

JOINT MECHANO RECEPTOR RESPONSES OF THE UROPODS IN *LIGIA EXOTICA*

Tsuneo Hatanaka and Mieko Kawamoto

ABSTRACT

The responses of mechanoreceptors at the uropodal basal segment-ramus joint are studied in *Ligia exotica*. The responses are classified into three types by the responsible direction of ramus movement, an open receptor, a close receptor and an open-close receptor. The open receptor is a unidirectional phasic-tonic position receptor with slow adaptation. The close receptor is also a unidirectional phasic-tonic position receptor but its adaptation is fast. The open close-receptor is a bidirectional phasic movement receptor with rapid adaptation. Almost units of this type have peculiar responsive ranges in ramus angle. The results of the dissection of a tendon or an arthroal membrane indicate that the open receptors and the open-close receptors relate with different structures.

INTRODUCTION

The structure and function of joint mechanoreceptors of crustacea decapoda have been intensively studied by number of works. In the limbs or walking legs, various mechano receptors have been observed and almost of these were chordotonal organ type structure (Bush and Laverack, 1982; Rossi-Durand and Vedel, 1982). From the response patterns, these mechanoreceptors were classified into two groups generally, such as a tonic position type and a phasic movement type. Laverack (1964) reported three types of response in antennule of *Panulirus* and Barber (1960) reported five types of response in the walking legs of *Limulus*. Bush (1965) reported that the responses of walking leg's receptor of *Caracius* revealed many types. While, the joint receptors of lower crustacea have been little studied. Alexander (1969) showed two types of response, a tonic position type and a phasic movement type in *Ligia* legs. He also mentioned briefly the mechanoreceptor response of the uropod (1971).

The uropod of *Ligia* is composed of basal segment and two rami, outer ramus and inner ramus. The distal portion of the inner ramus, a terminal spine is jointed. In a resting situation, the two rami are closed and the uropod itself is dropped. But in an active phase, the uropod is lifted up and the outer ramus is held almost erect, while, the inner ramus is bended ventrally, and the terminal spine of inner ramus still remains in contact with the ground, so two rami are opened. This posture with the open uropod seems to get ready for the stimulus perception. To recognize the state of uropodal ramus joint, some proprioceptors may exist. Alexander (1971) and Sttut and Laverack (1979) electrophysiologically investigated joint receptors of the uropod in *Ligia oceanica*. But they didn't determine the portion of the proprioceptors. So, we studied the properties of uropodal joint receptors and the effects of partial surgical dissection in joint structures in *Ligia exotica*.

METHODS AND MATERIALS

Ligia exotica was captured from a break water at the beach and preserved in a tank with seaweed and

fish meat (dried fish). The uropod of *Ligia* was dissected from a telson, and settled on an acryl chamber. Exoskelton, muscles and connective tissue of the basal segment were removed in about two thirds of more proximal part and, two uropodal nerves were exposed. The two nerves were hooked by Ag-Agcl electrode or platinum-iridium electrode, respectively or together. Nerve activity was introduced, amplified, and recorded by ordinal electrophysiological methods. Mechanical stimuli were derived from a micro-manipulator with a small ring of copper wire in which the ramus of the uropod was inserted. Sometimes, in order to avoid the risk of stimulation to mechano-sensitive sensilla over the ramus (Hatanaka, 1989), a glass micro tube was covered the ramus. A hand made stimulation set was made with a motor and cam system for a continuous stimulation. Usually, opening and closing stimuli were delivered to each ramus. When an angle between the ramus and a prolonged line of the basal segment axis was 0 degree, the ramus was closed (resting position). Each ramus was deflected to about 60 degrees; the outer ramus was elevated and the inner ramus was depressed.

RESULTS

1. Morphology and Anatomy

A joint portion between the basal segment and the two rami is elastic soft cuticle, arthroal membrane. Three tendons arose from a proximal part of the ramus, one joins abdominal part of the inner ramus, another joins dorsal part of the outer ramus and the other joins medial part of the outer ramus (Fig. 1). Many muscle bundles are attached to these three tendons. Two uropodal nerves (the sixth nerve from seventh pair of abdominal ganglia) join and run along the basal segment. They make a partial crossing near the distal end of basal segment and innervate to each ramus. Some nerve branches distribute among connective tissue of the joint region.

