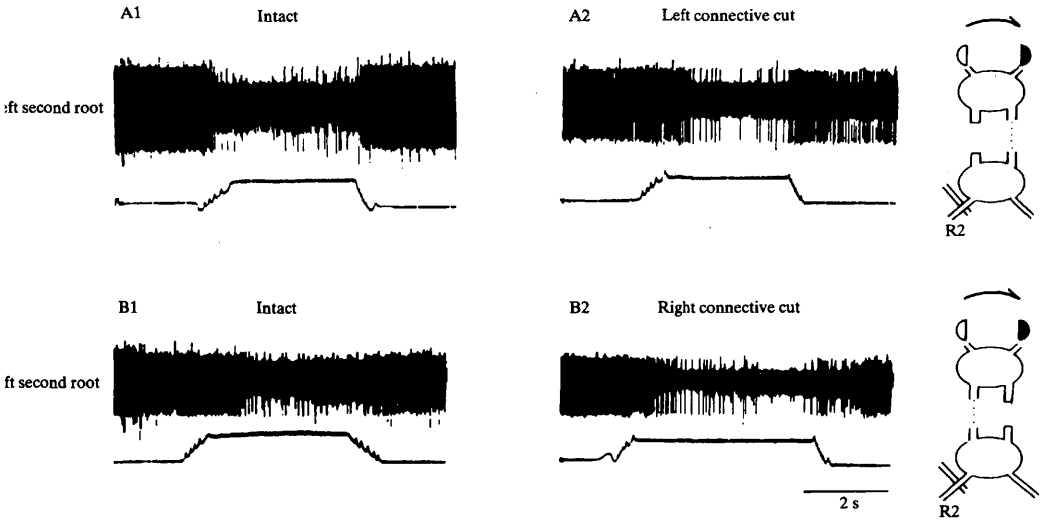


Fig. 9. Response of an unidentified opener motor neurone on the left side to body rolling in the right-side-down direction. In A, the intact animal was tilted. In B, the right statolith was removed. In C, the right abdominal connective was cut between the 5th and the terminal abdominal ganglia (solid line). The left connective was finally cut (broken line). All measurements were done in the same animal. The motor neurone activity was recorded *en passant* from the left third root.



g. 10. Inhibition of the uropod motor neurone activity during the steering movement. The activity of a putative C13 motor neurone was recorded *passant* from the second root on the left side. The right statolith had been removed. During the steering response to the right-side-down rolling, the 13 motor neurone was inhibited (A1, B1). After cutting the left connective between the 5th and the terminal abdominal ganglia, inhibition of the motor urone could still be observed (A2). After cutting the right connective in another preparation with the left connective intact, inhibition of the motor urone could also be observed (B2). The animal was tilted from 0° to 90° body position and returned to the initial body position.

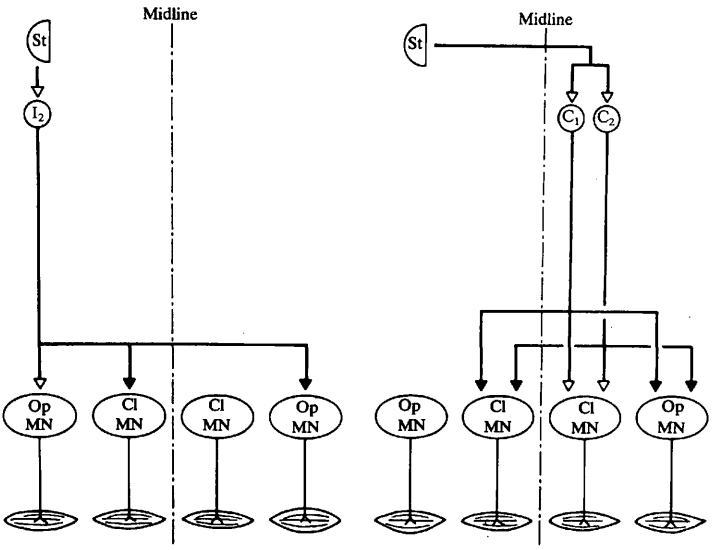


Fig. 11. Functional connections between a single statocyst (St) and the uropod motor neurones (MN) mediated by a set of statocyst interneurones. The ipsilateral pathway is shown on the left and the contralateral one on the right. The connections were deduced from the results of cord hemisection experiments. White and black triangles represent the excitatory and inhibitory connections respectively but do not necessarily indicate a monosynaptic link.

DISCUSSION

Role of statocysts in motor coordination

Three findings emerge from the present study about the function of a single statocyst in motor control.

Firstly, the neuronal pathway through which a single statocyst controls the bilateral movement of uropods has been clarified. That each single statocyst can control the bilaterally organized movement of appendages has been well appreciated (e.g. Schöne, 1951, 1954; Neil, 1975; Davis, 1968; Yoshino *et al.* 1980). However, it has long remained unanswered in what way a single statocyst controls the activity of motor neurones on both sides. We have shown in this study that a single statocyst controls the bilateral uropod movement by exciting the ipsilateral opener motor neurones and contralateral closer motor neurones through the ipsilateral statocyst interneurone (I_2) and the contralateral ones (C_1, C_2) respectively, and by inhibiting at the same time the ipsilateral closer and contralateral opener motor neurones through the interneurones descending both nerve cords (Fig. 11). Thus the distribution of statocyst information for controlling the motor neurones on both sides is primarily carried out in the brain, constituting a parallel descending system.

