Motor Pattern Changes During Central Compensation of Eyestalk Posture After Unilateral Statolith Removal in Crayfish

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ABSTRACT—Electromyographic recording was used to study how the activity of the eyestalk motor system is modified during the recovery of eyestalk posture following unilateral statolith removal in crayfish *Procambarus clarkii* Girard. Intact animals showed bilaterally balanced activity of the muscle 12 (eyecup-up muscle) in the upright body position. Body rolling caused an increase in the muscle activity on the lowered side and a decrease on the lifted side. Unilateral statolith removal caused imbalance in the bilateral muscle activity in the upright body position: the muscle 12 activity decreased tonically on the operated side and increased on the opposite side. Body rolling of the operated animal caused an increase in the muscle activity from the unbalanced level on the lowered side and a decrease on the lifted side. When the operated animal recovered its original symmetrical posture of eyestalks 14 days after operation, the muscle activity was found on both sides to return to the previous level observed before statolith removal, regardless of the post-operative condition in which the animal was maintained. In those animals that did not recover the original eyestalk posture, the unbalanced activity of bilateral muscles that was caused by unilateral statolith removal remained unchanged. The results indicate that the recovery of eyestalk posture is based on restoration of the original activity balance, rather than on fixation of the operation-induced activity imbalance, among bilaterally homologous sets of muscles in the course of central compensation.

INTRODUCTION

The body and appendage posture of crustaceans is primarily controlled by a pair of statocysts, each consisting of mechanosensory hairs and a statolith resting on them. Body tilting displaces the statolith to cause activation or inactivation of sensory neurons by deflecting the hairs connected with them in a specific direction. The postural control has been assumed to be based on the balance of activity of these sensory neurons on both sides (Davis, 1971). It has been pointed out, however, that the weight of statolith is not always balanced bilaterally in the same way since crustaceans grow larger by molting in which statoliths are newly formed by taking sand grains into the statocyst lumen from outside (Marler and Hamilton, 1966). Although no experimental support has been provided for this possibility, it has been further postulated that the central nervous system has an ability to compensate unbalanced inputs from bilateral statocysts (Marler and Hamilton, 1966). In fact, Schöne (1954) has demonstrated that the bilateral imbalance in statocyst inputs caused artificially by unilateral removal of statolith is compensated centrally to recover the

normal posture several days after operation. The physiological mechanism of this compensation remains unknown.

In a separate paper (Sakuraba and Takahata, 1999), we examined by behavioral observation the post-operative sensory conditions required for the postural recovery to be completed after unilateral statolith removal. It has been revealed that the recovery of normal eyestalk posture requires the presence of a leg substratum provided bilaterally. The recovery could be also completed when the leg substratum was provided unilaterally, only if it was accompanied by specific visual inputs. These findings raise a question regarding whether the recovery of normal eyestalk posture enabled by different sensory conditions is based on a common or different mechanisms.

The eyestalk posture is controlled by a set of 11 muscles (Mellon, 1977). Either an increase or a decrease in the activity of one muscle would alter the eyestalk posture while activity changes in an antagonistic set of muscles in the same direction would have no effect on the posture. In the uropod motor system of crayfish, it has been shown that both opener and closer muscles are activated during walking without affecting the symmetrical configuration of bilateral uropods whereas bilaterally homologous muscles are activated reciprocally to produce asymmetrical configuration during steering behavior (Takahata *et al.*, 1985). Behavioral observation of the eyestalk posture thus can provide by itself

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no definite clue for understanding the physiological mechanism underlying the postural recovery following unilateral statolith removal as well as the postural asymmetry just after the removal.

In this study, we first measured the weight of bilateral statoliths and examined the relationship between their balance and the eyestalk posture. We then made electromyographic recording from a pair of bilaterally homologous muscles that are responsible for lifting the eyestalk to examine the motor pattern changes in the course of central compensation that was artificially induced by unilateral statolith removal. The muscle activity change was studied in those animals that were reared in different sensory conditions after the statolith removal.

MATERIALS AND METHODS

Animals and preparations

Experiments were carried out on adult crayfish *Procambarus clarkii* Girard (8–12 cm in body length), which were obtained from a commercial supplier. They were kept in a laboratory tank until use and fed weekly on a diet of raw potato and liver. There was no significant difference in results between the sexes.

