

## The Neural Basis of Catalepsy in the Stick Insect *Cuniculina Impigra*\*

### 1. Catalepsy as a Characteristic of the Femur-Tibia Control System

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**Abstract.** Catalepsy in the femur-tibia joint can be characterized as follows: When the joint is passively bent and then released, the joint first extends rapidly by  $10^{\circ}$ – $30^{\circ}$  and then returns to its starting position with extremely low speed.

Catalepsy is a characteristic of the femur-tibia control system. This system is quantitatively described in the open-loop configuration (input: stimulation of the femoral chordotonal organ; output: movement of the tibia). The output shows a predominant dynamic portion which only responds to movement and a weak static portion which responds to position. The dynamic portion can be described by a high-pass and a low-pass filter in series. The time constant of the high-pass filter depends on input slope. The system possesses a large phase reserve and is therefore very stable in the closed loop configuration.

The results confirm the hypothesis that the high gain of the phasid control system evolved only under a selection pressure towards catalepsy.

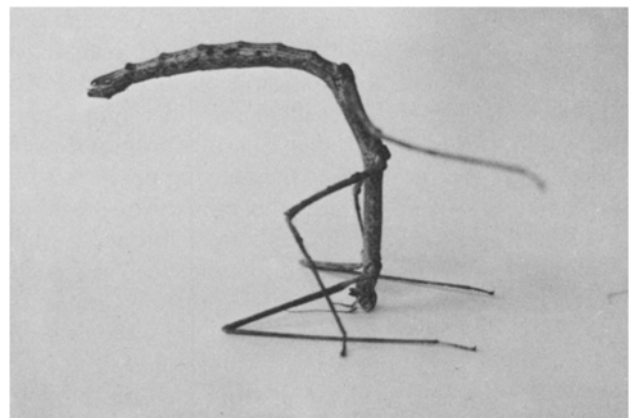
over  $10^{\circ}$ – $30^{\circ}$  towards the original position of the joint. It then abruptly slows down and returns to its original position with very low speed within hours (summary: Bässler, 1982a).

The femur-tibia control system also takes part in generating rocking movements due to its small phase reserve (summary: Bässler, 1982a).

In many somata of motor neurons of *Carausius* (at least in those of protractor and retractor coxae motor neurons) only very small spikes can be recorded (Graham and Godden, pers. comm.). For further analysis of the femur-tibia feedback system, which includes a causal analysis of catalepsy, the input-output relationships of the motor neurons as well as the characteristics of the femoral chordotonal organ, the sense organ of this feedback system, should be examined. The first is only possible with long lasting intracellular records which are much easier from the somata than from the neuropile. In preliminary experiments distinct spikes could be obtained from *Cuniculina* somata. This may be due to the fact that *Cuniculina impigra* is larger

### 1. Introduction

In the stick insect *Carausius morosus* one of the characteristics of the control system governing the femur-tibia joint is catalepsy. Catalepsy (*flexibilitas cerea*) can be described as follows: When the leg is forced into a certain position and kept there for some time it remains in approximately this position. All leg joints show catalepsy. Therefore it is possible to force the animal into quite unnatural positions (see Fig. 1) which are maintained for half an hour or longer. Quantitative measurements of the femur-tibia angle show, that after release the tibia first moves quickly



**Fig. 1.** *Cuniculina impigra* ♀. The legs were forced into appropriate positions without damage to the legs or muscles and the animal was placed on its head

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(mesothoracic ganglion appr. 0.8 mm long and 1.3 mm wide) than *Carausius morosus*. In *Carausius* it is impossible to record from the nerve coming from the femoral chordotonal organ. In *Cuniculina* the anatomy of coxa and trochanter is somewhat different so that records from the chordotonal organ nerve are possible. Therefore, the further analysis of the feedback loop was carried out in this animal.

This first article characterizes the feedback system and shows that catalepsy is one of its attributes. Further articles will focus on the neural basis of the control system.

## 2. Methods

The animals were restrained on a vertical corkplate so that the right middle leg was held perpendicular to the long axis of the body. The femur of this leg (the only subject of investigation) was horizontal as well as the plane of movement of the tibia (for details see Bässler, 1972). The position of the tibia was measured in the following way: A horizontal piece of aluminium foil was glued to one side of the tibia. It covered a semicircular slot below the tibia in such a way that at a femur-tibia angle of  $180^\circ$  the slot was completely open and at a femur-tibia angle of  $20^\circ$  (fully flexed joint) the slot was completely covered. Above the leg was a lamp, below the slot a photo cell (details of method see Ebner and Bässler, 1978).

