

# Modeling of the locust flight control network: Interaction of central network and sensory feedback.

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## 1 Introduction

The locust flight oscillator provides an excellent model system for the study of motor pattern generation on the neuronal network level. The central flight oscillator is electrophysiologically well-studied and sufficiently complex to exhibit emergent network properties (e.g. Robertson & Pearson, 1984). As yet, though, modeling studies of the flight pattern generator are basic (Grimm & Sauer, 1995) compared to those of many other rhythm generating systems.

The deafferented central nervous system of the locust produces a slow rhythm (10Hz, as compared to >20Hz intact wingbeat frequency, Wilson, 1961) that is otherwise similar to the intact flight motor pattern. Interaction of this central pattern generator (CPG) with proprioceptive feedback plays an important role in the (functionally adequate) patterning of motor activity (Wolf & Pearson, 1988). This proprioceptive feedback is provided by sense organs associated with the wing base, such as stretch receptors and tegulae. They signal upper and lower stroke reversals, respectively. The tegula is able to reset the wing stroke. While synaptic connections of the tegula to flight interneurons are well-known, the functional relevance of connections to core oscillator interneurons, as opposed to external reflex pathways, is not understood. Elucidating the functional relevance of such network properties through a modeling approach is the objective of our study.

## 2 Simulation Environment

Neurons and networks were modeled in the simulation environment madSim (Mader et al., 2003). A neuron was represented by a soma connected to three unbranched dendritic compartments. Active and passive neuron properties were implemented according to Hodgkin-Huxley equations (Hodgkin & Huxley 1952). The sodium and potassium currents were modified to enable high frequency firing.

## 3 Network Structure

We simulated a network structure based on Grimm & Sauer (1995; Fig.1), and previous electrophysiological analyses.

The present simulation does not account for the fact that most flight interneurons exist in more than one copy. First, there are bilateral pairs of neurons within a given ganglion (e.g. 301; Robertson and Pearson, 1983) and, second, in some cases there are additional segmental homologs in adjacent neuromeres (Robertson, Pearson & Reichert, 1982; e.g. neurons 501, 401, 201 and 504).

Robertson & Pearson (1985) describe a delayed synaptic connection between neurons 301 and 501 with inhibitory-excitatory properties. We modeled this connection according to the authors' assumption that it represents a disinhibitory pathway, with neuron 301 inhibiting in a graded manner the tonic release of transmitter from one or more unidentified interneurons. We hypothesize this interneuron to be neuron 511. 511 was shown to receive short-latency IPSPs from neuron 301, and in turn elicits short latency IPSPs in neuron 501 (Robertson & Pearson, 1985).

