

## Reversal of a Reflex to a Single Motoneuron in the Stick Insect *Çarausius morosus*\*

U. Bässler

Fachbereich Biologie der Universität Kaiserslautern, FRG

**Abstract.** In “inactive” stick insects ramp-wise stretching of the femoral chordotonal organ excites the slow extensor tibiae motoneuron. In “active” animals the same stimulus decreases the firing rate of this motoneuron. The time-course of increased and decreased firing rate is different. The same difference in reactivity of this motoneuron can be seen with triangular stimulation.

### Introduction

In electrophysiological literature dealing with the control of movement in arthropods there seems to be general agreement that reflexes are always working qualitatively in the same way. Only the gain of the reflex loop appears to change. As an example Burrows and Horridge (1974) report that the reflexes they studied in locusts “are stable, not easily blocked or changed in gain, and persist through other movements”. In behavioural studies on stick insects I have found that the reaction to a particular stimulus depends on the behavioural state of the animal (Bässler, 1973, 1974, in preparation). The different kinds of reactions in these different internal states of the animal could be due to activation of different motoneurons. To test this hypothesis the reversal of a relatively simple reflex should be examined in neuronal terms.

An example of such a simple reflex is the reaction to stretching of the femoral chordotonal organ in restrained stick insects. In “inactive” animals (animals which only move the stimulated leg) this stimulus causes an extension of the femur-tibia-joint of the stimulated leg. In “inactive” animals (animals which move also other legs) stretching the femoral chordotonal organ causes a flexion of the joint (Bässler, 1973, 1974). In order to examine this reversal at the

neuronal level recordings of the activity of the nerve supplying the extensor tibiae muscle were made. This muscle is innervated by three motoneurons. One of them, the slow extensor tibiae neuron (ET 1), is easily recognized by its spontaneous activity in resting animals (Godden, 1972). Therefore the firing rate of this neuron was examined as a function of movement of the chordotonal apodeme in “active” and “inactive” animals.

### Method

It is very difficult to make intact restrained animals “active” for long periods under daylight conditions. Therefore most of the experiments were performed with decerebrated animals. These are active for some time after a disturbance. The only disadvantage is that the gain of the “inactive” reaction is lower than in intact animals. The stick insects were decerebrated as described in 1973.

The animals were fixed ventral side down on a cork-plate, the femur-tibia-joint of the tested leg outside the edge of the plate. The animal was fixed in a way that at least two tibiae of non-tested legs were free to move. Round the inner two thirds of the femur of the tested leg there was a small basin filled with stick-insect-saline. The femur was opened from the dorsal side. The extensor tibiae muscle was removed. Then the receptor-apodeme of the femoral chordotonal organ and the nerve supplying the extensor-muscle are free. This nerve is a mixed nerve, its sensory part coming from tactile hairs and from sense organs near the femur-tibia-joint and the end of the apodemes of extensor and flexor muscles. To maintain the afferences from these sense organs the impulses were recorded *en passant* by a 50 µm silver-wire hook surrounded by petroleum jelly. The impulses were amplified by a Grass P 15 amplifier and recorded on tape (together with the stimulus).

The receptor-apodeme of the femoral chordotonal organ was held by a clamp. Before the receptor-apodeme was clamped the angle between femur and tibia was 90°. So in the experiments the mean position of the receptor-apodeme corresponds to a 90°-position of the joint. After fixing it, the receptor-apodeme was cut between clamp and tibia. Movement of this clamp was produced by a pen-motor. The amplitude of all stimuli was 300 µm.

From behavioural experiments it is known that the best way to obtain a definite “active” reaction is to use a rampwise stimulation of the chordotonal organ. Therefore the form of the most frequently used stimulus was a ramp with a time of rise of 100 ms. The interval between two ramps was between 0.5 and 5 s. In some

\* Supported by the Deutsche Forschungsgemeinschaft

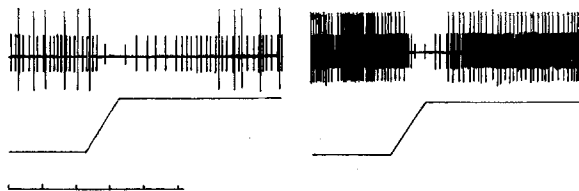
experiments steps and triangular stimuli were applied to the receptor-apodeme.

