

## A BIOLOGICAL FEEDBACK CONTROL SYSTEM WITH ELECTRONIC INPUT: THE ARTIFICIALLY CLOSED FEMUR–TIBIA CONTROL SYSTEM OF STICK INSECTS

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### SUMMARY

An experimental arrangement was constructed which is based on the open-loop femur–tibia control system of two stick insect species (*Carausius morosus* and *Cuniculina impigra*). It could be artificially closed in the following way: the position of the tibia was measured by an optical device and this value was used to drive a pen-motor which moved the receptor apodeme of the femoral chordotonal organ in the same way as in intact animals. This arrangement allows direct comparison of the behaviour of the open-loop and the closed-loop system as well as introducing an additional delay.

The *Carausius* system has a phase reserve of only 30°–50° and the factor of feedback control approaches 1 between 1 and 2 Hz. This agrees with the observation that an additional delay of 70–200 ms produces long-lasting oscillations of 1–2 Hz. The *Cuniculina* system has a larger phase reserve and consequently a delay of 200 ms produced no oscillations. All experiments show that extrapolation from the open-loop system to the closed-loop system is valid, despite the non-linear characteristics of the loop. Consequences for servo-mechanisms during walking and rocking movements are discussed.

### INTRODUCTION

In vertebrates and arthropods the positions of many limb joints are controlled by feedback systems. Such a feedback system stabilizes the joint against external forces acting on the limb. But there are also other mechanisms (muscle elasticity, friction etc.) which contribute to the resistance against external disturbances. Therefore, if one moves a joint passively and measures the forces resisting this movement, it is not possible quantitatively to attribute a certain part of this force to the resistance reflex produced by the feedback system and the rest to the mechanical impedance of muscles and joint or perhaps to other feedback mechanisms acting on the same joint (for discussion of this problem see Stein, 1982).

To study the characteristics of a certain feedback system independently of other mechanisms, the sense organ responsible for the feedback must be stimulated mechanically (e.g. by a length change) in the open-loop configuration and the reaction of

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the musculature must have the same unit of measurement as the stimulus (in this case also a length change). Only then is it possible to calculate the gain of the loop as output amplitude/input amplitude. When the characteristics of the input–output relationships are known (especially gain and phase shift between stimulus and response) and the system is linear, the characteristics of the closed-loop system can be calculated. The comparison of these characteristics with the properties of the whole joint allows one to attribute certain features of the joint resistance against external forces to characteristics of the feedback system (for details of this procedure see Bässler, 1983*b*; Stein, 1982).

If it is not possible to stimulate the sense organ definitely without interfering with the musculature (as in the vertebrate stretch reflex) calculations of the characteristics of the closed-loop system are only possible as very rough approximations. In the stick insect and some other orthopteroids it is possible to measure the input–output relationships of the open-loop feedback system which stabilizes the femur–tibia joint (for a summary see Bässler, 1983*b*). The sense organ of this loop is the femoral chordotonal organ. It lies outside the musculature and can therefore be stimulated without interfering with the musculature. To measure the input–output relationships of the open-loop system, the receptor apodeme of the chordotonal organ was cut and then moved in a defined way (stimulus). As reaction, the movement of the tibia was measured. From the attributes of the open-loop system, the characteristics of the closed-loop system were calculated using linear systems theory as a theoretical approach. But this system is non-linear and therefore these calculations can only be used as a first approximation. It is especially not possible to obtain exact data about the stability of the system. This would be very important because it has been suggested that resonance properties of this system contribute to the generation of rocking movements (Bässler, 1983*b*). If it is not possible quantitatively to calculate the characteristics of the closed-loop system, they have to be measured.

To be able to measure the characteristics of the closed-loop system and compare them with those of the open-loop system we constructed an experimental arrangement which is based on the open-loop system but which can be artificially closed. It allows direct comparison of the open-loop and the closed-loop systems in the same animal, specific alterations in gain and latency, disturbance of the closed-loop system by an extra electronic input and alteration of the sign of the feedback. With this system it is possible, for the first time, to study a closed-loop joint feedback system in isolation. And, with this system, it is also possible to investigate the role of feedback loops during active movements.

This first paper describes the experimental arrangement, compares the reaction of the open-loop and the closed-loop systems against external disturbances and investigates the stability of the system. The behaviour of the system during active movements will be described later.

The femur–tibia control system of stick insects consists of the following parts (Fig. 1). The femoral chordotonal organ contains approximately 500 sense cells (Füller & Ernst, 1973). There are position-, velocity- and acceleration-sensitive cells, and cells which respond to a combination of two of these parameters (Hofmann,

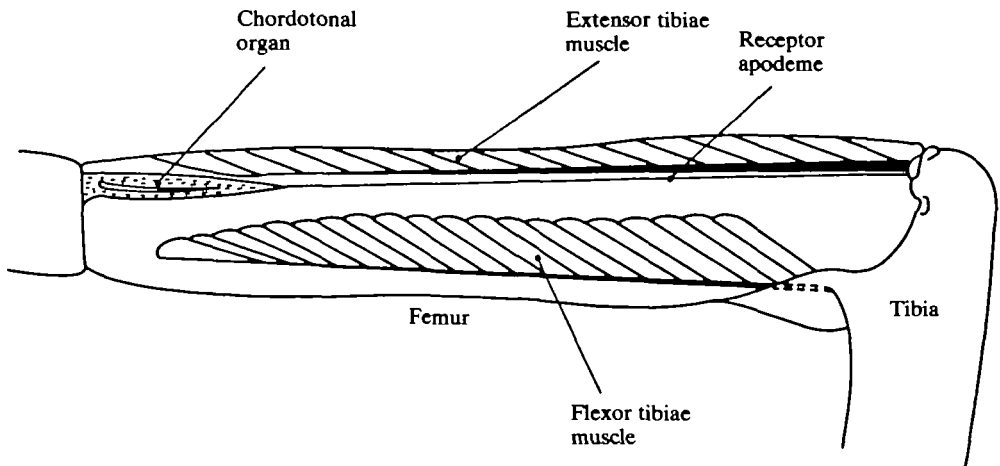


Fig. 1. Schematic presentation of the femur of a stick insect. Only those structures which are involved in the femur–tibia control system are drawn. Note that the femur length is reduced to improve the clarity of the drawing.