The chelipeds and rostrum were cut off before experiments. The operated animals were kept one day to allow the wounds to heal. The statocyst was disabled by first removing the hairs covering its aperture on the dorsal surface of the antennular basal segment with fine forceps. A jet of water was then directed with a pipette into the statocyst lumen to wash out the statolith. The operated animal was used for experiments after one hour of recovery period. In this study, the statolith was removed on either side. The data were pooled to be regarded as the results of unilateral statolith removal.

Post-operative conditions

All animals were reared at room temperature under a 12 : 12 light (86 ± 5.9 lux) -dark cycle made manually by turning on and off 2 fluorescent tubes (each 20W) located about 3 m above the aquarium. They were never fed after operation until the final measurement was done. Operated animals were kept in one of 3 specific sensory conditions for 14 days. In the first condition (condition #1 in Sakuraba and Takahata, 1999), the animal was individually maintained separately in a plastic aquarium (30 × 18 × 25 cm) filled with water (5 cm in depth). The animal could move around freely in the aquarium with visual input provided bilaterally. In other 2 conditions, each animal was kept separately in an aquarium of the same size as that used in the first condition equipped with a holding frame. The animal was fixed upright in the water to a metal rod of the frame with a nut glued onto the cephalothorax. In the second condition, the animal was provided with a leg substratum on both sides as well as bilateral visual inputs. The distance between the substratum and the thorax was held at 1 cm not to prevent animals from moving legs freely (condition #3). In the third condition, the animal was provided with a leg substratum only on the side ipsilateral to the statolith removal. The visual input was also restricted to the same side by surrounding the other sides of the aquarium with black paper (condition #10A).

Measurements

To measure the eyestalk posture in response to body rolling, the animal was suspended in the air with a metal rod, which was attached to a rotation apparatus (Yoshino *et al.*, 1980). No leg substratum was provided. The rod was connected with a nut that was glued on the cephalothorax. The eyestalk posture was video-recorded or photographed with a digital camera under bilaterally symmetrical light conditions about 300 lux. Measurement was done on the screen of a display monitor of a personal computer connected with these devices. Details are described in a separate paper (Sakuraba and Takahata, 1999).

In order to weigh the statolith, the pair of antennules were excised at the base and dried at 50°C for 8–12 hr. Contents of the dried statocyst, that were sand grains formerly constituting the statolith, were dumped into a measuring container and weighed using a microbalance with 1 μg readability and 0.8 μg repeatability (Mettler, MT5).

Electromyograms

Electromyographic recording was made from 41 animals. To investigate the change in muscle activities accompanying the compensation of eyestalk posture, a pair of electrodes made of steel insect pins (No. 00) insulated with enamel were implanted through the soft cuticle onto the eyestalk-up muscles (Muscle 12; Mellon, 1977) on both sides. Electrode implantation was adjusted so that the noise amplitude became almost the same on both sides in order to compare bilateral muscle activities. The electrical signals were fed through enamel coated silver wires (100 μm in diameter) to an electronic amplifier (Nihon-Kohden, MEG-2100) that was connected to an oscilloscope (Tektronix 5100) and a digital data recorder (Bio-Logic, DTR-1801). The tilt angle was monitored by a potentiometer mechanically coupled with the axis of the rotation apparatus. The other end of the axis was coupled with a DC motor (Mabuchi, RE-280) through a reduction gear to keep the tilt rate at 22°/sec.

RESULTS

Functional recovery of eyestalk posture

The eyestalk posture of crayfish is maintained bilaterally symmetrical in the upright (0°) body position both in the air and in the water when no substratum is provided to walking legs (Fig. 1). This symmetrical posture is primarily controlled by a pair of statocysts. However, measurement in 10 animals revealed that the balance of bilateral statolith weight varies from animal to animal (Fig. 2A). On average, the weight of heavier statolith was 175.9 ± 14.9 μg whereas that of the lighter one was 108.7 ± 12.5 μg (Fig. 2B). The difference was statistically significant (P < 0.01; two-sided Student's t-test). Despite the imbalance in sensory inputs from bilateral statocysts due to different statolith weight, the animal showed bilaterally symmetrical eyestalk posture (−0.28° ± 1.6°) in the upright body position.

When the animal body is rolled in the air without a leg substratum, both eyestalks move toward the opposite direction (○ in Fig. 1) showing bilaterally asymmetrical configuration. The eyestalk posture becomes asymmetrical even in the upright body position when the statolith is removed experimentally on one side. Body rolling causes eyestalk movements from this asymmetrical posture (● in Fig. 1). The eyestalks gradually recover the original symmetrical posture, however, if the operated animal is kept in an appropriate condition (■ in Fig. 1).

