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PHYSIOLOGY OF THE FEMORAL CHORDOTONAL ORGAN IN THE STICK INSECT, *CUNICULINA IMPIGRA*

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SUMMARY

The femoral chordotonal organ of the stick insect *Cuniculina impigra* Redtenbacher (Phasmida) can be stimulated precisely by moving the receptor apodeme. Single sensory units in the sensory nerve are recorded using glass microelectrodes. The units are classified according to their sensitivity to (a) position, (b) position and velocity and (c) velocity. Nearly all transitional forms exist between the position and velocity receptors. Both elongation- and relaxation-sensitive receptors exist, and also units which are bi-directionally sensitive. Many position receptors have their maximum frequency at one of the extreme joint positions, but others have their maximum frequency near the middle position of the joint. Some velocity-sensitive units respond with equal sensitivity over the whole operating range of the joint, whereas other velocity receptors respond only in a part of the operating range, thus providing further evidence of range-fractionation.

INTRODUCTION

The appendages of insects are copiously equipped with proprioceptors. Together with other sense organs (e.g. vibration-receptors) they play an important role in different behaviour patterns by feeding back the motor output (Bässler, 1967, 1977*b*; Cruse, 1979; Graham & Bässler, 1981; Pearson, 1972; Pearson & Iles, 1973; Pringle, 1940, 1961; Wendler, 1964; Wright, 1976). One important proprioceptor is the femoral chordotonal organ, which is involved in the control of leg movements, e.g. in the walking animal. Stick insects show a special behaviour, catalepsy, in which the femoral chordotonal organ is known to be a major part of the control loop (Bässler & Foth, 1982; see Bässler, 1983).

In the stick insect, the organ lies at the base of the femur and is connected with the tibia by a long cuticular apodeme (receptor apodeme). The organ consists of two strands with different dimensions, which are joined together at the base and at the origin of the receptor apodeme. The dorsal strand of *Carausius* contains about 200, the ventral strand about 40 scolopidia. Every scolopidium possesses two sensory cells. The pericarya of the cells lie in the common base of the two strands.

Key words: Stick insect, neuroethology, chordotonal organ.

The nerve leading from the chordotonal organ to the CNS contains two classes of axons, thin (0·2–0·9 μm diameter) and thick ones (1·1–2·2 μm diameter) (Füller & Ernst, 1973).

The first electrophysiological investigation of a femoral chordotonal organ was made by extracellular recordings from the chordotonal nerve (Burns, 1974; Usherwood, Runion & Campbell, 1968). Further investigations of chordotonal organs in insects have also used extracellular recordings (e.g. Young, 1970; Orchard, 1975; Hustert, 1982). More detailed results are available about the physiology of chordotonal organs in the legs of Crustacea (for review see Mill, 1976).

This paper describes an electrophysiological investigation of single sensory units of the femoral chordotonal organ in the stick insect *Cuniculina impigra* Redtenbacher (= *Baculum impigrum* Brunner) (Phasmidae). This animal was chosen because the sensory nerve of the chordotonal organ (nerve F1, Bässler, 1977*a*) is more accessible than in *Carausius*. Under the light microscope, the chordotonal organs of *Cuniculina* and *Carausius* look very similar. Therefore it is assumed that the electron microscopic structure is also identical to a great extent.

MATERIALS AND METHODS

The response pattern of individual units of the chordotonal organ was characterized by recording with microelectrodes from the chordotonal organ nerve.

Preparation

All experiments were performed on intact adult female *Cuniculina impigra*. The animal was placed dorsal side up on a foam-plastic plate (Versilic plates, 5 mm thick, produced by Verneret). All legs except the right hindleg were fixed parallel to the body with pins. The right hindleg was orientated perpendicular to the body. The coxa and femur was surrounded on three sides by a foam-plastic wall, the fourth side of the enclosure being the thorax. The floor of the enclosure was 1–2 mm higher than the rest of the foam-plastic plate to support the coxa at an appropriate angle. The coxa and the distal part of the femur were fixed to the foam-plastic base with dental cement (Scutan). The foam-plastic enclosure was filled with *Carausius*-saline (Bässler, 1977*a*) and the femur was opened from the dorsal side for 3–4 mm in its distal part (Fig. 1). The receptor apodeme was fixed in a small clamp made from a sharpened adjustable ink drawing-pen and cut further distal. The apodeme clamp was moved by a pen-recorder motor (see below). With no command voltage applied to the pen-motor, the position of the pen-motor was adjusted such that the receptor apodeme corresponded to a femur-tibia angle of 90°. Between 30° and 150° joint angle, the receptor apodeme movement is a linear function of joint angle, 10° of joint angle change corresponding to approximately 80 μm apodeme movement. *In vivo* flexion elongates the organ, which is wholly in series with its apodeme (no connection with any muscle). Therefore the organ is stimulated as *in vivo* by moving the apodeme. The distal processes of all the bipolar sensory neurones should be stretched by an elongation stimulus (but see Mill & Lowe, 1973).