Secondly, a demonstration has been made for the first time that inhibitory connections are involved in the control system of uropod steering, although they

have been assumed to be present between the statocyst and motor neurones in the neural models for equilibrium responses (Davis, 1968; Schöne, 1977). The functional significance of inhibitory pathways is still to be studied further. Since the bilaterally asymmetrical excitation of uropod motor neurones principally contributes to form the asymmetrical steering pattern, the role of inhibitory pathways seems to complement the excitatory pathways and to ensure the asymmetrical uropod configuration. Another possibility would be that the inhibitory pathways might play a crucial role in the central compensatory process after unilateral statolith removal (Yoshino *et al.* 1980). The mechanism underlying this process, however, remains open to future study.

Thirdly, the final form of the steering motor pattern was found to be shaped in the terminal ganglion. In the crustacean compensatory eyestalk movement, it has been shown that each single statocyst can control the bilaterally organized eyestalk movement in the full rotation although some phase shift does occur (Schöne, 1954; Neil, 1975). In the steering movement, however, we have shown that each single statocyst can control the bilateral uropod movement over a limited range of roll angle (Yoshino *et al.* 1980). This seems to be due to the low spontaneous discharge rate of the statocyst interneurones (Takahata & Hisada, 1982): they cannot represent by decrease in their own spike activity the decrease in the statocyst sensory neurone activity. The common feature to both the compensatory eyestalk movement and the uropod steering movement is that both statocyst inputs summate with each other to produce the bilateral movement in an intact animal (Yoshino *et al.* 1980). The cord hemisection experiment in this study (Figs 7, 8, 9) shows that the summation is carried out not on the statocyst interneurones in the brain but on the uropod motor neurones in the terminal ganglion. That the final motor output is represented not in the activity of premotor descending interneurones but in that of motor neurones gives a clue for understanding the function of statocyst interneurones in equilibrium control (see next section).

Role of statocyst interneurones in motor coordination

In the crab *Scylla serrata*, Fraser (1975) showed that direct stimulation of statocyst fibre A elicited the full righting reflex and that of fibres C and D elicited swimming behaviour. It seems that the statocyst fibres of this crab could function individually as the command neurone (Kupfermann & Weiss, 1978). In crayfish, by contrast, any one of the statocyst interneurones is unlikely to be capable of evoking the steering movement independently since each of them connects with only some of the motor neurones involved in steering (Fig. 11). Although the functional difference between interneurones C_1 and C_2 remains to be further studied, it seems that, to produce the bilateral uropod movement, all the three directional interneurones (C_1, C_2, I_2) and probably the non-directional one (I_1) have to cooperate and their outputs have to summate onto the motor neurone. In this sense, the set of statocyst interneurones seems to constitute a command system (Kupfermann & Weiss, 1978) as with the interneurones controlling the swimmeret beating of lobster (Davis & Kennedy, 1972). However, the nested structure of the behavioural organization in which the steering is normally released by body rolling only while the

animal is performing abdominal postural movement (Takahata *et al.* 1984) strongly suggests that statocyst input by itself is not sufficient for initiating steering movement. To determine whether the parallel system of statocyst interneurones exactly meets the criteria for a command system, it would be necessary to know which part of the circuitry the signals from the abdominal posture system act upon.

The fact that the final motor output is generated by summation of the activity of a set of statocyst interneurones at their output ends indicates that all the information necessary for controlling the steering movement is not entrusted to any single interneurone. This conclusion seems to be inconsistent with the report by Larimer & Kennedy (1969*b*) who could produce various kinds of bilateral uropod movement by electrically stimulating single interneurones in the abdominal nerve cord. The possibility that they were stimulating several statocyst interneurones seems to be unlikely since individual interneurones with different motor connections run in quite different parts of the ventral nerve cord (Takahata & Hisada, 1982).

The uropods are involved in many behavioural acts other than the steering in response to body rolling. A pinch to the abdomen on either side, for example, elicits the bilaterally asymmetrical configuration of uropods. It also occurs spontaneously without any definite external stimulus. Hence the alternative possibility would be that the interneurones reported by Larimer & Kennedy (1969*b*) mediate those uropod movements other than the steering during body rolling. The present conclusion should be confined to steering as an equilibrium response.

The control system of the steering movement seems to be unexpectedly complicated comparing with the general scheme in which the command neurone(s) activate(s) the motor pattern generator (e.g. Kupfermann & Weiss, 1978). The complication is due to the fact that the statocyst interneurones perform the functions both of a command set and of pattern transmission. In the steering system, there is no specific central pattern generator between the interneurone and motor neurone levels (Fig. 11). It may well be that the steering movement is so simple that no refinement or structuralization in the control system has evolved, the primitive form of motor control having been preserved. But the present study should provide a general model for understanding not solely the equilibrium but the visual, tactile and proprioceptive control and modulation of bilaterally organized behaviour in which asymmetry in the sensory input leads to an adaptive change in the motor output (e.g. Schöne, 1975 in shrimp; Reichert & Wine, 1983 in crayfish; Schöne, Neil, Stein & Carlstead, 1976 in lobster).

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