Muscle activity change during body rolling in intact and operated animals

When an intact animal is rolled, the eyestalk on the lowered side moves upward while the one on the lifted side
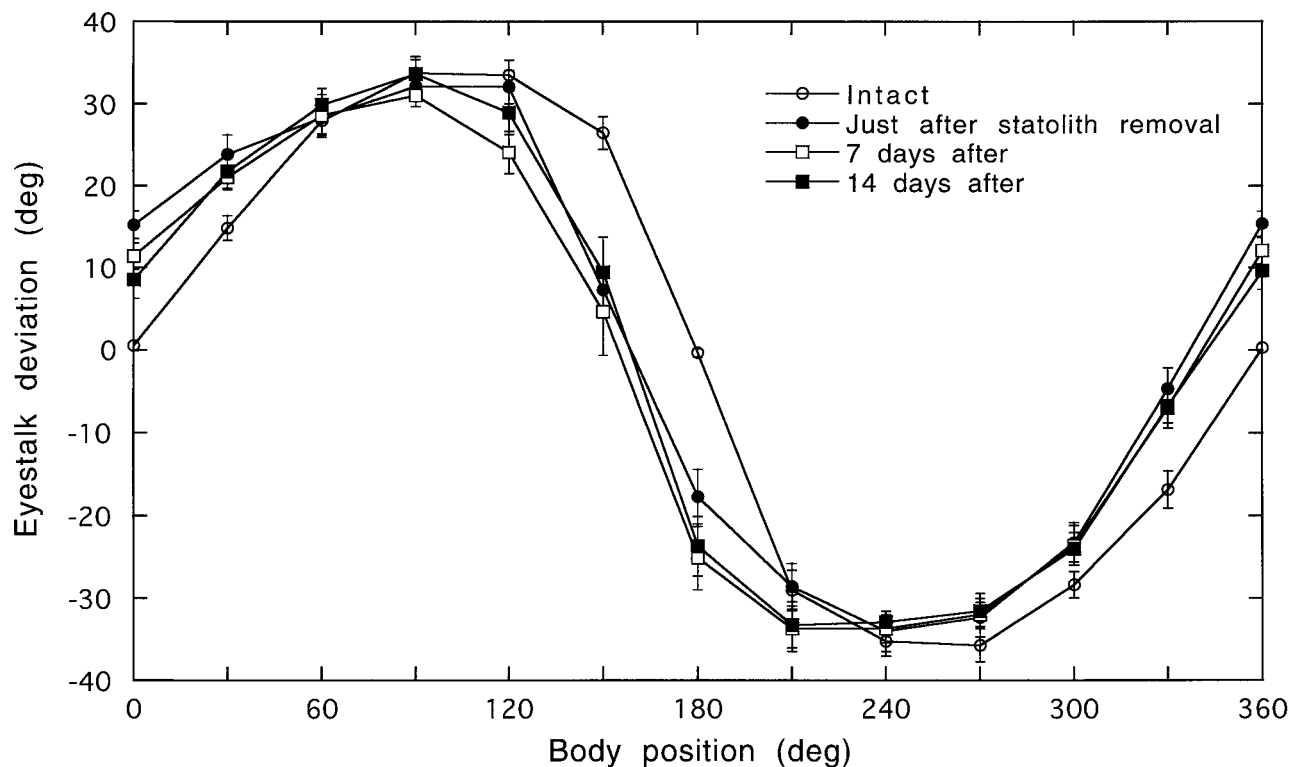
Fig. 1. Bilateral eyestalk movements in response to body rolling. The animal was rolled in the left-side-down direction from the upright (0°) body position. Eyestalk deviation is represented by the deviation angle of the bisector of an angle made by both eyestalks from the sagittal plane. Positive and negative values indicate deviation in the right and left direction respectively. Each point shows the mean and standard error for 10 measurements. After unilateral statolith removal, the animal was fixed in the water with unilateral leg substratum and visual input provided on the operated side. All measurements were done with no leg substratum provided.

moves downward (○ in Fig. 1). These movements of bilateral eyestalks are called compensatory movements (Schöne, 1961; Neil, 1982). Electromyographic recording from the muscle 12 (eyestalk-up muscle, Mellon, 1977) has revealed that the muscle shows spontaneous activity which is balanced bilaterally in the upright (0°) body position (Fig. 3A). In response to body rolling, the muscle 12 on the lowered side is further activated and maintains the increased activity as long as the body remains in the tilted position. This maintained muscle activity is consistent with the result of behavioral observation that the eyestalk response to body rolling is static (Schöne, 1954). On the other hand, the muscle 12 activity on the lifted side shows a decrease from the spontaneous activity level. This decrease also lasts as long as the body is kept tilted. Downward movement of the eyestalk on the lifted side is thus partly due to a decrease in the eyestalk-up muscle activity.