The femoral chordotonal organ was stimulated in the same way as in *Extatosoma* (Bässler and Pflüger, 1979) and *Carausius* (Bässler, 1972). The amplitude of stimulation was constant ( $100 \mu\text{m}$ ). In order to calculate the gain of the system the dependence of the movement of the receptor apodeme of the femoral chordotonal organ on the movement of the tibia in the intact system must be known. Between  $30^\circ$  and  $150^\circ$  joint angle a tibia movement of  $10^\circ$  produces a receptor apodeme movement of appr.  $80 \mu\text{m}$ .

## 3. Quantitative Description of Catalepsy

The animals were fixed in the set-up (plane of movement of the tibia of the investigated middle leg horizontal) and left there for about 2 h. The femur-tibia angle then assumed a constant value somewhere between  $90^\circ$  and  $180^\circ$  (starting position). After the rest period the tibia was rapidly flexed by hand to an angle of  $50^\circ$ , kept there for 30 s and then released (21 experiments). After release the femur-tibia joint extended rapidly over  $10^\circ$ – $30^\circ$  (fast phase), abruptly slowed down and then returned to the starting position with velocities between  $0.6^\circ/\text{min}$  (the velocity of the hour hand of a clock is  $0.5^\circ/\text{min}$ ) and  $10^\circ/\text{min}$  (mean value  $1.5^\circ/\text{min}$  – slow phase). The minimum speed as well as the mean value are somewhat higher than in *Carausius*, but the shape of the return-curve is the same in both animals. The speed of backward movement decreased when the starting position is approached. In most cases the starting position was reached after some time.

After cutting the receptor apodeme of the femoral chordotonal organ (operation technique: Bässler,

1965) the behaviour changed (10 experiments). (1) The return movement could no longer be divided into a fast and a slow phase. (2) The speed of backward movement was significantly higher (between  $8^\circ/\text{min}$  and more than  $30^\circ/\text{s}$ ).

## 4. The Femur-Tibia Control System

The femur-tibia control system was then investigated in the open-loop configuration. To do this the receptor apodeme of the femoral chordotonal organ was cut close to the joint and held by a clamp. The clamp was moved with an amplitude of  $100 \mu\text{m}$ . The reaction to such a stimulus was measured as movement of the tibia. After conversion ( $100 \mu\text{m}$  of receptor apodeme movement correspond to approximately  $12.5^\circ$  movement of the tibia) the input had the same dimension ( $^\circ$ ) as the output, and the gain of the system could be defined as output amplitude/input amplitude. Altogether 10 animals (only right middle legs) were tested.

The reactions to *sinusoidal stimulation* of different frequencies are shown by a Bode plot (Fig. 2). For each

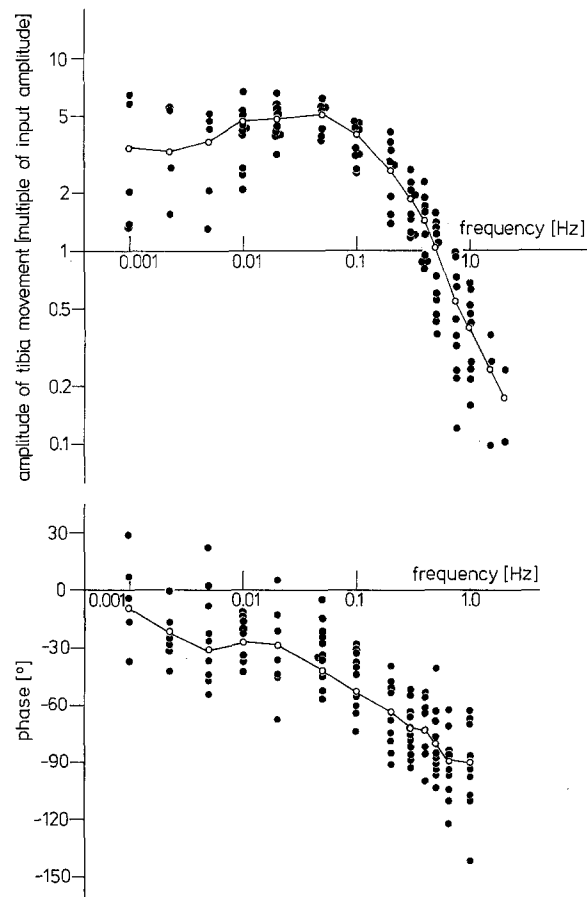


Fig. 2. Bode-plot of the open-loop system. ● mean for one animal, ○ mean of all experiments

