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

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SUMMARY

The femoral chordotonal organ of the stick insect *Cuniculina impigra* was stimulated by moving its apodeme with staircase-like waveforms having independently controllable acceleration and velocity values. Intracellular recordings were made of receptor units in the sensory nerve. Apart from receptors encoding position and velocity (see preceding paper, Hofmann, Koch & Bässler, 1985) specific acceleration receptors and also receptors responding to both the acceleration and the velocity of the stimulus could be distinguished. The pure acceleration receptors fall into two categories: units reacting only to one sign of acceleration (e.g. onset of relaxation *and* end of elongation) and units reacting to both signs of accelerations. Individual thresholds for each sign of acceleration were measured and analysed. Latencies of the receptors were determined and found to be dependent on the degree of acceleration.

A possible role for the acceleration receptors in an alarm system of the animal is discussed.

INTRODUCTION

Response characteristics of mechanoreceptors in arthropods have been described in great detail. Receptor cells can respond to static position of the stimulus ('P' response: 'tonic' receptors), velocity ('V' response: 'phasic' receptors) or acceleration ('A' response: vibration receptors), and response to any of these can be in one direction (+) or the opposite direction (−). Combinations of P and V responses (phasic-tonic receptors) have also been found (e.g. Bush, 1965*a*,*b*; Hofmann & Bässler, 1982; Mill & Lowe, 1972; Clarac & Vedel, 1975; Taylor, 1975; Zill & Moran, 1981).

In this paper we investigate whether A responses can be found in combination with P or V receptors in the femoral chordotonal organ of *Cuniculina impigra* Redtenbacher (= *Baculum impigrum* Brunner). This sensory organ has been shown in the preceding paper to contain receptors sensitive to acceleration in addition to those sensitive to position and/or velocity (Hofmann *et al.* 1985).

Key words: Stick insect, chordotonal organ, acceleration-sensitivity.

Stimuli with sinusoidal waveforms have often been used to study mechanoreceptors (e.g. Kalmring, Lewis & Eichendorf, 1978; Bart & Geethabali, 1982; Kühne, 1982), enabling Fourier analysis of a linear system with constant properties, but the analyses are not of great use in detecting and describing non-linearities such as range-fractionation or adaptation. To detect non-linearities and to determine the composition of phasic-tonic responses, trapezoidal or staircase stimuli are adequate. Sinusoidal stimuli are also inadequate to determine directionality of acceleration receptors, or to investigate a combination of acceleration response with the other responses. For this purpose it is necessary to use a stimulus containing position, velocity and acceleration in combinations that are individually controllable, e.g. by varying the acceleration into (and deceleration out of) a constant velocity (ramp function), or varying the ramp slope while holding the initial acceleration constant. In this work, this is achieved with a specially developed stimulating apparatus.

MATERIALS AND METHODS

Single unit recordings were made directly from the chordotonal organ nerve of intact female *Cuniculina impigra*, using glass microelectrodes, as described in the preceding paper (Hofmann *et al.* 1985). The receptor apodeme of the chordotonal organ was exposed by a small window in the distal part of the femur, fixed in a drawing pen clamp and cut distally. The clamp was moved by a loudspeaker (see below). The zero position of the clamp corresponded to an angle between femur and tibia of 90°. The position and the velocity signals of the apodeme clamp were stored, together with the amplified nerve potentials, on an FM tape recorder and displayed on a Mingograph or a standard pen recorder. In order to measure latencies, chart recordings were digitized on a graphic tablet connected to a DEC LSI 11-03 computer; this was also used for the statistical analysis of latencies. Mechanical movements with independently controllable values of acceleration, velocity and position were generated with a specially constructed waveform generator (Fig. 1). It consists basically of two integrators connected in series. The input to the first integrator, corresponding to the level of acceleration, can be varied in steps, independently for the start (acceleration) and stop (deceleration) phases of the movement. The output of the first integrator corresponds to velocity and is monitored by a level detector set to the desired value of velocity. On a starting command the acceleration voltage is switched to integrator 1, generating a linearly rising ramp. Once the preset velocity has been reached, current to integrator 1 is stopped. Velocity now remains constant. The velocity signal thus generated is integrated to form the position signal in integrator 2. At the output of integrator 2, a further level detector is set to the desired amount of displacement. Once this preset 'step size' is reached, the circuit switches to deceleration. Negative currents are now fed to integrator 1, reducing velocity linearly, until velocity zero is reached. Then, current flow to integrator 1 is stopped and velocity remains at 0, whereas the position signal stays at the new value reached after 'braking'. Under constant acceleration, velocity increases linearly with time, while position changes in the form of a parabola. Thus, the generator produces ramps of predetermined heights