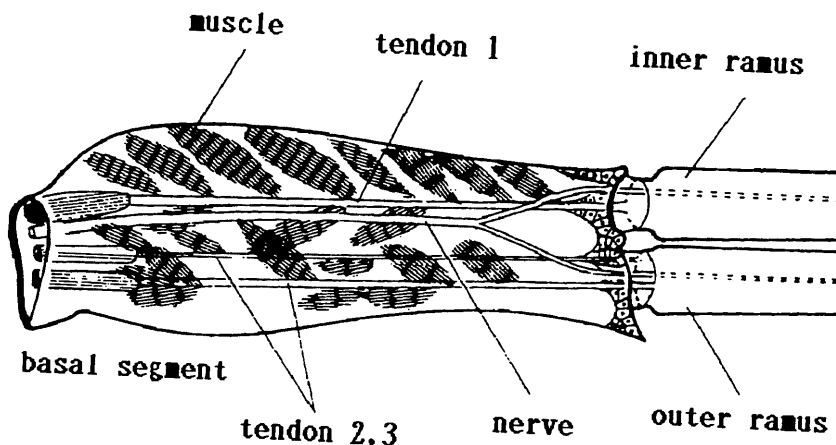


Fig.1 Internal structure of the uropod basal segment. Three tendons and attached muscle bundles are shown. Uropodal nerve which is composed of two nerves is separated and innervate to each ramus, and small branches distribute joint region.

2. Response Pattern

Response patterns to deflection and extension of each ramus were classified into three groups by responsible direction: open receptor, close receptor and open-close receptor.

i) Open receptor

These receptors responded to only the opening stimuli (elevation of the outer ramus or depression of the inner ramus) and closing stimuli (shift to the resting level) was not effective (Fig. 2). Impulse fre-

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quency was increased as the angle of deflexion was increased, and also as the speed of deflection was increased. When the deflective movement was ceased and the deflexion was sustained at some angle, the firing continued but decreased gradually according to adaptation (Fig. 2-B, Fig. 3).). So, these responses were showed two phases, high frequency of firing to the movement (phasic phase) and slowly decreasing firing according to the adaptation (tonic phase). Generally, the adaptation of the open receptor was far slower than other type neurons. When stepwise stimulus was delivered, the phasic-tonic responses was repeated, but the responses of both phases were increased as the beginning angle (Fig. 3, Fig. 4). When the opening angle was small, the adaptation was large and the phasic phase was not so remarkable, and the distinctive tonic level was noted above about 40 degrees. The fast velocity of deflexion caused large response of the phasic phase and the large adaptation (Fig. 4).