frequency the amplitude values for all animals were found to be normally distributed (Chi-square-test  $p < 5\%$ ). The phase shift was measured separately for flexion and extension of the joint. It was defined as the time interval between onset of movement of the receptor apodeme in one direction and onset of the corresponding tibia movement. For each frequency the values were normally distributed ( $p < 5\%$ ). The mean values for flexion and extension are not significantly ( $p < 1\%$ ) different.

In the amplitude-frequency-plot, the decrease towards smaller frequencies is not significant. In this region there are fewer values because each measurement required much more time. According to the Nyquist criterion (at a phase shift of  $180^\circ$  the gain must be smaller than 1 if the closed-loop system is stable) the closed-loop system is stable and possesses a relatively large phase-reserve (for more details of this method of description see Bässler, 1982a).

The results were different from animal to animal. Each animal increased its gain for some time when it was disturbed. Thus, *Cuniculina* is able to alter the gain of its reflex-loop in a wide range (for comparison with *Carausius* see Bässler, 1974).

*Step-stimuli* (amplitude  $100\ \mu\text{m}$ ) produced an extension when stretching the chordotonal organ and a flexion on release. After some minutes the tibia returned nearly to its starting position. The system behaves qualitatively like that of *Carausius* but it works in a symmetrical way and is not asymmetric like that of *Carausius*. With the exception of the direction all parameters did not differ significantly ( $p < 5\%$ ) for the responses to stretch and release stimuli (25 experiments each). The values of the reaction on stretch and release stimuli are therefore combined (mean value and standard deviation). The movement amplitude of the tibia was  $44.5^\circ \pm 21^\circ$ . This corresponds to a gain of  $3.6 \pm 1.7$ . The latency was  $140\ \text{ms} \pm 5\ \text{ms}$  and the half life of rise  $430\ \text{ms} \pm 60\ \text{ms}$ . The maximum amplitude was reached after  $2.34\ \text{s} \pm 1.32\ \text{s}$ . The time constant of fall was  $\tau = 27.5\ \text{s}$  (median). This time constant refers to the decline from maximum amplitude to the final position 10 min after stimulus. The final position differed from the starting position (residual deviation) by  $12.5^\circ \pm 6.7^\circ$ . The constant final position was reached after  $33\ \text{s} - 267\ \text{s}$  (mean value  $158\ \text{s}$ ).

The last type of input functions were *ramp-and-hold-functions* with an amplitude of  $100\ \mu\text{m}$  and different ramp slopes. Figure 3 shows the time interval between onset of stimulus and the time taken to reach the extreme tibia position. This time interval is shorter than the duration of the stimulus rise only for the lowest stimulus speeds. Only here did the reaction reach a plateau within the time of stimulus rise. After the end of the stimulus rise the tibia started to

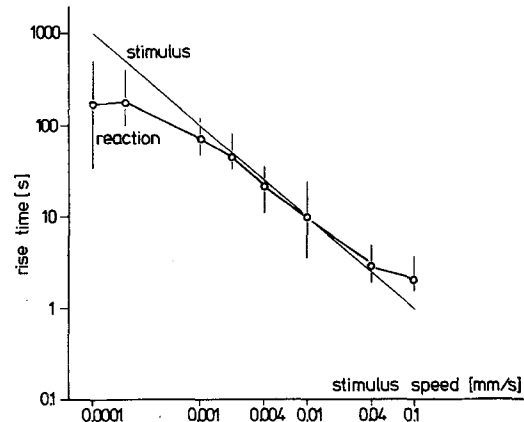


Fig. 3. Time interval between onset of stimulus and reaching the extreme tibia position as a function of stimulus speed (mean and extreme values). As a comparison the duration of stimulus rise is also plotted

