Interaction of sensory feedback and central network in the locust flight control system: a modeling study

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Introduction and Background

The deafferented flight (central) pattern generator 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.

The simulated network

Neurons were modeled in the simulation environment *madSim* (Mader et al., 2003) whith active and passive neuron properties according to Hodgkin-Huxley equations (Hodgkin & Huxley, 1952). The sodium and potassium ion currents were modified to enable high frequency firing.

We simulated a network structure based on Grimm & Sauer (1995). The synapse between neurons 301 and 501 was modeled as a delayed synaptic connection with inhibitory-exitatory properties according to Robertson & Pearson (1985).

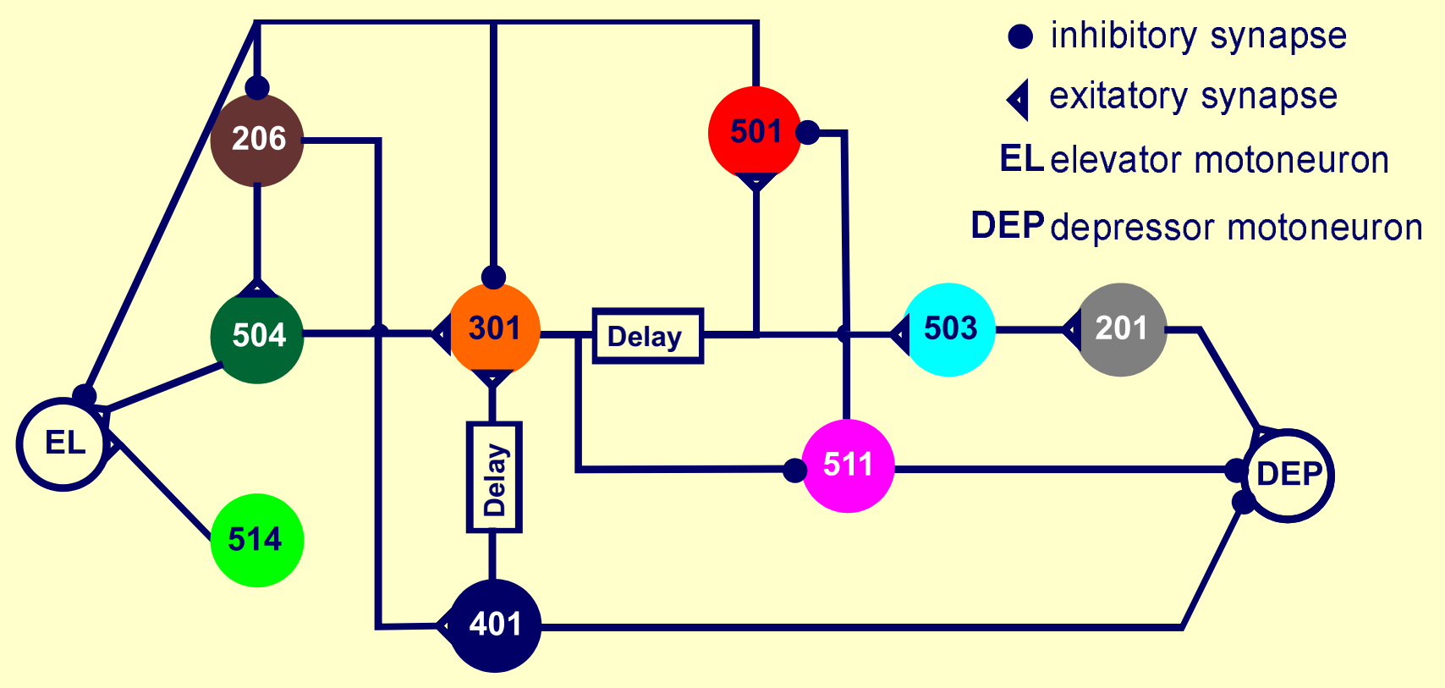

Fig. 1 Model network of the locust flight CPG. Numbers mark identified interneurons.

