

## Open Loop Analysis of a Feedback Mechanism Controlling the Leg Position in the Stick Insect *Carausius morosus*: Comparison between Experiment and Simulation\*

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**Abstract.** In the legs of the stick insect *Carausius morosus* a feedback mechanism exists to control the value of the angle between femur and tibia. It is possible to investigate the open loop system by moving as input experimentally the receptor apodeme of the femoral chordotonal organ, which acts as feedback transducer measuring the angle between femur and tibia (Bässler, 1965). As output the forces are measured separately which are developed by the two antagonistic muscles moving the femur-tibia joint. The response of this system to different step-, sine-, ramp- and  $\delta$ -functions are measured. An electronic analog model is constructed to simulate the biological system (Fig. 1). Although a number of different nonlinearities arise in the biological system, as a first-order approximation the model shows a sufficient fit to the experimental results (Figs. 2–9). The main characteristics of the model are as follows. It consists of two independent subsystems, the “flexor system” and the “extensor system”. Each subsystem again consists of two parallel branches with high-pass properties of different time constants. In each subsystem one branch is only excitable by input functions of a slope smaller than a certain degree. It is remarkable, that no mutual inhibitory influence between the subsystems controlling the antagonistic muscles is necessary in the model.

### A. Introduction

In the legs of the stick insect *Carausius morosus* there exists a mechanism, which controls the position of the femur-tibia joint of each leg. This mechanism works as a closed loop control system, which enables the tibia of this leg, to resist disturbance inputs (Bässler, 1965, 1967, 1972a, b, 1973, 1974; Bässler et al., 1974). These disturbance inputs are given for example by an experimental change of the angle of the femur-tibia

joint. If in the fixed insect, starting from any resting position of the tibia, you bend the femur-tibia joint, the forces developed by the extensor muscle of this joint (extensor tibiae) increase, whereas if you stretch this joint, the forces developed by the antagonistic flexor muscle (flexor tibiae) increase. Therefore these two antagonistic muscles act as the actuators of this closed loop control mechanism, as their forces try to resist the artificial disturbance input. This reaction nearly comes to zero, when the receptor apodeme is cut, which runs from a chordotonal organ lying in the proximal part of the femur to the tibia near the femur-tibia joint (Bässler, 1965). By this receptor apodeme the chordotonal organ is elongated, when the femur-tibia joint is bent and it is shortened, when the femur-tibia joint is stretched. Therefore this chordotonal organ can be regarded as the feedback transducer of this control system. In addition to the possibility of cutting the receptor apodeme and thereby switching off the closed loop control mechanism, the existence of this receptor apodeme has also the advantage, that you can use the position of the cut receptor apodeme as input to investigate the properties of the open loop system. This was first done by Bässler (1965) by cutting off the receptor apodeme, then by fastening it in fine forceps connected with a micromanipulator. By this method you can move the receptor apodeme and so lengthen or shorten the chordotonal organ, as it would be done in the intact animal by a movement of the femur-tibia joint. As an output Bässler measured either the movement or the force developed by the antagonistic muscle pair. In the force experiments the tibia is immovably fixed to a force meter.

In these investigations one cannot discriminate between the effects of the flexor muscle and those of the extensor muscle, since here only the sum of the forces of both muscles is measured. This work has therefore been continued by Storrer and Cruse (1975, 1977) in such a way, that the forces produced by the two antagonistic

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onistic muscles are now measured separately. The system under investigation then consequently has one input channel, the position of the receptor apodeme, and two output channels, the forces produced by the flexor tibiae and the extensor tibiae. With this system the input-output-analysis earlier started by Bässler has been continued by measuring step responses, frequency responses, ramp responses and  $\delta$ -responses of this system. The outcome of these investigations showed from the point of view of linear systems some unexpected and even contradictory results. Therefore parallel to these experiments an attempt has been made to build up an electronic analog model able to describe the experimental results. In this paper this model will be described and the corresponding data obtained by the experiments and by the electronic simulation will be compared.

## B. Methods

The method used in the experiments is described here only briefly, because it is discussed in detail in an earlier paper (Storror and Cruse, 1977). As mentioned above, inactive (i.e. not moving spontaneously) adult female stick insects (*Carausius morosus*) are restraint in a holder. The angle of the femur-tibia joint of the leg under investigation (middlelegs and hindlegs) is  $90^\circ$ . The axis of rotation of this joint is directed vertically. The tendon of the flexor muscle is cut off from the tibia and connected by fine forceps to a force meter (strain gauges). The forces developed by the extensor muscle are measured by a force meter, which is directly connected to the tibia. The corresponding lever arms are taken into account. The receptor apodeme of the chordotonal organ is also cut off from the tibia and connected by fine forceps to a micromanipulator. By means of this micromanipulator the receptor apodeme is moved forward and backward in the form of a sine function and a (limited) ramp function by a motor or in the form of a step function and a  $\delta$ -function by a special click-device. The slope of the steps used here is 25 mm/s. The duration of the  $\delta$ -function is about 100 ms. In order to describe the elongation of the chordotonal organ, the position of the forceps holding the receptor apodeme is measured. As the experiments usually start with an angle between femur and tibia of  $90^\circ$ , the corresponding position of the receptor apodeme is called 0  $\mu\text{m}$ . From this zero position in the experiments the receptor apodeme is pulled in distal direction until it maximally reaches a position of 500  $\mu\text{m}$ . This corresponds to stretching of the femur-tibia joint to an angle of  $25^\circ$ . The values of the input functions lie in this range with one exception, the ramp functions. In the following the angles between femur and tibia are given, which approximately correspond to the extreme positions of the receptor apodeme in the different input functions, if the tibia was freely movable and the receptor apodeme was not cut off: sine-function: 300  $\mu\text{m}$  ( $p-p$ ),  $90^\circ-35^\circ$ ; step function: 500  $\mu\text{m}$ ,  $90^\circ-20^\circ$ ; limited ramp function: 600  $\mu\text{m}$ ,  $150^\circ-35^\circ$ ;  $\delta$ -function: 400  $\mu\text{m}$ ,  $90^\circ-25^\circ$ .