The back of the animal was opened in the metathorax to prevent strong bleeding in the region of the coxa. To expose the chordotonal organ nerve, the joint membrane between coxa and trochanter was removed together with the dorsal roof of the coxa. The apodeme of the levator trochanteris muscle was cut near the insertion at the trochanter. The chordotonal organ nerve enters the crural nerve in the distal part of the coxa (see Fig. 1). Nerve Tr1 separates from the chordotonal organ nerve somewhat further distal. This nerve contains only sensory fibres and it innervates three groups of campaniform sensilla and one hair plate at the trochanter (Hofmann & Bässler, 1982). Another sensory nerve leaves the chordotonal organ nerve not far from the chordotonal organ. This nerve splits and runs through the whole femur as nerve F121 and F122 innervating a muscle-tension receptor, tactile spines on the femur and a multipolar sensory cell (RDAL) near the femur-tibia joint (Bässler, 1977*a*). In a series of control experiments, the possible influence of the sense organs described above on the recordings from the chordotonal organ was tested. No change in the recorded discharge patterns was found.

To make sure that the recorded potentials were coming from sensory fibres and to exclude excitations of the sense organs mentioned above *via* reflex activation of leg motoneurones, the leg was denervated in some animals. For this purpose the metathoracic ganglion was exposed through a small window in the sternite of the animal. Then the leg nerves were cut near the ganglion. Results from animals treated in this way were the same as from the others. Furthermore, it is very

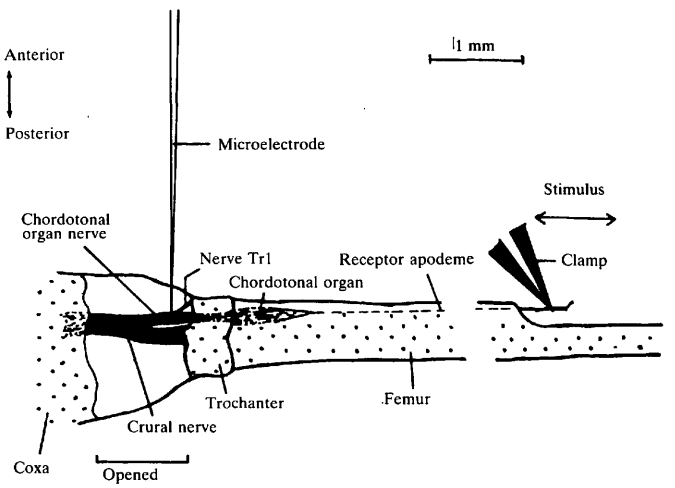

Fig. 1. Dorsal view of the experimental set-up, with anterior at top of the figure. Only the proximal and the distal part of the femur are shown, a piece of about 15 mm is omitted.

unlikely that efferent axons run in the investigated nerve for the following reasons. (1) By intensified cobalt-staining of the whole nerve F1 (common root of the chordotonal organ nerve, F121 and F122), only projections and no somata could be seen in the ganglion. (2) After cutting the nerve in the coxa, potentials could be recorded extracellularly only from the distal part, not from the proximal part of the nerve stump even after strong mechanical stimulation of the animal.

Recording technique

The sheath of the chordotonal organ nerve was softened by treatment with pronase solution (2·5 mg ml^{-1} in saline) for 5 min. The records were obtained using glass capillary electrodes which were filled with 3 mol l^{-1} KCl (40–50 MΩ) as shown in Fig. 1. The position of the microelectrode was controlled by a Leitz micromanipulator. The Ringer bath was connected to the reference electrode *via* a small plastic tube filled with Ringer solution.

The nerve potentials were amplified by a List Electrode Amplifier LM-1. The stimulus waveform and the action potentials were stored on a magnetic tape recorder. Earlier recordings were made on an audio tape recorder (Akai 202 D-SS), which distorted the shape of the action potentials. Later an FM tape recorder (Racal Store 4) was used.

The recordings were usually displayed on an oscilloscope. For further measurements and documentation they were displayed either on a high speed ink-jet chart recorder (Siemens Mingograph EEG 8) or, with reduced playback speed, on a Hellige HE 19 pen-recorder. In some cases spike frequencies were analysed using an automatic spike counter.

A total of thirty-five animals were investigated and analysed.

Stimulation technique

A Hellige pen-motor was used to move the apodeme clamp. It did not have electronic feedback. The performance of this system was measured using miniature inductive coils (Koch, 1983). The apodeme clamp motion pattern followed the electrical command signal with high precision. No overshoot and no vibrations could be measured up to velocities of 40 mm s^{-1}. The delay between electrical command and apodeme movement was 2·5 ms.

A variety of electrical command signals could be generated to drive the pen-motor. 'Trapezoidal' (ramp-and-hold) stimuli with a fixed amplitude of 400 μm or 200 μm (always symmetrical about the 90° joint position) and variable ramp slopes, corresponding to a linear speed of the apodeme between 3·3 μm s^{-1} and 70 mm s^{-1}, served to characterize velocity- and position-sensitive units. The trapezoidal waveforms could also be broken down into several small steps to produce a staircase, with slope per step variable between 80 μm s^{-1} and 8 mm s^{-1}. In staircase stimulation, the total amplitude of the apodeme movement was 1 mm, the physiological working range in the animal.