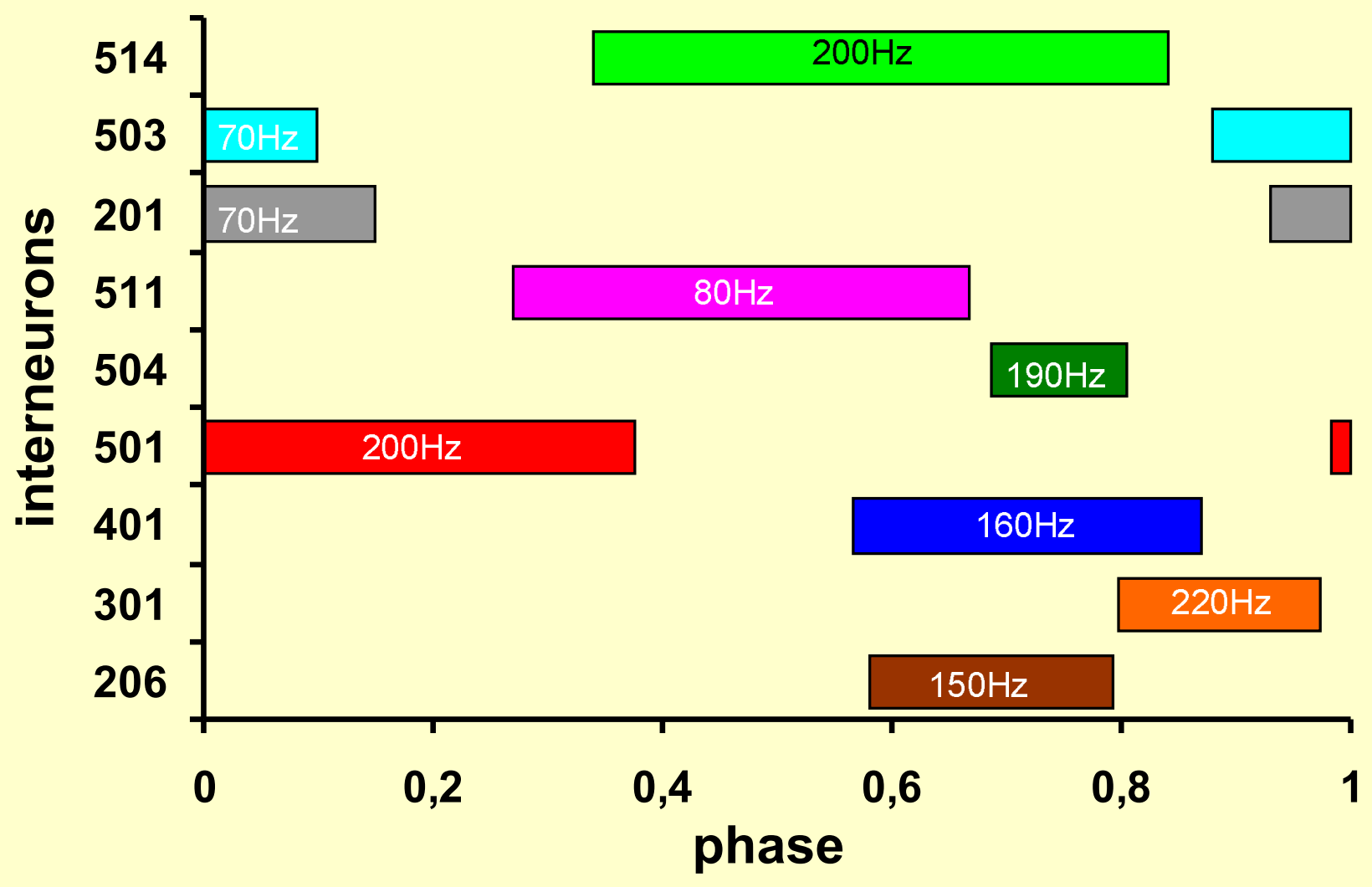

Fig. 2A Phase diagram of interneuron discharges and firing frequencies in the deafferented flight CPG. Activity patterns were evaluated from Robertson & Pearson (1985), Robertson (1991), Robertson & Pearson (1983) and Wolf & Pearson (1989). Phase related to depressor motoneuron activity.