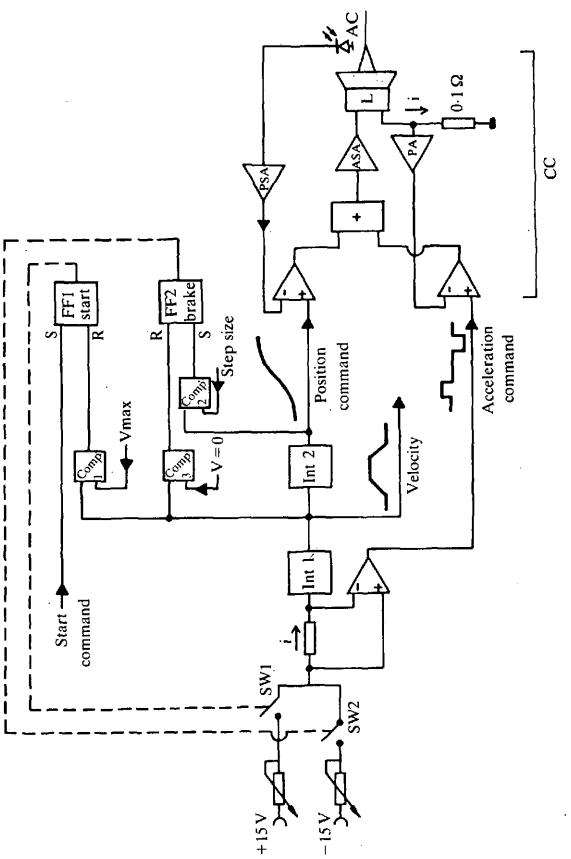

Fig. 1. Schematic drawing of the circuit to drive the apodeme clamp (AC, on far right) *via* the loudspeaker L. SW1, SW2, switches; FF1, FF2, flip flops controlling start and stop acceleration; Comp 1,2,3, comparators set to end start, linear slope and stop phases; Int 1,2, integrators producing velocity and position signals; CC, control circuitry ensuring accurate mechanical reproduction of the command voltages; PA, power amplifier; PSA, position-sensing amplifier; ASA, acceleration-sensing amplifier. Additional circuitry for producing velocities of opposite sign and series of identical steps (staircase) are omitted for clarity. i, current; R, Reset; S, Set.

(amplitudes) and slopes (velocities), and with parabolic curves instead of sharp edges at the beginning and end of each ramp. The degree of 'roundness' of the edges can be controlled by setting the acceleration value.

To transform these command voltages into precise mechanical motion of the apodeme, the signal was fed through a power amplifier connected to a low frequency loudspeaker (Visaton W 100, 30 W power rating, 100 mm diameter). Its coil carried a special paper-cone, on which the apodeme clamp was mounted. A feedback system containing two independent feedback pathways was used to ensure a precise transduction of the command voltages to the position of the apodeme clamp. The position of the apodeme clamp was measured using a light source and a photodiode detecting the transmission of a linearly graded optical wedge scale moving with the apodeme clamp. The linearity of this system was 0·8 %, the resolution 0·5 μm, and the response frequency limit 20 kHz. The acceleration of the loudspeaker was determined by the current through the moving coil, since the current is directly proportional to the force acting on the coil. Since $F = m \cdot a$, this force is proportional to the acceleration. Thus, one feedback pathway controlled the position of the speaker system whereas the other controlled the acceleration *via* the current going into the loudspeaker coil. Elaborate adjustment procedures were needed to ensure that the sensitivities of the control circuits for position and acceleration were suitably set, such that the combined control system worked without any overshoot. With an improvised acceleration meter mounted at the position of the apodeme clamp, the correct generation of the acceleration impulses was checked. Graded values of acceleration command voltages produced the expected graded values of acceleration. No deviation of the position signals from the required motion pathway were detected for accelerations up to 13·2 $m\,s^{-2}$.