Unilateral statolith removal caused a decrease in the muscle 12 activity on the operated side and an increase on the intact side in the upright body position (Fig. 3B). The muscle is still responsive to body rolling under this condition. When the animal was rolled so that the operated side was lowered, the muscle 12 increased its activity on the lowered side depending on the tilt angle. The muscle on the opposite side decreased its activity so that in a certain body position (shown with an asterisk in Fig. 3B) the muscle 12 activity

becomes balanced bilaterally. When the animal was rolled in the operated-side-up direction, the unbalanced activity of muscle 12 was further enhanced: on the operated side, the decreased activity of the muscle 12 shows a further decrease whereas the muscle activity is more enhanced on the opposite side (Fig. 3B).

It is noted in intact animals that the muscle activity increases transiently on both sides during body rolling (indicated by arrowheads in Fig. 3A). In the operated animals, the transient increase in muscle activity is also observed during body rolling in the operated-side-up direction as well as during return from the operated-side-down tilting (arrowheads in Fig. 3B). However, when the animal was rolled in the operated-side-down direction or returned from the operated-side-up to upright body position no transient increase was observed. Apparently, the transient increase of muscle activity is observed when the statocyst hairs are deflected laterally to activate phasic units and inactivate tonic units (Takahata and Hisada, 1979).

Muscle activity change 14 days after statolith removal

Even when the operated animals were kept in an appropriate sensory condition for 14 days, not all animals showed complete recovery of the normal eyestalk posture. Electromyographic recording from an animal that recovered the normal eyestalk posture in the free condition is shown in
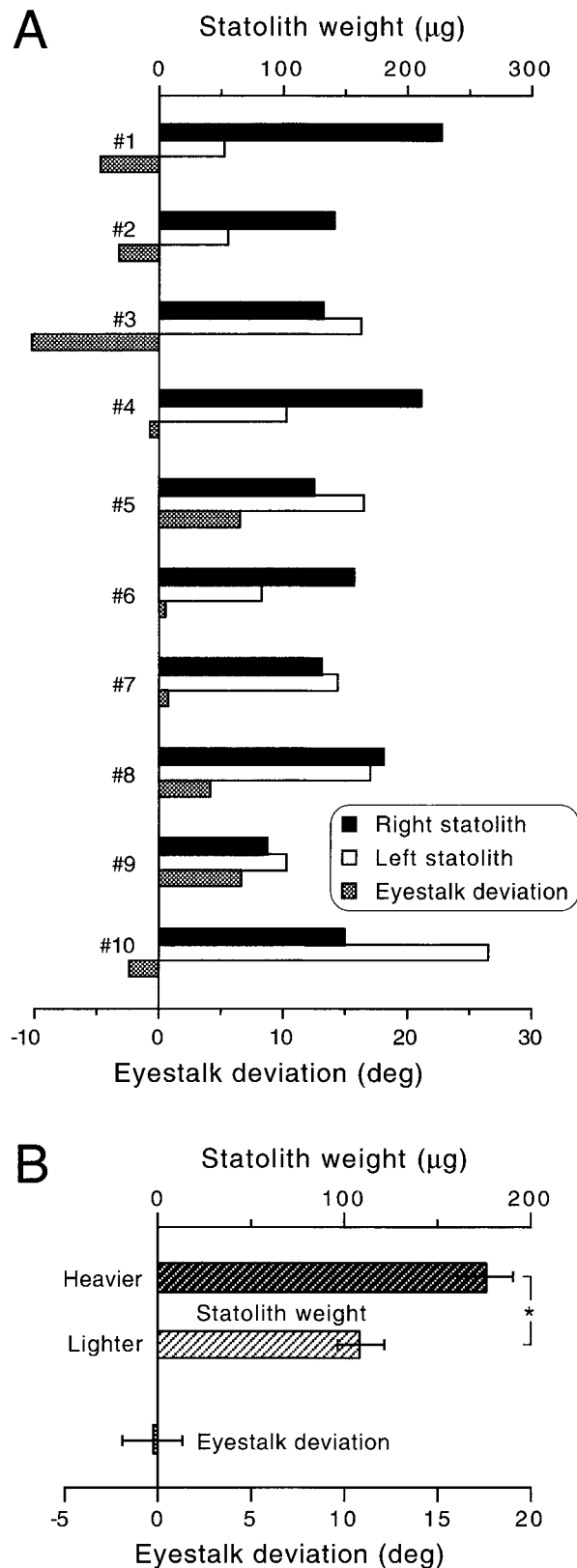
Fig. 2. (**A**) Dry weight of statolith measured in 10 animals (#1–10). The weight of right and left statolith is shown together with the eyestalk posture in the upright body position for each animal. (**B**) Mean statolith weight and eyestalk deviation. The mean weight of statolith is compared between heavier and lighter group. The difference was statistically significant (* P<0.01).

