フナムシ触角の機械受容器の性質

Properties of antennal mechano receptors in *Ligia exotica*

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ABSTRACT

Antennal joint receptors of carpus-flagella joint (C－F joint) and flagellar contact receptor of *Ligia exotica* were studied. Movable range of each antennal joint was obsered and nerve responses to C－F joint movement were recorded. The nerve responses to joint movement were classified to two type responses; one is tonic type response which continued firing as joint flexion, second is phasic type which showed fast adaptation. Almost of units (about 90%) responded with increase of firing to flexion but few units showed inhibition. Firing rate of the tonic type response depended on angle of the joint and, to a sustained flexion, the firing remained with steady rate depending on the angle. These tonic type receptors coded a joint position information. The phasic type receptor responded to a joint movement and a single cell responded to movement of only one direction (unidirectional), a flexion or an extension. Notwithstanding of steady rate of angular movement, the firing frequency reached maximum immediately after the initiation of the movement and rapidly adapted. Firing rate of these phasic unit depend on movement velocity. This phasic type response coded a movement direction and a rate. Unnatural opposite directional movement or lateral movement of the C－F joint which an animal cannot move itself caused also nerve responses. So it is suggested that these receptors have a rule not only as proprioceptors but also as extraceptors. Contact atimuli to the surface of flagellum caused nerve responses which seemed to be originated from tricorn like sensilla, indicating important rule for searching.

INTRODUCTION

Ligia exotica has two kinds of antenna at a head portion, small antenulla (first antenna) and large antenna (second antenna). The large antenna is composed by shaft portion of 5 segments (coxa, basipod, ischium, meropodite and carpus, respectively) and flagella with 30－40 small flagellum. In resting stage, the antenna was flexed and attached to lateral side of the body, but when animal is active, the antenna is protruded ahead and gropes their ways. In general, antennae of crustacea are used as olfactory receptors (Ache and Derby, 1985), gustatory receptors and contact mechano receptors with their sensillum

(Johnson and Ache, 1978; Seelinger, 1977, 1978). But antennal joint proprioceptors have also important role. These function of higher crustacea, lobsters and crabs were examined mainly, but studies of lower crustacea are few. Joint proprioceptors sense joint condition and, in turn, control their movement.

In higher crustaceans, it is known that there is at least one chordtonal organ at each joint. A chordtonal organ is formed by an elastic sheet or strand which spans the joint and insert on the cuticle of the proximal and distal segments. Bipolar sensory neurons have cell bodies on the sheet and axons which join a sensory nerve connected to the central nervous system. Many authors distinguished three categories of sensory cell, movement cells with dynamic sensitivity, position cells with static sensitivity and intermediate cells with both properties (Bush and Laverack, 1982; Taylor, 1966). But this chordotonal organ was not found in *Ligia* periopoda and the joint receptor of *Ligia* was thought to be more simple structure (Alexander, 1969). But two types of response, a phasic movement reception and a tonic position reception were recorded from the periopoda of *Ligia oceanica* (Alexander, 1969). An antenna has many segments and joints, so, the sensory information seems to be more complex than periopoda or other appendages. And moreover, Alexander (1977) examined the structure and function of sensilla which tufted antennal tip in *Ligia oceanica*. Same tricorn type sensilla on a dorsal tergnite in *Ligia exotica* have same mechanical and contact chemical sensations (Hatanaka, 1989).

In this experiment, response properties of joint receptors of antenna in lower crustacea, *Ligia exotica* were studied. Especially, responses to carpus-flagella (C－F) joint movement which seemed to be a most important joint movement, were examined.

MATERIALS AND METHODS

Experiments were perpormed on *Ligia exotica* captured at mole in Inage beach and caged in a laboratory. Animals of 25－35 mm large were used. One antenna was dissected from the head at the level of proximal joint, and an antennal nerve was exposed by eliminating the exoskelton, muscles and connective tissue from proximal three segments (coxa, basipod, ischium). The preparation was fixed on an acril experimental chamber. The exposed nerve was immersed in physiological saline solution and the cut end was sucked by a suction electrode. Nerve activity were recorded by ordinal electrophysiological techniques, amplified by AC coupled preamplifire, displayed on oscilloscope and recorded by electro photorecorder.

Flexion stimuli of the C－F joint was delivered by micro manipulator and monitored by mechano transducer. To avoid contact stimuli to flagella, a small glass tube with mineral oil covered the flagella and then the glass tube was moved to flex the joint by micro manipulator. Contact stimuli and deflection stimuli to flagella were delivered by a hand operated small needle.