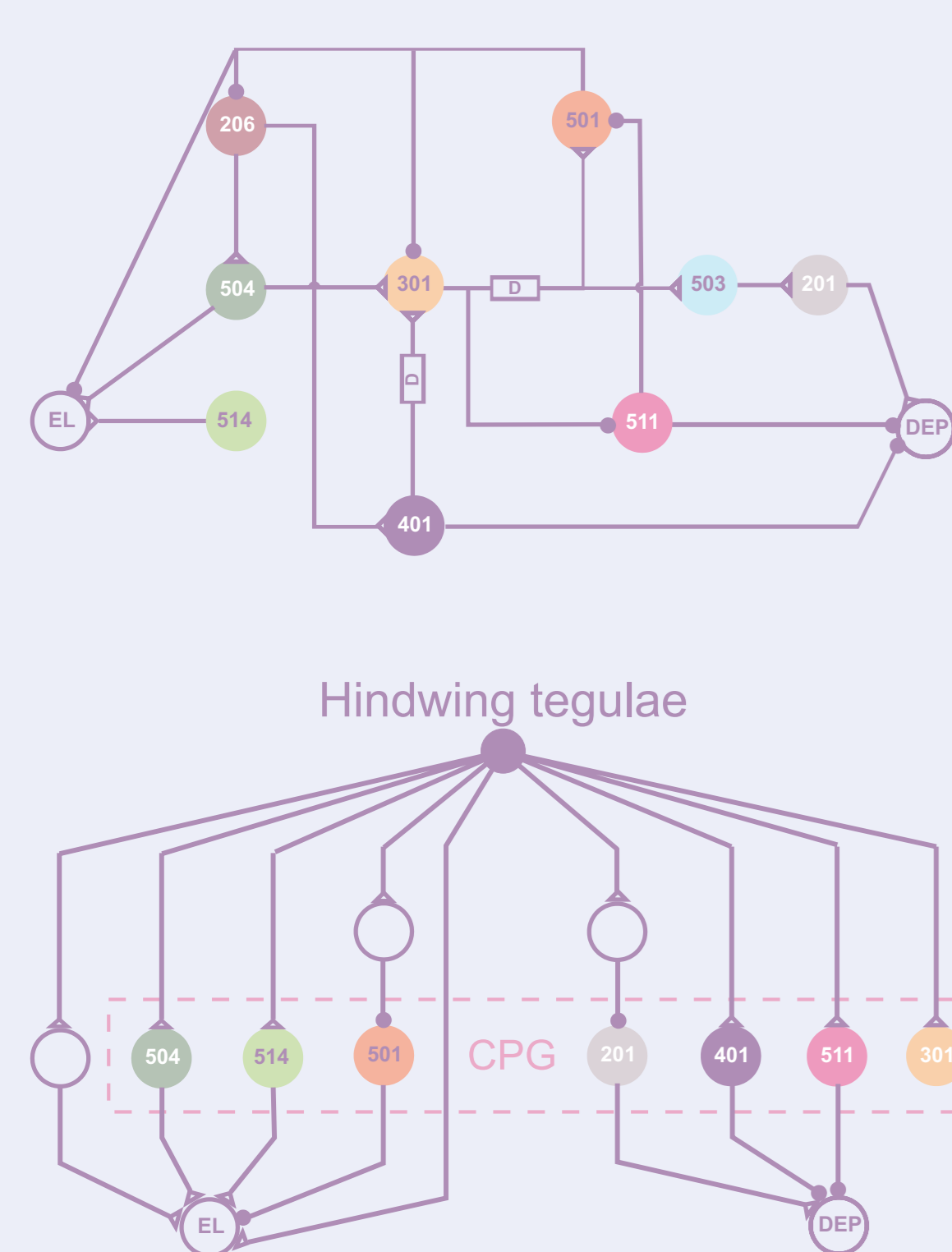
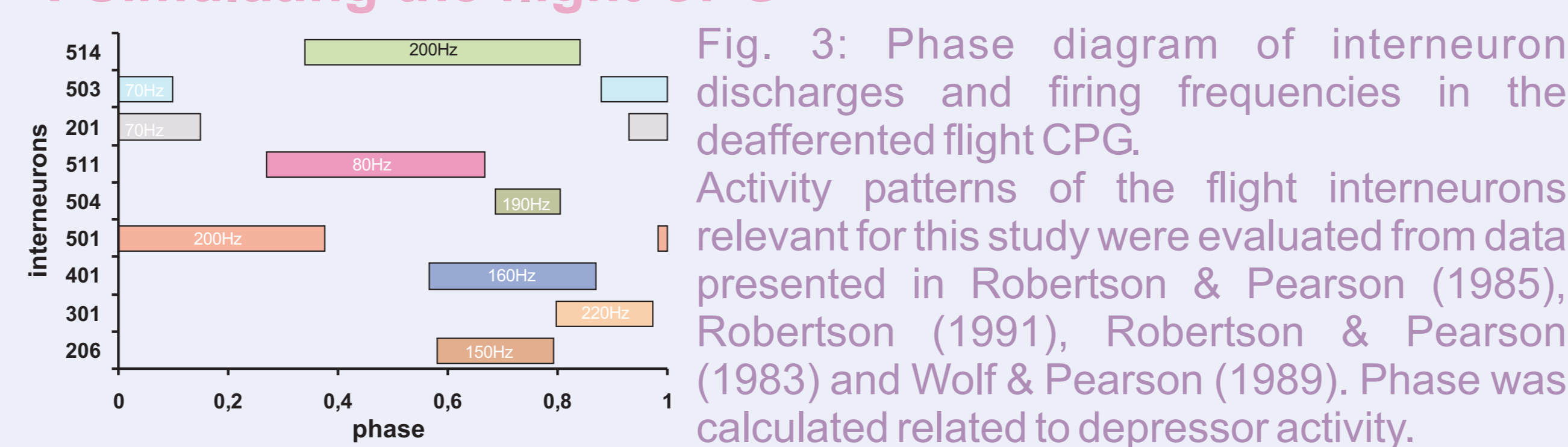