Koch & Bässler, 1985; Hofmann & Koch, 1985). Joint flexion elongates the organ and extension releases it. An unknown number of interneurons transfer this information to the motor neurones. There are two excitatory (fast and slow extensor tibiae motor neurones, FETi and SETi) and one inhibitory (common inhibitor, CI) motor neurone travelling to the extensor tibiae muscle (Bässler & Storrer, 1980) and at least 12 excitatory and two inhibitory motor neurones travelling to the flexor tibiae muscle (B. Debrod, in preparation), the two muscles which move the joint.

The experiments were performed on two species, *Carausius morosus* and *Cuniculina impigra*. As the open-loop systems in these two species differ in their upper corner frequency (Bässler, Cruse & Pflüger, 1974; Bässler & Foth, 1982) we expected that the stability properties of the closed-loop systems would also show differences.

#### MATERIALS AND METHODS

The experimental animals were adult females of *Carausius morosus* Brunner and *Cuniculina impigra* Redtenbacher (syn. *Baculum impigrum* Brunner) from the colonies at Kaiserslautern University.

The body was restrained in a vertical position (Fig. 2). One leg (for *Carausius* the left hind leg and for *Cuniculina* the left middle leg) was fixed at coxa and femur in such a way that the femur was horizontal and the tibia moved in a horizontal plane. The position of the tibia was measured using a horizontal piece of black paper glued to one side of the tibia. The paper covered a semicircular slot below the tibia (centre just below the axis of rotation of the joint) in such a way that at a femur–tibia angle of  $180^\circ$  the slot was completely open. Above the leg was a lamp, below the leg a lens and a photocell (for details see Bässler & Foth, 1982).

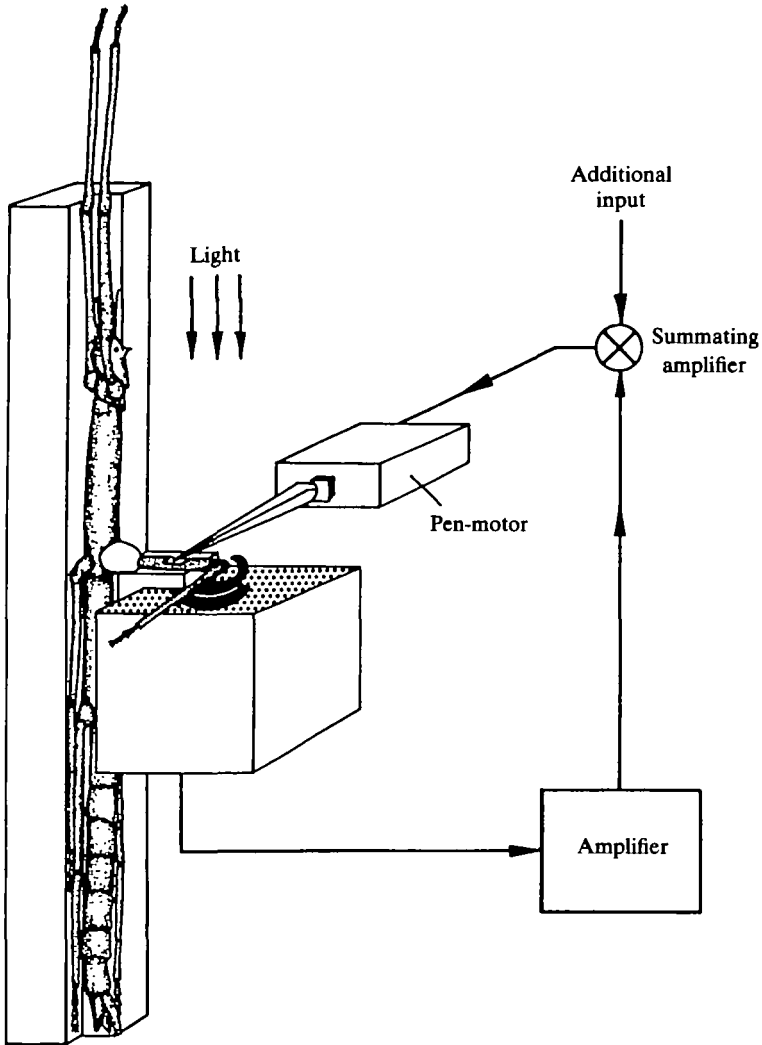


Fig. 2. Diagram of the experimental set-up. The box below the leg contains lens and photocell. The amplifier is a current-to-voltage amplifier. The power amplifier which drives the pen-motor is not drawn.

The output current of the photocell which was strictly proportional to the incident light intensity was fed into a current-to-voltage amplifier yielding a precise position signal. This in turn was used to drive a pen-motor (Hellige, upper corner frequency 100 Hz) which moved a clamp. This clamp held the receptor apodeme of the femoral chordotonal organ which was cut distal to the clamp (for details see Bässler & Foth, 1982). To mimic natural conditions the relationship between femur-tibia angle and receptor apodeme position as imposed by the pen-motor should be the same as in intact animals. Therefore, the position of the receptor apodeme was measured as a function of the femur-tibia angle in five intact animals of each species (Fig. 3). The gain of the amplifier between photocell and pen-motor was then adjusted to these

