J. exp. Biol. 133, 137–156 (1987)
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SENSORY FEEDBACK DURING ACTIVE MOVEMENTS OF STICK INSECTS

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Accepted 15 June 1987

SUMMARY

In the stick insect *Carausius morosus*, the role of the chordotonal organ was investigated using a new experimental arrangement which artificially closes the femur–tibia control system. The chordotonal organ was stimulated during voluntary movements by applying trapezoidal ramp stimuli in the closed-loop configuration.

The results demonstrate that the feedback loop is used to control the end points of joint movement. In addition, it was found that the control system counteracts experimentally applied velocity changes imposed during the middle part of the movements. Acceleration-sensitive units are shown to contribute to the reaction.

The results show that during active voluntary movements reflexes measured in the inactive animal are neither simply incorporated in a servo-system nor suppressed. Instead their characteristics are altered so that the voluntary movements are executed as intended by the animal. Thus reflexes cannot be considered as a fixed behavioural unit; rather their changing role must be analysed in the context of the behaviour studied.

INTRODUCTION

The control of limb movements is a problem that has been investigated using many different approaches in vertebrates as well as invertebrates. Many hypotheses have been developed concerning the question of which parameter is controlled during active movements. In a recent review (Stein, 1982), various muscle variables, such as force, length, stiffness, viscosity and velocity or acceleration of movement, were considered. It seems likely that a combination of these parameters is controlled.

When considering the role of sensory feedback during active movements, the question remains to be solved of the way reflex systems used in the inactive animal to stabilize posture are integrated into the active movement. In vertebrates, reflex systems can adapt to voluntary movements by coactivation of α- and γ-motoneurones. Arthropods also have resistance reflexes which stabilize joint angles and posture in the inactive animal. Since an efferent control of the position-sensing elements (e.g. chordotonal organs) does not exist in many arthropods, movement control cannot work on the same principle as in vertebrates. Thus, the resistance

Key words: stick insect, sensory feedback, active movements, velocity control, position control, servo-mechanism.

reflex chains must be modified or integrated into a servo-mechanism to permit coordinated movements.

Earlier experiments on stick insects demonstrated that these resistance reflexes can be suppressed, change sign or change gain depending on the behavioural state of the animal (Bässler, 1973, 1976, 1977). During walking, reflex activity is still present, but its gain is reduced and the time constant of reflex response is shortened (Cruse, 1981; Cruse & Pflüger, 1981; Cruse & Schmitz, 1983). The reflex action is then used to compensate for irregularities and disturbances occurring during walking over uneven surfaces. Cruse & Schmitz (1983) concluded that reflex systems are integrated in simple servo-mechanisms, which work in the standing and walking animal. But in the walking animal half-time values seem to be shorter, and the upper corner frequency lower, than in the resting animal.

This plasticity in reflex action was also demonstrated in locusts (Zill, 1985), in which the pattern of motoneuronal activity changes when the metathoracic legs work against a resistance and when this resistance is removed. In the first situation, a typical resistance reflex is found, whereas in the second case a complex change in reflex mode occurred. Experiments on crustaceans (Spirito, Evoy & Barnes, 1972; Barnes, Spirito & Evoy, 1972; Barnes, 1977) also demonstrated that there is reflex activity during active movements.

In all these experiments, the reflex loops were disturbed during active movements with stimuli in a way which did not permit a precise definition of the locus of stimulation, and it was not possible to stimulate directly the sense organ without disrupting the feedback loop at the same time. In vertebrates, muscle spindle organs cannot be stimulated separately from the effectors. Additionally, in investigations on walking animals, other sense organs may be involved in the reaction in many cases, for example, campaniform sensilla in insects, which have effects on timing during a step cycle (Cruse, 1985*b*; Bässler & Wegner, 1983). These experimental difficulties can be overcome using a new technique in which the femur–tibia control loop in the stick insect is closed artificially by an electronic system measuring leg position and transferring it to an appropriate mechanical stimulus of the chordotonal organ (Weiland, Bässler & Brunner, 1986). Using an electronic adding circuit, extra stimulation of the control loop can now be applied without disrupting the reflex activity produced by the moving limb. Using such an arrangement, it is possible to investigate more thoroughly the role of the control loop during active movements, since test stimuli can be applied at any phase without disturbing the active movement itself. In addition, one can test which parameters (e.g. position, velocity, etc.) are controlled in an active movement.

Four distinct working hypotheses can be formulated about a feedback loop during active movements.

(1) The characteristics of the feedback loop are the same as in the resting animal but a continuously changing reference input causes the actual output to follow the reference input (servo-mechanism). This hypothesis must be rejected for the femur–tibia joint of the stick insect because the closed-loop femur–tibia control

system is only able to follow a changing input at frequencies below 1 Hz (Weiland *et al.* 1986), which is too slow for faster active movements.

(2) During active movements the control system is integrated in a servo-mechanism but its characteristics are changed compared to the resting animal. Such a servo-mechanism may control position, velocity or acceleration or a combination of them. In addition, it is possible that a parameter (e.g. position) is controlled either over the whole trajectory of the movement or over a defined range of the movement (such as the end point).

(3) The feedback loop is switched off and therefore not involved in the system which controls active movements. The feedback system will not correct disturbances of the movement.

(4) The negative feedback of the system in the resting animal is changed into a positive feedback and is then used to reinforce an ongoing movement. In this case, small disturbances of the movement are not damped out, but instead are amplified. Such a system was described for the femur–tibia joint of the stick insect (Bässler, 1973, 1976, 1986) and the thoracico-coxal (TC) joint of *Pacifastacus* (Crustacea) (Sillar, Skorupski, Elson & Bush, 1986; Skorupski & Sillar, 1986).

The experiments described here were designed to investigate which of the above possibilities exists in the femur–tibia system of actively moving *Carausius morosus*.

MATERIALS AND METHODS

Artificially closed feedback loop

The experiments were performed on hindlegs of the stick insect *Carausius morosus* reared at Kaiserslautern University. The experimental set-up was an artificial closed-loop system with an additional electronic input, as described in detail by Weiland *et al.* (1986). The position of the tibia was measured using an optical detector, which had a voltage output proportional to the position of the tibia. This position signal was used to drive a pen motor bearing a clamp. The clamp moved the receptor apodeme, thus stimulating the chordotonal organ. The amplitude and offset of the pen motor movement were adjusted to the corresponding tibia movement, such that a tibia excursion caused a receptor apodeme displacement as in the intact animal. A summating amplifier, inserted in the feedback loop, allowed application of additional stimuli to the chordotonal organ in the artificial closed-loop control system. It was also possible to insert an analogue delay in the pathway between position amplifier and pen motor.

Stimulation procedures

Stimuli to the artificially closed feedback system were applied using four different protocols during active movements.