RESULTS

Overview

When the microelectrode penetrated through the nerve sheath, a potential change of about −20 to −50 mV was observed in most cases. After this penetration some large units could be observed extracellularly emerging from the background noise. Penetration of a sensory axon membrane was usually accompanied by a further potential drop of −20 to −50 mV. The size of the observed action potentials was very variable. The smallest action potentials had amplitudes of about 4 mV, the highest amplitudes were 70 mV. In the cases of the smallest action potentials the single unit recordings may have been extracellular. Extracellular recordings of more than one unit were made only in a few cases. The stability of the recordings was also very variable; some recordings were maintained for 20 min, others for only a few seconds. The following types of sensory units were found.

(1) Units which showed only a position-sensitivity (position receptors).

(2) Units which were stimulated by a movement of the apodeme with constant speed and which also showed a position-sensitivity (position- and velocity-receptors).

(3) Units which reacted only to the movement of the apodeme. The degree of excitation depended on the velocity of the stimulus (velocity receptors).

(4) Units which were adequately stimulated by acceleration of the receptor apodeme (acceleration receptors). These units are mentioned here only for the sake of completeness. They will be described in detail in the subsequent paper (Hofmann & Koch, 1985).

(5) Units which did not fall into one of the above categories.

In cases 1–3, stretch- and release-sensitive receptors could be distinguished. In addition, bi-directionally sensitive units were found among the velocity receptors.

Definition of abbreviations

In the following sections, the response characteristics of the sensory units are referred to by abbreviations. These were chosen to present all available information about the receptors in a convenient form and to gain a better systematic overview. If a tonic discharge exists, the unit is labelled with P (position-sensitivity). Spontaneous activity, which is independent of chordotonal organ length, is termed P0; when tonic activity increases with elongation it is called P+, or when it increases with relaxation the unit is labelled P−. Pm units show a mid-position-sensitivity. Likewise, the velocity-sensitive component is labelled with V. V+ describes a sensitivity to stretching, V− to releasing; V+− means that the unit reacts bi-directionally. In addition, the speed sensitivity range of the velocity-sensitive units is given by numbers indicating the stimulus velocity ($0 = 70\,mm\,s^{-1}$; $1 = 7\,mm\,s^{-1}$; $2 = 0{\cdot}7\,mm\,s^{-1}$; $3 = 0{\cdot}07\,mm\,s^{-1}$; $4 = 0{\cdot}007\,mm\,s^{-1}$). For example, a unit termed P+, V+, 0–4 means that the stationary frequency is increased by elongation, the unit increases its frequency also during stretching, and it is sensitive to stimulus velocities down to $7\,\mu m\,s^{-1}$. The bandwidth is indicated only if the unit was examined in detail.

The results and the number of records of each type are given in Table 1.

Table 1. *Summary of the results*

Classification	Response	Number of records
Position-sensitive	P+	11 (2)
	P−	3 (0)
	Pm*	3 (1)
Position- and velocity-sensitive	P+,V+	13 (5)
	P+,V−	1 (2)
	P−,V+	2 (0)
	P−,V−	3 (2)
	P+,V+−	0 (0)
	P−,V+−	0 (0)
Velocity-sensitive	P0,V+	12 (1)
	P0,V−	10 (0)
	P0,V+−	8 (2)

Note: the numbers without brackets (column 3) stand for units showing the corresponding response behaviour clearly. The numbers in brackets signify the receptors which either could not be investigated in detail or did not show the corresponding responses in a clear-cut manner; they can thus be classified only with reservation.

* These units also had a velocity-sensitive component, but were classified here because of their clear mid-position-sensitivity.

Position-sensitive units

Receptors that reached a new static frequency after a trapezoidal stimulus without a phasic component were classified as position receptors. They were found only rarely and the action potentials recorded had only small amplitudes. In addition, the recordings could not be held very long in most cases, which may be a consequence of a thin axon diameter. It is possible that a substantial part of the recordings was extracellular. Some units reacted to relaxation (P−), other units increased their frequency with elongation (P+). Staircase stimulation demonstrated that P+ units showed their maximum firing rate at maximum elongation of the organ, P− units at minimum elongation. In addition, position-sensitive units (Pm) were found with their maximum frequency near the middle of the operating range (near the 90° joint position Fig. 2A). Some position receptors fired over the entire operating range of the whole organ. Other units were silent during their minimum activation (Fig. 2B). Response of a certain unit in only one part of the operating range and coverage by different units of different parts of the range is called range-fractionation.