I have defined (Bässler, 1973) the "active" state as that state in which tibiae other than that of the tested leg move.

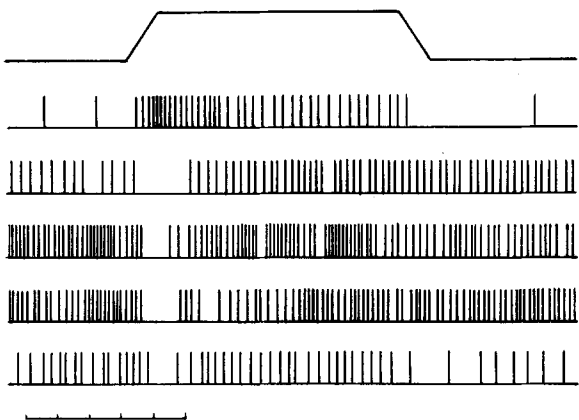
## Results

Figure 1 shows typical recordings from "active" animals. One can see three motoneurons active with different spike-amplitudes. The neuron with middle spike-amplitude is spontaneously active in "inactive", non-stimulated animals. It is therefore the slow extensor tibiae motoneuron described by Godden (1972). The large unit appears to be another excitatory unit while the small unit may be an inhibitory neuron. The sensory units running in the same nerve have much smaller spikes which are not to be seen in the figures. They will be described in another article.

In the following presentation I have only paid attention to the slow extensor tibiae neuron. Therefore in the other figures only the activity of this neuron is shown. This neuron has normally an impulse rate of



**Fig. 1.** Two records from the nerve supplying the extensor tibiae muscle during ramp-wise stimulation of the femoral chordotonal organ. Decerebrated "active" animals. Upper trace: Record from the nerve. The middle-sized spikes belong to the slow extensor tibiae motoneuron. Second trace: Stimulus. Upward means stretching the chordotonal organ. Third trace: Time (100 ms)



**Fig. 2.** Activity of the slow extensor tibiae motoneuron during ramp-wise stimulation of the femoral chordotonal organ. Upper trace: Stimulus. Upward means stretching the chordotonal organ. Second trace: Activity of the neuron in an "inactive" animal. Each vertical line corresponds to a spike. Third-sixth trace: "active" animals, otherwise like second trace. 3<sup>rd</sup>, 4<sup>th</sup>, 6<sup>th</sup> trace: decerebrated animals, 5<sup>th</sup> trace: intact animal. Last trace: Time (100 ms)

about 5/s to 10/s. When the animal becomes "active" the impulse rate increases very much. In "active" movements the impulse rate can change very quickly.

Figures 1 and 2 show some typical records from *decerebrated animals* with *ramp-stimulation*. They show that stretching the femoral chordotonal organ in "inactive" animals excites the neuron but in "active" animals the firing is stopped. That means, the same stimulus can give reverse reactions dependent on the state of activity of the animal.

One can see that the time between the beginning of the outward movement of the receptor-apodeme and the beginning of an increase in firing rate in "inactive" or reduction of firing rate in "active" animals is nearly equal. Evaluation of more than one hundred reactions in each state show that this time in "inactive" animals is between 10 and 45 ms, in "active" animals between 10 and 100 ms.

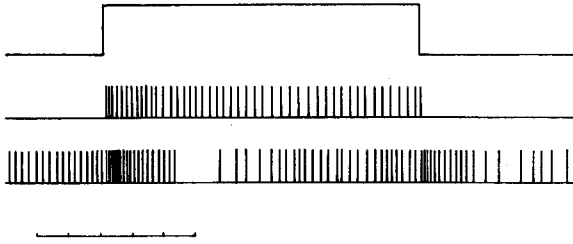
The increase in firing rate in "inactive" animals lasts a very long time. This was to be expected from behavioural experiments. However, the reduction of firing rate in "active" animals only lasts for a very short time. In 158 "active" reactions of four decerebrated animals the time during which no spike occurred was between 30 and 210 ms (mean value 110 ms).

In some animals the tibia was free to move. In other ones it was fixed in about a 90°-position. No difference between these two groups of animals could be seen.