Fig. 1: Model network proposed by Grimm & Sauer (1995; adapted from their Fig.1) for the locust flight CPG. Numbers mark identified interneurons, EL and DEP the wing elevator and depressor motoneurons, respectively. Inhibitory synaptic connections are represented by dots; 'D' signifies a central delay of several milliseconds. Only those neurons and connections are shown that were implemented in our simulation. Input to neuron 514 see section 4.

Fig. 2: Connectivity pattern of the tegula afferents, adapted from Wolf (1993). Open cells were not implemented as model neurons in our simulation, but represented by simple delays.

## 4 Simulating the flight CPG



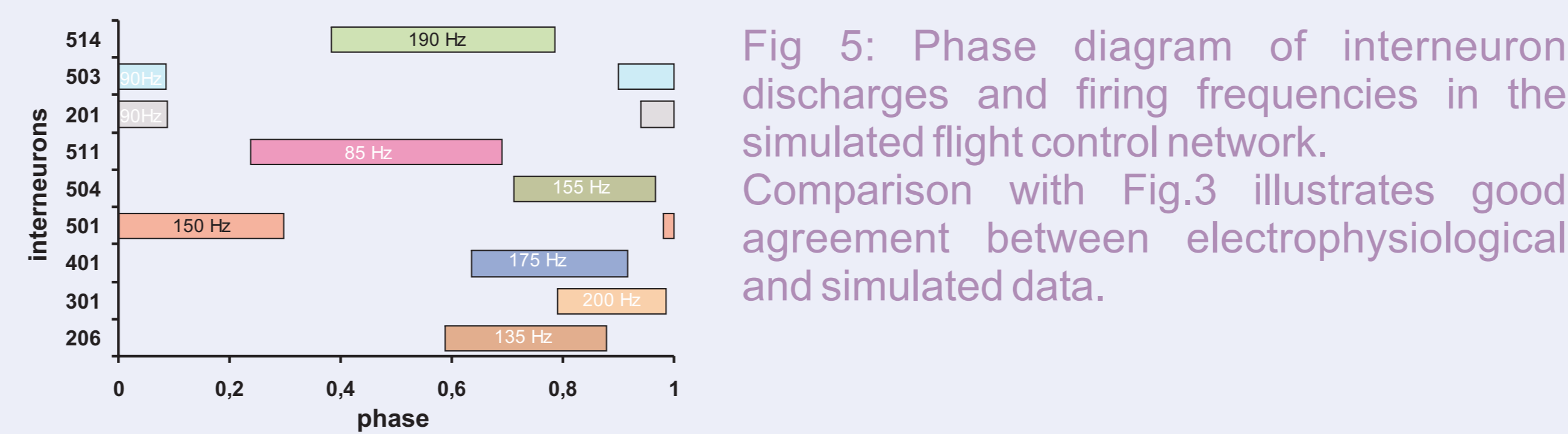
### High frequency firing

Several interneurons of the flight pattern generator sustain very high spike discharge rates, up to 220Hz (see Fig.3), in the deafferented as well as in the intact locust. To achieve these high frequencies, the Hodgkin-Huxley equations had to be adapted. Fig.4 illustrates the frequency range of the model neurons.



### Interneuron 514

Interneuron 514 is the only flight interneuron that has both, excitatory synaptic connections onto elevator motoneurons, and a discharge early enough in the wingbeat period to initiate the wing upstroke. It was thus essential to include interneuron 514 into our model network. However, interneurons which excite or inhibit 514 have not yet been identified. We therefore modeled interneuron 514 to be tonically active and to receive inhibition from interneurons 501 and 301.