RESULTS

1. General Structure

An antenna of *Ligia* consists of a shaft with large five segments and many small flagella (about 30−40 segments, Fig.1). First three proximo-distal segments are short and next two segments become to be long gradually. But an rock lobster has only three proximo distal segments. A proximal joint jointing the antenna to cephalotholax (C−C joint) moves antenna to all position about 10°. A joint between the coxa and basipod (C−B joint) moves the basipod dorsally about 90°, that between the basipod and ischium (B−I joint) moves the ischium dorsally abuot 90°, that between the ischium and meropodite (I−M joint) moves the meropodite dorsally about 90°, that between the meropodite and carpus (M−C joint) moves the carpus latelally about 90°, and C−F joint moves the flagella ventrally about 90°. Using these joints, *Ligia* moves antenna skillfully. The flagella is constructed by many segments, but their joint cannot be moved actually, and as a whole it is defleted passively only. The flagella is moved at C−F joint by three tendons which are originated from exoskelton of flagellum and connected to muscles. Large two tendons are useful for extension and flexion respectively and a amall one is supplementary. In the I−M joint and M−C joint, there are two tendons but first three joint (C−C joint, C−B joint and B−I joint) have no tendon.

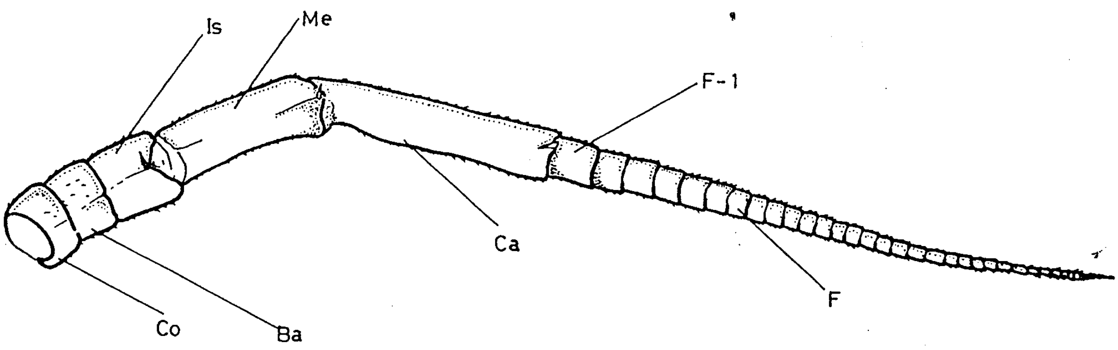

Fig. 1 Dorsal view of a *Ligia* antenna. Co;coxa, Ba;basipod, Is;ischium, Me;meropodite, Ca;carpus, F−1;first flagellum, F;flagella

2. Nerne Responses to the C−F Joint Movement

Immediately after the isolation of antenna, many injury spikes were recorded, but after dispersion of injury spikes, joint receptor responses could be observed. About 90% of responsive units to the C−F joint flexion were excitatory type with an increase of impulse frequency and the remainders were inhibitory type with a decrease or cease of firing. Almost same number of phasic movement receptor type response and tonic position receptor type response were recorded, and these two types of response were usually recorded simultaneously. In general, an amplitude of phasic movement receptor impulses was larger than that of tonic position type by 10−20 μv.

i) Responses of tonic position receptors

Typical responses of a position receptor at the C−F joint are illustrated in Fig. 2. As a increasing of flexion, an impulse frequency was increased, and when flexion was sustained at any position, the impulse frequency was almost stored. The impulse frequency in the flexion process and extension process of several units are demonstrated in Fig. 3.