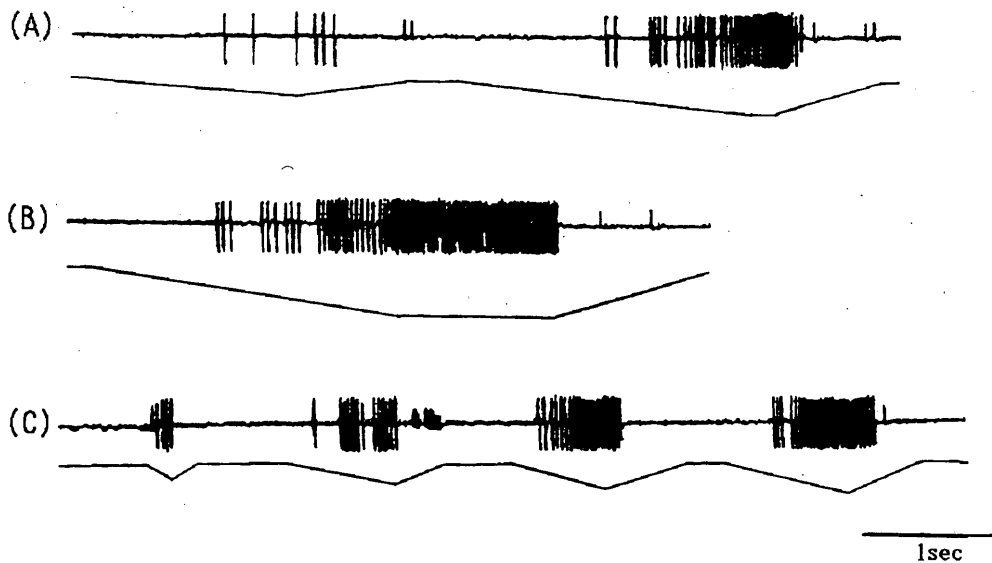


Fig.2 Response of open receptor. These receptor are sensitive to opening stimulus. A) Slow opening and closing with different strength are delivered. B) Opening stimulus is sustained and deflexion is maintained for a while. C) Quick opening and closing with different deflection angle is delivered. Lower trace of each recording indicates joint movement.

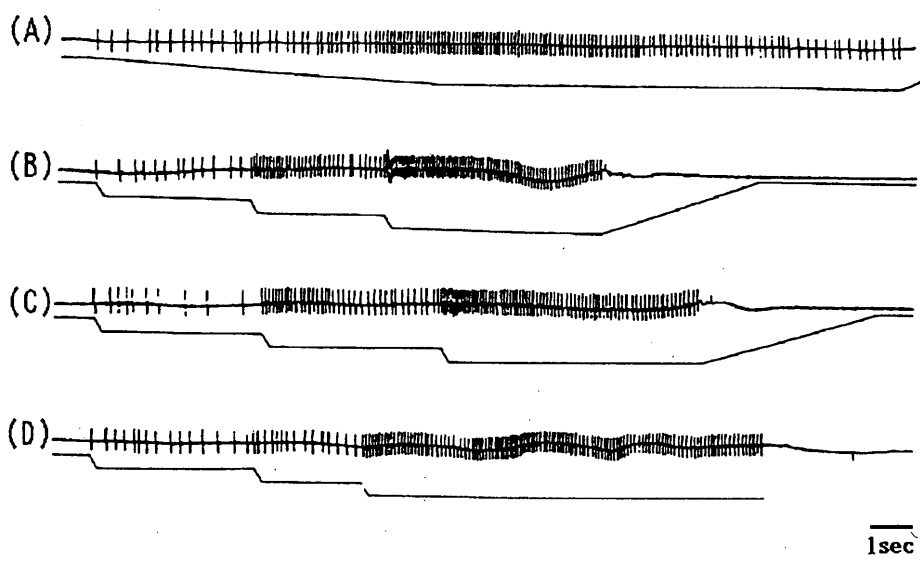


Fig.3 Responses of open receptors to stepwise stimuli. A) Successive stimulation. B),C),D) Stepwise stimulation with different velocity. Lower trace indicates joint movement.