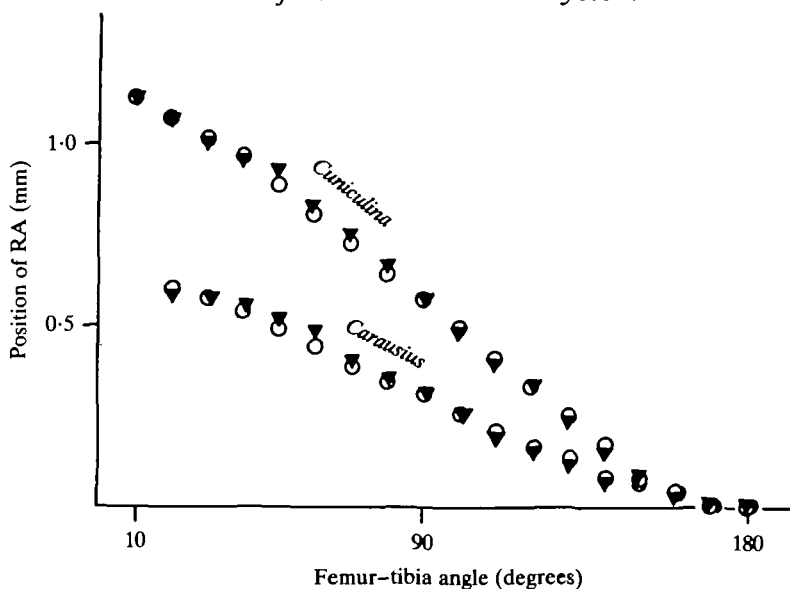


Fig. 3. The position of the receptor apodeme (RA) in intact animals (mean of five animals, triangles) and the position of the clamp attached to the pen-motor (circles) as a function of the femur-tibia angle.

values and the two ends of the semicircular slot were narrowed to produce a sigmoidal response curve modelling the non-linear relationship between femur-tibia angle and receptor apodeme position. This allowed a movement of the receptor apodeme in the artificially closed system which closely corresponded to that in the intact leg (Fig. 3).

A summing amplifier was inserted in the signal path between amplifier and pen-motor. It served to accommodate additional inputs. Between amplifier and summing amplifier there was a switch. When it was closed the pen-motor was driven by the sum of the amplified output of the photocell and the additional input (closed-loop condition, Fig. 4A). When the switch was open the pen-motor was only driven by the additional input (open-loop condition, Fig. 4B).

To examine the effects of an additional delay in the feedback signal path, a device was needed capable of delaying an analogue signal by about 100 ms. As the femur-tibia control loop has a strong tonic component, the device had to be capable of transmitting d.c. voltage. The delay was designed around a bucket brigade delay line (Reticon R5106). This is an integrated circuit containing an array of 512 capacitors alternating with FET transistor switches. At each clock pulse, the analogue voltage is transferred to the next capacitor in the array. These integrated circuits had been developed for use with a.c. audio signals, and the manufacturer only gives circuit proposals for a.c. operation. In order to permit d.c. transmission, a number of changes had to be made in the circuit. First, the input signal (between +2 V and -2 V) was shifted by +7.5 V using an analogue adding circuit. After passage through the delay line, the signal was shifted by -7.5 V back to the level of the input signal. Changing the setting of the delay value (50-200 ms was achieved) caused a small

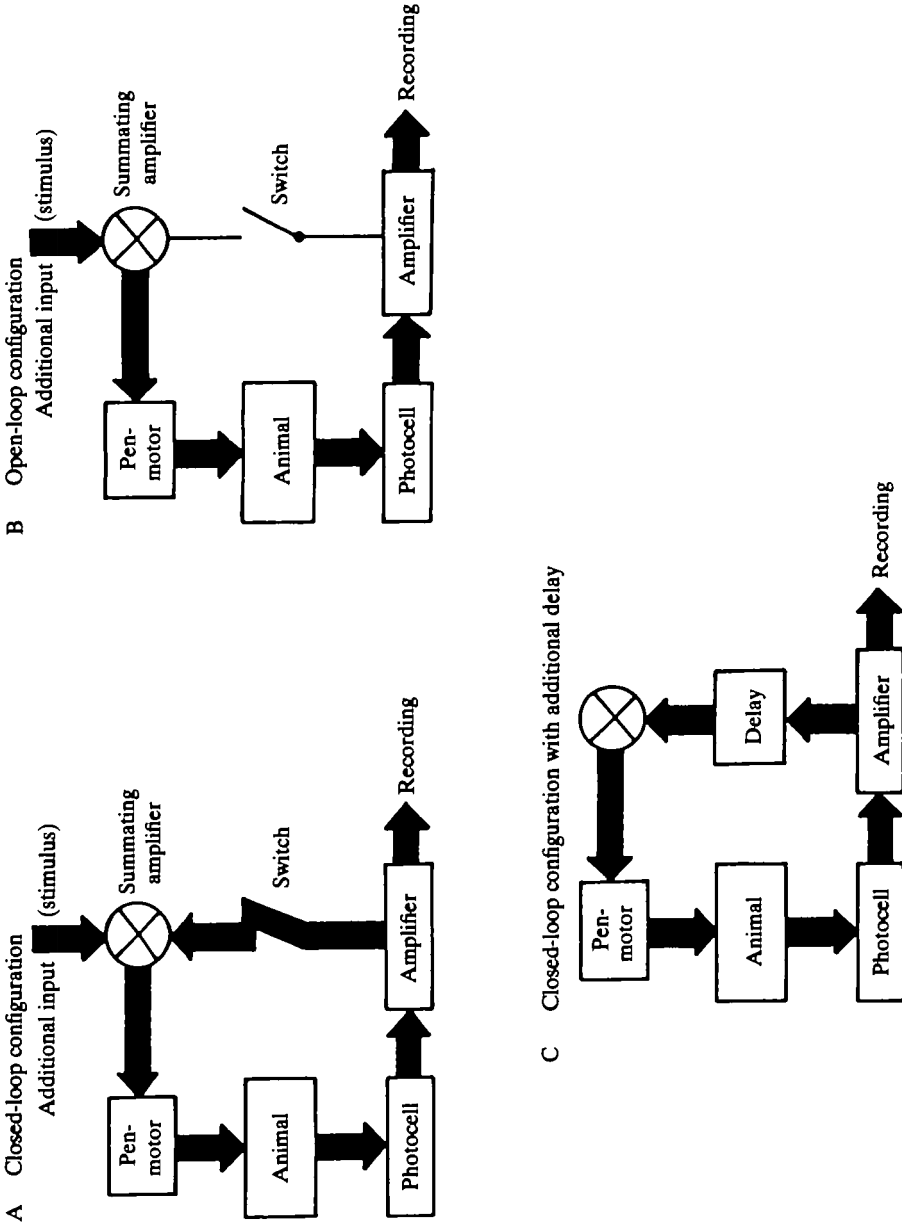


Fig. 4. Information flow in the closed-loop (A) and the open-loop configuration (B) (thick lines) as well as in the closed-loop configuration with additional delay (C).

additional offset of the signal. This was compensated by a finely controllable offset voltage which was set to the appropriate values for each setting of the delay. Finally, the attenuation (approx. 3 dB) inherent in the delay line was compensated by a suitable post-amplifier. As in all bucket brigade delay systems, the ripple resulting from the clock pulses must be removed from the output. A four-stage R-C filter with a corner frequency of 100 Hz was used for this purpose.