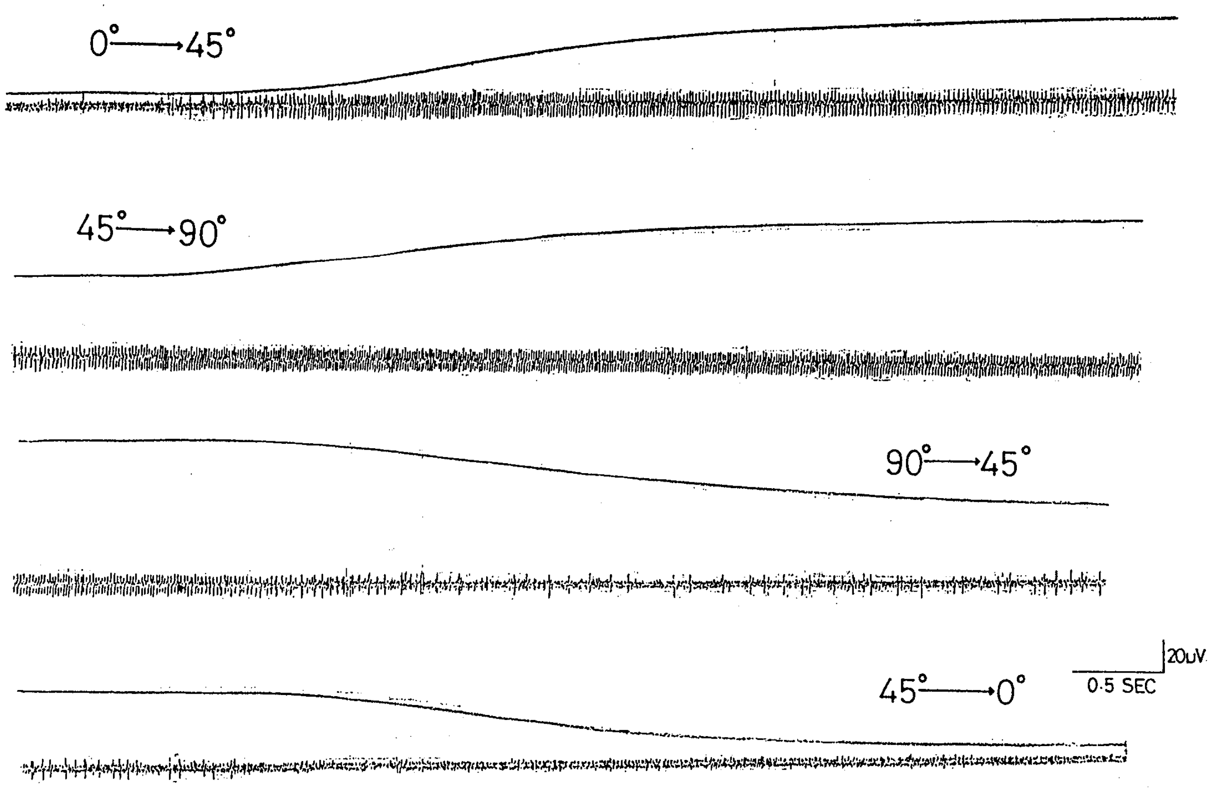

Fig. 2 Responses of a tonic position type receptor to flexion and extension of each 45 degrees' movement. Solid lines above each record indicate joint movement, and an upper decline indicate flexion.

Because of an adaptation, the extension process showed lower frequency at same degree than flexion. These position type receptors barely effected by movement velocity. Unit in Fig. 4 showed a little velocity dependency.

ii) Responses of phasic movement receptors

This type unit responded phasically to joint movement and ceased firing when the movement was stopped. A single unit responded to flexion or extension only (unidirectional). In Fig. 5, these phasic responses are shown multiply. Responses of these units depended on velocity, and a higher velocity increased firing frequency and number of impulse (Fig. 6). Threshold of velocity was higher than that of the tonic type response. To demonstrate the temporal patterns of response, the impulse frequency of each 0.2 sec response was graphed