RESULTS

To demonstrate clearly that a unit in the chordotonal organ nerve was an acceleration receptor, the following scheme was used: two ramp signals of equal step height were generated. One, (A) had low velocity (0·4 $mm\,s^{-1}$) with high acceleration (1·3 $m\,s^{-2}$) while the other, (B) had high velocity (1·3 $mm\,s^{-1}$) with low acceleration values (0·1 $m\,s^{-2}$) (see Fig. 2). If the unit were velocity sensitive, it should respond better to stimuli of type B, whereas a pure acceleration receptor should respond better to stimulus A. In Fig. 2, only one step out of every staircase series is shown. The responses clearly demonstrate a true acceleration sensitivity. Units of this type showed action potentials with high amplitudes (30–100 mV). In most cases, it was possible to maintain the intracellular recording for long periods (up to 30 min). Therefore it is assumed that the A receptors have rather large axons. In comparison with position receptors and velocity receptors (see preceding paper, Hofmann *et al.* 1985), acceleration receptors were easier to impale.

The response characteristics of the receptors are conveniently summarized using abbreviations, as indicated in the Introduction. Thus A+ is an acceleration receptor reacting only to positive acceleration (increase of elongation velocity and decrease of relaxation velocity). An A− unit is sensitive only to negative acceleration (increase

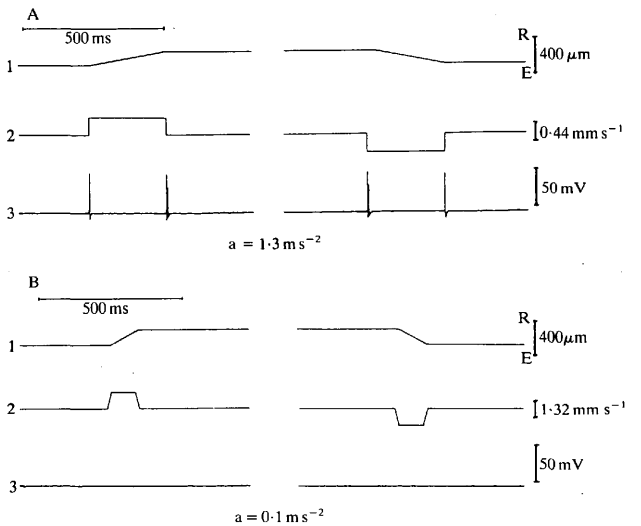

Fig. 2. Reaction of an acceleration-sensitive unit to stimuli with different velocities and accelerations. (A) Lower velocity, higher acceleration, $1{\cdot}3\,m\,s^{-1}$; (B) higher velocity, lower acceleration, $0{\cdot}1\,m\,s^{-1}$. Only the stimuli with the high acceleration elicit action potentials. In each recording three traces are shown. Trace 1, stimulus position (output of the position encoding photodiode), E, elongation; R, relaxation. Trace 2, velocity profile (command voltage). Trace 3, nerve record. Although the velocity is three times higher in B, the unit responds only to the stimulus situation in A, where acceleration is higher.

in relaxation velocity or decrease in elongation velocity). An A+− unit responds to both positive and negative acceleration.

The numbers and types of units found and characterized in this work are summarized in Table 1, together with the units described in the preceding paper (Hofmann *et al.* 1985).

General features of acceleration receptors

As shown in Table 1, the largest fraction of A receptors were of the A+− type, followed closely by A− receptors. These two types of receptors are labelled pure acceleration receptors. In a smaller number of cases, A,V receptors reacting to acceleration and velocity with individual thresholds were clearly identified.