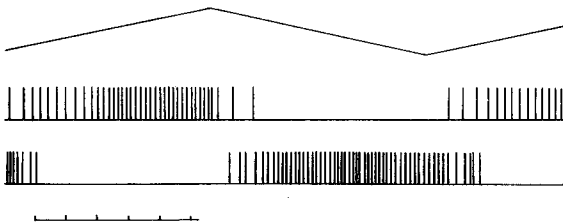
Releasing the chordotonal organ (inward movement of the receptor-apodeme) in "inactive" animals reduces the firing rate of the slow extensor tibiae motoneuron. In "active" animals no response to this kind of stimulus could be seen. This agrees with results of behavioural experiments where only stretching the chordotonal organ had an influence on leg-movement in "active" animals. At the end of a period of activity the animal not being totally inactive, sometimes stretching and releasing the chordotonal organ reduces the impulse rate of the neuron (Fig. 2, 6<sup>th</sup> trace). The reaction on stretching seems to be an "active" one, the reaction on releasing seems to be an "inactive" one. Similar results have been obtained in behavioural experiments (Bässler, 1974).

Some experiments were performed with *intact animals*. The results were more or less the same as in decerebrated animals (Fig. 2, 5<sup>th</sup> trace).

*Step-wise stretching* the femoral chordotonal organ in "inactive" animals excites the slow extensor tibiae motoneuron with latencies of about 10 ms (Fig. 3). Very rarely, in "active" animals a reduction of firing rate is seen. An example is given in Figure 3. The latencies of these "active" responses are large. They



**Fig. 3.** Activity of the slow extensor tibiae motoneuron during step-wise stimulation of the femoral chordotonal organ. Decerebrated animals. Signature and time as in Figure 2. First trace: Stimulus. Second trace: "inactive" animal. Third trace: "active" animal



**Fig. 4.** Activity of the slow extensor tibiae motoneuron during triangular stimulation of the femoral chordotonal organ. Decerebrated animals. First trace: Stimulus. Second trace: "inactive" animal. Third trace: "active" animal

are for 40 definite "active" responses of four decerebrated animals between 100 and 300 ms. The time during which no spike occurred is within the same range as that following ramp-wise stimulation.

*Triangular stimulation* in "inactive" animals causes an excitation of the neuron during stretching the chordotonal organ. In "active" animals during the same stimulus a decrease in firing rate is observed (Fig. 4). The duration of this phase is much longer with this kind of stimulation. Thus with this kind of stimulation the slow extensor tibiae motoneuron is active in "inactive" animals during stretching the chordotonal organ and in "active" animals during releasing the chordotonal organ: The reaction is reversed.

## Discussion

The experiments show that the effect of stretching the femoral chordotonal organ on the slow extensor tibiae motoneuron depends upon the state of activity of the animal. The changes are not merely alterations in the latency or strength of the reaction but involve a complete reversal of the sign of the reflex. Thus a resistance reflex in the "inactive" animal becomes an assistance reflex in the "active" animal. As the time course of increased firing rate in "inactive" and of decreased firing rate in "active" animals is different, one must argue that the information for increasing and decreasing the firing rate flows over different channels. It is not clear whether these different channels are formed only by different interneurons or also by different units of the chordotonal organ.

The decrease in firing rate in "active" animals is unlikely to be a central programme only triggered by stretching the chordotonal organ. Otherwise it must be more stereotypic in length.

## References

- Bässler, U.: Zur Steuerung aktiver Bewegungen des Femur-Tibia-Gelenkes der Stabheuschrecke *Carausius morosus*. *Kybernetik* **13**, 38—53 (1973)
- Bässler, U.: Vom femoralen Chordotonalorgan gesteuerte Reaktionen bei der Stabheuschrecke *Carausius morosus*: Messung der von der Tibia erzeugten Kraft im aktiven und inaktiven Tier. *Kybernetik* **16**, 213—226 (1974)
- Bässler, U.: Sensory control of leg movement in the stick insect *Carausius morosus* (in preparation)
- Burrows, M., Horridge, G. A.: The organization of inputs to motoneurons of the locust metathoracic leg. *Phil. Trans. R. Soc. Lond. B.* **269**, 49—94 (1974)
- Godden, D.: The motor innervation of the leg musculature and motor output during thanatosis in the stick insect *Carausius morosus*. *J. comp. Physiol.* **80**, 201—225 (1972)

Received: April 30, 1976

Prof. Dr. U. Bässler  
 Fachbereich Biologie der Universität  
 Postfach 3049  
 D-6750 Kaiserslautern  
 Federal Republic of Germany