The delay was used in the closed-loop configuration between amplifier and summing amplifier (Fig. 4C).

In most experiments the activities of FETi and SETi were recorded as described by Bässler & Storrer (1980) using 50  $\mu\text{m}$  steel wires inserted through small holes in the cuticle. The cross-talk from flexor myograms is relatively large with freely moving tibia but the nerve spikes from FETi and SETi can clearly be distinguished from the much longer myogram potentials.

The data were stored on tape (Racal Store-4) and displayed on a Hellige He 19 pen-recorder. To evaluate amplitude and phase-shift, the chart records were analysed using a Houston Instruments digitizer connected to an LSI 11-03 microcomputer (Plessey). Evaluation programmes were written in BASIC. Since the amplitude of the reaction becomes smaller from cycle to cycle during continuous stimulation (Kittmann, 1981) the same number of stimulus cycles were always evaluated. For stimulus frequency 0.005 Hz cycles 2-4 were evaluated, for stimulus frequency 0.01 Hz cycles 2-5 were evaluated, otherwise cycles 2-11 were evaluated. Phase shifts were measured as the relative time interval between stimulus maximum and start of flexion of the tibia as well as relative time interval between stimulus minimum and start of tibial extension.

In all cases the animals were inactive (for definition see Bässler, 1983b), i.e. only the stimulated leg moved.

## RESULTS

### *Tibia movement of Carausius*

The gain of the feedback loop can vary considerably for the same animal. It is high after the animal has been disturbed and declines gradually when the animal is left undisturbed (for summary see Bässler, 1983b). To obtain values for low as well as for high gain two different series of experiments were performed, the first one for low gain and the second one for high gain.

Four animals were used in the first series. After an animal had been fixed in the apparatus it was left undisturbed for 15 min. The apparatus was in the open-loop configuration (Fig. 4B) and the receptor apodeme was in a position corresponding to a 90° position of the femur-tibia joint. A sinusoidal input (stimulus) producing a movement amplitude of the receptor apodeme of 100  $\mu\text{m}$  was introduced as additional input to the summing amplifier (Figs 2, 4). The frequency of the input was between 0.005 and 2.5 Hz. The mean of this input was zero, i.e. the input corresponded to a movement of the joint of  $\pm 10^\circ$  around 90° (in the open-loop configuration). A resting period of 4 min was inserted between stimulus presentations.

Each stimulus frequency was first tested in this open-loop configuration (no connection between amplifier and pen-motor). Then the switch was closed (closed-loop configuration) and the same stimulus frequency was presented again. The sequence of stimulation frequencies was different for different animals.

The form of the tibia movement for both configurations resembled that given by Bässler (1972) and Bässler *et al.* (1974). From the records the amplitude of tibia movement and the phase shift between stimulus and tibia movement was evaluated. The mean amplitudes of tibia movement are much smaller in the closed-loop configuration, especially at lower frequencies (Fig. 5). They always remain below the gain-1 line. Gain 1 means that input and output amplitude are identical. In the intact leg, a 100- $\mu\text{m}$  receptor apodeme displacement corresponds to a joint angle change of  $20^\circ$  in the large, middle part of the operating range (Fig. 3). Thus, gain 1 corresponds to a tibia amplitude of  $20^\circ$ . At higher frequencies the amplitude of tibia movement became equal for both configurations.

The phase shifts for both configurations lie within the range given in Bässler *et al.* (1974) for the open-loop system and are therefore not shown here (but see Fig. 6B).

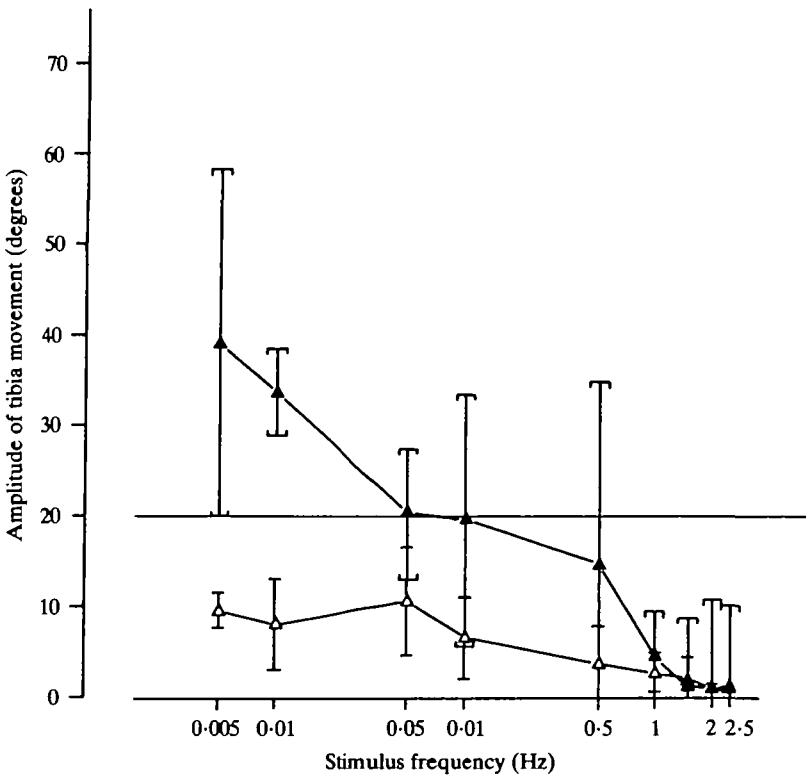


Fig. 5. Amplitude-frequency plot of tibia movement for undisturbed *Carausius* (low gain) under open-loop (filled triangles) and closed-loop conditions (open triangles). Means and full ranges of measured values in four animals. Gain 1 is shown as a horizontal line.