Thresholds

In a large number of cases the recordings were held so long that it was possible to measure thresholds of the A and A,V units by varying acceleration and keeping ramp velocity and step size constant. Acceleration was varied between $3{\cdot}88\,m\,s^{-2}$

Table 1. *Summary of the results (including the position and velocity receptors)*

Classification	Response	Number of records
Position-sensitive	P+	11 (2)
	P−	3 (0)
	Pm(V)	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	V+	12 (1)
	V−	10 (0)
	V+−	8 (2)
Velocity- and acceleration-sensitive	V+,A+	0 (0)
	V+,A−	2 (3)
	V+,A+−	0 (1)
	V−,A+	0 (0)
	V−,A−	4 (1)
	V−,A+−	0 (0)
	V+−,A+	0 (0)
	V+−,A−	0 (0)
	V+−,A+−	5 (0)
Acceleration-sensitive	A+	0 (1)
	A−	12 (3)
	A+−	16 (7)

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

In addition to the receptors listed above, 14 A receptors and 2 V,A receptors were found but could not be classified further.

and $0{\cdot}01\,m\,s^{-2}$. The thresholds measured ranged between $0{\cdot}44\,m\,s^{-2}$ (less sensitive units) and $0{\cdot}02\,m\,s^{-2}$ (most sensitive units). No units with thresholds above $0{\cdot}44\,m\,s^{-2}$ were found. When remaining unstimulated, a large fraction of the receptors showed no activity. The rest, however, showed 'spontaneous' activity.

In a large fraction of spontaneously active units, thresholds could be measured, and turned out to be at levels comparable to the non-spontaneously active units. There was, however, a smaller number of units which had a very high spontaneous activity. The pattern of action potentials often had multiplett structures. In these cases, it was not possible to measure a threshold, because reactions to the smallest stimuli ($0{\cdot}01\,m\,s^{-2}$) could not be distinguished from the high frequency background. It is possible that these units had thresholds below $0{\cdot}01\,m\,s^{-2}$ and were continuously responding to residual vibration signals in the apparatus, originating either from building vibrations or from electronic noise in the control circuit.

Above threshold behaviour

Once above threshold, higher acceleration values were generally answered with

larger numbers of action potentials. In many cases, the instantaneous action potential frequency was so high that some action potentials fell in the partially refractory phase and therefore showed a reduced peak height (Figs 2A, 3A).

The latency between onset of acceleration and the first action potential also depended on the amount of acceleration above threshold: the latencies were reduced at higher acceleration, latencies as short as 2–3 ms were reached. This behaviour was analysed for a selection of three A and one A,V receptors. In Fig. 4, latency values are plotted *versus* acceleration in a logarithmic coordinate system. The data points can be fitted well by straight lines, which means that latency depends on acceleration in a power function. For the acceleration values of $3{\cdot}88\,m\,s^{-2}$ and $0{\cdot}88\,m\,s^{-2}$ the latency histograms of a total of four acceleration-

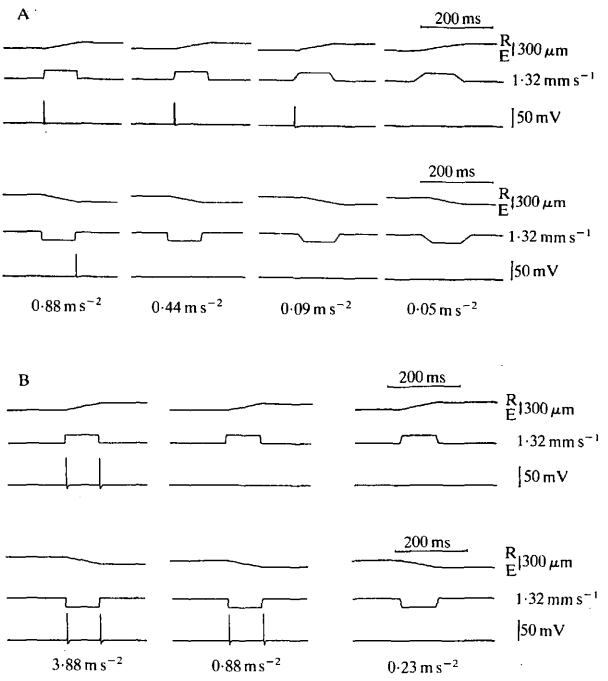

Fig. 3. Reaction of two pure A receptors to stimuli containing always the same maximum velocity, but different levels of acceleration. The stimuli are only answered at higher accelerations of the stimulus. The unit shown in part (A) reacts only to one sign of acceleration (A−). The reaction depends also on the sign of the velocity. Part (B) shows a unit reacting to both signs of accelerations (A+−). A slight preference for the positive velocities seems to exist here. Upper traces, position signal, E, elongation; R, relaxation. Middle traces, velocity signal (command voltage). Lower traces, nerve record.

