Modelling of the Active Reaction of Stick Insects by a Network of Neuromimes

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Abstract. Depending on the activity status of the animal, the control system of the femur-tibia joint in stick insects exhibits either a resistance reflex, or the "active reaction", a totally different action pattern (Bässler 1988a). Using analog electronic neuron models, several different neuronal circuits are explored that model the active reaction with all its features. The models differ in complexity, redundancy and the robustness against small variations of network parameters (e.g. coupling strengths). The circuit with the highest robustness and redundancy requires interneurons with special features, such as found in real animals. When inserted into a closed loop modeling movement and sensory feedback from the periphery, this circuit produces oscillations similar to searching movements found in the real animal. In addition to intracellular recording methods, the authors propose modeling with realistic neuromimes as a complementary method in the investigation of neuronal networks which have well documented input-output relationships.

Introduction

The position of the femur-tibia joint in locusts and stick insects is measured by the femoral chordotonal organ. A flexion of the joint stretches the chordotonal organ, and extension results in a relaxation (Bässler 1983).

The mechanical connection between the chordotonal organ and the joint can be severed (opening of the feedback-loop) and well defined mechanical stimuli can be applied to the chordotonal organ. Stretching of the organ now signals a fictive flexion of the joint. This stimulus elicits totally different reactions depending on the internal state (active or inactive) of the stick insect. In the inactive animal, the stimulus produces a strong excitation of both excitatory motoneurons of the extensor tibiae muscle. Since the stimulus mimics a passive flexion, this reaction can be described as a resistance reflex (negative feedback) (for a review see Bässler 1983). In the active animal, the same stimulus elicits a more complex reaction, the so-called active reaction. The resistance reflex is obviously switched off in this condition (Bässler 1988a).

Relaxation of the chordotonal organ in the inactive animal also produces a strong resistance reflex (excitation of flexor tibiae motoneurons). In the active animal, there is no clear response to the stimulus. Since the active reaction only occurs in response to stretch stimuli, we will restrict the following description to these stimuli.

The following description of the active reaction is based on experiments on the stick insect Cuniculina impigra (Bässler 1986, 1988a). The appropriate stimulus is a rampwise stretching of the chordotonal organ, signalling a fictive flexion of the joint of a substantial amount (e.g. from 120° to 50°). If the ramp velocity is lower than approximately 200°/s, the excitatory motoneurons of the extensor tibiae muscle are inhibited at the start of the stimulus. At the same time, the excitatory motoneurons of the flexor tibiae muscle are excited (Fig. 1a). This signifies a positive position feedback reaction, and thus represents the opposite of the reaction in the inactive animal. When the chordotonal organ signals a rather flexed joint position, the flexor motoneurons are inhibited and the extensor motoneurons are excited strongly. In one preparation, this transition from flexor to extensor activity always takes place at the same joint position. We will label this position the "transition point". Thus, the transition point is independent of the stimulus velocity, provided that the stimulus is sufficiently slow to elicit the active reaction at all. At stimulus velocities higher than approximately 500°/s, there is no active reaction. In this case, the extensor motoneurons start to fire at the
Fig. 1a and b. Excitation level of extensor and flexor motoneurons, schematic presentation. a Active reaction found in Cuniculina front legs. b Hypothetical active reaction if position and velocity information were superimposed linearly (for details see text).

onset of the stimulus, in the active animal as well. Thus, the system shows negative position feedback characteristics at high stimulus velocities, just as in the inactive animal. When the stimulus velocity is in the range of 200–500°/s, the system may show one or the other type of reactions.

During the first part of the stimulus, there is positive position feedback, if the stimulus velocity is small. If the femur-tibia control loop were closed, this would lead to an acceleration of slow flexion movements. On the other hand, high stimulus velocities elicit negative position feedback. In the closed system, this would result in braking fast flexion movements. The system producing the active reaction thus accelerates slow and brakes fast flexion movements. It may therefore be considered as some kind of a velocity control system for flexion movements. Since with slow flexion speeds the transition point is only dependent on joint position, the system also controls the end-point of a flexion movement (i.e. the transition from flexion to extension).

The neural system producing the active reaction is very likely to be a subunit of the walking pattern generator. In the front leg, the flexor activity corresponds to the stance phase, whereas the extensor activity corresponds to the swing phase of a step (Bässler 1986, 1988a; Nothof and Bässler, in preparation). It is likely that the active reaction also controls flexion movements of the femur-tibia joint in searching movements. During searching movements, the flexion movements of this joint show a position-dependent end-point control and a continuous velocity control involving the chordotonal organ (Weiland and Koch 1987).

A reaction very similar to the active reaction described above was found in the thorax-coxa joint of the crayfish Pacifastacus leniusculus (Skorupski and Sillar 1986). Thus, it is possible, that this type of reaction is common to a larger number of systems. In this work, we have tried to gain new ways to ask precise questions concerning the analysis of the interneurons involved in the production of the active reaction. To this aim, we have tried to construct a network using electronic analogue neuron-models which would be able to produce the active reaction.

The output of this network was used to generate simulated muscle forces and a simulated movement of the joint. When these movement parameters were used as "sensory" input to the network, the system represents part of the closed femur-tibia control loop. The closed network model showed oscillations. This proves that the system that produces the active reaction is also sufficient to generate rhythmic joint movements.

Choice of Model Neurons

In the locust it was shown that the afferents of the chordotonal organ project either directly on motoneurons, or on non-spiking interneurons or on spiking interneurons, see, e.g. Burrows (1987a); Burrows et al. (1988). In the stick insect, the resistance reflex of the inactive animal has a shorter latency than the active reaction (Bässler 1988a). This means, that the active reaction is mediated by a longer neural pathway, which in analogy to the locust (cf. Burrows 1985) might look like the following chain:


In a series of experiments, the active reaction was studied while stimulating trochanteral campaniform sensilla in addition to the chordotonal organ. The results led to the conclusion, that the active reaction is formed in a two-step process. In a first step, the basic pattern of the active reaction itself is formed. In the second step, this pattern can be somewhat modified by other influences yielding the final motor output (Bässler 1988a). This led to the assumption, that the basic pattern of the active reaction is formed by the spiking interneurons being the first part of the chain quoted above. The modifying influences would then be added in the stage of the nonspiking interneurons. This assumption was verified: if the ventral median part of the ganglion is destroyed, the animal can no more produce an active reaction. The resistance reflex of the inactive animal, however, remains unchanged (Bässler 1988b). In this region of the ganglion, the only...