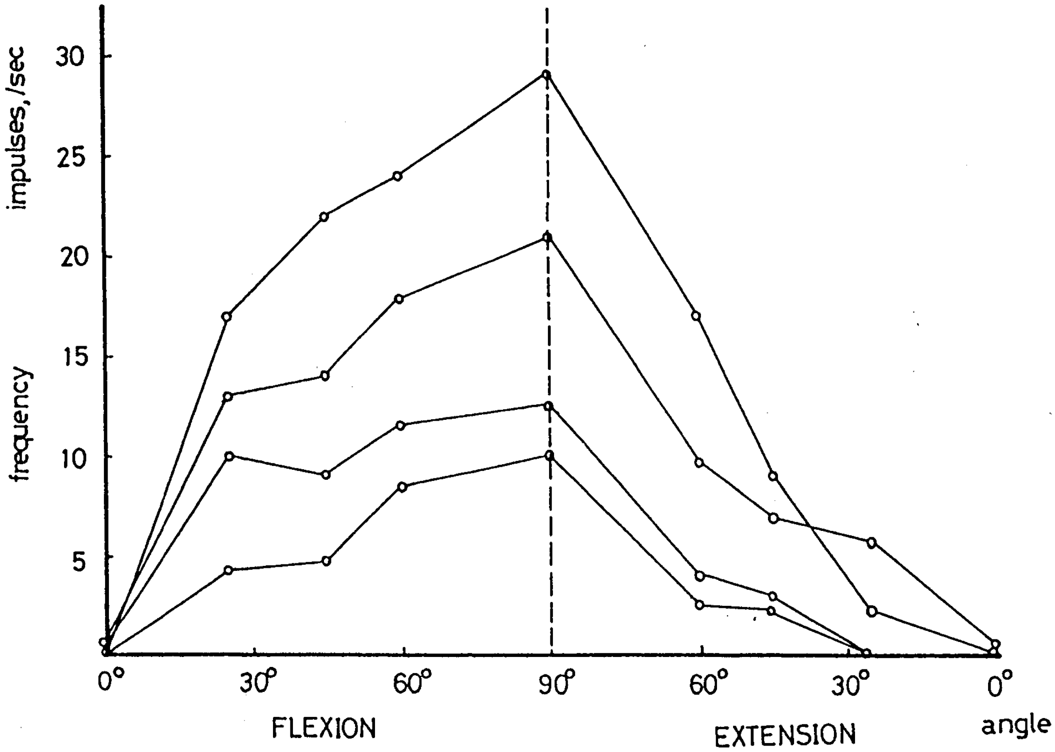

Fig. 3 Relation between the impulse frequency and flexion angle of 4 units in the flexion and following extension. A firing rate in extension process is lower than that in flexion because of adaptation. The ordinate indicates impulse frequency and the abscissa indicates flexion angle.

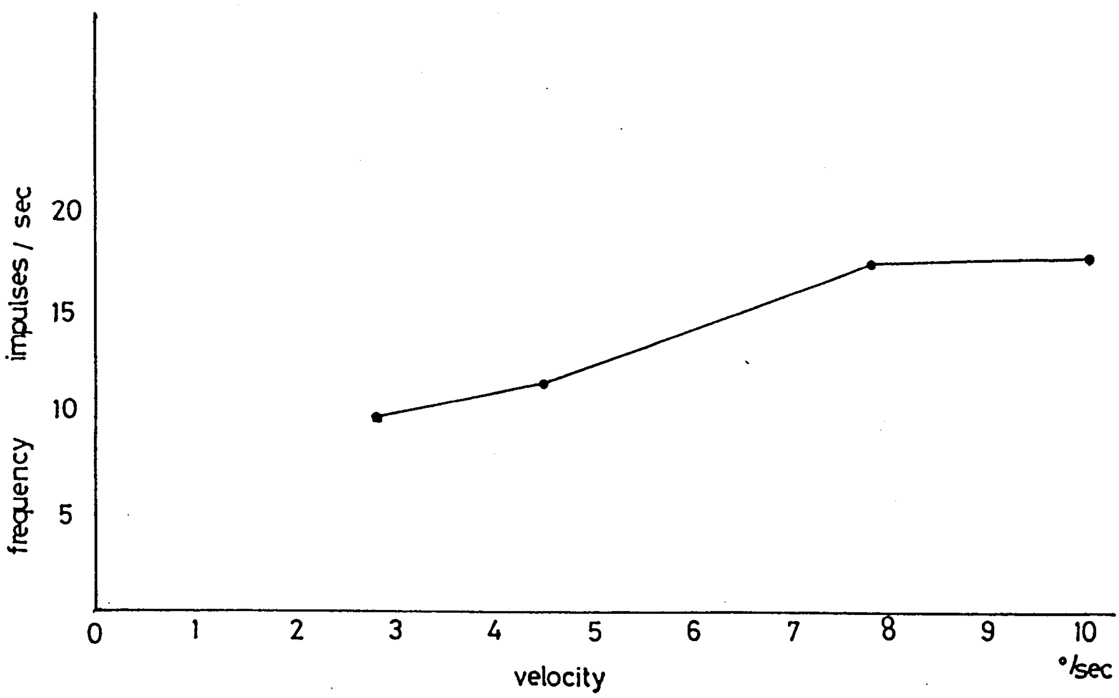

Fig. 4 Influence of the velocity to a tonic type response. The ordinate indicates impulse frequency and the abscissa indicates movement velocity.