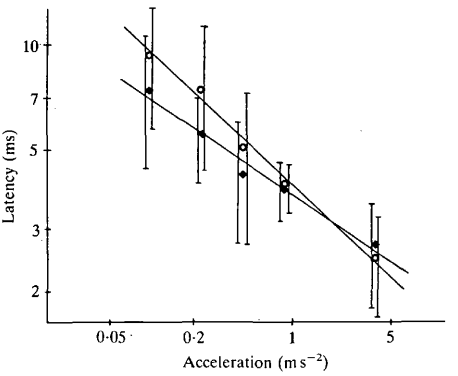

Fig. 4. Latencies between onset of acceleration and first action potential plotted *versus* acceleration. Averages of four selected units (one V,A and three A units). Bars, ±S.D. ◆, Latencies at the begin of the stimulus (84 measurements in total); $y = 0{\cdot}27x + 1{\cdot}32$, $r = 0{\cdot}988$. ○, Latencies at the end of the stimulus (74 measurements in total); $y = 0{\cdot}37x + 1{\cdot}39$, $r = 0{\cdot}989$.

sensitive units are shown in Fig. 5. In the histograms the shift to longer latencies at the lower accelerations can clearly be seen. Pure acceleration receptors reacted very well to sinusoidal stimuli at frequencies above 20 Hz even at small amplitudes. In this respect, they correspond to the classical 'vibration receptors'.

Symmetries and asymmetries

Assuming a more or less constant axon diameter for all types of pure A receptors, the fact that 12 A− and no A+ receptors were found is highly significant.

Even in a large fraction of the A+− units, the two signs of acceleration are not answered quite symmetrically. At values near threshold, negative acceleration is generally answered more strongly, and thus thresholds for positive acceleration are somewhat higher than for negative acceleration. Thus, near threshold, A+− units may react as A− units. Only one exception to this rule was found, where one A+− unit behaved as an A+ unit in the range of 0·4 m s^{-2}.

In most units reacting asymmetrically to the two signs of acceleration, the sign of the velocity also appeared to have an effect on the reaction pattern. With positive velocities (i.e. elongation), the A+ component was enhanced, whereas with negative velocities, the A− component could react more strongly. Another way to describe this phenomenon is to say that the acceleration is answered more vigorously at the onset of a stimulus movement than at the end of the stimulus. Thus, an A− receptor may react more strongly to the onset of relaxation than to the end of elongation (e.g. Fig. 3A). In cases where the beginning of the stimulus was answered more strongly than the end, this tendency was not dependent on the sign

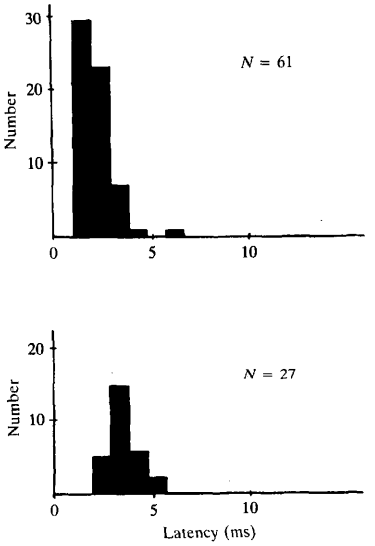

Fig. 5. Histograms of the latencies at the stimulus accelerations 3·88 m s^{-2} (upper) and 0·88 m s^{-2} (lower). The reactions of four receptors are pooled. Stimulus velocity, 1·3 mm s^{-1}.

of the acceleration. This is also shown in the latency plot of Fig. 4. Here, latencies increased to larger values near threshold for reactions to the end of a stimulus. Even in A+− receptors where no evident preference of either acceleration sign was found, a preference to react better on one velocity direction than the other could be found (e.g. Fig. 3B).