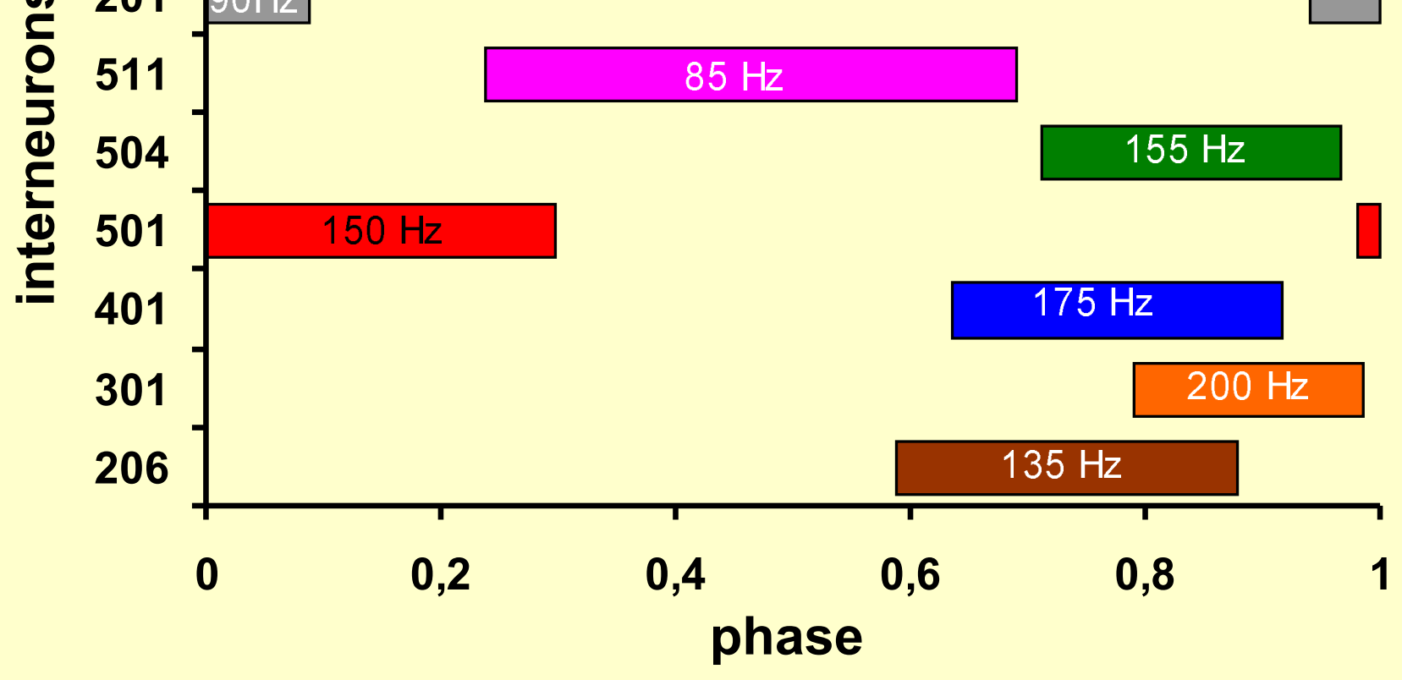

Fig. 2B Phase diagram of interneuron discharges and firing frequencies in the simulated flight control network.