(1) In a first series of experiments ramp-and-hold stimuli were applied during active movements. The stimuli corresponded to $\pm 200\,\mu m$ of apodeme movement. They were released arbitrarily by the experimenter. These experiments were carried

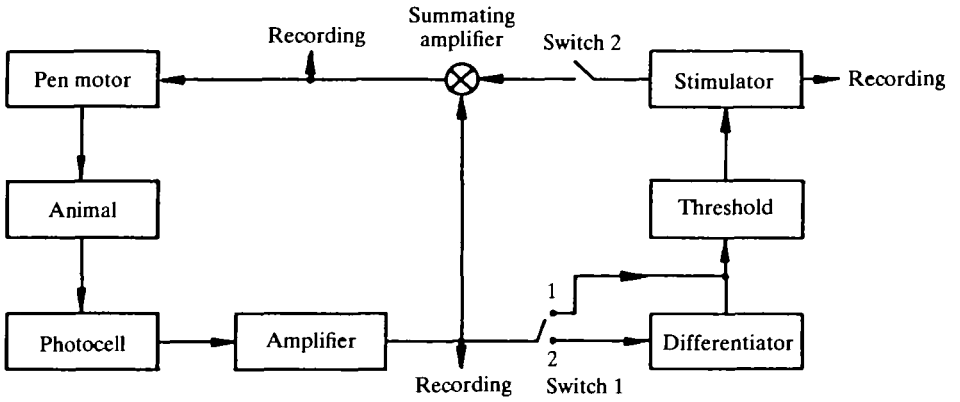

Fig. 1. Information flow of the closed-loop system with stimulation at a predetermined position level (differentiator bypassed) and with stimulation at a predetermined velocity level (differentiator enabled).

out with several animals. The results from three animals were analysed quantitatively.

In the following three stimulation protocols, the stimulus was always released at a specified phase of the active movement.

(2) In this series, the point of stimulus release was a predetermined joint position (90° joint angle for flexion, 115° for extension movements). For this, a Schmitt trigger circuit was adjusted to the appropriate output voltage of the position detector. The trigger released the trapezoidally shaped stimuli (rise and fall time, 20 ms; amplitude, $100\,\mu m = 20°$ joint angle; plateau duration, 12, 30 and 90 ms) which were connected to the summating amplifier (Fig. 1, switch 1 in position 1). To measure the average motion without an intervening stimulus, the trigger impulses were recorded, but the stimuli were disconnected from the summating amplifier (switch 2). A set of gates and time delays was used to avoid too frequent stimulus releases which could have led to habituation. Data from seven animals were analysed in this experiment.

(3) In this series, the point of stimulus release was a predetermined velocity of the joint motion. For this, the position signal was transformed to a velocity signal using an analogue differentiator adjusted to reproduce faithfully the velocities occurring in active leg movements, and a low-pass filter was used to cut off high-frequency noise (Fig. 1, switch 1 in position 2). A Schmitt trigger set to the desired velocity level was then used to release the stimulus (position value of trapezoidal shape; rise and fall time, 20 ms; amplitude, $100\,\mu m = 20°$ joint angle; plateau duration, 45 ms; velocity of rising and falling part, $1000°\,s^{-1}$). In these experiments the velocity of the tibia movement was obtained using an analogue differentiator. The results from seven animals were analysed.

(4) In this series of experiments the stimulus was again released at a predetermined level of velocity using the same triggering set-up as in series 3. However, here the stimulus consisted of inserting an analogue delay into the

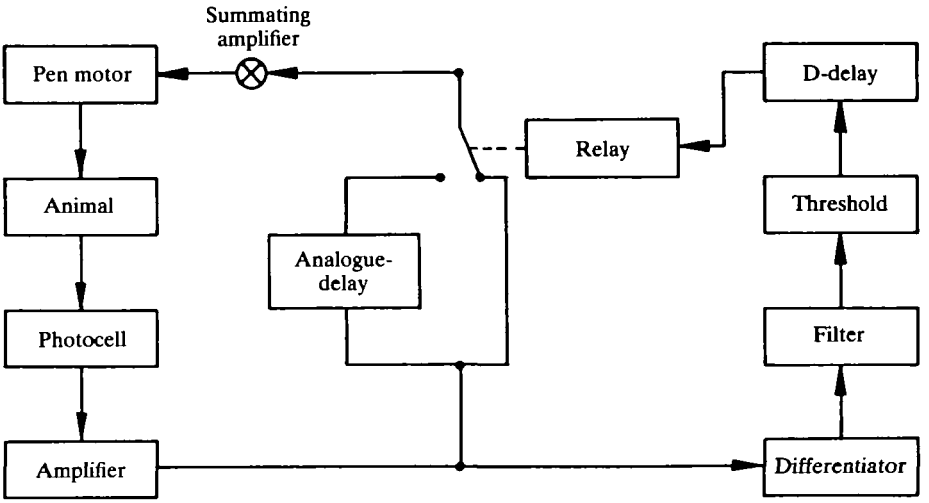

Fig. 2. Information flow of the closed-loop system with an additional delay in the pathway. Depending upon the setting of the relays either the delayed or the undelayed position signal is transmitted to the chordotonal organ.

feedback loop using a fast reed relay activated by the trigger circuit. The delay time was 200 ms. The results from two animals were analysed quantitatively (Fig. 2).

Data recording and evaluation

In addition to the position signal and stimulus waveform, the electrical activity of the extensor nerve F2 was recorded using 50 μm diameter steel wires inserted through small holes in the cuticle (Bässler & Storrer, 1980). In these nerve recordings, muscle potentials from the flexor muscle may be seen due to cross-talk. These potentials were normally larger than the potentials from the extensor motoneurones, but could be distinguished from the extensor nerve spikes by their longer duration. All data were stored on a tape recorder (Racal Store 4) and displayed on a chart recorder (Hellige He19 and Gould 220).

To evaluate series 2 and 3, the position signal shapes (in series 2) or the velocity signal shapes (in series 3) were averaged using a DEC-LSI 11 computer equipped with an A/D converter and a plotter output. Correct triggering of the averager passes was ensured using the onset of the stimulus ramp. To obtain a short part of the pre-stimulus movement, the position signal was fed through an analogue delay of 50 ms prior to A/D conversion. The averaged position and velocity signals were plotted on an x,y-plotter for each animal and also stored on disk files. The results from individual animals were later summed using a BASIC computer program. For the other experiments the data were evaluated quantitatively from the chart records. The electrical activity of the extensor nerve was evaluated using a storage oscilloscope (Minirec, Lutz Neumann) which had a pretrigger, so that the activity before the onset of the stimulus could also be evaluated. The impulses were either counted directly on the monitor or displayed on a chart recorder (Gould 220) and counted afterwards.