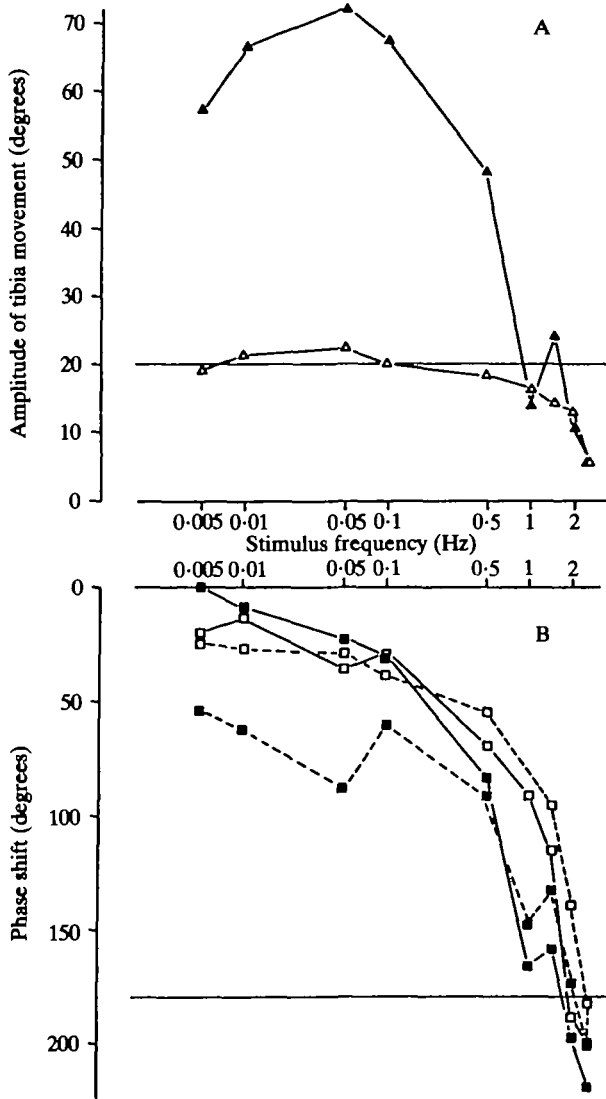


Fig. 6. Amplitude-frequency plot (A) and phase-frequency plot (B) of tibia movement for a *Carausius* briefly disturbed before each stimulation (high gain). Open-loop condition, filled symbols; closed-loop condition, unfilled symbols. Phase shifts were evaluated either as phase of beginning of extension movement with respect to beginning of chordotonal organ elongation (dotted lines) or as phase of beginning of flexion movement with respect to beginning of chordotonal organ release (solid lines). Gain 1 and 180° phase shift are given as horizontal lines.

In the second series of experiments two other animals were used. The abdomens of these animals were touched before each measurement to obtain a high gain of the loop (Bässler, 1983b). An amplitude-frequency plot for one of these animals shows that all amplitude values were higher than in the undisturbed animals but the shape of the curve was similar (Fig. 6A). Again, the values of the open-loop and those of the

closed-loop system were not significantly different at stimulus frequencies above 1 Hz. The other animal showed the same characteristics, but there was no 'valley' at 1 Hz and no peak at 1.5 Hz.

In Fig. 6B the phase shift is shown as a function of the stimulus frequency. The phase shift values lie within the range obtained in the undisturbed animals of Fig. 5 and are similar to those obtained by Bässler (1972) and Bässler *et al.* (1974) in the open-loop system with another method.

#### *Behaviour of the SETi-neurone of Carausius*

In both series of experiments described in the preceding section the activity of the extensor motor neurones was also recorded. Fig. 7 shows the mean maximum spike frequency of the SETi-neurone for the same animals as in Fig. 5 (solid lines) for the open-loop and the closed-loop condition. It also shows the maximum spike frequency of the SETi-neurone for one of the animals with high gain (not the animal in Fig. 6; but the animal in Fig. 6 showed the same characteristics). In all cases SETi was silent during relaxation of the chordotonal organ. FETi discharged only in response to the higher stimulus frequencies and often only with some spikes during the first few

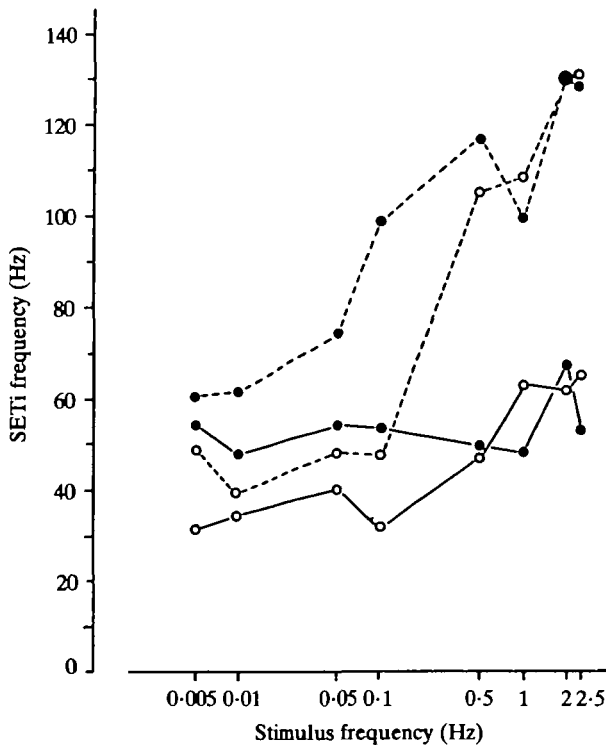


Fig. 7. Maximum spike frequency of the SETi-neurone for the open-loop (filled circles) and for the closed-loop conditions (unfilled circles). Solid lines are means from the four animals of Fig. 5. Dashed lines are values from an animal briefly disturbed before each stimulation.

cycles. In all animals the maximum SETi frequency was considerably higher in the open-loop configuration than the corresponding values of the closed-loop system at frequencies below 1 Hz. The two configurations did not significantly differ above 1 Hz.