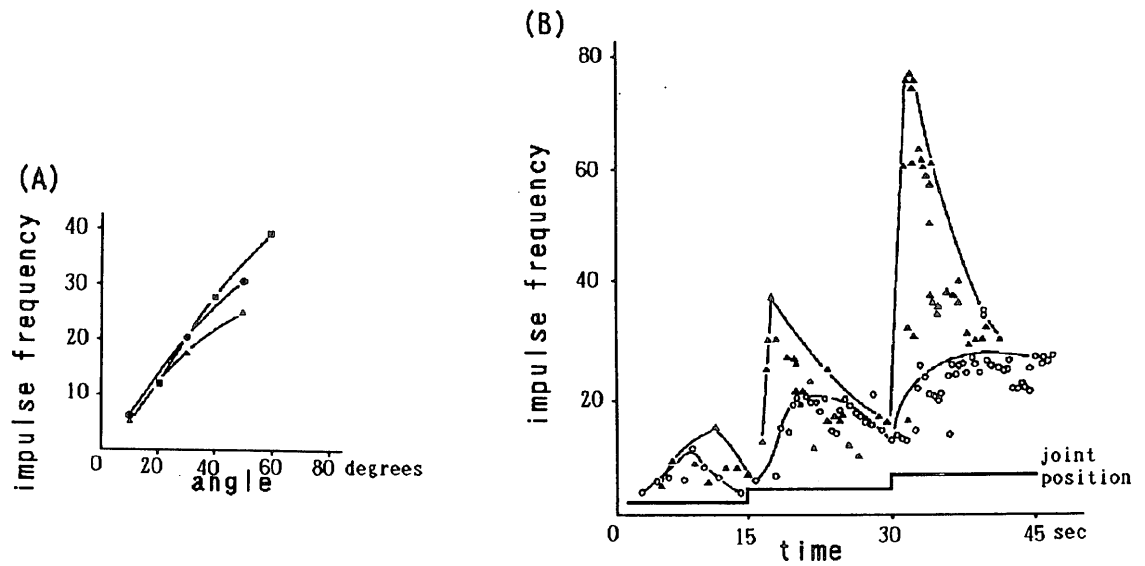


Fig.4 Response properties of open receptors.

A) Relation between impulse frequency (ordinate) and deflexion angle (abscissa).

B) Time course of adaptation to stepwise stimulus. Rapid stimulus (\blacktriangle) causes larger phasic responses and more rapid adaptation than slow stimulus (\circ). The ordinate indicates impulse frequency and the abscissa indicates time.

ii) Close receptors

This type of receptor responded to the close stimuli (shift to the resting level) only, and there were very few (Fig. 5). This type of receptor showed the dependency to the flexion angle like open receptors, so the large deflexion caused large response and the decrease of deflexion angle reduced the firing rate. But this receptor is, in a certain sense, a movement receptor because this unit didn't respond to the steady deflexion and became firing with close movement. The dependency to the movement velocity was also equipped, and the high speed closing showed high frequency response (Fig. 5-C).

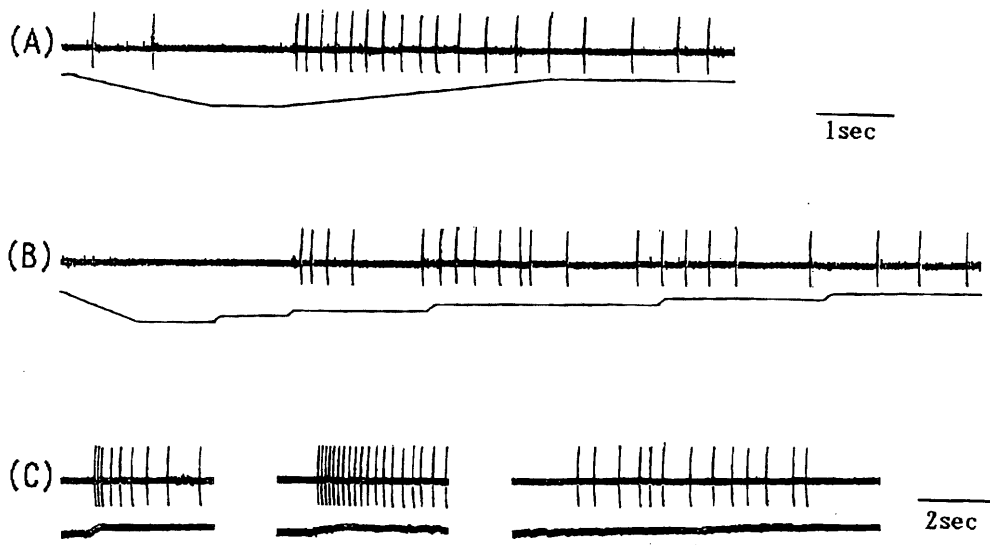


Fig.5 Responses of close receptor. This receptor responds to close stimulus only and the frequency of response decreases as the decrease of deflexion. A) Slow stimulus. B) Stepwise stimulus. C) Close stimulus with different velocity. Lower trace indicates joint movement.