RESULTS

Experiments with ramp-and-hold stimuli

Before recording was started, active movements were elicited by touching the abdomen of the animal. After the onset of a ramp-and-hold stimulus clear changes in the movement trace could be observed: a stimulus which added a fictitious flexion shifted the movements to a more extended position and a stimulus which added a fictitious extension shifted the movements to a more flexed position than normal (Fig. 3). The shifting of the movement traces by the stimulus was limited by the maximal angles that the joint could actually attain (minimum: 20°, maximum: 175°). Therefore, the movement amplitudes appeared to be reduced in the stimulated situation. Due to the reduction in amplitude the shape of the movement was sometimes also affected (Fig. 3A).

To evaluate the effects of the stimulation quantitatively, the means of extreme values of the trace just before and after the stimulus onset were computed. The differences of these means represent the shift of the extreme position caused by the stimulation. The mean value of shifts determined in this way was 40·5° ± 16·4° for extension and 40·3° ± 16·4° for flexion stimuli, which corresponds very well to the stimulus amplitude of 40·0°.

Experiments with stimuli released at a fixed position

Stimuli resulting in an additional elongation of the chordotonal organ signal that the joint is more flexed than in reality. However, a stimulus resulting in an additional

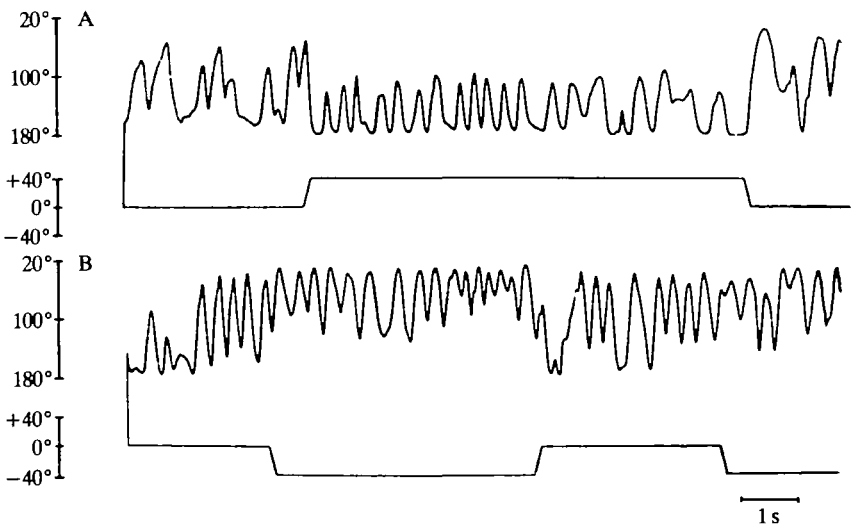

Fig. 3. Original records of active movements. Upper trace: tibia movement. The ordinate corresponds to the angle of the femur–tibia joint. Lower trace: stimulus. A value of +40° (A) stands for an elongation stimulus mimicking a decrease of the femur–tibia angle of 40°. Likewise a stimulus value of −40° (B) stands for a relaxation stimulus equivalent to an angle increase of 40°.

relaxation of the chordotonal organ signals a less flexed position than actually exists. Thus, one would expect from the previous results that elongation stimuli would reduce the extremes of flexion movements and enhance the extremes of extension movements. Likewise, relaxation stimuli should increase the extremes of flexion and reduce the extremes of extension movements. These effects were clearly confirmed by the results.

When stimuli were applied during flexion movements, the effects were less obvious in individual recordings (e.g. Fig. 4) but became clearer in the averaged position recordings (Fig. 5). The reactions to the stimuli were as expected: the amplitude of the movement was reduced with a stimulus signalling a more advanced position, and increased whenever a less advanced position was mimicked. In addition, the observed changes in the movement amplitudes were larger for longer stimulus durations (see Discussion).

The latencies between the onset of the stimulus and the beginning of the antagonistic movement were calculated from the averaged position signals of individual animals. For flexion movements, the latencies (mean ± S.D.) were 59·3 ± 12·7 ms after the start of chordotonal organ elongation and 127 ± 31·5 ms after the beginning of chordotonal organ relaxation (undisturbed animals 110 ms after passing the 90° position). For extension movements the latencies were 135 ± 35 ms after the start of elongation and 76·6 ± 14·5 ms after the beginning of relaxation of the chordotonal organ (undisturbed animals 111 ± 33·8 ms after passing the 110° position).

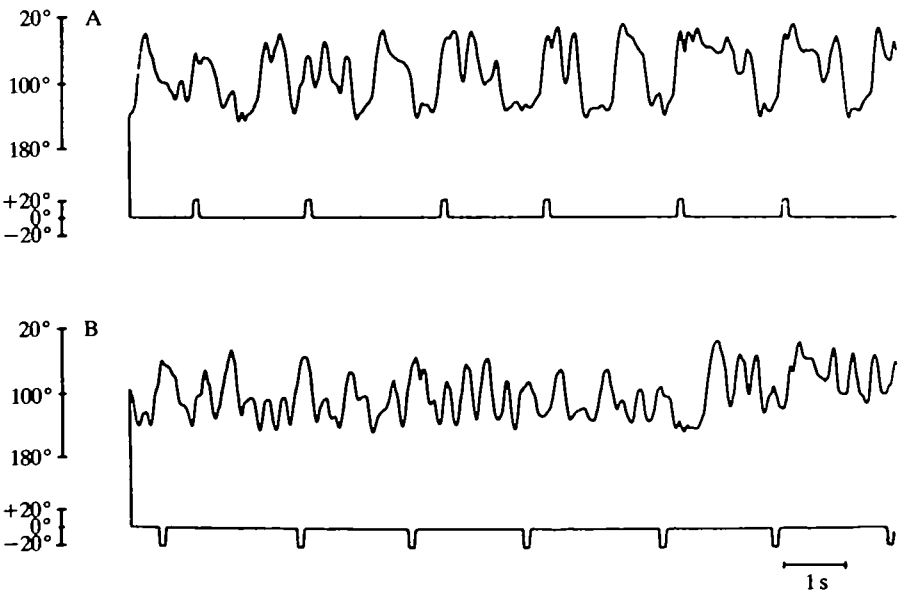

Fig. 4. Original movement recordings with elongation (A) and relaxation (B). Stimuli applied during a flexion movement at a predetermined position level. The trigger level was at 90° joint angle. The upper traces represent the movement, the lower traces the stimulus.