Position- and velocity-sensitive units

To be classified as position- and velocity-sensitive, a receptor had to fulfill the following criteria:

(1) a response to the movement of the apodeme similar to the pure velocity receptors (see below);

(2) a static discharge depending clearly on the position of the apodeme. Units which showed some such dependence, but not clearly, were classified simply as velocity-sensitive. If the static part of excitation depended only weakly on the

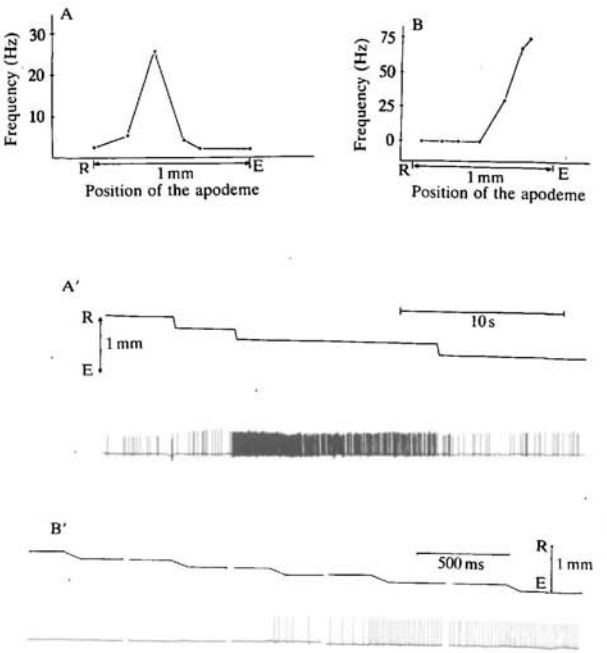

Fig. 2. Two position receptors (A and B), showing range fractionation. Static response frequency plotted *versus* apodeme position. Each point represents the mean frequency for a set period of 2 s. (A) Maximum discharge frequency appears in the middle part of the operating range. (B) The maximum frequency appears at the elongated end of the operating range. (A'),(B') Original recordings of the behaviour of units A and B. Upper traces: stimulus command voltage, E, elongation; R, relaxation. Lower traces: nerve record.

position of the receptor apodeme but in the opposite direction to the dynamic part (e.g. Fig. 10), the units were also classified as velocity receptors. When this dependence was more marked, however, they were described in this category. To some extent, this distinction is arbitrary.

Position- and velocity-sensitive units were recorded more frequently than the pure position-sensitive ones. This is probably due to a larger axon diameter of the former. In general, the recordings obtained also showed a larger spike amplitude.

Concerning their stimulus-response behaviour, the position- and velocity-receptors formed a broad transition group between the pure velocity-sensitive and the pure position-sensitive units. The velocity-sensitive component of excitation could be strongly marked and then appeared also at lower stimulus velocities.

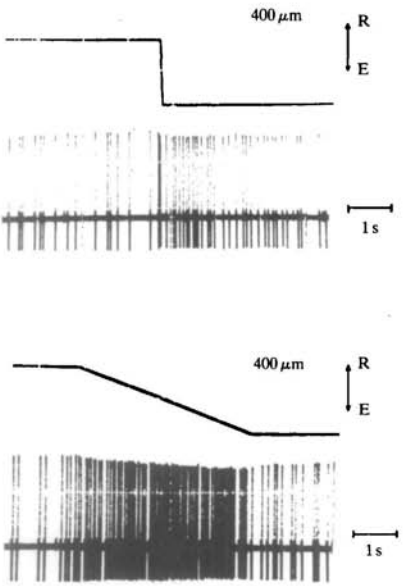

Fig. 3. Oscilloscope recording of response of a P+, V+, 0–3 unit to trapezoidal stimulations with two different velocities (7 mm s^{-1}, 70 μm s^{-1}). The dynamic part is very marked. AM-recording. E, elongation; R, relaxation.

Fig. 3 shows such a response behaviour (P+, V+, 0–3). On the other extreme, the velocity-sensitive part only appeared clearly at higher velocities. Both stretching- and releasing-sensitive receptors existed. When stimulated with staircase waveforms, most P,V receptors showed a dynamic response amplitude that was only weakly dependent on the length of the chordotonal organ, whereas the stationary frequency increased with elongation or relaxation. Fig. 4 demonstrates the response behaviour of such a P+, V+ unit with the static and dynamic characteristics.

The static response of the P,V units often showed hysteresis. At a given position of the receptor apodeme, for example, an elongation-sensitive unit had a higher static frequency when this position was reached by elongation, and a lower frequency when this position was reached by relaxation (e.g. Fig. 4).

Other P,V units showed an even more complex behaviour. The reaction to one direction of the stimulus, e.g. relaxation, was tonic. But the elongation produced a strong movement discharge, after which the unit fired with a lower frequency than before the elongation stimulus. Fig. 5 shows the response behaviour of such a unit (P−, V+) to staircase stimulation. This unit showed a relatively constant velocity-