The time constant of the output functions could not always be measured, as because of the limited range of the ramp function the plateau of the output function was not reached in all measurements. Therefore all transient output functions are described by their *half time*. That is the time, in which the output reaches half the value of its maximum value. In some cases, when the functions could be described by an exponential function, the time constants  $\tau$  are calculated from the half times. In the simulation it is done in the same way. Therefore the corresponding values are comparable. Corresponding to the definition of the position of the receptor apodeme a movement of the receptor apodeme will be said to have a *negative slope*, when

the receptor apodeme is pushed in a proximal direction, which would correspond to a stretching movement in the femur-tibia angle, and the movement will be said to have a *positive slope*, when the receptor apodeme is pulled in the distal direction, which would correspond to a bending movement in the femur-tibia angle. In the same sense the expressions positive or negative step and positive or negative ramp will be used in the following, when the step or the ramp have either a positive or a negative slope. Referring to an earlier paper (Storror and Cruse, 1977) a positive step is produced by a pull ("Zug") and a negative one by a push ("Schub") at the receptor apodeme.

The forces produced by the flexor and by the extensor muscles are measured in p ( $1 \text{ p} \approx 10 \text{ mN}$ ). Individual muscles can only produce forces directed in one direction, but by means of the different points of fixation of the muscle tendons at the tibia relative to the point of rotation of the femur-tibia joint both antagonistic muscles act against one another. Because of this reason in the following the forces developed by the extensor shall be signed positive, and the forces developed by the flexor shall be signed negative. Using as input function a positive step function, a positive force will be developed by the extensor, using a negative step function, a negative force will be developed by the flexor muscle.

*Simulation:* In order to find out, if the different results obtained by the experiments could be described by one single model, an analog computer-like device was constructed. This device consists of small electronic units, which contain either a first-order high-pass filter (HPF), a first-order low-pass filter (LPF), each of variable time constant  $\tau$ , a rectifier, an (inverting) amplifier, an integrator, a summing element, a voltage follower or a characteristic of changeable form. Additionally to these rather simple circuits in order to simulate a pure time delay an integrated circuit consisting of a chain of different sample and hold amplifiers (ITT, type TCA 350) is used. Two other types of nonlinear units will be described below. All these units are charged by a  $\pm 15 \text{ V}$  source with exception of the frequency filters, which are passive elements. These electronic units can be connected in an arbitrary manner to form different electronic circuits. The input functions for such a circuit are obtained as voltage over time functions by a function generator (Tektronix, type FG 501).

In order to simulate the experiments mentioned above by this electronic device, the values of the experimental input functions given in  $\mu\text{m}$  have to be represented in voltage values. In the simulation used here a movement of 50  $\mu\text{m}$  corresponds to a change of the input voltage of 1 V. The total range of input values in the experiment from  $-300 \mu\text{m}$  to  $+500 \mu\text{m}$  therefore corresponds to an input range from  $-6 \text{ V}$  to  $+10 \text{ V}$  in the simulation. In the same way as above a step or a ramp function is called positive, when the value of the voltage is increasing and is called negative, when these values are decreasing. With this definition two further electronic elements with nonlinear properties used in this simulation can be described. In two cases high-pass or low-pass filter like elements were used which however show nonlinear properties in a way that they show different time constants when responding to a positive or a negative step function. Such "asymmetric filters" were constructed by using instead of one resistor as in the linear passive filter now two different resistors connected in parallel and each of them connected in series with a diode in opposite direction. The time constant when responding to a negative step function is then called  $\tau'$ , and that when responding to a positive step function is called  $\tau$ . The two output functions (flexor and extensor forces) are displayed together with the input function either a storage oscilloscope or on a three channel penrecorder (Hellige He 18). All simulations are done in real time mode. To be able to make a simple but clear discrimination between the results obtained by the investigation of the biological system and those obtained by that of the electronic model, the former always will be called results of the *experiment*, the latter results of the *simulation*. In the figures the experimental results are shown by crosses, those of the simulation by open symbols, usually circles.

### C. Basic Properties of the Model

As shown in detail by Storrer and Cruse (1977) when moving the receptor apodeme in form of a positive step function with an amplitude of 500  $\mu\text{m}$ , the force developed by the extensor rises to a maximum value within about half a second and then decreases more slowly to zero within about 50 to 150 s. This shows that this system qualitatively has the property of a high-pass filter. As this step response can be approximated by an

exponential function  $f(t) = \text{const} (1 - e^{-\frac{t}{\tau_1}}) e^{-\frac{t}{\tau_2}}$  the underlying system could be regarded as a band-pass filter with the time constant  $\tau_1$  describing the fast ascending branch of this response (low-pass filter property) and  $\tau_2$  describing the slowly falling branch (high-pass filter property). The half time of the ascending branch is  $ht_1 = 0.14$  s, that of the falling branch  $ht_2 = 15.0$  s. The corresponding time constants to approximate this response are  $\tau_1 = 0.22$  s and  $\tau_2 = 22.0$  s. If one starts a negative step function when the force developed by the extensor was zero before, no change of the force can be seen. This depends on the fact that muscles can produce forces only by contraction, not by elongation. To model this behaviour, a rectifier has to be added to the band-pass filter. If this rectifier was put in front of the band-pass filter, this would only have the effect to limit the input range but not to prevent negative output values. Therefore the rectifier must be put behind the high-pass filter. No necessary statement can be made on the position of the low-pass filter, but as at least a part of this low-pass properties are due to the inert properties of the muscle, at least this part of the low-pass filter must be put behind the rectifier. Results of Iles and Pearson (1971) allow the assumption, that the low-pass properties measured here are indeed mainly due to the properties of the muscle, although of course all other elements of this system also have low-pass properties.