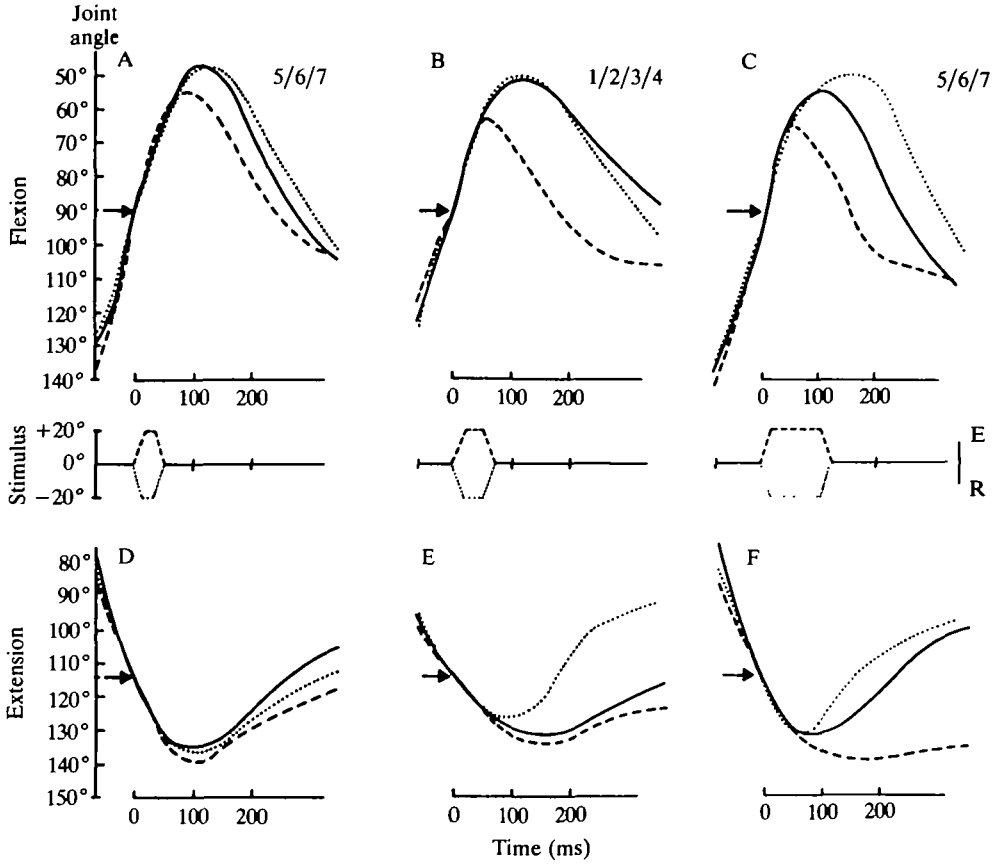

Fig. 5. Averaged position trajectories with additional stimuli released at 90° for flexion movements and at 115° for extension movements. The dashed lines show averaged position signals with elongation stimuli, the dotted lines those with relaxation stimuli applied. The solid lines represent movements without stimulus. Between 38 and 69 movement cycles were averaged. The arrows mark the onset of the stimulus. Seven animals were analysed quantitatively. Four of them (1, 2, 3, 4) were treated with medium stimulus durations, three of them (5, 6, 7) with short and long stimulus durations.

To test the statistical relevance of the different averaged movement curves, all flexion movements of one animal were plotted and the means and their standard deviations were calculated for a selection of points in time. The data for elongation stimuli were significantly different from the data for relaxation stimuli, as can be seen from the lack of overlap between the standard deviations (Fig. 6).

Activity in the extensor nerve was recorded during extension (Fig. 7A) and flexion (Fig. 7B) movements and stimuli of 130 ms duration were applied. The data were analysed by counting spikes between 45 ms before and 110 ms after the onset of the stimulus (this was the beginning of the falling slope of the stimulus). For evaluation of flexor motor activity (indicated by 2 in Fig. 7) only the large spikes, such as the first and the third in Fig. 7A and the last four in Fig. 7B were counted.

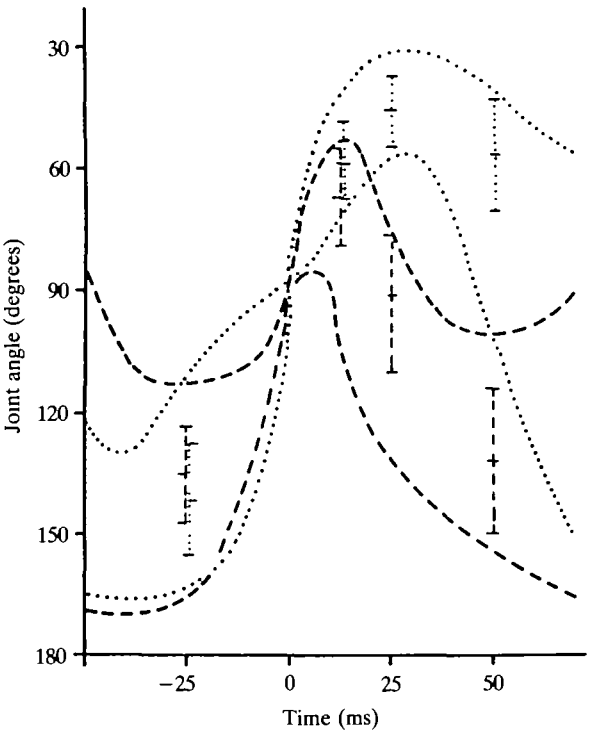

Fig. 6. Range of movement traces of all flexion movements of one animal. The dashed curves include all movement traces ($N = 12$) for elongation stimuli (duration 130 ms). The dotted curves include all movement traces ($N = 12$) for relaxation stimuli lasting 130 ms. At selected points the individual position values were averaged. The mean values and standard deviations are indicated. This demonstrates that the traces are significantly different in the two stimulus situations.

The results of the analyses are shown in Fig. 8. During *flexion* movements, an elongation stimulus (signalling an experimentally superimposed flexion) led to a strongly increased extensor activity. Relaxation stimuli (signalling a superimposed extension) produced no significant changes. During *extension* movements an additional elongation produced a small increase in extensor activity but the relaxation stimulus was only followed by a very small increase in flexor activity. These findings are in agreement with the results of the position recordings: stimuli working in the same direction as the existing movement (elongation stimuli for flexion movements and relaxation stimuli for extension movements) counteract the movement; stimuli working in the opposite direction prolong the movement but do not significantly accelerate it.

Experiments with stimuli released at a predetermined velocity level

Velocity stimuli ($1000°s^{-1}$) were released at $274°s^{-1}$. In, for example, a flexion movement, this means that an elongation stimulus mimicked a very strong increase in velocity, whereas a relaxation stimulus signalled not just a reduced flexion velocity,

but a velocity of opposite sign. Velocity recordings from seven animals were averaged.

During *flexion* (Fig. 9A), six of the seven animals reacted with a velocity decrease to an elongation stimulus (arrow) with a mean latency of 50–60 ms. A little more than 100 ms after the start of stimulation (about 40 ms after the stimulus began to decrease), the velocity increased again (with three exceptions). In comparison to the disturbed movements, the undisturbed movement trajectory is smoother (Fig. 9A).