## 5 Testing the validity of the model

Measuring the cycle period of the rhythm during injection of depolarising current into 301 or 501 was used as a test for the validity of the model.

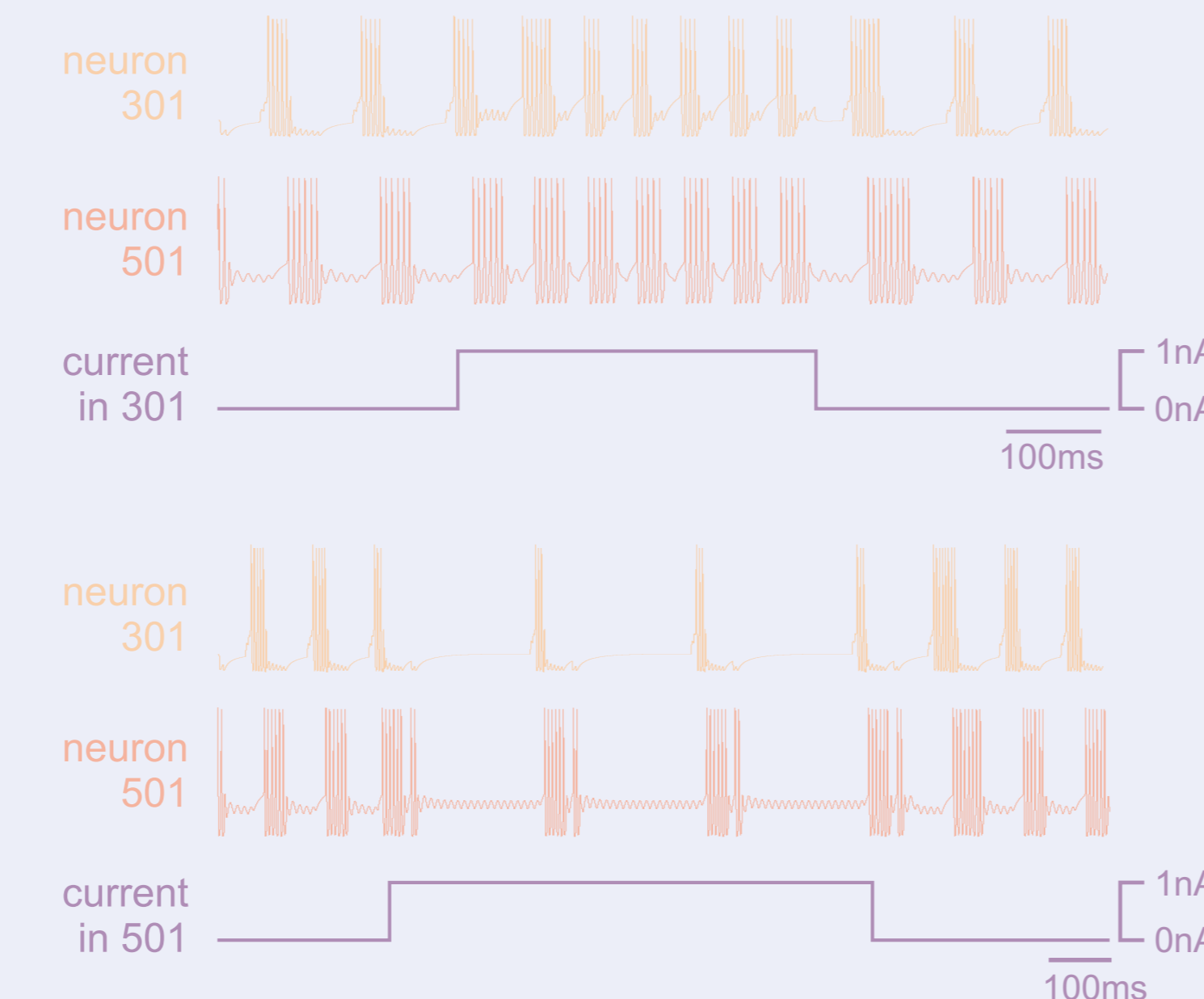


Fig. 6: A pulse of depolarising current delivered to neuron 301 caused the frequency of the flight rhythm to increase from 10 Hz to 18 Hz.