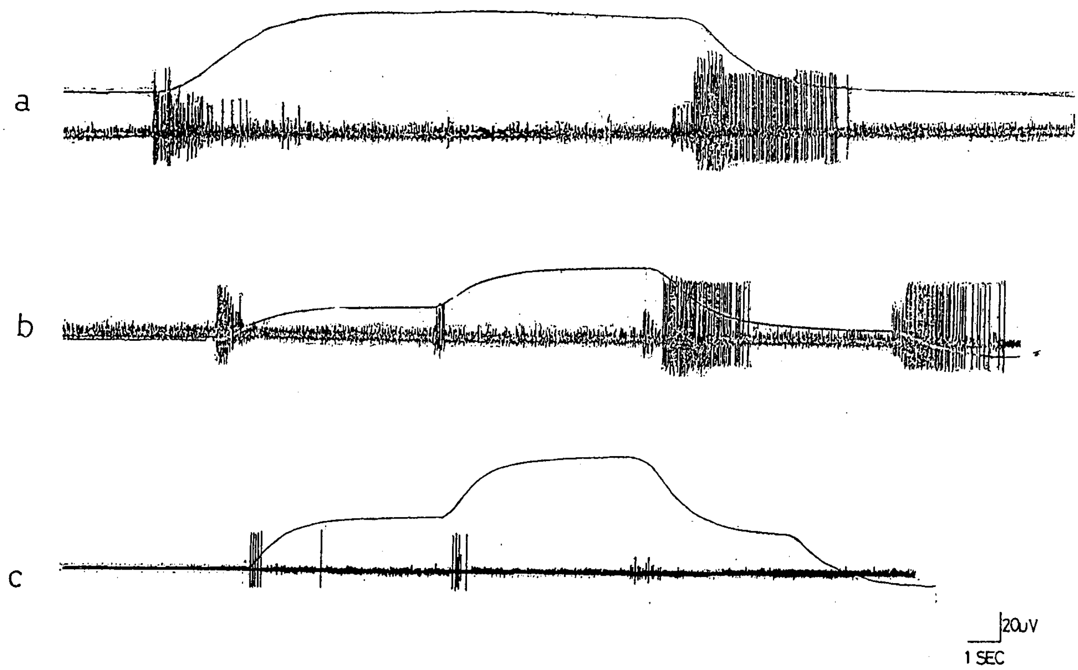

Fig. 5　Rrsponses of phasic movement type receptors. Each record was recorded from different preparations. Different units with different amplitude responded to unidirectional movement, only flexion or extension. Solid lines indicate joint movement and an upper displacement indicates flexion.

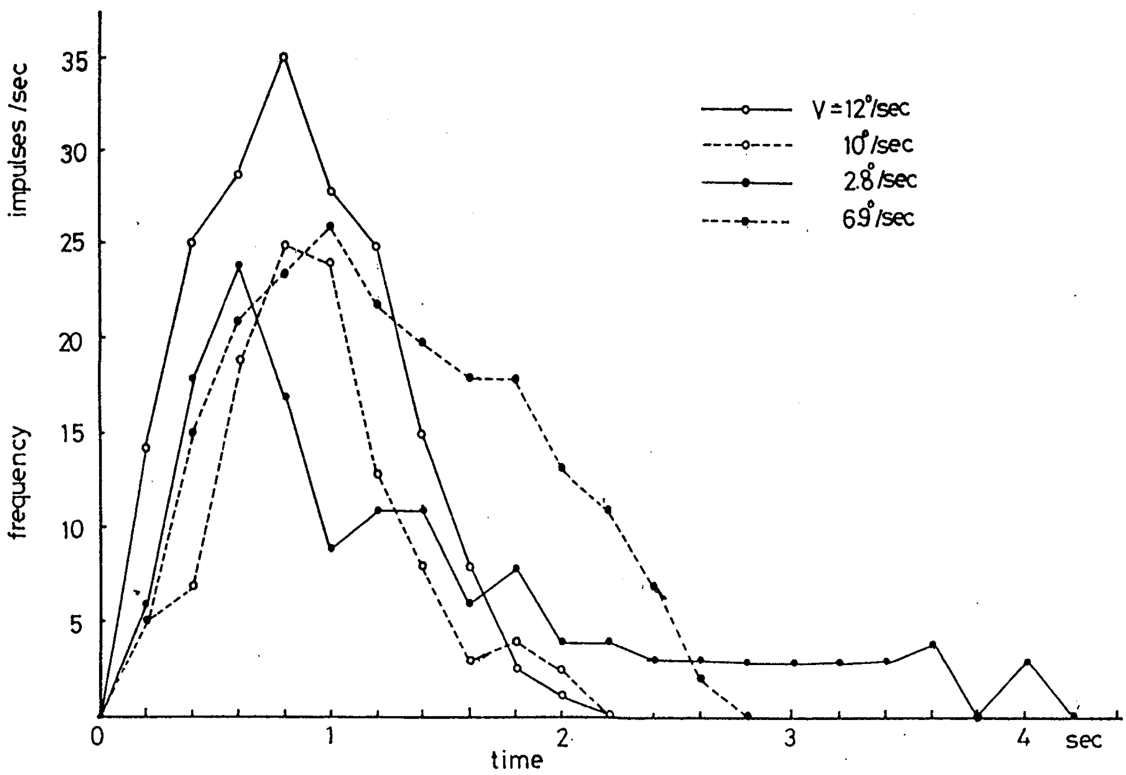

Fig. 6　Temporal patterns of phasic response to the flexion with different velocity. The ordinate indicate impulse frequency and the abscissa indicate time from initiation of the movement. Each response reached maximum in 1.5−2 sec and then decrease for adaptation. Higher velocity cause faster adaptation.