Sensory feedback to the flight CPG

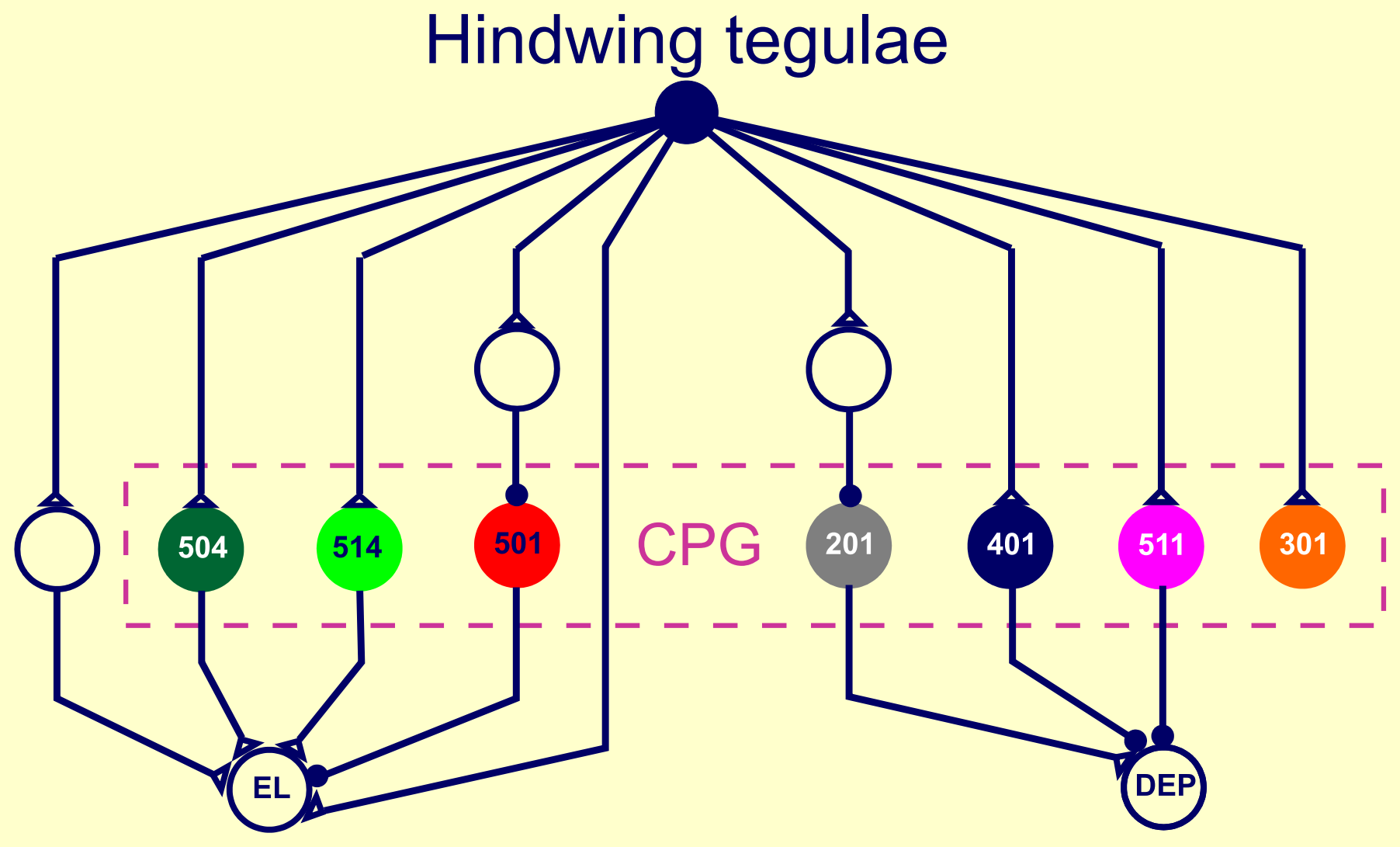

Fig. 3 Connectivity pattern of the tegula afferents, adapted from Wolf (1993). Open cells were not implemented as model neurons in our simulation, but represented by simple delays.

Latency of tegula discharge was determined from motoneuron activity on a wingstroke cycle-by-cycle basis, according to Fischer et al. (2002). Tegula activity was terminated by the start of the subsequent upstroke movement (elevator motoneuron discharge).