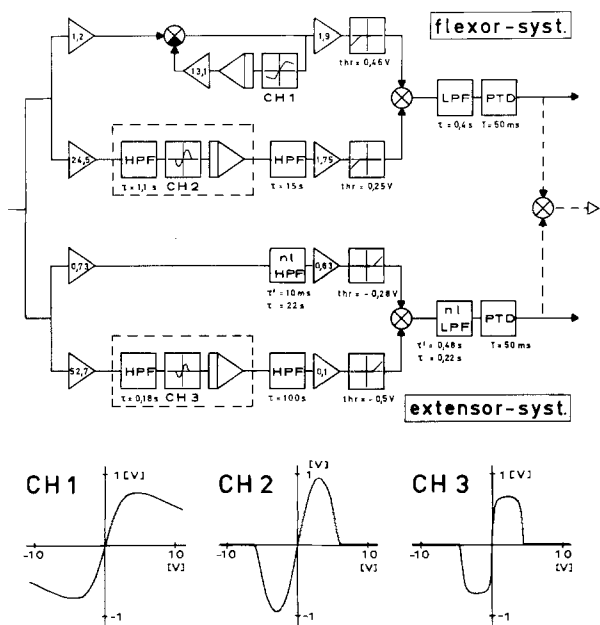
Additionally a measurable value of dead time is found in the experiments. As this dead time beside others is caused by the finite velocity of signal propagation and is therefore distributed over the whole system between the receptor apodeme and the muscle force development in an unknown way, it is lumped in the model and put at the end of the circuit as a pure time delay. For the above reasons a preliminary model describing the input-output relationships of the extensor system might consist of a high-pass filter, a rectifier, a low-pass filter and a pure time delay connected one behind the other in this order. The preliminary model of the flexor system shows the same combination, because its step responses have qualitatively the same properties ( $\tau_1 = 0.4$  s;  $\tau_2 = 1.5$  s). But as this muscle starting from zero force responds only to negative steps, the rectifier has to be inverted in the "flexor branch" of the model.

If one intends to investigate a system with non-linear properties it is appropriate to use different kinds of input functions. As biological systems in general are expected to have nonlinear properties, the responses of the whole system to step functions, sine functions, ramp functions and approximative  $\delta$ -functions are examined. Most of these results cannot be described by the preliminary model, which therefore requires a number of additional changes. As is shown below this system can be divided up into two independent subsystems; the "flexor system" and the "extensor system". Since both subsystems show qualitatively different properties, they will be treated separately.

### D. Flexor System: The Structure of the Final Model

The output of the flexor system in response to two approximative  $\delta$ -functions, one starting with a positive step, the other with a negative one (Fig. 2, trace 1) can be qualitatively described by the response of the preliminary model. Quantitatively however the time constant of the falling part of the response to the first  $\delta$ -function (starting with a positive step) is too small. The upper corner frequency  $\nu_1$  of the amplitude frequency plot of the preliminary model can be calculated as  $\nu_1 = \frac{1}{2\pi\tau_1} = 0.4$  Hz. This corresponds qualitatively to the upper corner frequency estimated from the amplitude frequency plot measured in the experiments. The lower corner frequency of the amplitude frequency plot calculated from the values of the step response of the preliminary model is  $\nu_2 = \frac{1}{2\pi\tau_2} = 0.1$  Hz. However,

the experimental value of  $\nu_2$  can be estimated from the amplitude frequency plot as being smaller than 0.005 Hz (Fig. 3, upper part, crosses). Therefore one finds an essential difference between the biological system and the preliminary model. When comparing the experimentally found responses to ramps of different slope (Fig. 4, crosses) with those expected by the preliminary model one again finds strong disagreements. With the band-pass filter, by which the step responses can be described sufficiently, especially in ramp functions with very small slope the maximum amplitudes should be much smaller than they are in the experiments. One possibility to understand these experimental results is to assume that the gain of the system is increased when the slope of the input function decreases (Bässler, 1972a). However, not only the maximum amplitude, but also the time constant of the high-pass filter increases with decreasing slope. Since in the ramp response of a linear high-pass filter the maximum output amplitude is proportional to the ramp slope and the time constant, the increase of the time constant



**Fig. 1.** A schematic diagram of the electronic model. Triangles represent rectifiers. Their gain is written within the triangle. Integrators are shown by a triangle with a rectangular base. The circles with oblique crosses inside indicate a summation of the inputs. A black sector denotes inversion of the corresponding input. thr: threshold; PTD: pure time delay; LPF: low-pass filter; HPF: high-pass filter; nl LPF, nl HPF: low- or high-pass filter with nonlinear properties described in the text in detail. For further explanations see the text

might possibly be the only reason for the increase of the maximum amplitude. This change of the time constant might additionally be the reason for the unexpected high gain in the amplitude frequency plot for low frequencies.

When measuring the responses of the biological system to steps of different amplitude, one also finds a change of the time constant of the high-pass filter. The time constant increases with increasing input amplitude. Now the question arises, whether it is possible to find a model able to describe all these nonlinearities. An attempt was made to solve this problem by using a model for the flexor system consisting of two parallel channels, the outputs of which are summed (Fig. 1). One channel has a high-pass filter with a large time constant ( $\tau = 15$  s). Input functions of high slope can however not exit this filter because of a speed-sensitive "slope window", which is put in front of the high-pass filter. The second channel consists of a system which has the properties of a high-pass filter, the time constant of which however depends on the amplitude of the input function.

Instead of simply connecting a resistor and a condenser, a high-pass filter can also be constructed by using a negative feedback loop which contains an integrator. The gain of this feedback loop is proportional to the time constant of the high-pass filter. A nonlinear system as required above can be constructed by using a nonlinear

characteristic in front of the integrator (Fig. 1, CH 1). The shape of this characteristic CH 1 causes high gain for small input amplitudes and low gain for large ones<sup>1</sup>. The half times of this system vary between 0.3 s and 1.1 s. The slope window used in the other channel is constructed by a differentiator (high-pass filter with a small time constant), a nonlinear characteristic (Fig. 1, CH 2), which produces zero output values for high speed input values and by an integrator at the end. In Figure 1 this circuit is framed by dashed lines.