in Fig. 7. The impulse frequency reached maximum after only 0.5−1.5 sec from the beginning of movement, then decreased gradually, and firing was failed in spite of continual movement with steady velocity. As the velocity was increased, an adaptation became large and the firing was stopped faster. Stepwise stimulation indicated that in a steady velocity, a starting position effected to response pattern a little (Fig. 8).

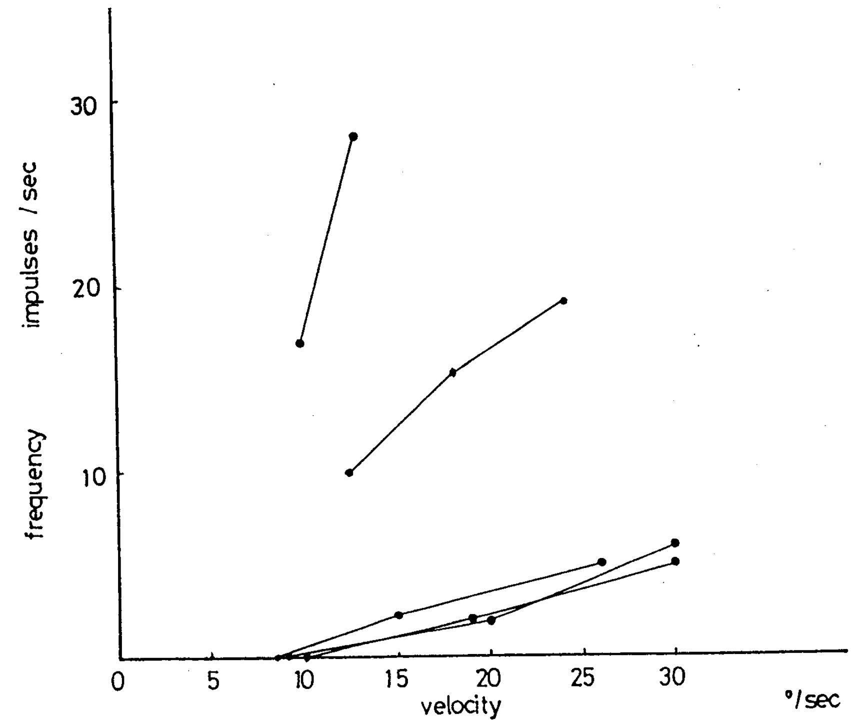

Fig. 7 Relation between the impulse frequency and movement velocity of 5 movement receptors. The ordinate indicates impulse frequency and the abscissa indicates velocity.

iii) Response to abnormal flexion

In general, a positive antennal movement is restricted in movement plane and direction, but if abnormal mechanical stimuli are delivered, the antenna can be bent passively. A lateral movement of the flagella caused nerve responses (Fig. 9−a). Several phasic responses (large impulses of 40 μv) and tonic amall impulses (30 μv) appeared by lateral flexion, and tonic one continued firing as the flexion was preserved. An opposite flexion to dorsal position at C−F joint caused phasic type responses (Fig. 9−b). At beginning of flexion and extension, phasic type responses were observed.

3. Nerve Response to Mechanical Stimuli to Flagellum

As reported by Alexander (1979) for *Ligia oceanica*, contact stimuli to the antennal tip yielded several impulse firings (Fig. 10−a). A stroke stimulus to the flagella surface