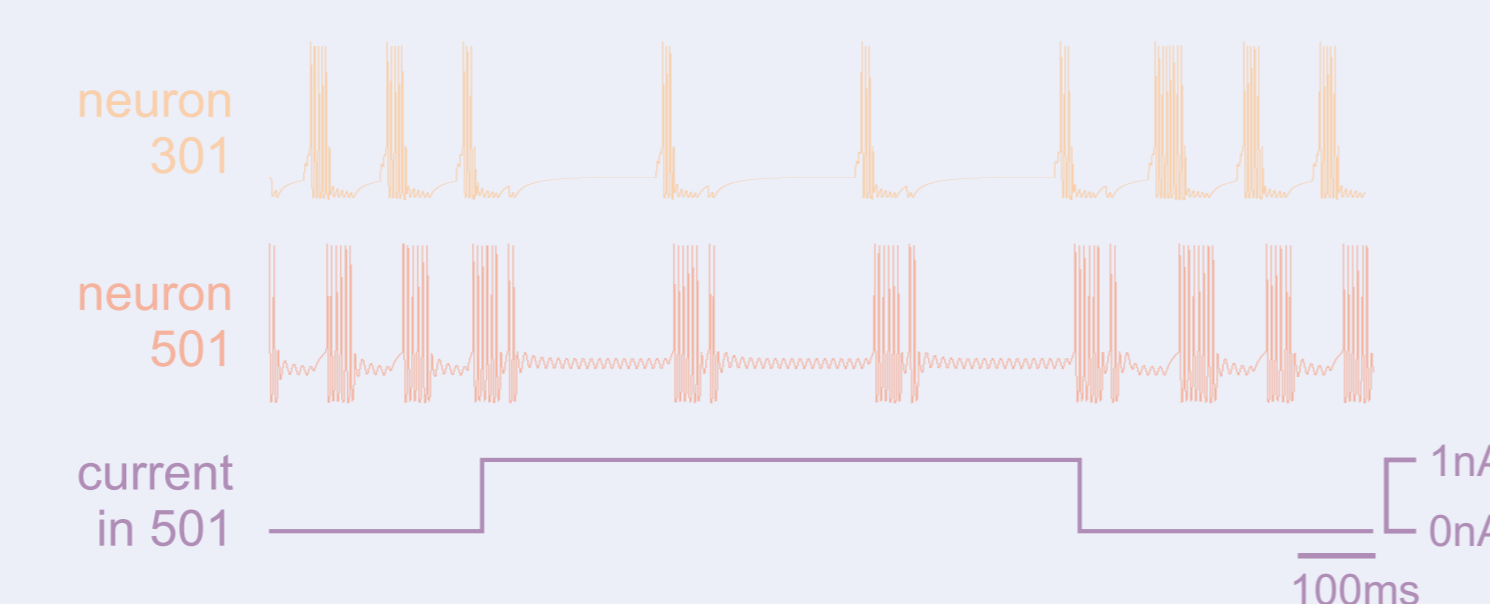


Fig. 7: A similar pulse of depolarising current delivered to neuron 501 caused the frequency of the flight rhythm to decrease from 10 Hz to 2 Hz.

Both experiments revealed similar results to those presented in Robertson & Pearson (1983).

## 6 Sensory feedback to the flight CPG

Feedback from the tegula onto flight interneurons and motoneurons was implemented into our network model. Tegula discharge was determined from motoneuron activity on a wingstroke cycle-by-cycle basis, according to the data of Fischer et al. (2002). Critical parameters of tegula discharge are (i) latency with regard to the wing downstroke and (ii) discharge duration. (i) The latency of tegula discharge was increased with increasing cycle period, according to the relationship measured by Fischer et al. (2002) (Fig. 8). (ii) In our model the tegula discharge was terminated by the start of the subsequent upstroke movement (elevator motoneuron discharge).