These two channels can act together in such a way that for a slow ramp input the high-pass filter with the large time constant determines the output, while for high slope ramps and steps the high-pass filter with the small time constant controls the output behaviour. For ramps of intermediate slope both channels are active. This should result in a half time value between the extreme values determined by the time constants of the two single channels. The dead time values varying in a large range seem to be connected with the maximum slope of the output functions. This led to the assumption, that these dead times might be produced by a threshold. In the model this threshold is combined with the rectifier mentioned in the preliminary model at the end of each branch. After the summation the signals have to pass the low-pass filter and finally the lumped pure time delay.

It is certainly possible to find circuits to simulate separately the individual responses to the different input functions, but we have tried to create a single model capable of responding correctly to a wide range of inputs. If such a model is found one can assume with a certain probability that all the essential properties of the biological system have been found. This probability increases as the ratio of necessary to sufficient elements and connections is increased.

### E. Flexor System: Comparison Between the Results of the Experiment and the Simulation

As stated in Section D, in the  $\delta$ -response one finds only qualitative agreement between the experimental results and the responses of the preliminary model. However, it can be seen in Figure 2, that for the revised model even with respect to the value of the time constant the results agree quantitatively with those of the biological system. The responses to sine functions of constant amplitude ( $300 \mu\text{m} \approx 6$  V) and frequencies between 0.005 Hz and 2.5 Hz are shown in Figure 3. In this figure and all following ones the results of the simulation are shown by open symbols, usually circles, while the experimental results are shown by crosses. If in the simulation the accuracy of measurement is larger than the size of the symbols, this is shown by thick vertical bars without horizontal closing. In these ex-

<sup>1</sup> This circuit is based on an idea of Dr. M. Pandit, Kaiserslautern

periments the animals can change the gain of the system over a wide range (Bässler, 1972b), so that in some measurements the values of each single animal have small standard deviations, but the mean values of different animals differ considerably. In these cases the range of the mean values is shown by dashed vertical bars. [The corresponding mean standard deviations of the different animals can be found in Storrer and Cruse (1977)]. If the distribution of the single values is a normal one, the standard deviation is given by thin vertical bars. If the experimental results are insufficient to compute standard deviations, these mean values are shown in brackets. In the upper part of Figure 3 the amplitude frequency plots for the experiment and the simulation are compared. Here as well as when measuring the amplitude frequency plot for small input amplitudes ( $80 \mu\text{m} \cong 1.6 \text{ V}$ ), no significant difference between experiment and simulation can be seen. These results are not shown explicitly.

The middle part of Figure 3 shows the change of the dc-shift with frequency. As a measure to describe the dc-shift the minimum values of the sine responses are used (offset). Although one finds a sufficient description of the dc-shift for higher frequencies, the experimental values seem to be too high for lower frequencies. If one however regards the distribution of the single values measured in the experiments, one finds skewed distributions because values whose moduli are smaller than zero are not possible. Because of the skewed distributions the mean values shown in Figure 3 differ from zero, while the mode values for 0.005 Hz and 0.05 Hz are zero. The agreement between experiment and simulation is therefore much better than it seems to be at first sight.

In the lower part of Figure 3 the phase shift between input function and output function is shown. As the shape of the output function is significantly different from that of a sine function, the way of measuring the phase difference between input and output function has to be specially defined. With reference to Bässler (1974) this has been done by measuring the time between the beginning of a movement of the input function in one direction (=extreme value) and the

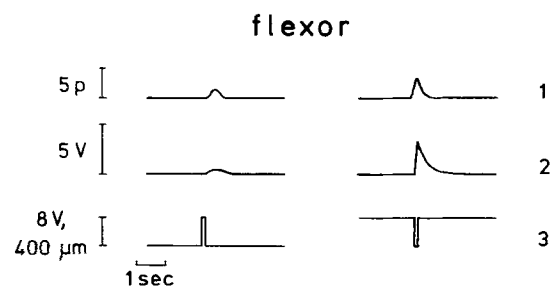


Fig. 2. Flexor system: comparison between the  $\delta$ -responses of the experiment and the simulation. 1: Experimental responses. 2: Simulation responses. 3: Input functions

## FREQUENCY RESPONSE FLEXOR

input amplitude (p-p):  $300 \mu\text{m}$  (+ experiment)  
 $6 \text{ V}$  (o simulation)

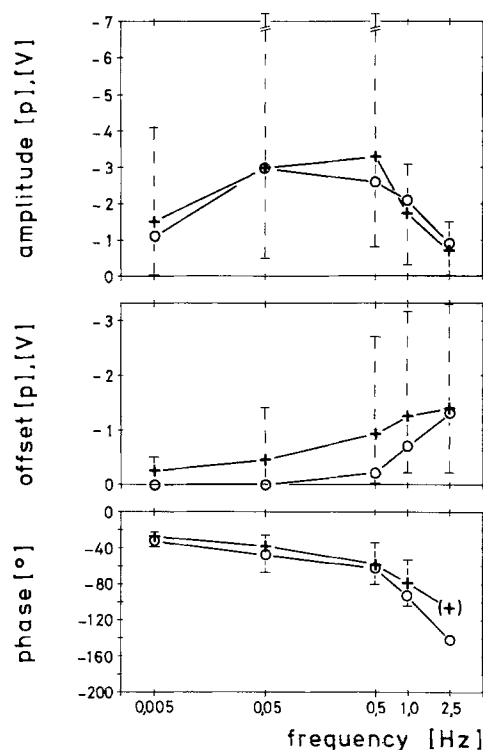


Fig. 3. Flexor system: the frequency responses of the experiment (+) and the simulation (o). For further details see the text

beginning of force development in the same direction in the corresponding output function. This is measured in the same way for both the experiment and the simulation. Again the agreement between model and biological system is sufficient.