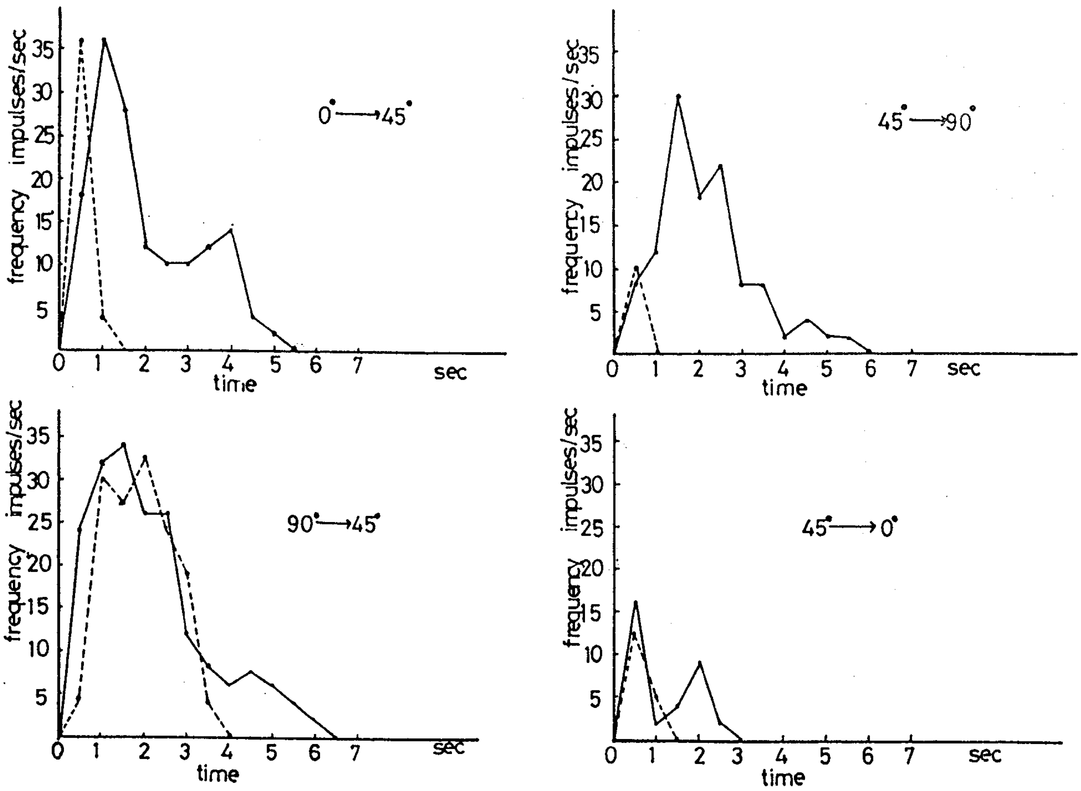

Fig. 8 Temporal patterns of response to stepwise flexion and extension (from 0° to 45°, from 45° to 90°, from 90° to 45°, and from 45° to 0°). In each process, two different units are demonstrated, and second stimuli (from 45° to 90°, or from 45° to 0°) caused amall response.

Fig. 9 Response to unusual deflection of the C−F joint. a) A lateral flexion causes large phasic impulses and small tonic impulses. b) Opposite directional flexion caused phasic responses.

caused several kinds of impulse. These units belonged to many tricorn like sensilla along the flagella. Ventral deflection of the flagella at the portion of lcm apart from antennal tip showed phasic response only (Fig. 10−b,c).