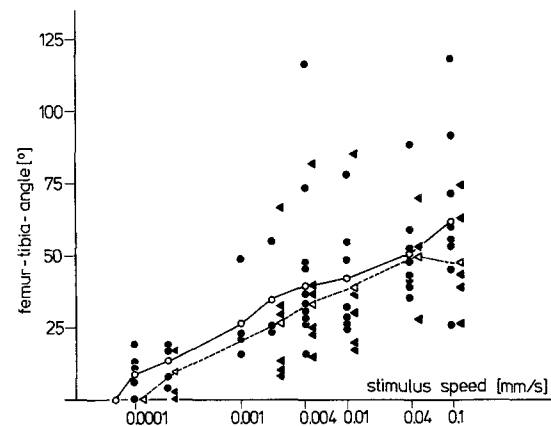


Fig. 4. Amplitude of tibia movement as a function of stimulus speed during ramp-and-hold stimuli. Circles: flexion movements resulting from release stimuli. Triangles: extension movements resulting from stretch stimuli. Filled symbols: mean for one animal. Open symbols: mean of all experiments

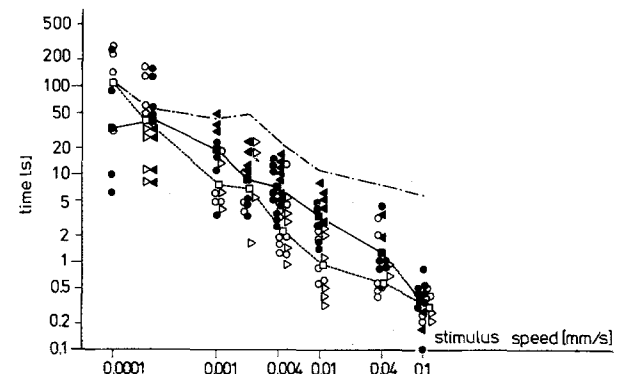


Fig. 5. Latency, half-lives of rise and fall as a function of stimulus speed during ramp-and-hold stimuli. — and filled symbols: latency, --- and open symbols: half life of rise. - · - · mean of half-lives of fall after stretch stimuli

approach the starting position. This starting position was not reached. The maximum amplitude of tibia movement increased with increasing ramp slope (Fig. 4). At the same time the half-lives of rise and fall (Fig. 5) as well as the latency (Fig. 5) decreased.

## 5. Discussion

### 5.1. Characteristics of the Control System

The control-system is similar to that of *Carausius*. It can be divided into a weak static and a much stronger dynamic portion. The static portion responds to the position of the receptor apodeme and is the cause for the residual deviation after step and ramp stimuli. The dynamic portion responds only to a movement of the receptor apodeme (for details see Bässler, 1982a, b).

The dominant dynamic portion may be characterized as follows. The falling branch of the amplitude-frequency plot towards high frequencies can be approximated by a straight line. The phase-shift in this region is approximately  $90^\circ$ . This is the behaviour of a first order *low-pass filter*. The upper corner frequency derived from the amplitude-frequency-plot is 0.1–0.15 Hz. This corresponds to a time constant of the low-pass filter of 1.6–1.1 s. In a first order low-pass filter the phase-shift is close to  $45^\circ$  at the corner frequency. This is the case here too (*t*-test, normal distribution present). The rising branch of the step response is mainly influenced by the low-pass filter. The low-pass filter time constant calculated from the half-life of rise of the step response is 0.6 s. The time constants obtained by these two methods agree within the accuracy of measurement but it is more likely that a certain difference exists. Perhaps the system reacts differently to repetitive stimuli (sinusoidal stimuli) than to single (step and ramp) stimuli (see Bässler et al., 1982).

The amplitude-frequency plot also decreases towards lower frequencies. This behaviour indicates a band-pass filter. It consists of a low-pass filter and a high-pass filter in series. The *high-pass filter* produces the decrease of response after a step-stimulus. The corresponding time constant is 27.5 s. A high-pass filter with such a time constant shows a lower corner frequency of approximately 0.005 Hz. The amplitude-frequency plot does not decrease significantly at this frequency. The evaluation of the lower corner frequency from the amplitude-frequency plot is not absolutely clear (small number of measurements at low frequencies). Therefore, the time constant of the high-pass filter is approximated from the ramp responses. The half-life of rise of the ramp response is mainly determined by the high-pass filter, especially at low velocities. In a linear high-pass filter it is as large as the half-life of fall, when the reaction reaches a plateau

during the time of stimulus rise. (The latter was only the case during low ramp velocities where the half-lives of rise and fall are similar.)