Because of the limited range of the ramp functions as mentioned above, the half times of the "rising phase" of the force have been measured. After the input function has reached a constant value because of the limitation of the range of the ramp, the modulus of the output function falls to zero as can be expected from the step response. The half times are also measured for this "falling phase". These half time values together with the maximum amplitudes and the values of the different dead times are compared in Figure 4. A strong difference between experiment and simulation can here be found in the half times of the falling phase of the  $60 \mu\text{m/s}$  ramp and to a smaller degree in the half time of the rising phase of the  $60 \mu\text{m/s}$  ramp. This is astonishing, as no difference can be seen in the corresponding values of the maximum amplitudes. When assuming that no change in gain appears, either the amount of the maximum amplitude should be smaller in the biological system or the values

RAMP RESPONSE FLEXOR

input amplitude: 600  $\mu\text{m}$  (+experiment)  
12 V (o simulation)

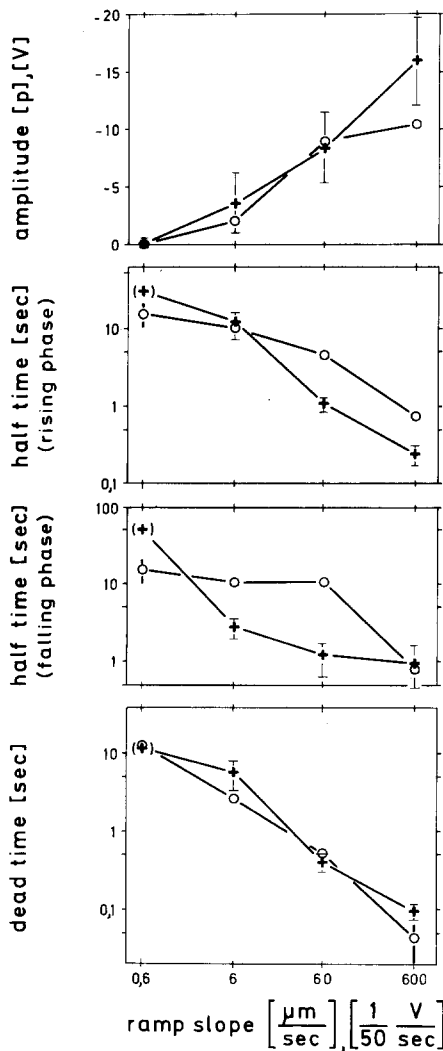


Fig. 4. Flexor system: the ramp responses of the experiment (+) and the simulation (o). For further details see the text

of the half times should be higher (as they are in the model). One possibility to explain these results is to assume that the flexor system consists not only of two but more parallel channels with different "slope windows". It may then be possible, that in some of these channels the gain is changed too. With the exception of these deviations an unexpectedly good fit between the experimental and the simulated results is found, at least in the order of magnitude.

In Figure 5 two parameters describing the step responses of the flexor system to steps of different amplitudes are compared. These are the half time of the falling phase and the maximum amplitude. The half times of this model show a good agreement with those

STEP RESPONSE FLEXOR

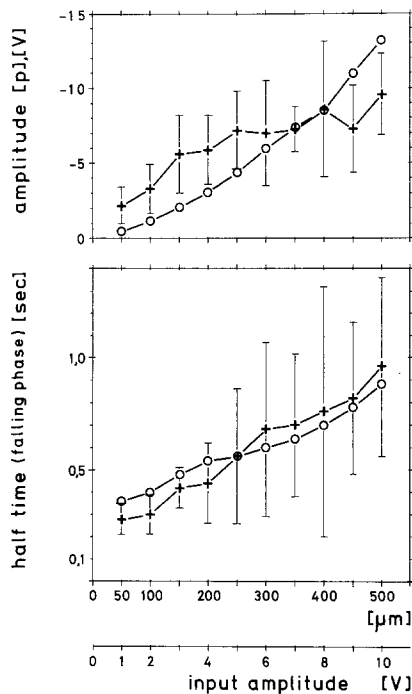


Fig. 5. Flexor system: the maximum amplitudes and the half times of the step responses of the experiment (+) and the simulation (o)

of the experiment. However, significant deviations can be seen when comparing the maximum amplitudes. These might be reduced by using an additional non-linear characteristic. Because of reasons discussed in Section H, in the present simulation this has however not been performed.

When shortening the temporal distance between a positive and a following negative step function, the maximum amplitude of the flexor response to the negative step function is diminished as the distance between both step functions is decreased. This can be seen in the  $\delta$ -response (Fig. 2) as an extreme example of a very short interval between the two steps. According to the model the amplitude should increase with increasing temporal interval exponentially with the time constant of the falling phase of the flexor step response. This is shown to be the case in Storrer and Cruse (1977, Fig. 8).

F. Extensor System:  
The Structure of the Final Model

Qualitatively the extensor system corresponds to the flexor system with two exceptions. Regarding the responses to steps of different amplitudes, the extensor system is much simpler, as here the value of the time constant of the falling phase is constant and therefore not dependent on the input amplitude. While in this

respect the extensor system coincides more with the preliminary model (Section C), the  $\delta$ -response cannot be described by this preliminary model as was possible at least qualitatively in the flexor system. The response of the extensor system to a  $\delta$ -function starting with a negative step should then look like the response of the flexor system to a  $\delta$ -function starting with a positive step (Fig. 2, trace 1). The real response of the extensor system however looks as if the high-pass filter did not assume negative values (Fig. 6, trace 1), because even after this short time interval no diminuation of the maximum amplitude of the response to the positive step appears.

This nonlinear behaviour is simulated by an "asymmetrical" high-pass filter (Section B). The time constant of responses to positive steps is  $\tau=22$  s, that to negative steps is  $\tau'=10$  ms. This part of the  $\delta$ -response is suppressed by the following rectifier. This suppressed part of the response can effect the total response only when a superposition of repeated events of a frequency higher than 50 Hz occurs, which however is never the case in this investigation.