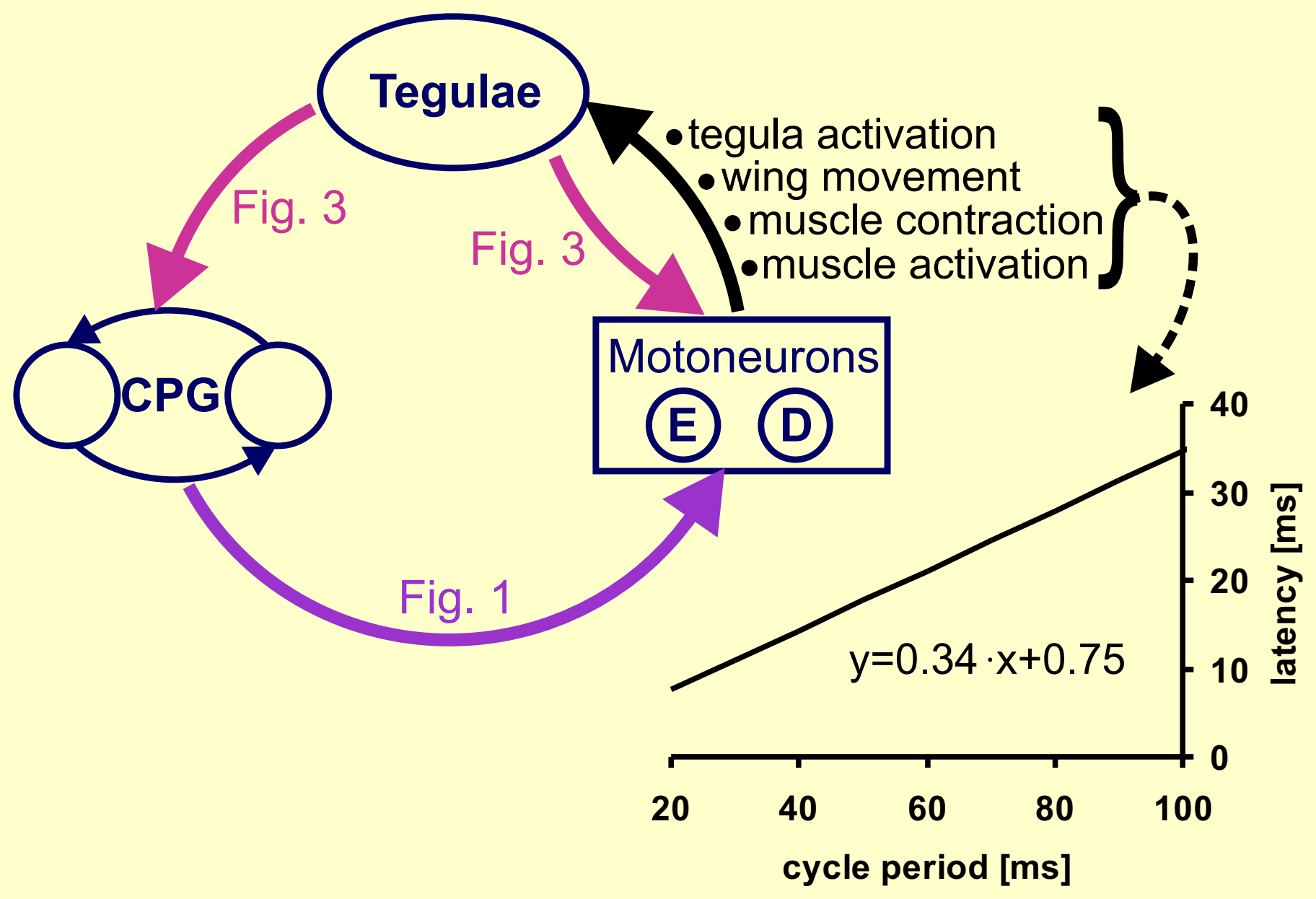

Fig. 4 The transfer function used to translate cycle period into latency (interval between depressor and tegula discharges), according to Fischer et al. (2002).

Tegula feedback onto interneuron 301 is sufficient to raise cycle frequency

Cycle frequency increased from 10 to 17Hz. The wingbeat rhythm, however, was irregular. Occasionally, interneurons 206 and 504 missed cycles (➚).