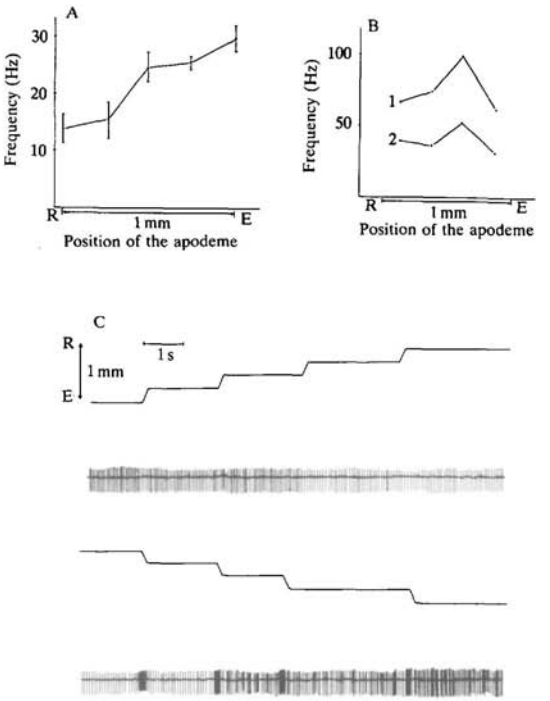

Fig. 4. Response of a P+, V+ receptor unit to staircase stimuli. (A) Static frequency plotted *versus* the position of the apodeme. The bars indicate the standard deviation (seven measurements; in three cases the position was reached by elongation, in four cases by relaxation). Each point represents the mean frequency for a set period of 1 s. (B) Mean frequency of the action potentials during elongation steps plotted against the middle of each movement step; each point represents the mean frequency over the whole movement period (one measurement). Velocities: 1·8 mm s^{-1} (1) and 0·4 mm s^{-1} (2). (C) Example of the nerve record (AM-recording). Upper trace: stimulus (command voltage); E, elongation; R, relaxation; lower trace: nerve record.

dependent response to stretching over the whole operating range. But the position-dependent response decreased with progressive stretch applied to the organ. Receptors reacting in this way may show a rather weak position-sensitivity. Thus, there is a continuous transition to the class of velocity-sensitive units with spontaneous activity (see Fig. 10).

Velocity-sensitive units

These units were spontaneously active (sometimes with very low frequency) and reacted only to the slope of a trapezoidal stimulus. In some cases even a velocity as

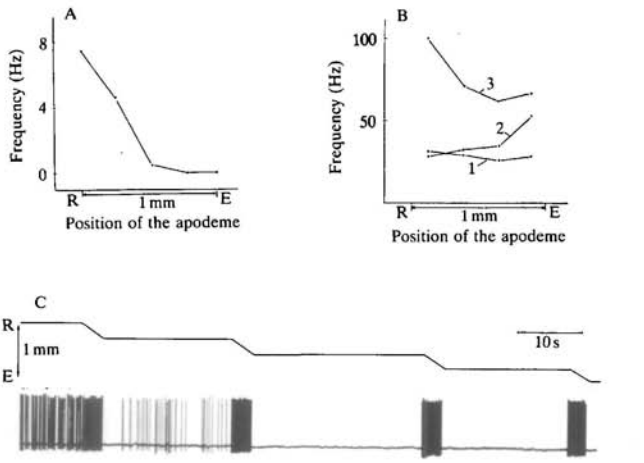

Fig. 5. Response of a receptor unit (P−, V+) reacting tonically to relaxation and phasically to elongation. (A) Static frequency *versus* apodeme position. Each point represents the mean frequency for a set period of 5 s. (B) Mean frequency of the action potentials during apodeme movement plotted against the middle of each movement step (measured as described in Fig. 4). Stimulus velocities: (1), 0·08 mm s^{-1}; (2), 0·8 mm s^{-1}; (3), 8 mm s^{-1}. The data are from a single stimulus sequence. E, elongation; R, relaxation. (C) Reaction to staircase stimulation with a constant step size and velocity (0·08 mm s^{-1}). Upper trace: stimulus (command voltage), lower trace: nerve record (FM-recording); E = elongation, R = relaxation.

low as 6–7 μm s^{-1} was answered in a distinct way. The recordings of such units were mostly characterized by the high amplitude of the action potentials and could be held for a long time in several cases. Therefore, a large axon diameter is assumed. Fig. 6 shows the reaction of a relaxation-sensitive unit (P0, V−, 0–4) to trapezoidal stimulations with different velocities. It can be seen that the unit reacted to all stimuli but especially well to the slower stimuli. When such a unit reacted to one direction of the stimulus with an increase in frequency, the spontaneous frequency was decreased during the reverse stimulus (Fig. 7A, P0, V−, 0–4). However, other units were found which did not react in this way to the opposite direction of the stimulus. Finally, this group also contains receptors reacting with a frequency increase to both stretching and releasing. Such receptors were recorded less often. Fig. 7B shows one example (P0, V+−, 0–3). The response frequency of the velocity receptors depended on the velocity of the stimulus. Fig. 8 shows this dependence for a selection of stretching- and releasing-sensitive receptors.