With very few exceptions, acceleration receptors seem to react evenly over the whole operating range of the chordotonal organ; thus no significant range fractionation was observed.

Velocity- and acceleration-receptors

V,A receptors were recorded less frequently than A receptors. In principle, nine combinations of V and A sensitivity are possible (see Table 1), but only three were found: V+−, A+− units (e.g. Fig. 6), V+, A− units and V−, A− units (e.g. Fig. 7). A,V receptors with an A+ component were not found at all; this is in agreement with the results for pure A receptors.

The reaction of the V,A units to the velocity component of the stimulus is similar to the reaction of pure velocity receptors (described in Hofmann *et al.* 1985). Even low velocities were answered clearly (see Fig. 6). Above the acceleration threshold,

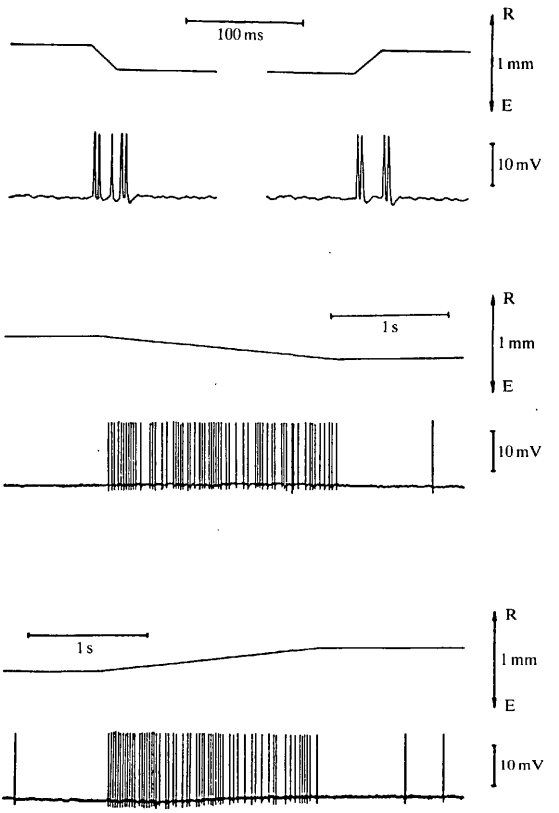

Fig. 6. Response behaviour of a V+−,A+− unit to stimulation with fast (upper) and slow (lower) trapezoidal stimuli. In the first case, mainly the acceleration, in the second case only the velocity is answered. Upper traces, stimulus; E, elongation; R, relaxation; lower traces, nerve record.

reaction also occurred to the acceleration component in the stimulus. In one case a V,A receptor could be investigated in detail (Fig. 7). Here the latencies were in the same range as those of the pure acceleration receptors. The threshold of the unit shown in Fig. 7 for acceleration was between 0·02 and 0·05 m s^{-2}, the threshold for the velocity component of the stimulus was lower than 0·13 mm s^{-1}. V,A receptors were recorded less frequently than A receptors.

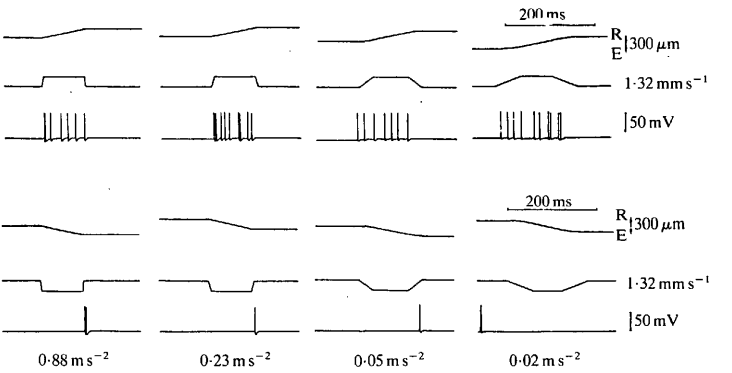

Fig. 7. Reaction of a V−,A− unit to stimuli containing always the same maximum velocity but different accelerations. The begin of relaxation and the end of elongation are answered only at higher acceleration levels. In contrast to this, the stimulus-velocity is answered during every relaxation independently of the acceleration. The spike in the last record is spontaneous. Upper traces: position signal; E = elongation, R = relaxation. Middle traces: velocity (command voltage). Lower traces: nerve record.