#### *Carausius with an additional delay in the feedback loop*

In a linear system one can predict from the Bode plot (combination of amplitude-frequency and phase-frequency plot as in Fig. 6) of the open loop whether the closed-loop system is stable. If the gain in the open loop is greater than one for the frequency with a phase shift of  $180^\circ$ , oscillations will show up in the closed loop (Nyquist criterion). Fig. 6 demonstrates that a relatively small increase in phase shift should produce oscillations, provided the linear theory can be applied here. To test whether this conclusion can also be drawn in this non-linear system the phase shift was increased artificially. Therefore, in a third series of experiments (eight animals) the variable analogue delay (50–200 ms, upper corner frequency 100 Hz) was added between amplifier and pen-motor in the closed-loop system (Fig. 4C). The experiments started with the minimum delay value of 50 ms. The animal was briefly disturbed to obtain a high gain. The delay was then increased steadily until the tibia started to oscillate regularly. In most cases these oscillations started with delay values of 70–150 ms. In some cases they lasted for about 30 min, in other cases they disappeared after several minutes. In the latter case they reappeared after a brief disturbance or a further increase of the delay value.

The amplitude of the first cycle of an oscillation was always smaller than the following ones (Figs 8, 9). The amplitude was maximal during the second or third cycle and then declined steadily to a relatively constant value (Fig. 9). A further increase of the delay produced an increase in oscillation amplitude (Fig. 9).

The frequency of the oscillations was between 1.6 and 2.0 Hz at the beginning and 1.2 and 1.4 Hz after habituation. An increase in the delay value caused a very small drop in oscillation frequency in all cases (Fig. 9).

Fig. 8 shows that the motor neurones were rhythmically active during the oscillations. FETi and SETi fired during the extension movements (to be able to distinguish these spikes from flexor myograms, the time base must be much larger than in Fig. 8) and the flexor motor neurones fired during the flexion movements (the flexor motor neurones can be seen as cross-talk on the extensor recording).

#### *Undisturbed Cuniculina*

Three animals were treated as in the first series of experiments with *Carausius* (but the amplitude of the stimulus corresponded to 200  $\mu\text{m}$  receptor apodeme movement). Fig. 10 gives the amplitude-frequency plot for the open-loop and the closed-loop configuration. The amplitudes of tibia movement were much smaller in the closed-loop configuration for the whole frequency range. The phase shifts were similar to those described by Bässler & Foth (1982). Fig. 11 shows the maximum SETi frequency. The minimum SETi frequency was zero in all cases. The maximum

SETi frequency was larger in the open-loop configuration for the whole frequency range.

### *Disturbed Cuniculina*

An animal which was disturbed in the same way as in the second series of *Carausius* experiments responded more strongly than the undisturbed animals but showed no important difference (Fig. 12). In contrast to *Carausius*, the amplitude values of the closed-loop system were larger than the corresponding values of the closed-loop system for the whole frequency range. Another animal behaved in the same way.

Introducing the delay produced no oscillations in all cases (three animals).

### DISCUSSION

Closed-loop systems with negative feedback may become unstable. In a linear system, the stability of the closed-loop system can be predicted from the Bode plot of

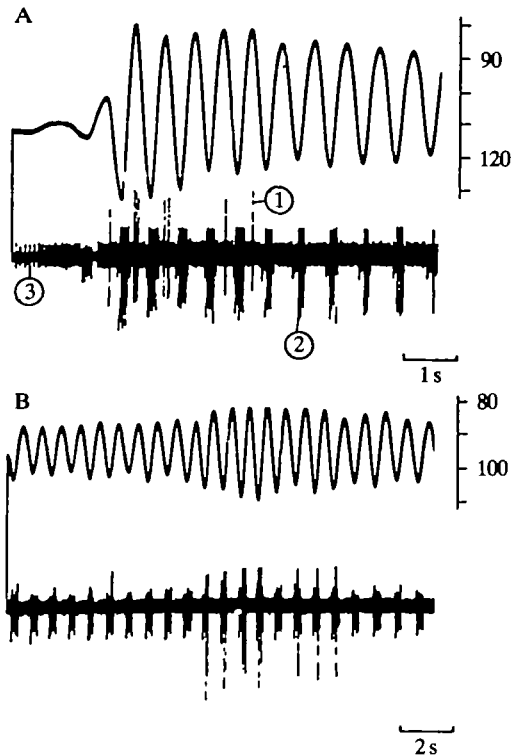


Fig. 8. Original records of the onset of an oscillation in the closed-loop system caused by insertion of the delay (A) and from an increase in oscillation amplitude produced by an increase of the delay (B). In the extracellular recording the large, more upwardly directed spikes, occurring close to maximum flexion, belong to FETi (1). Flexor myogram spikes have a larger downwardly directed component (2). The small, more upwardly directed spikes at the beginning belong to SETi (3).

the open system (see Results, *Carausius* with an additional delay). If at gain 1, the measured phase shift,  $A$ , does not reach  $180^\circ$ , a phase reserve  $R = 180^\circ - A$  exists. The higher the phase reserve, the more stable is the system.

The measurements confirm earlier results obtained for the open-loop system in *Carausius* (Bässler, 1972; Bässler *et al.* 1974) and in *Cuniculina* (Bässler & Foth, 1982). These earlier results suggested for *Carausius* with a high gain of the feedback loop that the phase reserve is small ( $30^\circ - 50^\circ$ ), i.e. the system is close to instability. In our experiments the minimum phase reserve was within the same range. In animals with low gain the phase reserve is much larger. If the *Carausius* system were to be linear an increase of phase shift of  $30^\circ - 50^\circ$  in animals with high gain would produce oscillations of maximum amplitude and a frequency of 1–2 Hz. But this system is non-linear. Therefore, oscillations of non-maximal amplitude may occur, but it cannot be deduced from open-loop experiments that they really are produced by increasing the phase shift by  $30^\circ - 50^\circ$ . This has to be proved experimentally. At a frequency of 1.5 Hz (the middle range of frequencies which should occur after increasing the phase shift) a phase shift of  $30^\circ - 50^\circ$  corresponds to a delay of 55–90 ms. This closely fits our finding that the minimum delay producing oscillations was 70 ms. Thus, the system really has a small phase reserve and is close to instability and has the ability to produce oscillations of non-maximal amplitude