Fig. 4A. It shows bilaterally balanced activity of the muscle 12 in the upright body position. As the normal animal (Fig. 3A), the recovered animal responds to body rolling with an increase in the muscle 12 activity on the lowered side and a decrease on the lifted side. The change in muscle activity lasts as long as the animal is kept tilted. It is also noted that the muscle now shows a transient increase in its activity on both sides just as in intact animals.

Results obtained in an unrecovered animal are illustrated in Fig. 4B. In the upright body position, this animal still shows bilaterally asymmetric activity in the muscle 12. Responses of the muscle to operated-side-up and down rolling, including the transient increase in muscle activity that was characteristically observed during the body tilt in specific directions, are also similar to those observed right after operation (Fig. 3B). Thus, the muscle 12 that is less active than its counterpart in the upright body position further decreases or increase its activity depending on the roll direction whereas the other shows opposite changes (Fig. 4B).

Muscle activities in animals reared in different sensory conditions

Electromyograms from the muscle 12 on both sides in the upright body position are compared in Fig. 5 among those animals that were kept in different sensory conditions but commonly showed recovery of the normal eyestalk posture 14 days after unilateral statolith removal. The animal was kept in the free condition with bilateral visual input (Fig. 5A). The animal shown in Fig. 5B was fixed in the water with a leg substratum and visual input provided bilaterally whereas the one shown in Fig. 5C was also fixed with a leg substratum but the visual input provided only on the operated side. These post-operative sensory conditions have been shown to be as effective as the free condition for attaining the functional recovery of the normal eyestalk posture (Sakuraba and Takahata, 1999). The results illustrated in Fig. 5 indicate that irrespective of the sensory condition, the recovered animals commonly show bilaterally balanced activity in the muscle 12 which once showed bilaterally unbalanced activity right after the statolith removal, although the animal shown in Fig. 5A is not typical in that the statolith removal did not cause a clear decrease in the muscle activity on the operated side.