Fig. 9 demonstrates the response of a P0, V+ unit to staircase stimulation of the chordotonal organ. The response occurred over the whole operating range and depended only weakly on the degree of elongation of the organ (compare the diagram and the nerve records). Other velocity-sensitive units were found in which the response amplitude depended clearly on the elongation of the chordotonal

organ. Fig. 10 shows such a receptor, sensitive to stretching (P0, V+). The spontaneous activity of this unit decreased weakly with the length of the organ. The dynamic response appeared during elongation, but only when the organ was rather relaxed. In the elongated organ, no reaction to stretching is observed. Thus, some spontaneously-active velocity receptors showed their response over the whole operating range while others only reacted in a part of the operating range (range-fractionation).

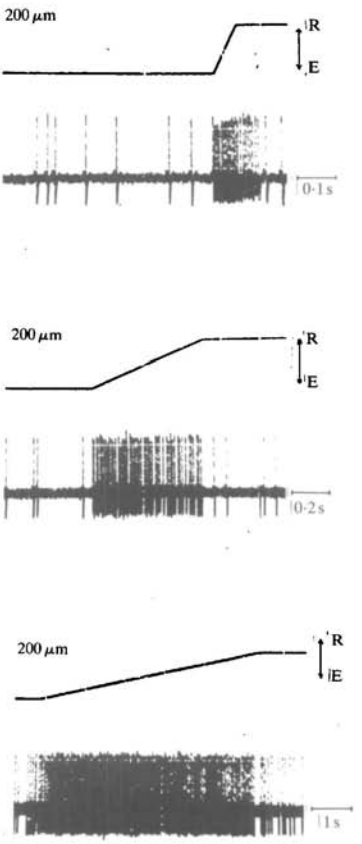

Fig. 6. Response of a P0, V−, 0–4 unit to different trapezoidal stimulations (AM-recording). R, relaxation; E, elongation; stimulus amplitude, 200 μm.

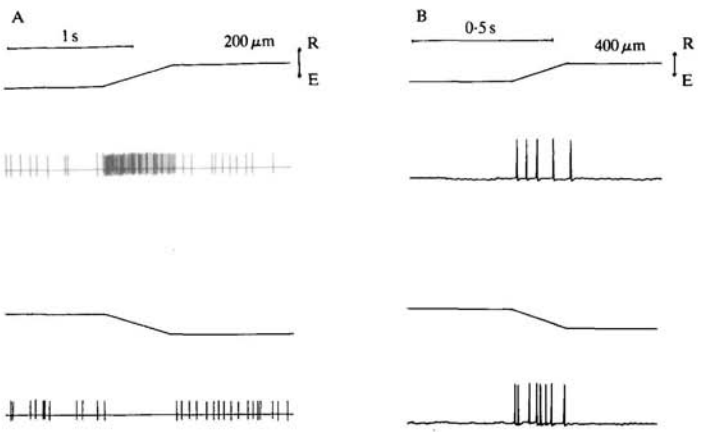

Fig. 7. Comparison of unidirectional (A) and bidirectional (B) V receptors. Upper traces: stimulus (command voltage); R, relaxation, E, elongation. Lower traces: nerve records. (A) P0, V−, 0–4; AM-recording. Note the inhibition to stretching. (B) P0, V+−, 0–3; FM-recording.

Other units

Acceleration-sensitive units, which are described in the subsequent paper (Hofmann & Koch, 1985) were relatively often penetrated.

Finally some units were found which did not respond to any kind of elongation or relaxation stimulus applied to the chordotonal organ. They probably originated from other sense organs, for example tactile spines on the femur or, when recordings were made more proximally (only in a few cases), from campaniform sensilla or the hair-plate at the trochanter.

DISCUSSION

A large variety of units in the chordotonal organ have been found and classified. However, it cannot be excluded that the chordotonal organ contains other units showing responses not described above.

The femoral chordotonal organ in *Cuniculina* contains unidirectionally-sensitive velocity receptors, position-sensitive units and position- and velocity-sensitive units. This is in agreement with results from Crustacea (for review see Mill, 1976) and insects (Burns, 1974; Young, 1970). The bi-directionally-sensitive velocity receptors found here have also been described in Crustacea (Taylor, 1975) and in an abdominal chordotonal organ of the stick insect *Carausius* (Orchard, 1975).

Velocity and position receptors

Velocity-sensitive units, which fire only in a small part of the operating range and which also react to slow movements, have been described in the MCO 2 organ of