DISCUSSION

A sensitivity to acceleration has also been described for other mechanoreceptors in insects and crustaceans (e.g. subgenual organ, Schnorbus, 1971; complex tibial organ, Kalmring *et al.* 1978). However, in most cases the acceleration sensitivity has been demonstrated by the dependence of the receptor thresholds on the frequency of sinusoidal stimuli. Such stimulation does not allow differentiation between A+, A− or A+− units.

Acceleration- or vibration-receptors have also been described in other chordotonal organs, e.g. in the crayfish antenna (Taylor, 1975) and at the wing base of the cricket (Möss, 1971) owing to their increased activity at velocity changes. Bush (1965*b*) described phasic movement fibres in the coxo-basal chordotonal organ of the crab. Evidence for the existence of vibration sensitivity in the tibio-tarsal chordotonal organ in the cockroach was found by Young (1970), but this response was not studied systematically. In an extracellular electrophysiological investigation of the femoral chordotonal organ in the locust, strong responses were produced by vibrations of the tibia (Burns, 1974). In this study the tibia was also moved with trapezoidal stimuli. Thus, at the beginning and at the end of the stimulus, spikes appeared, which were much bigger than those occurring during the rest of the movement. They were classified as purely phasic. We suggest that they originated from acceleration receptors homologous to the ones described in this paper. In all cases quoted above, the acceleration sensitivity could not be analysed with respect to the different signs of acceleration. In agreement with Taylor (1975), the acceleration receptors have the largest axons in the nerve and therefore presumably also the highest conduction velocity.

In the present work acceleration-sensitive receptors are shown to exist in the chordotonal organ of *Cuniculina impigra*. For the first time, it has been possible to analyse the sensitivity to each sign of acceleration independently; accordingly, both A+− and A− receptors were found, but no A+ units were encountered. Receptors sensitive to both acceleration and velocity were postulated by Taylor (1975). These have now been shown unambiguously to exist, and to have distinct thresholds for velocity and acceleration. In addition, their directionality combination is described.

The most sensitive A receptors investigated here have threshold values of about 2–5 $cm\,s^{-2}$, in the cases where the threshold could be measured. However, we believe that among the spontaneously active units, some exist with thresholds below 1 $cm\,s^{-2}$. In comparison with this, the thresholds of the most sensitive units in the cockroach subgenual organ have values of about 0·04–4 $cm\,s^{-2}$, dependent upon the experimental set-up (Schnorbus, 1971). Thus the threshold values of the units of the femoral chordotonal organ of *Cuniculina* are in the same range as the thresholds of the subgenual organ in *Periplaneta*. Because of the extracellular investigation of the subgenual organ, the probability of encountering the most sensitive units is greater than with the intracellular recording technique used here. Therefore it is possible that the chordotonal organ of *Cuniculina* contains units with a higher sensitivity than the receptors described in this study.

Some of the asymmetries found in the reaction patterns of the A receptors are very pronounced, e.g. the disparity between A+ and A− receptors. This might be caused by the construction principles of acceleration-sensitive units in general. Another interesting possibility is that all A receptors are A− receptors at threshold and then, at higher accelerations, A+ sensitivity is added. A− receptors then would only be A+− receptors with a very high A+ threshold. It was not possible in this study to use high enough accelerations to test this hypothesis. The observation that, in many cases, acceleration at the onset of a movement is answered more strongly than deceleration at the end of a movement might be explained by inhibition. That is, the acceleration at the onset of the movement could inhibit the reaction of the unit at the end. Stimulation with asymmetrical accelerations (slow start – fast brake or fast start – slow brake) could be used to analyse these phenomena further.

The fact that among the A,V receptors no A+ components were found, underlines the asymmetries in the pure A receptors. However, the relatively small numbers of A,V receptors are not sufficient to indicate a significant bias in their existing combinations. Thus further investigations might reveal V+,A+−, V−,A+− or V+−,A− units. If measurements on a larger scale could be made, significant asymmetries in the combinations of V,A as well as P,V receptors might be established. This might suggest important principles as to the construction of functional models of these types of receptors.