In the responses to sine- and ramp functions only quantitative differences relative to the flexor system can be seen. The time constant of the rising phase of the step response is  $\tau_1=0.22$  s, that of the "slow" falling phase is  $\tau_2=22$  s. As in the flexor system, the upper corner frequency calculated from the time constant  $\tau_1$  of the step response is the same as the value which can be estimated from the amplitude frequency plot. As the corresponding lower corner frequency of  $\nu_2=0.007$  Hz is not essentially higher than the lowest frequency used in the amplitude frequency plot, it is not possible to say if a contradiction arises between the step response and the frequency response as was found in the flexor system. However, the values of the maximum amplitudes of the ramp responses are too high for slow ramps, because in a linear system these values should be proportional to the ramp slope. Therefore qualitatively the same contradiction as in the flexor system appears. Since the time constant of the extensor system seems also to depend on the slope of the input function, apart from the nonlinearities just described the extensor system was again simulated by a circuit of two parallel channels with high-pass filters of different time constants, one of which has a "slope window" in front of the high-pass filter. When a negative input step occurs before the output value to an earlier positive step has dropped to zero, this negative input step causes a fast fall in the output. This "fast" falling phase has a larger time constant than that of the fast rising phase in response to a positive step, while in the flexor system both values are equal within the accuracy of measurement. To describe these different time constants, an "asymmetric" low-pass filter (Section B) is used in the model. All other properties of the modelled extensor system are in principle the same as in the flexor mentioned above.

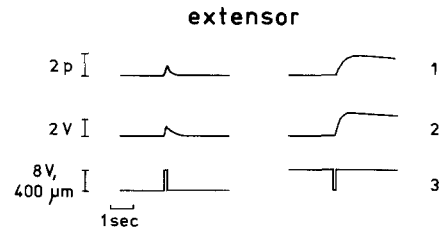


Fig. 6. Extensor system: comparison between the  $\delta$ -responses of the experiment and the simulation. 1: Experimental responses. 2: Simulation responses. 3: Input functions

## FREQUENCY RESPONSE EXTENSOR

input amplitude (p-p): 300  $\mu$ m (+ experiment)  
6 V (o simulation)

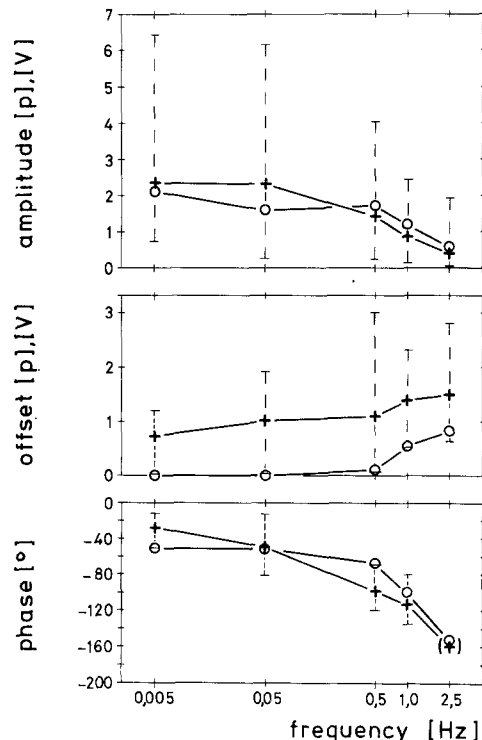


Fig. 7. Extensor system: the frequency responses of the experiment (+) and the simulation (o). For further details see the text

## G. Extensor System: Comparison Between the Results of the Experiment and the Simulation

The comparison between the  $\delta$ -response of the biological and the simulated system shows a good fit (Fig. 6). This is also true when regarding the amplitude frequency plot (Fig. 7, upper part). The dc-shift measured in the same way as in the flexor system (Section E) however shows significant differences, which cannot be explained in a similar way to those in the flexor system, because here the single values were distributed symmetrically. As the mean values measured in the

## RAMP RESPONSE EXTENSOR

input amplitude:  $600\ \mu\text{m}$  (o experiment)  
 $12\ \text{V}$  (+ simulation)

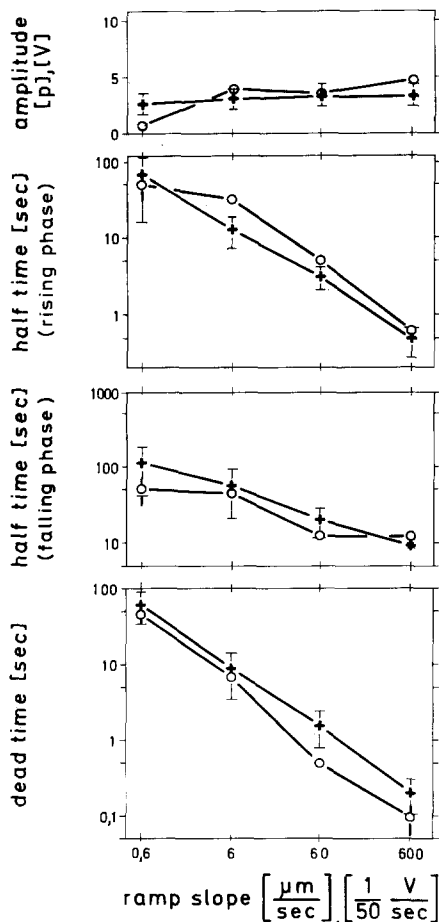


Fig. 8. Extensor system: the ramp responses of the experiment (+) and the simulation (o). For further details see the text

experiments are higher than those measured in the simulation by an almost constant value, a possible reason for this difference may be a spontaneous discharge rate very often found in the extensor motoneuron ET 1 ("slow" axon), but never in those of the flexor (Godden, 1972, 1974). As Godden could show in electrophysiological experiments, the effects of stimulating the chordotonal organ are superposed on the different but in individual animals constant discharge rates of the extensor slow axon. This superposition may therefore be the reason for the higher mean values in the experiment. This can be supported by the fact, that also in our experiments in individual animals for slow frequencies the values really fall to zero as expected in the simulation.

The phase frequency plots again show a good fit between experiment and simulation. This is also true for the values of the ramp responses (Fig. 8). Only the

maximum amplitude in the slowest ramp is too small in the simulation. This might easily be corrected by using a third parallel channel with a higher time constant and a different slope window. This is not done for the same reason as in the flexor system. The measured parameters (i.e. the time constants) of the step response and the responses to a negative step occurring shortly after a positive one are not shown here, because they completely coincide with the mean values of the experiments.