When the stimulus began with a relaxation stimulus during flexion (Fig. 9A), the velocities increased (three exceptions) and became greater than those in the other experimental situations. Since the transitions were slow, it is impossible to define a latency for the onset in this case. During or just after the plateau phase and the falling slope of the stimulus, the velocity decreased in all cases, first slowly, then rapidly. The latency between the beginning of stimulation and the decrease of velocity was $45 \pm 7{\cdot}4$ ms. Afterwards the velocity increased again (one exception). Immediately

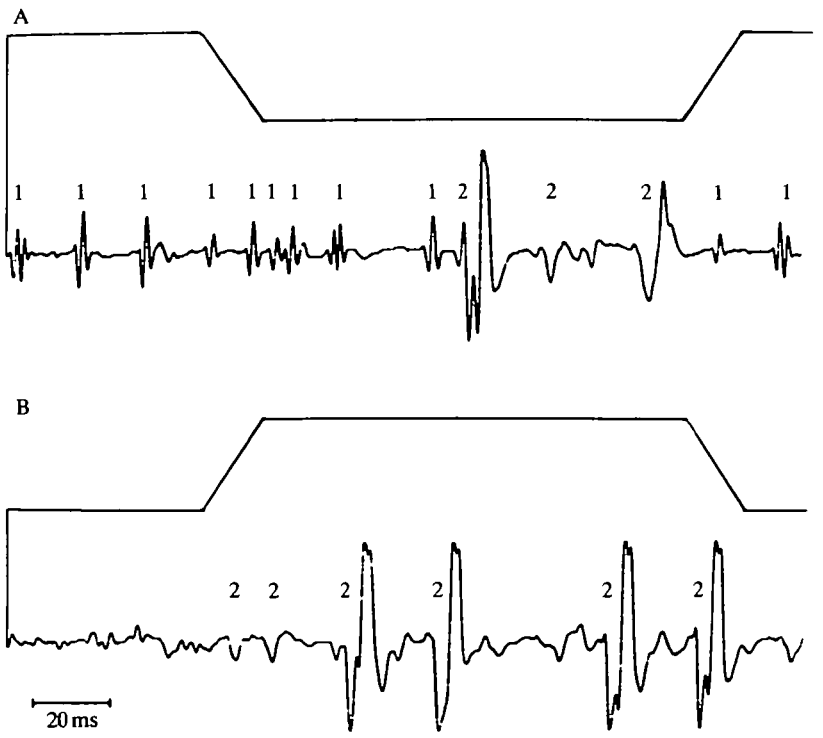

Fig. 7. Original recordings of the extensor nerve activity. Upper traces: stimulus. The lower traces show extensor motor activity of the slow and fast extensor tibia (1). We have not attempted to discriminate between slow (small) and fast (large) spikes. The potentials labelled with 2 result from muscle potentials from the flexor muscle which are also picked up by the recording electrodes. (A) An active extension movement with an additional relaxation stimulus; (B) an active flexion movement with an additional elongation stimulus. In B, no extensor activity can be observed because the flexion movement persists.

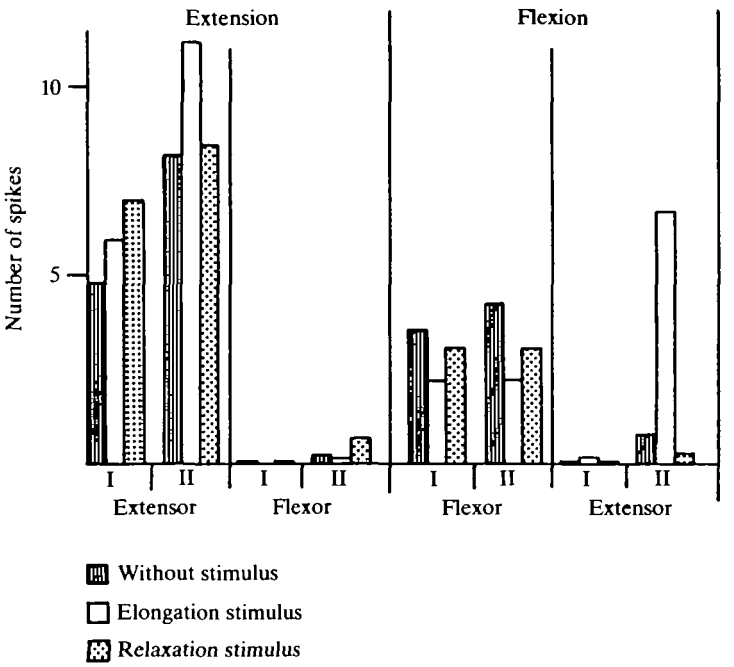

Fig. 8. Evaluation of the extensor nerve activity and flexor EMG for one animal. The absolute mean number of spikes was calculated for the last 45 ms before the onset of the stimulus (I) and during stimulation (II, from the beginning of the stimulus to the falling edge, 110 ms).

after the onset of an elongation or a relaxation stimulus, the velocity of the flexion movement increased. It is highly probable that this reaction is elicited by acceleration-sensitive units in the chordotonal organ (Hofmann & Koch, 1985) (see Discussion).

For *extension* movements (Fig. 9B) a decrease of velocity was found approximately 50 ms after the stimulus onset when relaxation stimuli were applied (one exception). In some cases there was again an increase of velocity after the trailing edge of the stimulus. For elongation stimuli (Fig. 9B), there was an increase of velocity after the stimulus (two exceptions). In most cases, the absolute velocity that was reached was higher than in the other experimental conditions. This can also be seen in the weighted mean of all animals.

In all investigated animals, the reactions were rather weak, especially during extension movements, but it can be seen that stimuli signalling an increase of velocity were followed by a decrease of velocity and stimuli signalling a decrease of velocity caused an increase of velocity. The latencies between the onset of the stimulus and the reaction were around 50 ms. Evaluation of the extensor nerve activity showed no significant differences between disturbed and undisturbed movements (Fig. 10). During flexion movements a small increase of extensor activity could be seen after elongation of the chordotonal organ.