DISCUSSION

The central compensation of appendage posture following unilateral statolith removal has long been known in crustaceans (Schöne, 1954, 1961; Yoshino *et al.*, 1980) although the physiological mechanism still remains unknown. In a previous study, we have shown that attainment of the central compensation is significantly facilitated when the animal is maintained in specific sensory conditions after statolith removal (Sakuraba and Takahata, 1999). In the present study, we have examined the neural activity change for the first time in the course of compensation by making
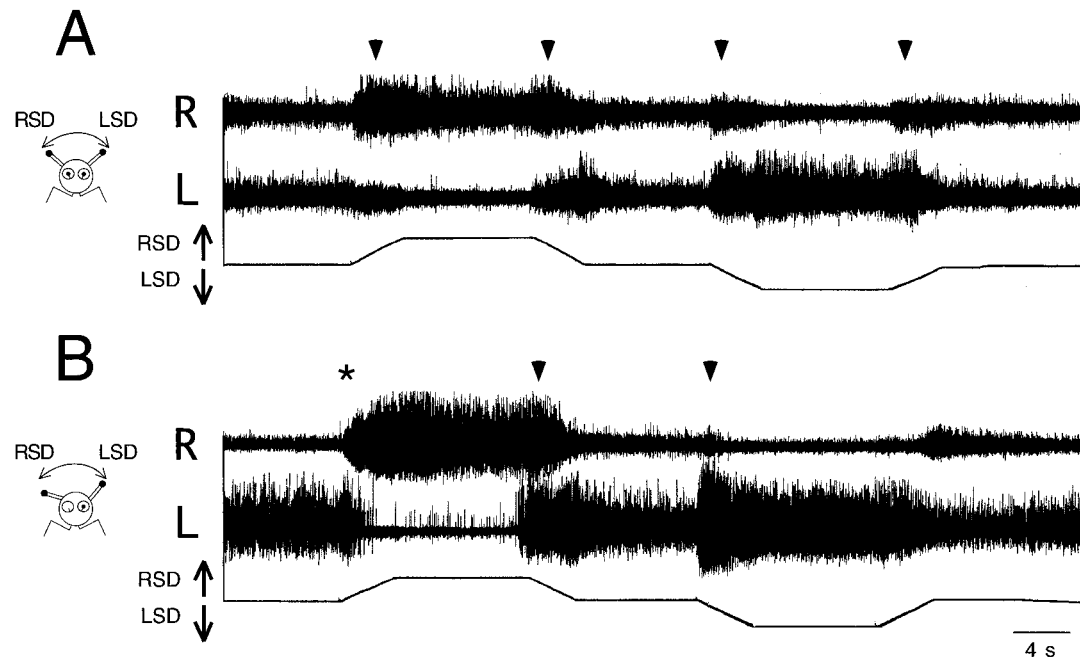
Fig. 3. (**A**) Electromyographic recording from the eyestalk-up muscle during body rolling in an intact animal. (**B**) Eyestalk-up muscle activities in response to body rolling just after the right statolith was removed. Upper and lower traces in each record show the muscle activity on the right (R) and left (L) side respectively. The bottom trace in each record indicates the body position. The animal was tilted from 0° to 90° body position in the right-side-down (RSD, upward deflection of the bottom trace) and left-side-down (LSD, downward deflection) direction. A transient increase in the muscle activity was observed during rolling regardless of its direction in A (arrowheads). The transient increase is observed only during the body roll in specific directions in B. Right after the statolith removal, the bilateral muscle activity becomes balanced not at the upright body position as in A but at a tilted body position (indicated by * in B).
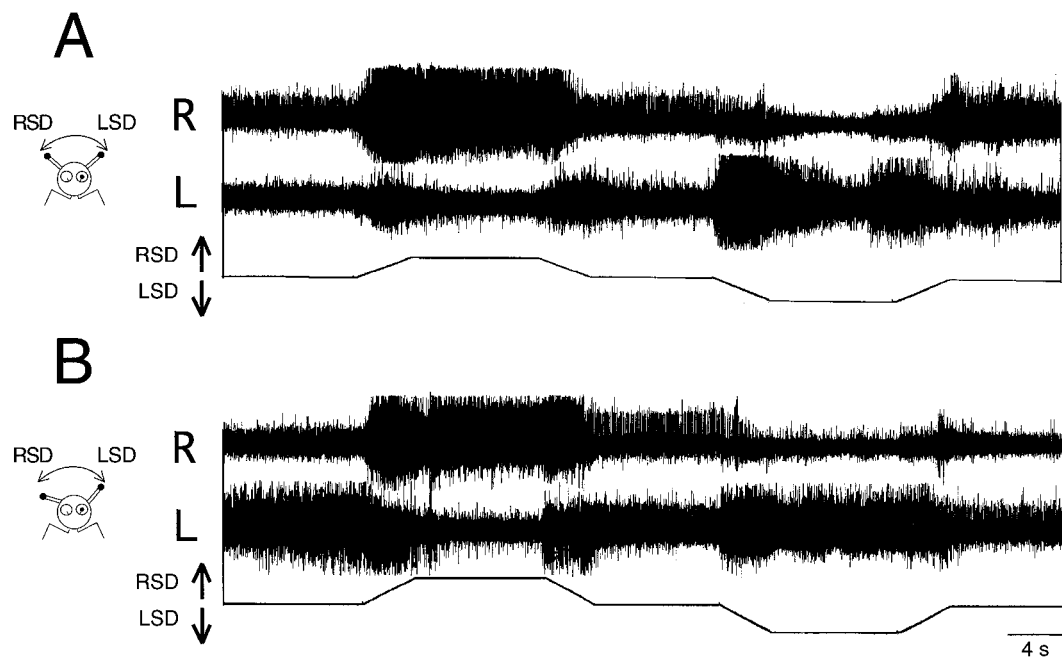
Fig. 4. (**A**) Electromyographic recording from the eyestalk-up muscle during body rolling in an animal that recovered the original posture of bilateral eyestalks 14 days after the statolith removal. The animal was reared in the free condition. (**B**) Eyestalk-up muscle activities in an animal that did not recover the original eyestalk posture.
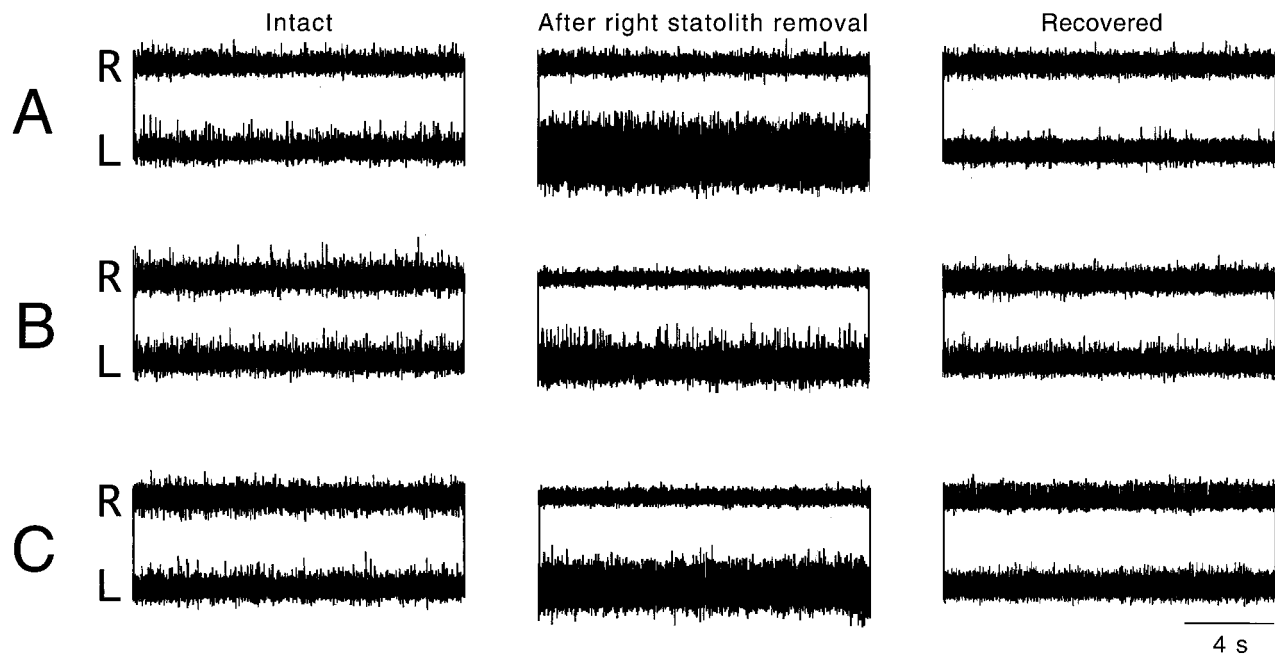
Fig. 5. Activities of the eyestalk-up muscle on the right (R) and left (L) sides in the upright body position. Electromyograms recorded in the intact condition (left column), just after removal of the right statolith (middle column) and after restoration of original posture of bilateral eyestalks (right column). The animal was kept free in a tank with light from above (**A**), fixed in the water with bilateral leg substratum and visual input provided (**B**), and fixed with unilateral leg substratum and visual input on the operated side (**C**). Different animals were used for each recording.