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iii) Open -close receptor

These receptors responded to both opening and closing of the ramus (Fig. 6). Generally, this type receptors were encountered more frequently than other type receptors, and the impulse amplitude of this receptor was smaller than others. These receptors showed the fastest adaptation, so responded in only movement phase, suggesting the nature of so called phasic movement receptors. These units had a responsive range of angle, and generally responded to the stimulus of narrow special angle range. When the opening stimuli or the closing stimuli passed through a special angle, these units fired phasically (Fig. 6). Impulse frequency was depended to the velocity of movement. Fig. 7 shows examples of the range of sensitive angle. The ordinate indicates impulse amplitude and the abscissa indicates deflection angle. The position of bars in the ordinate indicates impulse amplitude. The width of bar shows relative impulse frequency and figures near the bars indicate the maximum impulse frequency. Many receptor have a narrow responsive range near 30 degrees.

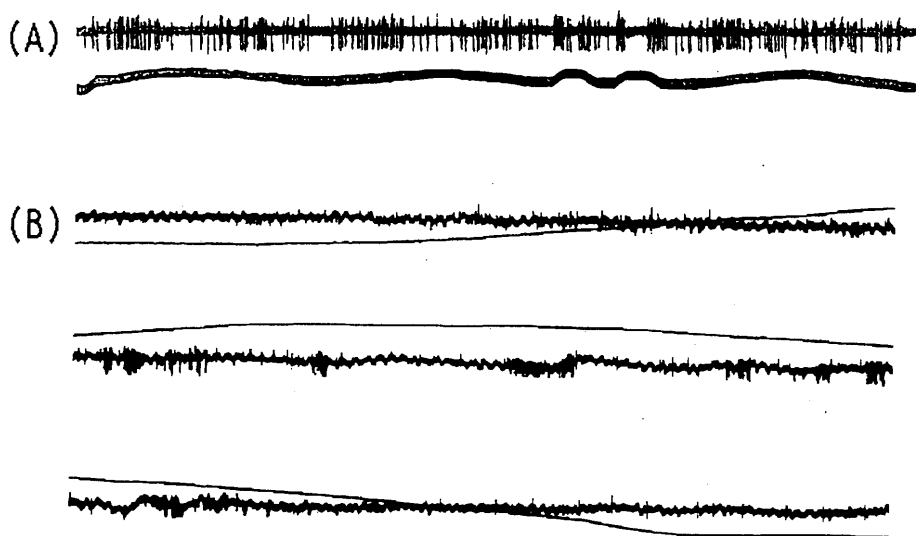


Fig.6 Responses of open-close receptors. A) Open-close stimuli with different velocity are delivered continuously. B) Same response are caused at same angle of open phase and close phase.