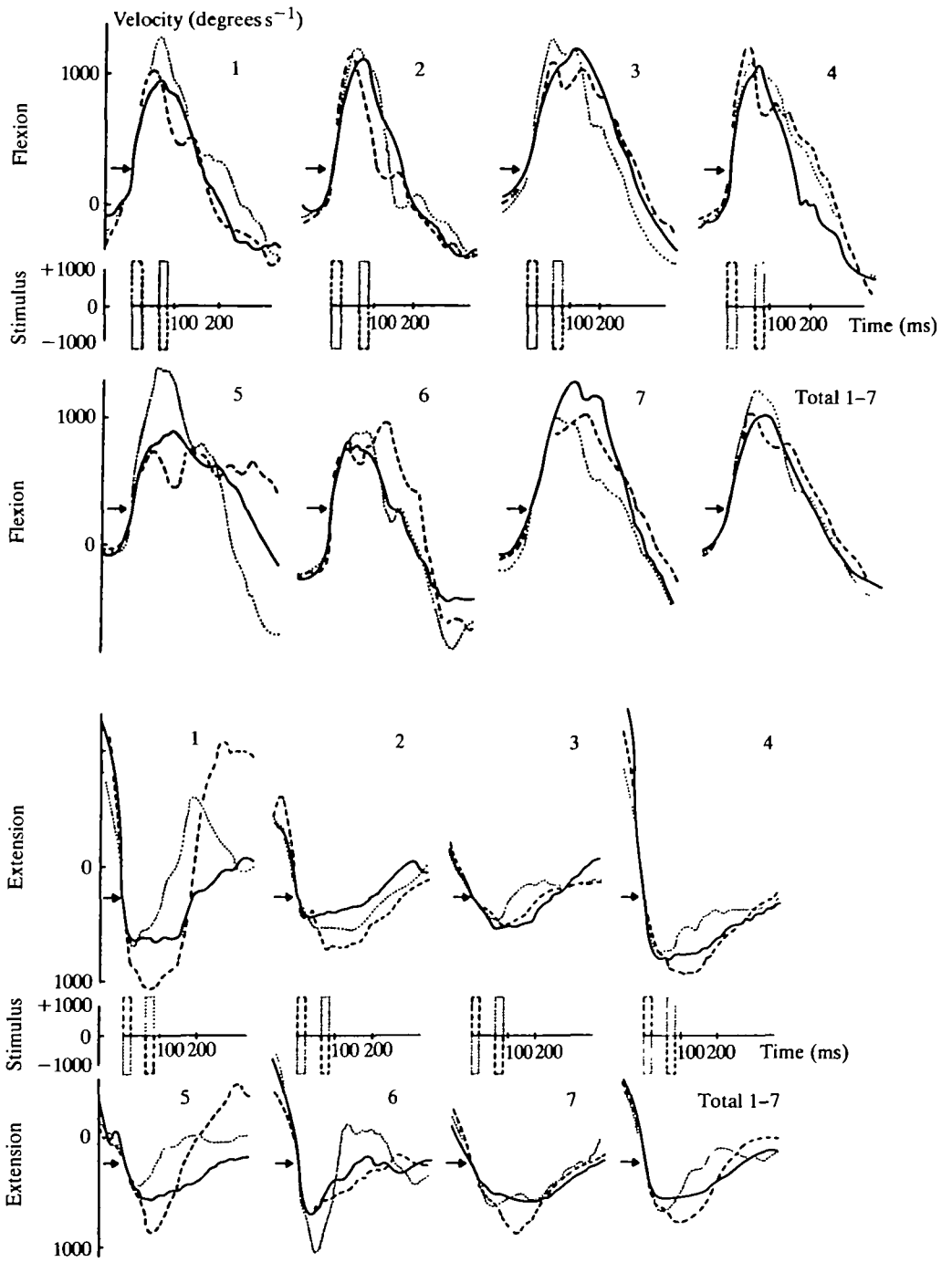

Fig. 9. (A,B) Averaged velocity traces for flexion (A) and extension (B) movements for seven animals. Movements without stimulus are represented by the solid lines, those with an elongation stimulus by the dashed lines and those with a relaxation stimulus by the dotted lines. The arrows mark the onset of the stimulus.

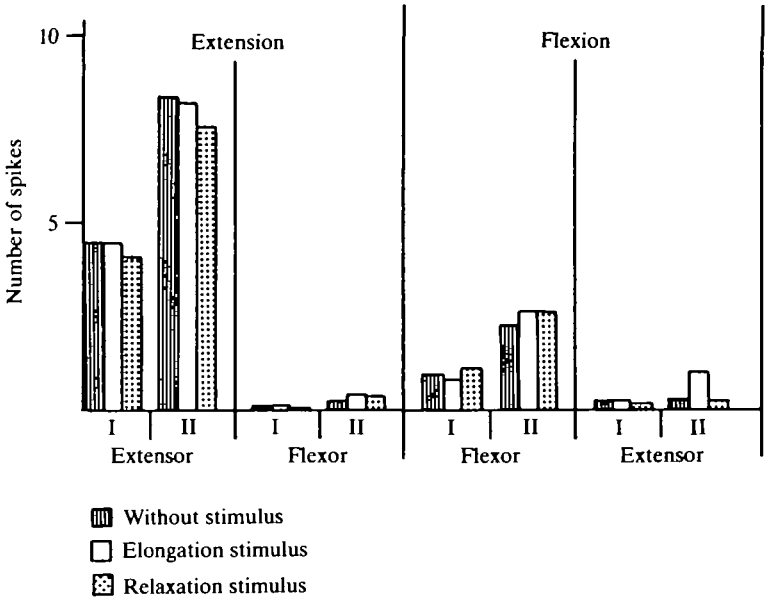

Fig. 10. Evaluation of extensor nerve activity for one animal when stimuli were released at a predetermined velocity level. The absolute number of spikes was calculated 45 ms before the onset of the stimulus (I, 45 ms) and during stimulation (II, from the beginning of the stimulus to its falling edge, 65 ms).

Experiments with an additional delay in the feedback loop during active movements

An analogue delay introduced into the feedback loop in the inactive animal has been found to cause oscillations of the control system (Weiland *et al.* 1986) provided that in the feedback loop the gain is greater than one and the total phase shift is larger than 180° in the open-loop system. The delay values necessary to achieve oscillation range from 70 to 200 ms.

When, during active movements, a delay of 200 ms was introduced into the feedback loop, the active movements became more regular and their amplitude increased (Fig. 11). The frequency of flexion and extension movements with delayed feedback was about 1 Hz, whereas normal movements varied in amplitude and frequency from cycle to cycle. The amplitudes of normal active movements were between 40° and 90°. Insertion of the delay increased this amplitude to values between 90° and 130°.

DISCUSSION

The results of the experiments indicate that the second hypothesis described in the Introduction is most likely to be correct.

First, ramp-and-hold stimuli applied during active movements shift the whole range of movement towards flexion or extension, depending on the direction of the stimulus. A stimulus which elongates the chordotonal organ tonically, signals a more

flexed position. This results in a shift to a more extended position. A stimulus signalling a more extended position shifts the movement range towards flexion. The amount of shift corresponds to the amplitude of the applied stimulus. These results can be a consequence either of a general position control or of a control of the end points.

Second, the results of the stimuli released at a predetermined position can be explained in detail by the following assumption. Whenever the position-sensitive units of the chordotonal organ signal a critical position value (on average approximately 133° for extension and 55° for flexion) the antagonistic muscles are activated. After a certain latency the existing movement is terminated and movement starts in the opposite direction. Since there is some latency, the actual end point is beyond the critical position values. We have labelled the whole process 'end point behaviour'. The critical position (= threshold position) thus triggers the end point behaviour. When the stimulus is superimposed on the undisturbed flexion movement trace, one finds for a stimulus signalling a more flexed position that the threshold position is reached earlier than in the unstimulated case for all stimulus durations (Fig. 12A–C, dashed traces). Thus the end point behaviour is triggered earlier in all cases as found in the experimental results (Fig. 5A–C).