electromyographic recording from eyestalk muscles. The results show that the recovery of eyestalk posture is based on restoration of original activity balance between bilateral homologous muscles regardless of the post-operative sensory condition.

Central compensation of unbalanced statocyst input

Functional recovery of the bilateral eyestalk posture following unilateral statolith removal (Fig. 1) apparently reflects the ability of the crayfish brain to centrally compensate the sensory imbalance for keeping appropriate postures of the body and appendages. The central compensation is crucial for the crustacean posture control because, every time the animal molts, the amount of sand grains taken into the statocyst to form a new statolith is not necessarily balanced on both sides (Marler and Hamilton, 1966). Our measurement of the statolith weight has revealed for the first time that it significantly differs on each side (P < 0.01) whereas the eyestalk posture was bilaterally symmetrical (Fig. 2B). This finding indicates that the central nervous system of crayfish compensates the sensory imbalance after every ecdysis to restore the symmetrical eyestalk posture.

Compensatory functions of the central nervous system for dealing with partial sensory deprivation have been widely reported in both invertebrates (Vardi and Camhi, 1982a, b; Wolf and Büschges, 1997; Kanou et al., 1999) and vertebrates (Deliagina, 1997; Dieringer, 1995; Smith and Curthoys, 1989). In crustaceans, however, the compensatory function is not only employed to manage accidental sensory imbalance but also crucially involved in recalibration of bilateral statocyst inputs in the course of molting as a physiological process for normal growth. Thus, in the natural condition, it is likely that the compensation after molting that is under control of ecdysterone (Hampshire and Horn, 1966; Krishnakumaran and Schneidermann, 1969) is attained by cooperation of hormonal and neuronal processes. In the experimental study by unilateral statolith removal, however, only the neuronal mechanism can be investigated as a first step toward understanding the physiological mechanisms of central compensation.

Neuronal mechanisms underlying the central compensation

The eyestalk posture is controlled by balanced activity of 11 muscles on each side (Mellon, 1977). We made electromyographic recording from the eyestalk-up muscle (muscle 12) to find that its activity is bilaterally balanced when an intact animal is kept in the upright body position (Fig. 3A). Although we did not make recordings from other muscles in this study, it would be safe to assume that the activities of other muscles are also balanced in the upright body position since imbalance in their activity would inevitably lead to postural asymmetry of bilateral eyestalks just as in tilted body positions (Fig. 3A).

Electromyograms reflect the electrical activities of motoneurons innervating the recorded muscle. Our results thus indicate that the motor activity of the eyestalk system shows a temporary decrease when the statolith is removed on the same side whereas it shows an increase on the opposite side (Fig. 3B). This temporary activity change is

gradually canceled after operation, provided that the animal is kept under appropriate sensory conditions (Fig. 4A). Neither increased nor decreased activity of the muscle 12 is maintained when the central compensation is successfully attained. In those animals that did not show compensation, by contrast, the unbalanced activity appears to be sustained (Fig. 4B). The symmetrical posture of bilateral eyestalks can be attained by balanced activity of antagonistic sets of muscles on each side. Thus a possible explanation of the recovery of bilateral eyestalks would be that increased activity of the eyestalk-up muscle becomes counteracted in the course of compensation by increased activity of the eyestalk-down muscle on one side whereas decreased activity of the eyestalk-up muscle becomes counteracted by decreased activity of the eyestalk-down muscle on the other side. However, the results of our study makes this possibility unlikely. It is concluded instead that the temporary changes in any motor activity following the statolith removal is not fixed but brought back to the original level in the eyestalk posture system. The restoration of original muscle activity is not dependent on the post-operative sensory condition, always observable when the central compensation is successfully attained (Fig. 5).

In many studies of compensation following partial ablation of sensory organs, the sensory neurons are also injured so that the central effect of their regeneration and degeneration have to be considered to understand the physiological mechanism of compensation (Büschges *et al.*, 1992; Wolf and Büschges, 1997; Kanou *et al.*, 1999). In the statolith removal experiment, however, the mechanosensory neurons remain intact although the stimulative stretch formerly exerted by the statolith is lost (Sakuraba and Takahata, 1999). Even in the absence of statolith, however, the statocyst sensory neurons continue to discharge spikes spontaneously (Takahata and Hisada, 1979). It is therefore unlikely that the synaptic connection between sensory neurons and central interneurons is functionally modified in the course of compensation. Furthermore, no efferent control system is present in the crustacean statocyst, unlike in the mollusk statocyst (Wollf, 1970) and vertebrate equilibrium sense organs (Galiana *et al.*, 1984). Hence more plausible is the possibility that the unbalanced statocyst input due to statolith removal is recalibrated in the central nervous system by other sensory cues including visual and leg proprioceptor inputs to provide bilaterally balanced motor outputs. This possibility is supported by the convergence of visual, statocyst and leg proprioceptor inputs onto interneurons (NGIs) that are presynaptic to eyestalk motoneurons in the brain (Okada and Yamaguchi, 1988; Yamaguchi and Okada, 1990; Okada *et al.*, 1994; Furudate *et al.*, 1996). Nakagawa and Hisada (1990) further reported many local interneurons in the brain receiving statocyst inputs. Further study by direct recording from these interneurons including NGIs in the course of central compensation is needed to clarify its neurophysiological mechanisms.

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