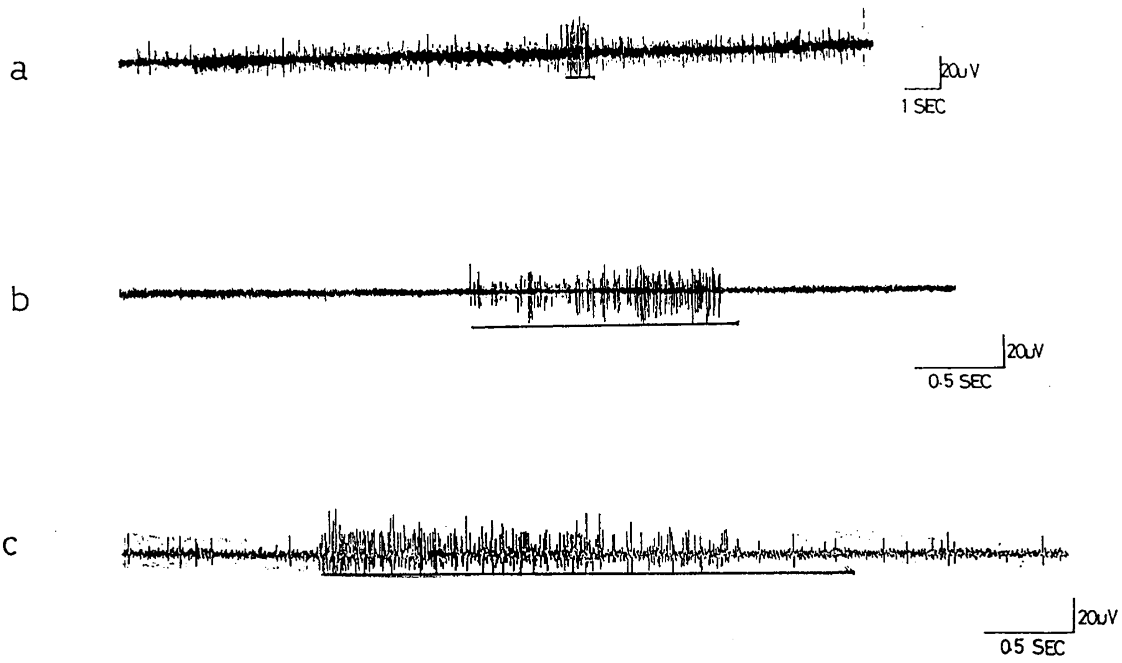

Fig. 10 Response to stimuli delivered to the flagella. a) Contact stimuli to the antennal tip caused response. b) and c) Deflection of the flagella on different portion yield nerve responses. Solid lines under each record indicates a period during stimulation.

DISCUSSION

To a flexion and extension of the C−F joint of *Ligia* antenna, typical two types of response were recorded. Slow adaptive tonic type response showed dependency of angular position. So, as the angle of flexion increased, the impulse firing frequency also increased. These properties are similar to that of tonic position receptor of higher crustacea like lobster and crab (Wyse and Maynard, 1964; Rossi-Lurand and Vadel, 1982). These tonic receptors send information of joint position to a central nervous system. Although the response of these position receptors are influenced by movement velocity to some extent, these unit can reveal exact position information when a movement is stopped. In joint extension process, impulse firing frequency to the some angle is lower than that in flexion process because of adaptation to large flexion that is experienced just before. In the C−F joint, many tonic receptors increase firing rate as increase of deflection. This joint is extended in resting animal, and when they search on substrate, this joint became bend in order to reach antennal tip to the substrate. So, the information of flexion is seemed to be more important. Some position type responses which decreased firing as increase of flexion are observed. These units would code the extension state.

Phasic type responses have fast adaptation, so fire during joint movement. These unit respond to the movement of only one direction, flexion or extension, and sometimes multi units are recorded simultaneously. These units change firing frequency depending on velocity of the movement, so this type unit coded the direction and velocity of movement. Some phasic type receptors which had an angle specificity and responded to only narrow range of special angle were observed at the uropodal joint of *Ligia exotica* (Hatanaka, in preparing). But this type response was not reported by Stutt and Laverack (1979) in *Ligia oceanica*. These angle specialized phasic receptors cannot be observed in antennal C—F joint. So phasic receptor of antennal C—F joint cannot send the position information. Generally, phasic type impulses have higher magnitude than tonic type impulses. This means that phasic fibers are thicker than tonic fibers. Generally, the conduction velocity of nerve fiber depends on thickness. So, the information of movement direction reaches to the brain before that of accurate position information (probably, in the case of passive movement of the antenna, it seems to be useful to avoid danger). Extraordinary lateral flexion and opposite directional flexion of the antennal joint also cause nerve impulse. *Ligia* cannot moves the antennal C—F joint to these directions intself, but it is likely that during searching by antenna, some objects or substrate stimulate so. But it cannot be made sure that these units responding to unusual deflection are the same units which respond to normal joint flexion.

As joint mechamoreceptors, several structures have been observed (Bush and Laverack, 1982). In the antenna of rock lobster, a large chordotonal organ which spans 2 joints from S2 proximo-distal segment to first flagellum, and contains about 400 sensory cells (Rossi-Durand and Davel, 1982). In the antenna of *Ligia*, such chordtonal organ have not been reported. And a simplicity of recorded responses indicates that the joint receptor of *Ligia* antennal C—F joint seems to be more simply. Alexander (1969) studied pereiopod of *Ligia oceanica* and found that there was no chordtonal organ in any joint examined. He reported simple structures which consisted of single or two-cells suspended by two or three processes between exoskelton and either nerve or muscle. While, in antennule of *Ligidium*, only first joint has chordtonal organ (Risler, 1978). So, further observation of morphology *Ligia* antennal joint is demanded.

The flagella have no muscle and tendon, so it cannot bend itself. But nerve bundle is innervated to the antennal tip, so it is reasonable to suppose joint receptors between flagellum. Deflection of flagella in spiny lobster caused both tonic type and phasic type responses (Laverack, 1964). In *Ligia* antenna, typical tonic type response was not observed, but existence of extroceptor which receive passive bending of flagella was demonstrated.

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