During stimuli signalling a more extended position (dotted lines), however, the point at which the threshold position is reached is only delayed when the stimulus duration is long. For shorter stimuli, the average undisturbed (control) movement has not reached the threshold after the decay of the stimulus (Fig. 12A,B) and thus the stimulation has no effect. In Fig. 12C, however, the stimulus signalling a more extended position is maintained beyond the time usually taken to reach the threshold. Now the end point behaviour occurs at a more flexed position (40°) and is delayed compared with the control curve, as found experimentally (Fig. 5C, dotted trace).

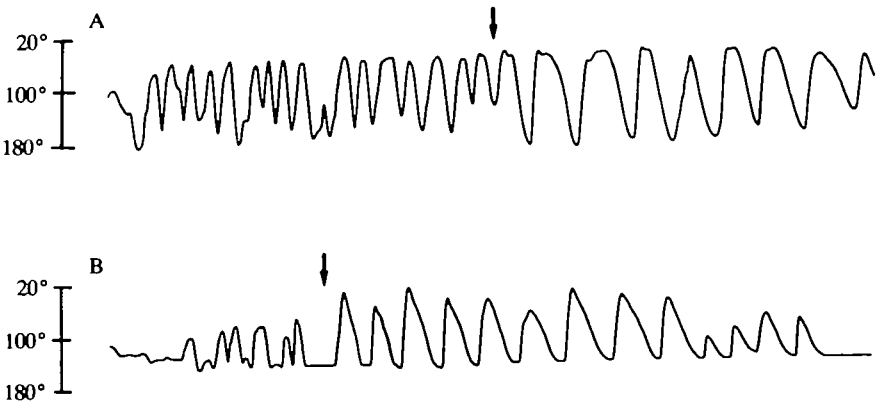

Fig. 11. (A,B) Two original recordings of a movement when an additional delay was inserted in the feedback path during an active movement. The arrow marks the time of delay insertion.

The reactions during extension can be explained in the same way. There are three main differences from flexion movements. (1) The position where the stimulus is released is closer to the natural end point than with flexion movements. (2) With extension movements the curve is flatter and therefore does not extend far towards the threshold position. (3) The reaction is somewhat weaker.

For stimuli signalling a less extended position (Fig. 12D–F, dashed traces), a delay in reaching the threshold should be expected. For short stimuli (Fig. 12D,E), however, the stimulus has decayed before the threshold is reached, explaining why no reaction is seen in Fig. 5D,E (dashed lines). For the longest stimulus duration (Fig. 12F), there is a significant delay in crossing the threshold and the end point behaviour is delayed accordingly (cf. Fig. 5F, dashed line). In the case of stimuli signalling a more extended position, threshold crossing should occur earlier by the same amount for all three stimulus durations (Fig. 12D–F, dotted traces). Thus, one would expect the end point behaviour to occur earlier in all these cases. While the experimental results show no clear reaction to the short stimulus (Fig. 5D, dotted traces), reactions to the longer stimuli show that the end point behaviour occurs earlier than in the unstimulated case, as expected (cf. Figs 12E,F, 5E,F).

The scheme of the end point behaviour being released at a position threshold is also able to explain the results of the active animal with an additional delay in the feedback loop. Since the position signal is delayed compared to the normal case, the

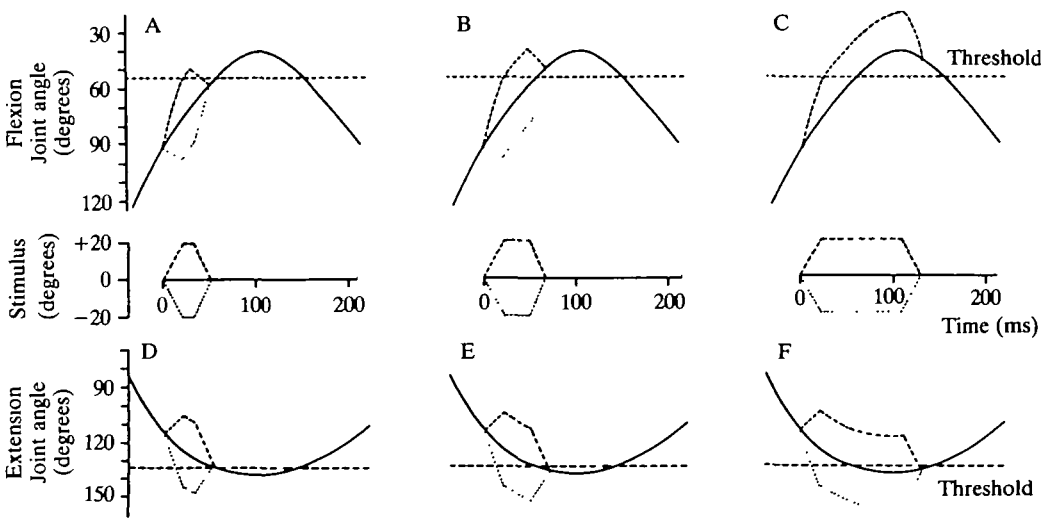

Fig. 12. Schematic diagram of joint angle movement traces during flexion (A–C) and extension (D–F). The solid lines represent the undisturbed movement traces. The time course of the different stimuli is plotted. When the stimulus is introduced into the control loop, the joint angle as perceived by the chordotonal organ differs from the actual movement trace. For stimuli simulating an additional flexion, this deviation is indicated by a dashed line, while stimuli simulating additional extension cause a deviation along the dotted line. As a consequence of the stimulation, the thresholds for end point behaviour are crossed at times different from the unstimulated case, provided that the stimulus has not decayed before the threshold is reached. These shifts in threshold crossing times provide detailed explanations of the movement trace alterations as measured in Fig. 5.

threshold-crossing signal triggers the end point behaviour at a later time. As in the other experiments, this leads to an increased movement amplitude.

Our results agree with the observation that position information is a decisive parameter in ending a stance phase (Cruse, 1985*b*). Experiments on decerebrate *Cuniculina* in the active state show similar results (Bässler, 1986). A ramp-wise stretching of the chordotonal organ with high amplitude and low velocity elicits the so-called 'active reaction'. In its first part, the flexor motoneurones are activated and the extensor motoneurones are inhibited. This reaction corresponds to a positive feedback mechanism. In the second part of the reaction, the activity of the stance phase muscles (flexor tibiae) declines and the swing phase muscles (extensor tibiae) become active. The transition between the first and second parts of the reaction always occurs at a similar level of the ramp. The second part of the reaction corresponds to the position-sensitive end point behaviour found in our experiments. If a predetermined position is reached, a transition from flexion to extension takes place. Although the animal was restrained in our experiments and was performing struggling movements with its freely movable tibia, it seems that use was made of the same motor programme (or parts of it) that is normally used during walking to trigger the transition between stance and swing phase.