For both the extensor and flexor system stair functions and those consisting of the ascending or the descending branch of a sine function were examined (Storrer, 1976), but as the results gave no additional informations, they will not be treated here. The transient oscillations which were found in the experiments when starting a sine input function at its maximum are not investigated in detail but show qualitative agreement with the corresponding behaviour of the model. Finally it should be mentioned that the threshold of that step input function which produces no measurable output amplitude was found to be somewhat smaller than  $20\ \mu\text{m}$ . With the corresponding input function in the model ( $0.4\ \text{V}$ ) one gets an output function with a maximum amplitude of  $130\ \text{mV}$  ( $\pm 130\ \text{mp}$ ). As the minimum accuracy of measurement in the experiment was  $\pm 100\ \text{mp}$ , this also fits the experimental results.

## H. Discussion

The model discussed here represents a simplification of the biological system as some properties found in the experiments are not taken into account in the simulation. The most significant of these effects appears in the step responses. A step function can only be approximated experimentally by a limited ramp function with a slope as great as it is possible to achieve with the experimental device used. In linear systems the maximum amplitude of the response to a limited ramp increases with increasing ramp slope. When varying the slope of the "step" in these experiments it was however found that for very fast steps (slope greater than  $500\ \mu\text{m/s}$ ) the amplitude of the step responses decreases with increasing slope (Storrer and Cruse, 1977) in both, the flexor and the extensor system. This additional nonlinearity was not considered in the simulation, because it does not influence the other results except for the amplitudes of the step responses at high amplitudes and the amplitude frequency plot for the highest frequencies. Another nonlinear property of the biological system was found by Bässler (1965), when measuring the movement of the tibia as an output. Using step input functions with a small, constant amplitude but different range, the system provides a larger output amplitude to positive and negative steps, when the movement of the receptor apodeme starts at a high elongation of the chordotonal organ (corresponding to a small femur-tibia angle). To simulate this nonlinearity an additional input characteristic might be



used, which enlarges the gain for higher input values. Since this effect is relatively small in the range of all input functions used here except of the small values of the ramp functions, this nonlinearity is also neglected in the simulation. The stronger effect of this nonlinearity on the ramp responses might at least partially explain the differences between experiment and simulation for these particular input functions. Because of these reasons the model discussed here can only be regarded as a first-order approximation.

When evaluating the agreement between experiment and simulation an additional factor has to be taken into account. These animals show a considerable individual variability in the parameters measured here. The standard deviations of the individual animals in each series of experiments are relatively small, while the mean values of different animals vary in a large measure. This is obvious when for example comparing the shape of the ramp responses obtained by Storrer and Cruse (1977) and those by Bässler (1972, Fig. 17). Especially, the gain of the system can be changed even within the same animal (Bässler, 1972b). As the different experimental series could only be performed with different animals for technical reasons, between these series changes have to be expected, which however are not to be seen in the simulation. Therefore especially for such parameters which vary over different decades, a coincidence in the order of magnitude may be a sufficient description in this first-order approximation. In this sense a good agreement between experiment and simulation can be stated, although on the basis of linear systems theory strong contradictions have been found. Those cases which show large differences can be explained either by the reasons just mentioned or by enlarging the model by additional parallel channels with different "slope windows" (see also Sections E, G). Such a circuit might also diminish a difference between experiment and simulation, which cannot be recognized from the parameters shown in the figures. The shape of the simulation response of the flexor system to a sine function of 0.5 Hz falls into two parts, equivalent to the response of each channel, while in the experiment as in all other cases of the simulation no such decomposition can be seen. Nevertheless such an enlargement of the model has not been performed, because the actual knowledge about the biological system is not sufficient to justify a more detailed model. This should not be done until electrophysiological investigations have been made.

In the following it will be discussed to what extent the structure of the model can be called necessary in the mathematical sense and at the same time whether single elements of the model could be connected with known morphological structures. The necessity of the arrangement of the high-pass filter, the rectifier and

the low-pass filter is mentioned in Section C. There is a theoretical argument in addition to the morphological one (Section C) for putting the low-pass filter at the end because the dc-shift shown in Figures 3 and 7 is only possible when the low-pass filter is behind the rectifier. This rectifier can be represented by the rectifier properties of the muscles (Section C) or by those of any interconnecting neurons or even by such properties of the sensory cells of the chordotonal organ. However, in each case the high-pass filter must lie in front of this rectifier.

The biological system contains the chordotonal organ with its sensory cells and the muscles with their motoneurons, and probably several interneurons. The branching between the flexor system and the extensor system has to be in front of the motoneurons, because the motoneurons are different for each muscle [3 motoneurons of the extensor tibiae, 4 motoneurons of the flexor tibiae, Godden (1972)]. Some of these may be inhibitory neurons, the role of which is unknown. [As Iles and Pearson (1971) showed that the firing of an inhibitory neuron accelerated the decay of the force at the end of an excitation of a muscle, it may be possible, that the different time constants of the extensor system to positive and negative steps may be traced back to different innervation by inhibitory neurons.] The branching may even arise in the chordotonal organ itself. Füller and Ernst (1973) describe it as consisting of two groups of sensory cells, one group of about 420, the other of about 80 cells arranged pairwise. This arrangement might possibly indicate such a physiological division.