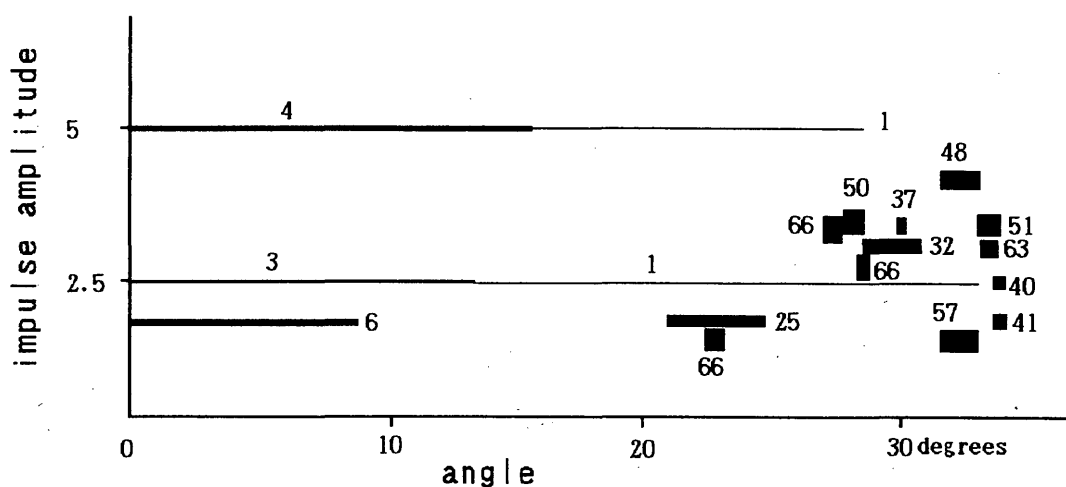


Fig. 7 Examples of the responsive range of open-close receptors. The ordinate indicates impulse amplitude, and the abscissa indicates deflexion angle. The length of the bar indicate responsive range of each unit. The width of the bar indicates relative impulse frequency and figure near the bars is impulse frequency.

3. Recording from Two Nerves

The responses recorded from the two nerves were not always specialized to each ramus. In some cases the response to the outer ramus elevation and that to the inner ramus depression were recorded from different nerves (Fig. 8-B). In other case, a synchronizing firing was recorded from each nerves simultaneously (Fig. 8-A).

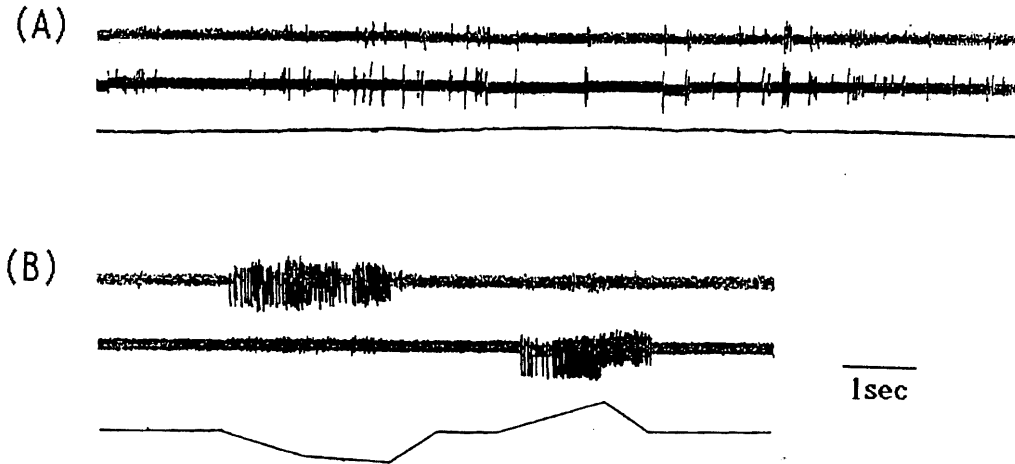


Fig.8 Simultaneous recording from two nerves. Upper two records indicate nerve activity and lower trace indicates joint movement. A) A synchronizing open-close type responses are simultaneously recorded from different nerves. B) Depression of the inner ramus (the first half) and elevation of outer ramus (the latter half) caused the responses of different nerve respectively.

4. Position of Receptors

From histological preparations, the structure of the joint mechano-receptors failed to be demonstrated. Some partial surgical procedures changed the response. When the tendon for the depression of the inner ramus was cut at the proximal region, the inner ramus depression without the movement of the tendon caused tonic open receptor response, and the movement of the tendon without ramus depression caused only a phasic open-close receptor response. When the arthroal membrane was cut at the dorsal part of insertion of the inner ramus, the response of a tonic open receptor to the ramus depression was disappeared.