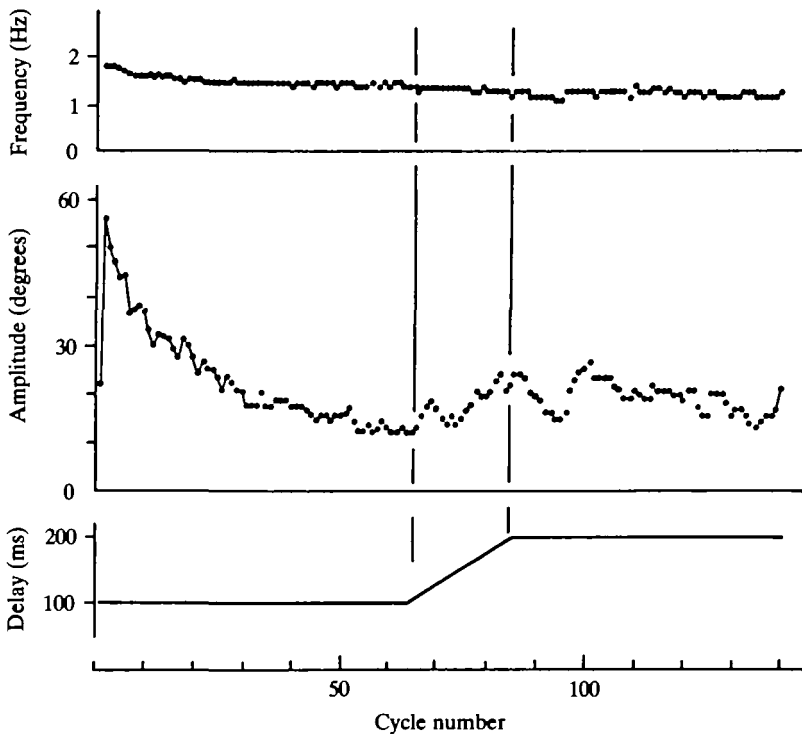


Fig. 9. Frequency and amplitude of the oscillation caused by the additional delay as functions of the cycle number. Between cycles 65 and 85 the delay value was increased.

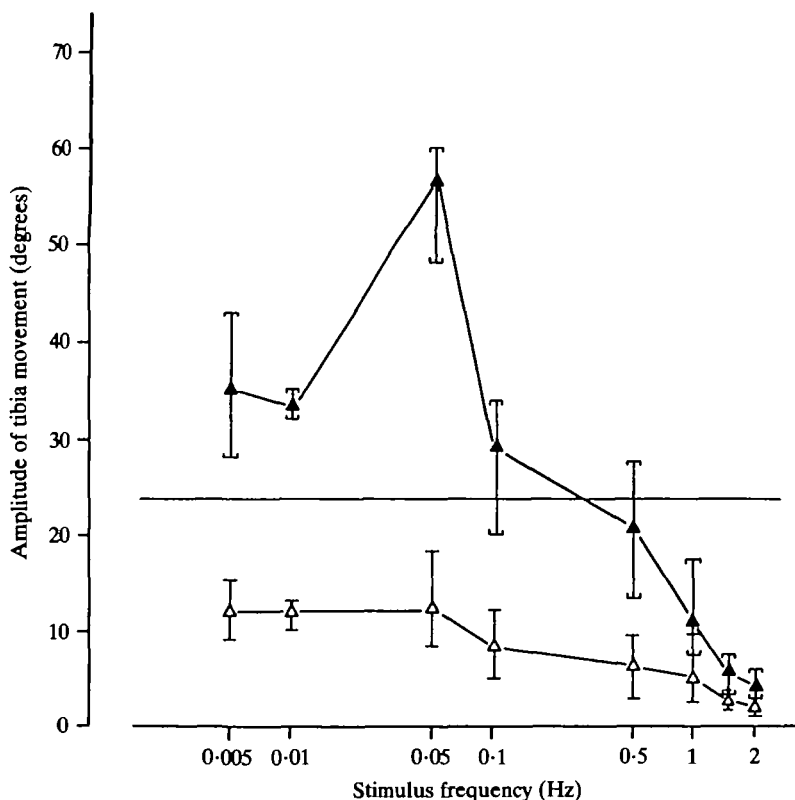


Fig. 10. Amplitude–frequency plot of tibia movement for *Cuniculina* under open-loop (filled triangles) and closed-loop conditions (unfilled triangles). Means and full ranges of measured values in three animals. Gain 1 corresponds to the horizontal line at  $23^\circ$ . Undisturbed animals.

provided the gain is high. As the gain declines gradually after a disturbance, oscillations should disappear after some time but should reappear if either the gain or the phase shift is increased. This was confirmed experimentally.

A feedback system with small phase reserve is likely to possess ‘resonance’ properties (Bässler, 1983*b*). The ‘resonance’ frequency should be between 1 and 2 Hz.

The amplitude–frequency plots of the closed-loop system in Figs 5 and 6A show no significantly increased amplitude at this frequency. But the values for the open-loop and the closed-loop system were identical in this region. Because the absolute values were small, this could have been caused by inaccurate measurements. But the values for the SETi frequency were also identical in this region (Fig. 7) whereas they differed significantly at lower frequencies. Apparently the ‘resonance’ properties of the system are expressed by the fact that the factor of feedback control (amplitude of the closed-loop system divided by the amplitude of the open-loop system) for sinusoidal inputs becomes 1 at the ‘resonance’ frequency and not larger than 1 as in a system with a stronger ‘resonance’. That the increase of the factor of feedback control is really produced by resonance properties is confirmed by a comparison with the

results obtained for *Cuniculina*. The *Cuniculina* system has a considerably larger phase reserve (Bässler & Foth, 1982) and, therefore, no distinct 'resonance' point. In this case the amplitude values and SETi-frequencies of the open-loop system are higher than those of the closed-loop system for the whole frequency range and the factor of feedback control is always smaller than 1.