The existence of the two parallel branches in each of the subsystems is not necessary. One can also think of one channel constructed in a way that the half time of the rising phase of a ramp response depends on the ramp slope. It is also possible to describe the different half times of the falling phase in the same way. Then, however, a complicated memory circuit is necessary because, during these falling phases of different shapes, the input function in all cases has the same constant value. The multi-channel model described here does not require such a circuit. The greater simplicity and the fact, that in biological systems parallel processing is very common support the hypothesis of the multi-channel model. A possible morphological substrate might be the different parallel motoneurons, which control "slow" and "fast" contractions of the muscles and which show different dynamic properties (Godden, 1974). In the same way as in the branching of the two subsystems, the splitting of the branches of each subsystem can occur at all levels of interneurons and even in the sensory cells of the chordotonal organ itself. It is hoped that this question may be answered by electrophysiological investigations. The circuit pro-

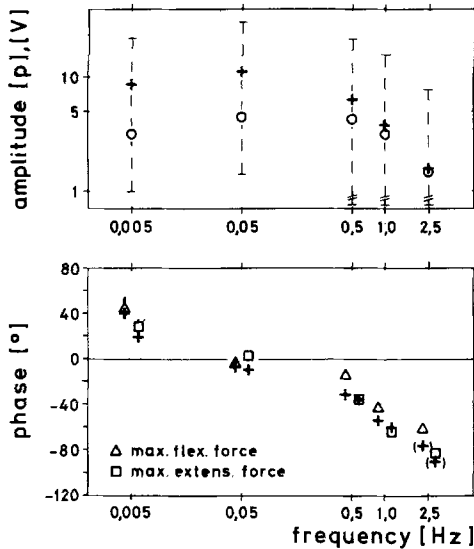


Fig. 9. The amplitude frequency plot and the phase frequency plot of the total system (Figure 1, dashed lines, output). Comparison between experiment (+) and simulation (O, Δ, □). For further details see the text

viding the "slope window" and the high-pass filter with a time constant dependent on the input amplitude could be constructed electronically in different ways, which here however are not explained further.

The response of the extensor system to a positive step following a negative one shows the same behaviour as a simple phasic sensory cell (Fig. 6) because negative spike frequencies are not possible. This type of response is therefore not unusual from an electrophysiological view. The response of the flexor system to a negative step following a positive one however requires on the neuronal level a more complicated system. One possibility to obtain a behaviour like that of the flexor system is to have a neuron with the phasic properties of the corresponding high-pass filter but with a constant spontaneous frequency when not excited. If the following neuron had a threshold precisely at this spontaneous frequency, these two neurons would show exactly the behaviour of the flexor system. Another possibility is to take two phasic neurons connected in parallel, one excited only by input functions with positive slope, the other only by those with negative slope. The output of both neurons is summed with different sign on a third neuron. These two parallel connected neurons may either be in the flexor system with both having the same time constant or, the one responding to negative steps may lie in the flexor system, while the other branches from the extensor system behind its high-pass filter, acting as an inhibitory pathway from the antagonistic system. In this case the

dynamic properties of this neuron have to be different from those of the corresponding neuron in the flexor branch. Both latter possibilities however work only when the two parallel neurons are unidirectionally sensitive. This however would have the consequence, that on input functions consisting of repetitive events as for example sine functions the mean spike frequency of both neurons would reach very high values when acting against each other. This appears to be very uneconomic, thus the possibility discussed first seems to be the more probable one.

As a last comparison between experiment and simulation the frequency response of the whole system may be examined. This is done in measuring the sum of the forces acting on the tibia by both antagonistic muscles by simply connecting the tibia to a force meter without cutting either muscle tendon. In this experiment the system has one input and only one output. In Figure 1 this is symbolized by dashed lines in the output. The upper part of Figure 9 shows the amplitude frequency plot of the experiment and the simulation. Remembering the possible change of the gain in different animals one finds a sufficient agreement between both results. In the lower part of Figure 9 the corresponding phase frequency plot is shown. The phase differences between the maximum of the input function and the maximum of the flexing force (□) and those between the minimum of the input function and the maximum of the extending force (Δ) are compared separately. The results of the experiment are shown by crosses and are drawn in the same vertical line as the corresponding simulation values. This phase frequency plot shows a much better correspondence to what one expects from a band-pass filter than those shown in Figures 3 and 7, as positive phase shifts are found for slow frequencies. This is because the strong nonlinearity which is caused by the rectifiers in both subsystems is cancelled by the summation of the outputs of both subsystems. Again close agreement between experiment and simulation is found. Bässler (1974) performed the same experiments in a smaller frequency range and found corresponding results.

As mentioned above (Section A), the system regarded here represents a closed loop feedback mechanism, which is broken experimentally in front of the feedback transducer in order to investigate the open loop system. One could suppose, that this feedback mechanism acts in the animal as a servomechanism that controls the position of the tibia relative to the femur in the static animal. Another possibility is that it acts as a servomechanism that controls active leg movements (e.g. walking movements). The question arises at which positions of the open loop model the reference input could act on the closed loop system.

The investigation of this system when the legs were showing active movements has shown that fundamental changes in the system can be seen (Bässler, 1973, 1974). As an example, positive feedback appears in the active state. Therefore only the system working in the static animal is discussed in the following section. Results of Godden (1974) show that a sort of reference input exists, as a constant discharge rate in one of the three extensor motoneurons (ET 1) controls the value of the femur-tibia angle. If the frequency of ET 1 is zero, the femur-tibia angle is about  $90^\circ$  which corresponds to the state when the position of the tibia is only determined by the elastic properties of both unexcited muscles. The higher the constant discharge rate of the unit ET 1, the higher is the value of the femur-tibia angle. One can assume that the input on the extensor motoneuron is added in the extensor system behind the high-pass filter, because the value of this discharge rate can show no changes over several hours. If this connection arose in front of the low-pass filter, the difference in the dc-shift of the extensor system (Fig. 7) could be explained by this additional input found by Godden (1974). No such constant discharge rates could be found in the flexor muscle. A simple possibility to understand the experimental results would therefore be that the reference input acts only on the extensor system and is summed up behind the high-pass filter.

The phasic behaviour of this feedback mechanism as well as its high sensitivity to input ramps of very small slope are unexpected properties of a normal biological feedback mechanism. Both properties however seem to have biological significance. When a constant, strong disturbance input on the static animal arises, the phasic behaviour appears to be appropriate, as it would be undesirable to oppose this disturbance input over possibly several hours during which the animal may remain in one position. It is the phasic property of the system which permits these forces, caused by the control system, to diminish to zero after some time. The high sensitivity to ramps of very small slope provides a possible explanation of another behaviour of the animal, the "flexibilitas cerea" (Bässler, 1972b).

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