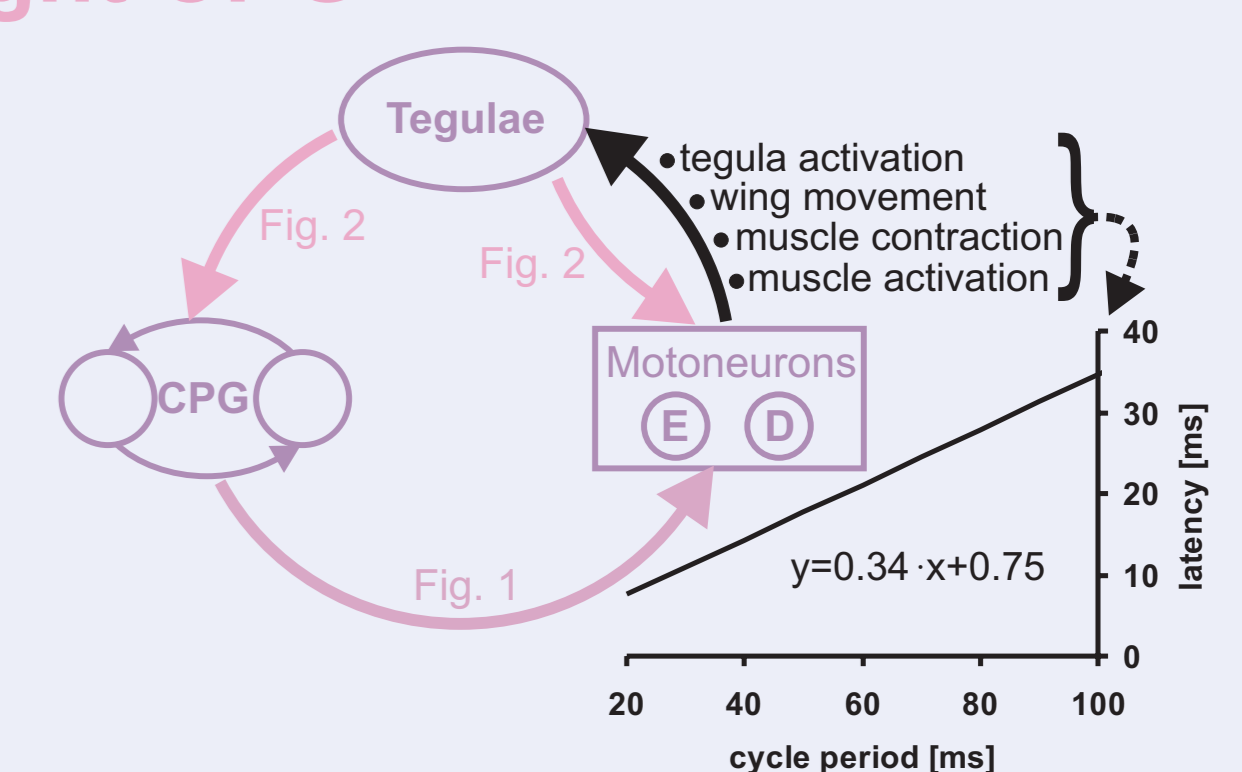
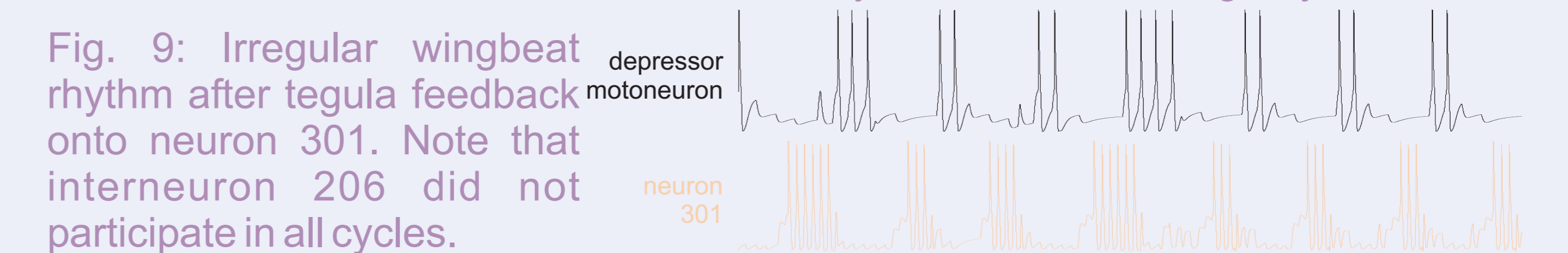