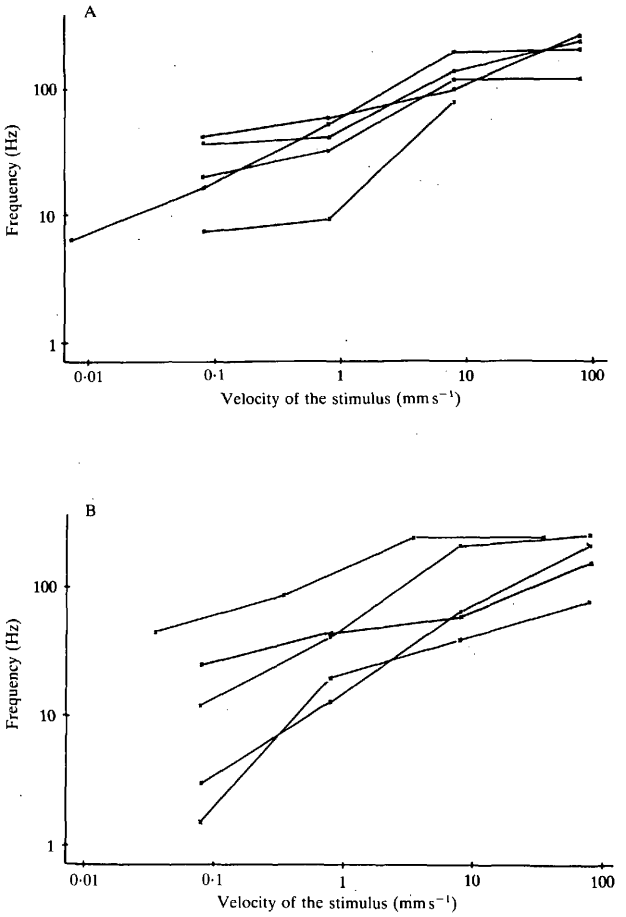

Fig. 8. Comparison of responses of different V receptors. Mean frequency of action potentials during apodeme movement plotted *versus* velocity of the stimulus, measured as described in Fig. 4. Trapezoidal stimuli, 400 μm. Every line corresponds to a single receptor unit. (A) Selection of five V+ receptors; (B) selection of five V− receptors.

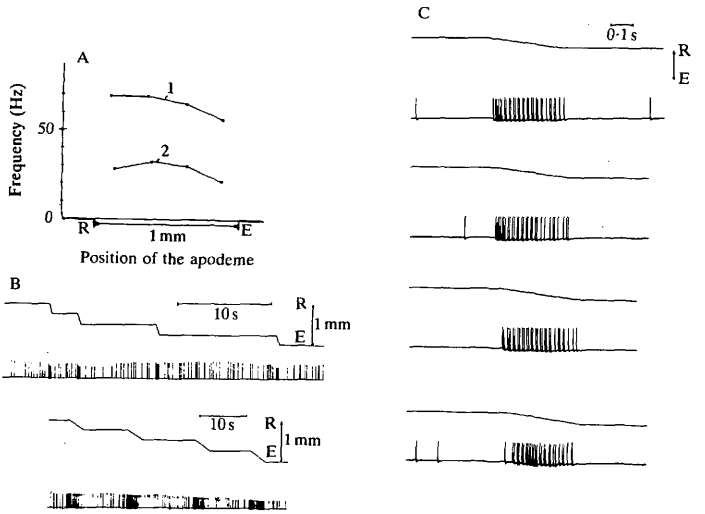

Fig. 9. Response of a P0, V+ unit which reacts to stretching. (A) Dynamic characteristic (mean frequency of action potentials during apodeme movement plotted against the middle of each movement step). 1, stimulus velocity, 0·8 mm s^{-1}; 2, stimulus velocity, 0·08 mm s^{-1}. (B) Illustration of the corresponding records (FM-recording). *Upper:* stimulus velocity 0·8 mm s^{-1}, lower: stimulus velocity 0·08 mm s^{-1}. In each record the upper trace is stimulus (command voltage) and the lower trace is nerve record. R, relaxation; E, elongation. (C) Expanded view of the response to the four stimuli with a velocity of 0·8 mm s^{-1} (FM-recording). Occasional spikes with a very high instantaneous frequency occur within the partial refractory state of the axon. Therefore, the amplitude of these spikes is reduced.

Crustacea (Cohen, 1963, 1965). Range-fractionation, as found here in the position and velocity receptors, could be useful to encode position information with very high resolution and improved stability since position information would depend much less on changes in the thresholds of the receptor cells. If the velocity-sensitive component of the response is also range-fractionated, information about movements is available together with the position at which they occur.

Receptors showing the complex behaviour in the position- and velocity-sensitive components (P+, V− and P−, V+, see Fig. 5) have also been described in the PD-proprioceptor of *Nephrops* (Decapoda) (Mill & Lowe, 1972). This response behaviour was named 'post-excitatory-depression' in Decapoda. It seems that it also plays a role in the femoral chordotonal organ of Phasmida. Such stimulus-response behaviour is difficult to explain. This is especially true in the analysis of ultrastructure, where function models for tonic (position-sensitive), phasic-tonic (position- and velocity-sensitive) and phasic (velocity-sensitive) units have already been described (Mill & Lowe, 1973; Lowe, Mill & Knapp, 1973).