When in *Carausius* the delay is increased until oscillations occur, the initial cycles have smaller amplitudes than the following ones. This is to be expected if these oscillations are feedback system oscillations. Additionally, oscillations should only occur if the gain is high (oscillations of a feedback system only occur if the gain is higher than 1 at the frequency where the phase shift is  $180^\circ$ ). This was also observed. Also at a somewhat smaller gain (but still larger than 1) the delay must be larger to obtain oscillations, and *Cuniculina* with its larger phase reserve should produce no oscillations with an additional delay of 200 ms. This was also observed.

After a certain maximal oscillation amplitude had been reached the amplitude decayed to a smaller constant value. This is in accordance with Kittmann (1981) who found that repetitive sinusoidal stimulation in the open-loop configuration habituates the system. That an increase in delay value increased the oscillation amplitude and decreased the oscillation frequency is also to be expected if these oscillations are feedback oscillations: an increase in phase shift causes a  $180^\circ$  phase shift at a smaller frequency value where the gain is higher.

Figs 5, 6, 10 and 12 show that at frequencies larger than 0.5–1 Hz the factor of feedback control approaches 1 (in *Cuniculina*) or becomes 1 (in *Carausius*). During

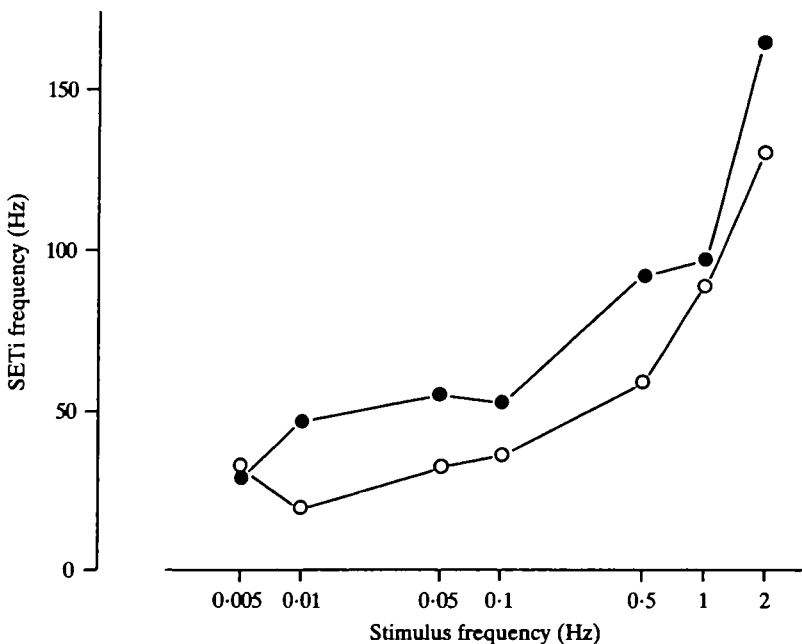


Fig. 11. Maximum spike frequency of the SETi-neurone for the open-loop (filled circles) and for the closed-loop system (unfilled circles). Means from the three animals of Fig. 10.

normal walking the femur–tibia joint often moves with frequencies larger than 1 Hz (maximum stepping frequency for *Carausius* is 3 Hz). If in walking animals the femur–tibia control system functioned in the same way as in resting animals, a feedback control of walking would only be possible at low stepping rates. A feedback control over the whole range of stepping frequencies is only possible if the characteristics of the system are adjusted to this situation. In fact, Cruse & Pflüger (1981) and Cruse & Schmitz (1983) suggested that the high-pass filter time constant of the system (Bässler, 1983a) is smaller during walking (this would produce a higher upper corner frequency) than during resting.

It has been previously suggested that the resonance properties of the *Carausius* system are used to amplify the oscillations produced by a central pattern generator for rocking movements (Bässler, 1983b, based on findings from Pflüger, 1977). As no increase of the amplitude was found at the resonance point, this hypothesis must be rejected. The reason 'why' the animal tunes the frequency of the rocking generator to the resonance point of the control system is apparently not that the control system

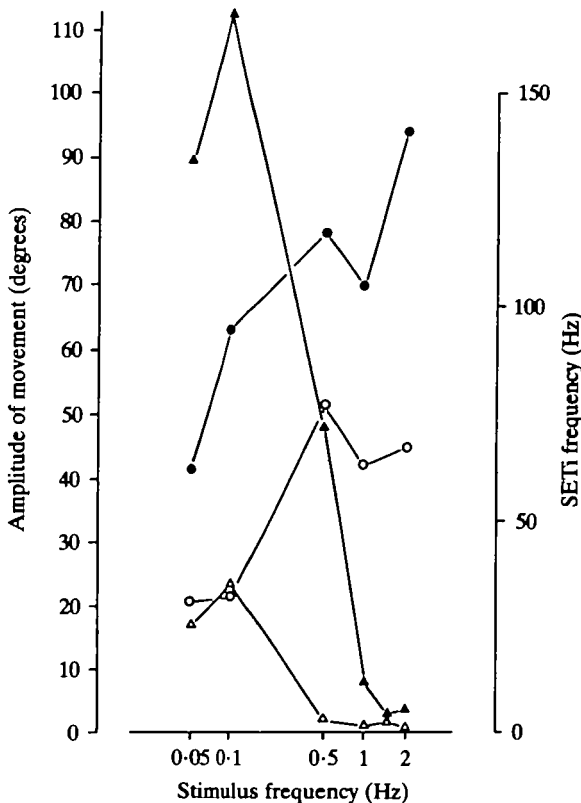


Fig. 12. Amplitude–frequency plot (triangles and left ordinate) and maximum SETi frequency (circles and right ordinate) for the open-loop (filled symbols) and the closed-loop systems (unfilled symbols) for a *Cuniculina* briefly disturbed before each stimulation.



amplifies the rocking generator output but that it does not reduce its amplitude at that frequency.

When the body of a *Carausius* is passively moved up and down strong forces are produced by the animal to oppose these movements. The forces do not change in amplitude up to 10 Hz of up and down movement (Kemmerling & Varju, 1981). These movements also move the femur-tibia joints. The measurements presented here show that the femur-tibia control systems do not substantially contribute to force production at high frequencies.

Our experiments have clarified several problems of the feedback control of the femur-tibia joint. In all cases the set-point of the system was constant. But, this system can also be used when the animal performs active movement, i.e. when it changes the set-point. These experiments will be reported later.

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