Fig. 8: Latency of tegula feedback. The transfer function used to translate cycle period (interval between the onsets of subsequent depressor motoneuron discharges) into latency (interval between depressor and tegula discharges), according to Fischer et al. (2002).

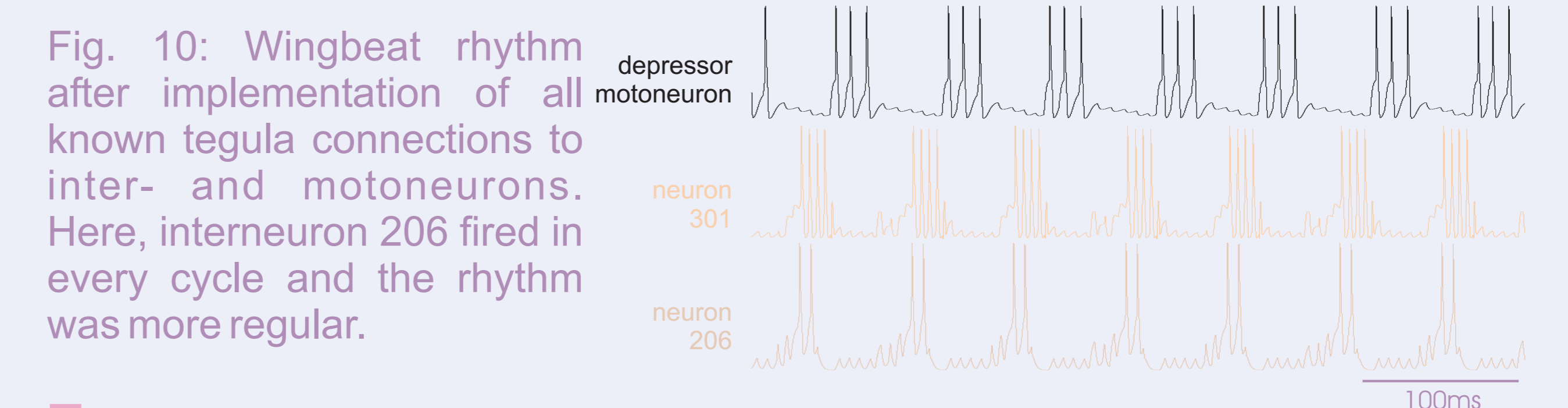
### Tegula feedback onto interneuron 301

Feeding tegula discharge back onto interneuron 301 alone was sufficient to raise cycle frequency from 10 to 17 Hz, with appropriate synaptic coupling strengths. The wingbeat rhythm was irregular under these conditions, however, and sometimes interneurons 206 and 504 did not follow the rhythm and missed single cycles.



### Tegula feedback onto interneurons and motoneurons

Providing tegula feedback to further flight interneurons and motoneurons stabilized the wingbeat rhythm and entrained all neurons into the rhythm.



## 7 Conclusions

Our model network of the locust flight oscillator exhibited the key characteristics of the biological rhythm generator, and it truthfully reproduced experimental data from electrophysiological experiments. It therefore appears as an adequate platform for analysing the functional relevance of network properties that cannot be tested in the real animal. In particular, the model should be adequate to test the function of sensory feedback, namely tegula input.

Implementing tegula feedback accelerated the wingbeat rhythm - as it does in electrophysiological experiments. This finding validates the transfer function we used to implement tegula feedback. Acceleration of the wingbeat rhythm was already observed when tegula feedback impinged on just single interneurons.

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Support: Studienstiftung des Deutschen Volkes; travel grant University of Ulm