Looking at the distribution of the P and P,V receptors in *Cuniculina*, a strong predominance of the P+ and P+,V+ receptors is obvious (see Table 1). Assuming equal axon diameters for its symmetrical partner (P−,V−) the assymetry in the P,V

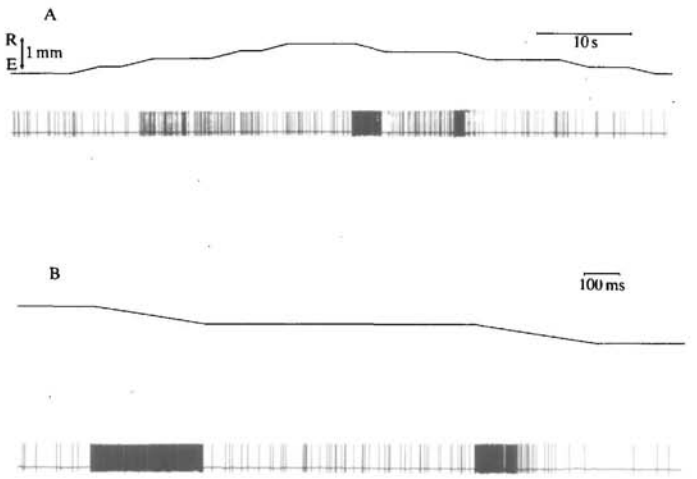

Fig. 10. Response of a unit (P0, V+) only reacting in a part of the operating range. (A) Recording over the whole range. (B) Recording in the adequate range only. Upper trace, stimulus (command voltage). Lower trace, nerve record (FM-record). R, relaxation; E, elongation.

receptors is significant. The preference for the P+ type in the P receptors seems to agree well with the predominance of the P+,V+ in the P,V receptors. In addition, it is noteworthy that no P,V receptors with a bi-directional component were found, although pure V+− receptors exist. The total number of P,V units found is not large enough to indicate with statistical significance that P,V+− receptors do not exist.

On the other hand, the distribution of directionality in the pure V receptors seems quite even, with a substantial fraction of the V+− type.

Integration of the afferences in the CNS

How is the information of the different sensory units processed in the CNS? The P and the P,V receptors provide information about the position of the femur-tibia joint to the CNS continuously even over long durations. The position receptors often show range-fractionation. Especially those units having a narrow peak in their response characteristic (Fig. 2A) should be able to provide precise information about joint angles lying between both extreme positions.

The most sensitive velocity-receptors still respond to a velocity of $3–4\,\mu m\,s^{-1}$ with a weak increase of the discharge frequency. Stimuli with a lower velocity could not be produced by the apparatus used, but the threshold of the single cell recorded is probably not much lower. In contrast to this, the threshold of the whole femur-tibia control system lies at a velocity of the receptor apodeme of $0{\cdot}03\,\mu m\,s^{-1}$

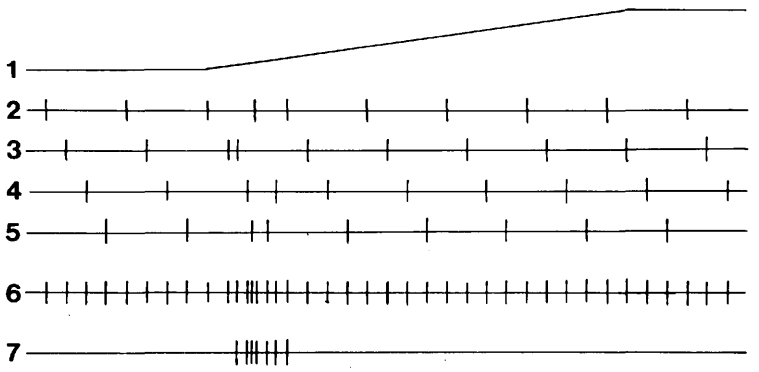

Fig. 11. A five-unit model giving increased sensitivity to slow movements by summation of spontaneously active sensory units with moderate motion sensitivity: four sensory fibres (trace 2–5) scarcely react to the stimulus (trace 1). Each of these fibres only reacts at the beginning of the stimulus (range-fractionation). All fibres converge to a single interneurone. The summed input to this interneurone is shown in trace 6. Because of the threshold of the interneurone the 'spontaneous activity' disappears and the velocity response is clearly visible now in trace 7. Of course, more interneurones could be involved in such a mechanism.

(Bässler, 1972). In catalepsy behaviour the velocity of apodeme movement lies between $20\,\mu m\,s^{-1}$ and $0{\cdot}013\,\mu m\,s^{-1}$. Such a high sensitivity of the system does not seem to be explicable only on the level of single sensory units. Perhaps, the appropriate sensory units have not yet been found. However, an increase of the sensitivity could also be obtained in the following way: there are many sensory fibres reacting to very slow stimuli with a weak response, where the frequency change cannot be distinguished from accidental changes of the spontaneous frequency in the single unit case. If many such units all reacting in the same part of the operating range were to be summated, a distinct stimulus response could be produced in the CNS. Such an integration could happen at the interneuronal level. Fig. 11 shows a hypothetical example. If the extremely low velocity detection threshold is obtained by using this or a similar mechanism, then the large number of scolopidia in the chordotonal organ could be understood.

In the femur-tibia control system the chordotonal organ, together with possibly associated interneurones, represents a lead-lag-system (high-pass filter with a tonic part) with its half-time depending on the velocity of the stimulus (Bässler, 1983). It is still unclear whether all or only a fraction of the sensory units of the chordotonal organ are used in the feedback system of the femur-tibia joint. Therefore it remains an open question to what extent the high-pass filter properties in the feedback control system are due to the properties of the chordotonal organ.

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