In every mechanical stimulus, acceleration reaches its maximum value earlier than velocity and position. Therefore acceleration receptors are able to detect any change in the mechanical conditions faster than other receptors. They could be a part of an alarm system reacting to the onset of very fast movements. The morphological and physiological organization of the femoral chordotonal organ would present optimal conditions for such a function: acceleration is quickly transmitted from the distal part of the leg to the chordotonal organ apodeme by the

cuticle. Because of its stiffness, the apodeme also transmits acceleration very quickly to the receptor cells. Short stimulus-response latencies imply a rapid transduction into action potentials. The large axon diameters of the acceleration-sensitive units guarantee a high conduction velocity. All these conditions improve the ability to react as rapidly as possible to potential danger-signals to the animal.

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REFERENCES

BARTH, F. G. & GEETHABALL (1982). Spider vibration receptors: threshold curves of individual slits in the metatarsal lyriform organ. *J. Comp. Physiol.* **148**, 175–185.

BURNS, M. D. (1974). Structure and physiology of the locust femoral chordotonal organ. *J. Insect Physiol.* **20**, 1319–1339.

BUSH, B. M. H. (1965*a*). Proprioception by chordotonal organs in the mero-carpopodite and carpo-propodite joints of *Carcinus maenas* legs. *Comp. Biochem. Physiol.* **14**, 185–199.

BUSH, B. M. H. (1965*b*). Proprioception by the coxo-basal chordotonal organ, CB, in legs of the crab, *Carcinus maenas*. *J. exp. Biol.* **42**, 285–297.

CLARAC, F. & VEDEL, V. P. (1975). Proprioception by chordotonal and myochordotonal organs in the walking
legs of the rock lobster, *Panilurus vulgaris*. *Mar. behavl Physiol.* **3**, 157–165.

HOFMANN, T. & BÄSSLER, U. (1982). Anatomy and physiology of trochanteral campaniform sensilla in the stick insect, *Cuniculina impigra*. *Physiol. Entomol.* **7**, 413–422.

HOFMANN, T., KOCH, U. T. & BÄSSLER, U. (1985). Physiology of the femoral chordotonal organ in the stick insect, *Cuniculina impigra*. *J. exp. Biol.* **114**, 207–223.

KALMRING, K., LEWIS, B. & EICHENDORF, A. (1978). The physiological characteristics of the primary sensory neurons of the complex tibial organ of *Decticus verrucivorus* L. (Orthoptera, Tettigonioidae). *J. comp. Physiol.* **127**, 109–121.

KÜHNE, R. (1982). Neurophysiology of the vibration sense in locusts and bushcrickets: response characteristics of single receptor units. *J. Insect Physiol.* **28**, 155–163.

MILL, P. J. & LOWE, D. A. (1972). An analysis of the types of sensory unit present in the PD – proprioceptor of decapod crustaceans. *J. exp. Biol.* **56**, 509–525.

MÖSS, D. (1971). Sinnesorgane im Bereich des Flügels der Feldgrille (*Gryllus campestris* L.) und ihre Bedeutung für die Kontrolle der Singbewegung und die Einstellung der Flügellage. *Z. vergl. Physiol.* **73**, 53–83.

SCHNORBUS, H. (1971). Die subgenualen Sinnesorgane von *Periplaneta americana*: Histologie und Vibrations- schwellen. *Z. vergl. Physiol.* **71**, 14–48.

TAYLOR, R. C. (1975). Physical and physiological properties of the crayfish antennal flagellum. *J. Neurobiol.* **6**, 501–519.

YOUNG, D. (1970). The structure and function of a connective chordotonal organ in the cockroach leg. *Phil. Trans. R. Soc. Ser. B* **256**, 401–428.

ZILL, S. N. & MORAN, D. T. (1981). The exoskeleton and insect proprioception. I. Responses of tibial campaniform sensilla to external and muscle-generated forces in the american cockroach, *Periplaneta americana*. *J. exp. Biol.* **91**, 1–24.