DISCUSSION

Generally, the joint mechano-receptors of crustacea are classified into two groups, tonic receptors with slow adaptation and phasic receptors with rapid adaptation. And it is supposed that the tonic receptors code the information of position and the phasic receptors do the information of movement. In this experiment, pure tonic position receptors were not found. The response of the open receptor is a phasic-tonic type response and this phasic-tonic type response was also reported in uropods of *Ligia oceanica* (Stutt and Laverack, 1979). This open receptor is resembled to the hermit crab intermediate fiber (Tayler, 1966). The tonic phase response of the hermit crab intermediate fiber increased as the deflexion angle was increased but the phasic phase response of that was decreased as the angle was increased. While, the open unit of *Ligia* increases the response in both phasic and tonic phase as the angle increase. If the movement velocity is steady, the open receptor can inform an accurate angle position. Because this unit shows also

the dependency on velocity, when the ramus is moving, this receptor cannot inform an accurate position but only direction of movement, opening. The ramus of uropod remains the opening position in active state, so in such a case, the tonic open receptor may send the position information. The close type receptor showed a phasic movement type response, but in a certain sense, this unit can pass on the information of position at the beginning of the ramus movement. It is difficult to guess the actual stimulation process of these receptor dendrite with the ordinal mechano-receptor mechanism. At least, this unit can inform that the moving direction is closing. The open-close receptors are the phasic movement receptors. Generally the movement receptors have a uni-directional sensitivity, but this type receptor in *Ligia* has a bi-directional properties, and moreover, many of these units are restricted in responsible range. The receptors with a restricted sensitive range were also reported in the lobster which have most responsive angle at 75 (Bush, 1965) and the crab in which many receptors with various sensitive range gathered to cover the all range (Cohen, 1963). So the receptor of *Ligia* uropod with a restricted sensitivity is not so rare case. These receptors can inform both the movement velocity and the angle position, but not the movement direction. In a conclusion, the open receptor informs the movement direction of opening, and the state of closing or opening of the two rami. The close receptor informs the movement direction of closing. The open-close receptor informs the movement velocity and the passing position of angle. Uni-directional tonic position receptors like open receptor and bi-directional phasic movement receptor with restricted responsible range like open-close receptor also exist in the antennal joint in *Ligia exotica* (Hatanaka and Konno, 1994).

The structure of the uropod was reported by Alexander (1971), and Stutt and Laverack (1979) in *Ligia oceanica*. In the latter case, four muscles (extensor and flexor of outer ramus, extensor and flexor of inner ramus) for ramus movement were reported. But in *Ligia exotica*, only three tendons are found. Stutt and Laverack (1979) did not mention about the tendon, but generally, it is not likely that two extensor muscles of the outer and inner ramus attached to one tendon. In *Ligia exotica*, it seems that the two tendons act as flexors of each ramus and one acts as a common extensor. It is interesting that the muscle system is not similar in two species of *Ligia*.

The two uropodal nerves corresponded to the nerve II and the nerve III named by Alexander (1971). He demonstrated that the nerve II responded to the depression of inner ramus and vibration of inner ramus terminal spine and that the nerve III responded to the elevation of outer ramus. So two nerves innervate two rami differently. In this experiment, both nerve responded to the stimulation of inner ramus and outer ramus each together, and simultaneously, synchronizing activity were recorded in two nerves. The recordings of a synchronized activity from the two nerves probably suggest that the electrically coupled neurons sent off the axons in distinct two nerves, because it is not likely that one neuron sent two axon branches in different nerves. In spite of a whole recording of the nerve trunk, the simultaneous recording of multiple open receptors was rare case, but many open-close receptors were encountered. So, the open receptors and the close receptors are few and the open-close receptors are many to cover all range of movement. The result of the partial surgical operation suggested that the open receptor has some relation to the arthroal membrane, and the open-close receptor relates to the tendons. Small nerve branches in joint region were observed but the chordotonal organ was not found so far.

The role of uropod is still undefined. The distal spine of the inner ramus is always in contact with the substrate. So the mechano-receptive function to investigate the situation of the substrate or the sensation of vibration by the possible predators or incoming tide are reasonable. But the role of outer ramus can not be determined. The two rami of opposite direction can be measure the some spatial feature. It seemed that the Y-shaped uropod is useful for flattened *Ligia* to locomote in the limited lower space. In such a case, the fundamental proprioceptors may act as extroceptors. The sensitive range of many open-

close receptors crowd about 30 degrees, so the fine information near this angle may be important for *Ligia* size.

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