The time constant of rise and therefore also the time constant of the high-pass filter depends on stimulus slope (Fig. 5). During a small stimulus slope the time constant is large and vice versa. The same kind of dependences was also found for the half-lives of fall. In *Carausius* a similar non-linearity was measured. Thus, the dynamic portion of the control-system can be described by a band-pass filter. The high-pass filter is non-linear. The low-pass filter is to a first approximation first order.

The control system has a large phase reserve and is therefore very stable. This can also be derived from the following experiment in which the tibia of an intact animal is coupled to an inert mass (a weight hanging from the ceiling). In *Cuniculina* no long lasting oscillations occur like in *Carausius* (Bässler, 1982a). As the phase-frequency plot of *Cuniculina* is similar to that of *Carausius*, this is only the result of the markedly smaller upper corner frequency in *Cuniculina*. The control system of *Cuniculina* therefore does not possess a small phase reserve like that of *Carausius*.

### 5.2. Catalepsy as a Characteristic of the Closed-Loop System

Let us assume that the angle between the femur and the tibia in an intact leg has a starting position close to  $180^\circ$ . Bending of the joint (to  $50^\circ$  for example) meets with an opposing force which is made up of two components. Component 1 is the dynamic portion of the control system plus the viscosity of the extensor muscle. The amount of this component increases with increasing velocity of tibia movement (Fig. 4) and becomes zero when the movement stops. Component 2 consists of the static portion of the control system plus the elastic properties of the extensor muscle. Component 2 is independent of the velocity of tibia movement.

If the tibia is held in the  $50^\circ$  position for some time, component 1 decreases to zero or to a very small value, but component 2 still acts on the tibia to bring it back to its starting position. Thus, after being released, the tibia will move towards the starting position. This extension produces an opposing tendency in the dynamic portion of the control system to slow the movement down. Since this tendency first comes into effect after expiration of the latency, the tibia should move quickly at first and then abruptly slow down. Precisely this behaviour is observed and is termed the fast phase of the return movement.

After completion of the fast phase the tibia comes under the influence of two opposing tendencies. One

produced by component 2 (independent on velocity) moves the tibia toward the starting position. The other produced by the velocity-dependent component 1 acts as a brake on this movement. At a certain velocity both components have equal value but opposite sign. This velocity of counterbalance will be the velocity of backward movement. As component 1 responds strongly at very low velocities, the speed of backward movement will be correspondingly slow. The velocity of counterbalance must decrease as the tibia approaches the starting position, because component 2 decreases as well. This behaviour was also observed in catalepsy.

This explanation of catalepsy is confirmed: (1) After cutting the receptor apodeme (destroying the feed-back loop) catalepsy no longer occurs. (2) The variation of velocity of backward movement during catalepsy is as large as the variation of the gain of the reflex loop. In *Carausius* there exists a negative correlation between velocity of backward movement and gain (Summary Bässler, 1982a).

The complicated high-pass filter properties seem to be a modification for generating the cataleptic state. They ensure that the system has a small time constant after a rapid flexion. The resulting rapid decline in the response is responsible for the small amplitude of the fast phase of catalepsy. The time constant is large during slow movements, i.e., the response is high even during very slow extension. In conjunction with the high gain this produces very low velocities during the slow phase of catalepsy.

### 5.3. Evolution of the Characteristics of the Control System in Phasmids

The *Cuniculina* control system has a high gain like that of *Carausius* but has a larger phase reserve and the animal only rarely shows rocking behaviour. This confirms the hypothesis that the higher gain of the phasmid control systems was only produced by a selection pressure towards catalepsy (detailed dis-

cussion of the evolutionary aspect: Bässler, 1982a). A small phase reserve and with it a "resonance frequency" is not a necessary concomitant phenomenon of a high gain, because it does not occur in *Cuniculina*. Another fact points in the same direction: All phasmids studied so far have the same kind of nonlinear high-pass filter which is favourable for producing catalepsy.

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