Lastly, if position was controlled over the whole trajectory of a movement the trajectories of movements with and without stimulation should rejoin after the end of the stimulus. As a consequence, the movements must be halted or accelerated, depending on the direction of the stimulus, until the movement follows the predetermined trajectory again. The results of Fig. 9 show a different behaviour. The movement follows a new trajectory after the end of the stimulus (the plane below the velocity curves is different for the three conditions). This indicates that the trajectory of a movement is not centrally preprogrammed.

The results of the velocity measurements during flexion movements can be explained by the following assumptions.

(1) The onset of the stimulus releases a reaction with short latency (about 20 ms) serving to enhance the existing movement, regardless of the stimulus direction. This reaction is likely to be mediated by the bidirectional acceleration receptors found in the chordotonal organ of *Cuniculina impigra* by Hofmann & Koch (1985). Intracellular recordings of the extensor and flexor motoneurones in resting animals show a rapid activation of extensor motoneurones and inhibition of flexor motoneurones as a result of stimulation of the acceleration receptors (Bässler, Hofmann & Schuch, 1986).

(2) This short-latency reaction does not appear to any great extent at the end of the stimulus, although acceleration is present at the same level. This we attribute to a refractory effect in the receptors. Successive stimulation in such short intervals was not investigated in the study of Hofmann & Koch (1985), thus such an effect may exist. In the resting animal only the acceleration at the start of a relaxation stimulus had an effect, not the acceleration at its end (Bässler *et al.* 1986).

(3) The velocity stimuli release a corrective 'regulating' reaction with a longer latency (50 ms) which is always directed to reduce the changes in velocity imposed

onto the system. The regulating efficiency is modest: it amounts to an amplification factor between 0·25 and 0·3 (stimulus velocity, $1000°s^{-1}$; range of the compensatory velocity change, $250–350°s^{-1}$).

If these three reaction patterns are added to the velocity trace of the undisturbed movement, the shape of the observed velocity traces (averaged over all experiments) can be reproduced quite clearly (Fig. 13).

In the averaged results of individual experiments with flexion movements (Fig. 9A) some of the assumed effects are enhanced, others are diminished. Thus the sharp peaks produced by animal 3 (dashed and dotted curves) show the fast reaction very clearly. One can also observe the marked depression of the dashed curve at about 100 ms after stimulus onset in all seven records.

About 100 ms after the termination of the disturbing stimulus, the velocity returns to the value of the unstimulated situation, or at least follows the general shape of the

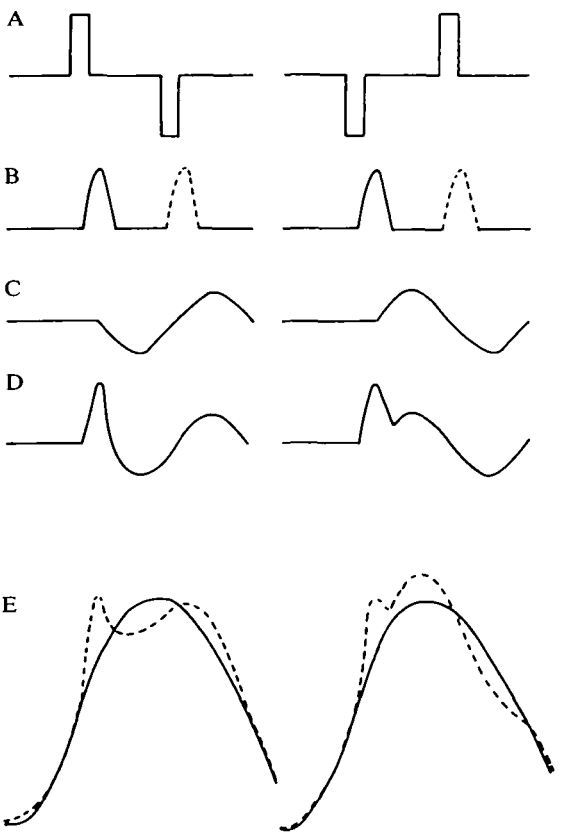

Fig. 13. Schematic drawing of the expected velocity reactions when a stimulus is released at a predetermined velocity level. (A) Stimulus. (B) Reaction of acceleration units to a stimulus. The second part does not occur because of refractoriness. (C) Reaction of velocity-sensitive units to a stimulus. (D) Reaction of velocity- and acceleration-sensitive units. (E) Velocity trace for an undisturbed flexion movement (solid lines) and with stimuli applied (dashed lines).

velocity trace again. Thus, we can say that velocity is a controlled parameter during the whole flexion movement.

For extension movements, the reactions can be explained in the same way. First, there is a short-latency reaction (about 20 ms) which increases the velocity regardless of stimulus direction. Again, we attribute this effect to the reaction of acceleration-sensitive units in the chordotonal organ. Then, with a latency of about 50 ms, there is the onset of the velocity-dependent reaction, which depends on the direction of the stimulus, and is directed to compensate for the imposed velocity changes. While the reactions are clear for the first part of the stimulus, the reactions to the trailing edge deviate somewhat from the anticipated scheme. The reaction to extension stimuli (dotted curve), particularly, shows smaller velocity values than expected near the end of the reaction.

Our results are supported by findings that, for ramp-wise stretching of the chordotonal organ, the first part of the active reaction is velocity-dependent (U. Bässler, unpublished observation). Whenever stimuli with high velocity were used, reactions similar to the resistance reflex in undisturbed animals occurred. This means that if the velocity is too high, a negative feedback mechanism is used to decelerate the movement. However, if the velocity is too low, a positive feedback mechanism occurs to accelerate the movement.

Our results are also in agreement with those of Cruse (1985*a*) who postulated a velocity-servo-control during the stance phase. In his experiments, performed on stick insects walking on a treadwheel, the motor output of the investigated leg standing on a movable platform increased if the actual velocity of this leg became zero. Otherwise, the motor output decreased if the actual velocity of this leg increased.

To summarize, a velocity control system is active during the voluntary movements of *Carausius morosus*. Furthermore, a position control exists for the end points of movements (transition between, for example, stance and swing phase). To accomplish this, sensory signals must influence the timing of the motor output. Thus proprioceptive information can influence a central pattern generator. Therefore, a central pattern generator cannot be conceived as operating in a fixed pattern mode, but it must be modifiable by afferences and its mode must be varied depending on the behavioural context of the animal. Dean (1984) and Dean & Cruse (1986) showed that the same principles are also active during the swing phase. The position information is used to determine the end point of the swing phase whereas the velocity is controlled during the movement.

The results are also in agreement with results from vertebrates, which have demonstrated that signals from sensory systems influence the motor pattern (Grillner, 1985). This versatile reflex action was also shown by Lennard & Hermanson (1985), who concluded that a temporal reflex organization exists. Experiments performed on cats have shown that phase-dependent proprioceptive modulation is used to refine the locomotor activity and to determine the timing in a rhythmic locomotory pattern.

Thus, a similar concept of temporal reflex organization in the stick insect would be able to explain a large number of experimental results found by different investigators.

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