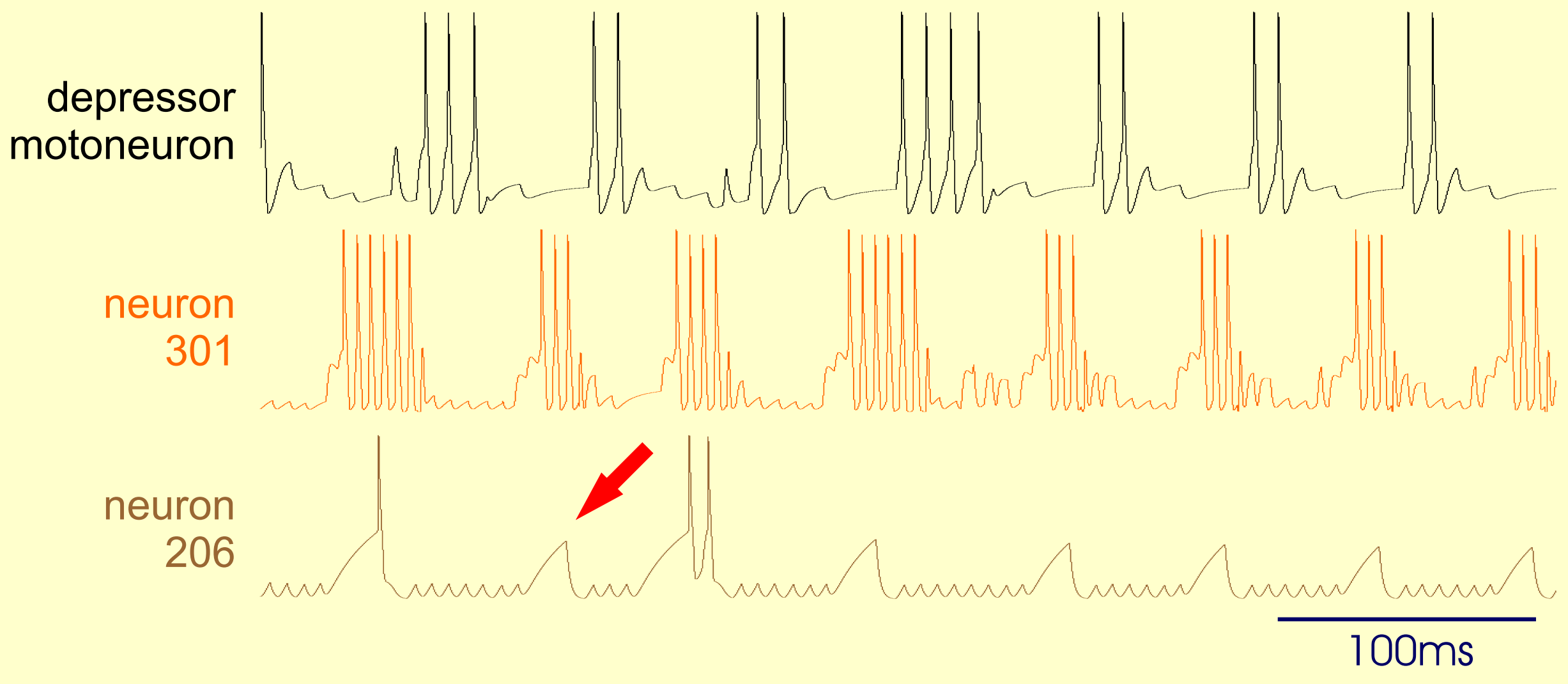

Fig. 5 Irregular wingbeat rhythm after tegula feedback onto neuron 301.

Tegula feedback onto interneurons and motoneurons improves stability of the rhythm

Additionally, all neurons were entrained into the rhythm.

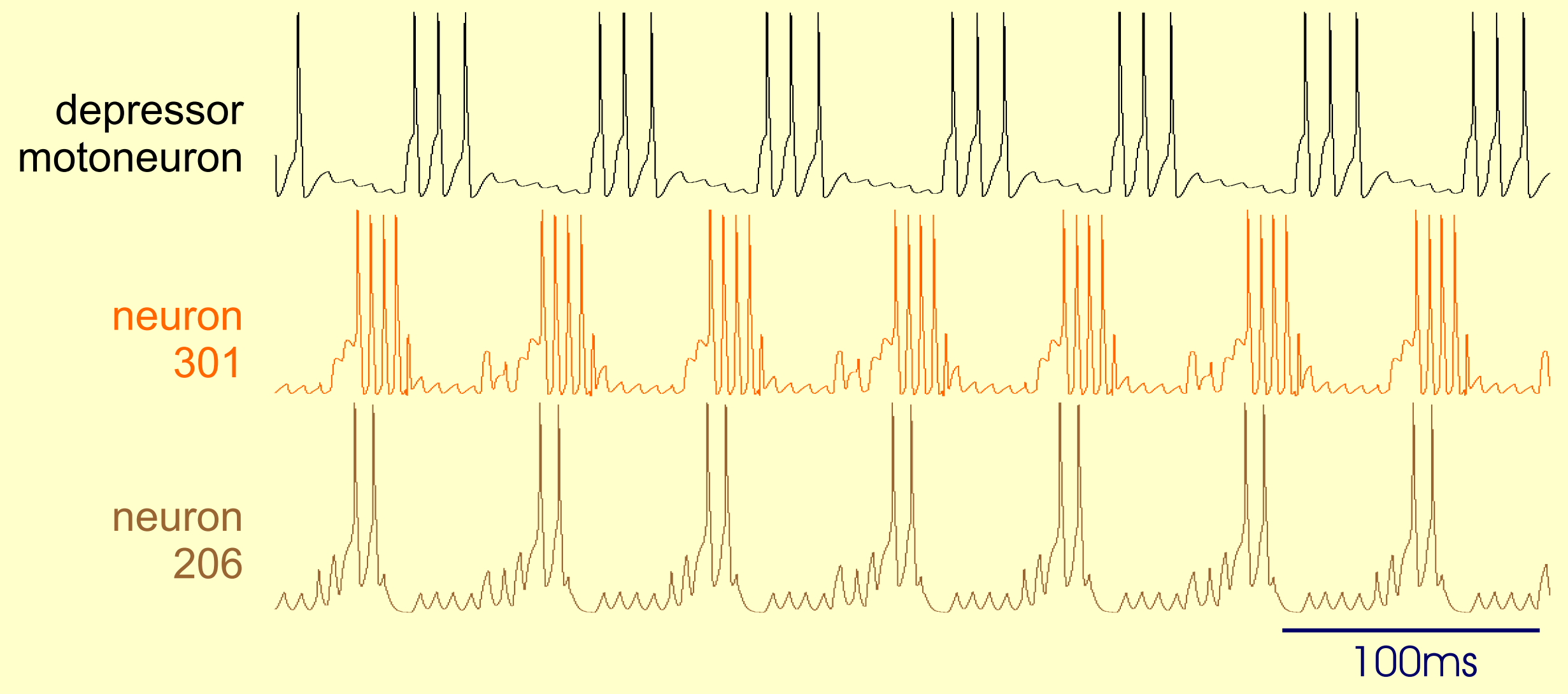

Fig. 6 Wingbeat rhythm after implementation of all known tegula connections to inter- and motoneurons.

Tonic *versus* phasic tegula effects

Connecting the tegula to interneuron 301 sped up the rhythm (Fig. 5). Was this due to a phasic effect on 301, or the result of a general increase of excitation?

Test for tonic effects

We compared cycle period in 3 situations. 1) Phasic tegula input onto 301. 2) Tonic tegula input *with equal amount of excitation* (and thus lower amplitude). 3) Tegula removed.

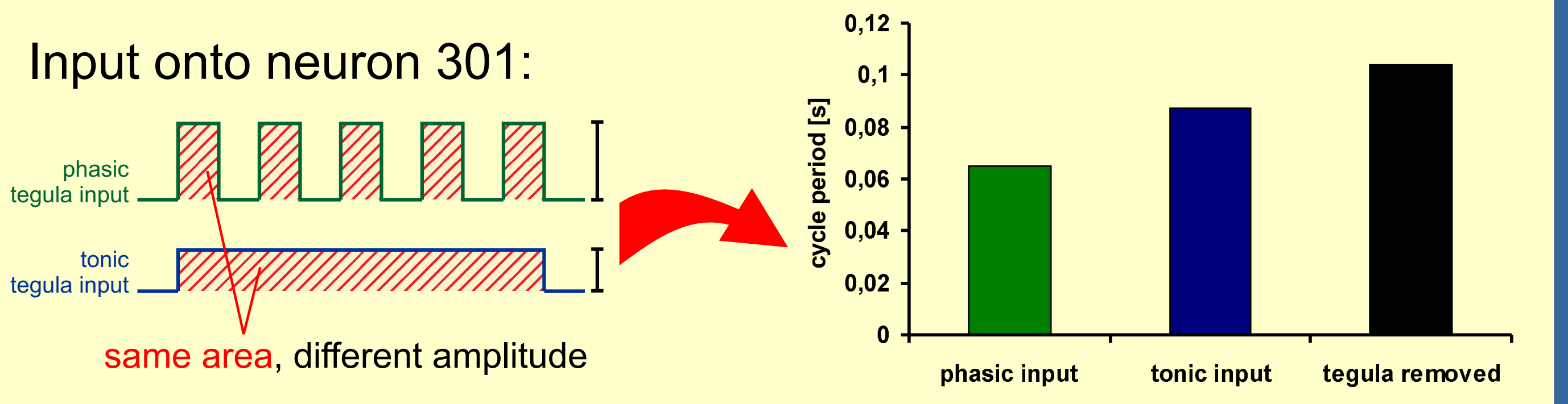

Fig. 7 shows that a purely tonic influence of the tegula on neuron 301 was not sufficient to explain the observed changes in cycle period.

Test for phasic effects

To test whether the tegula effects were due to the strength of the excitation of 301, we decreased the *amplitude* of the phasic input so that it matched the tonic excitation.

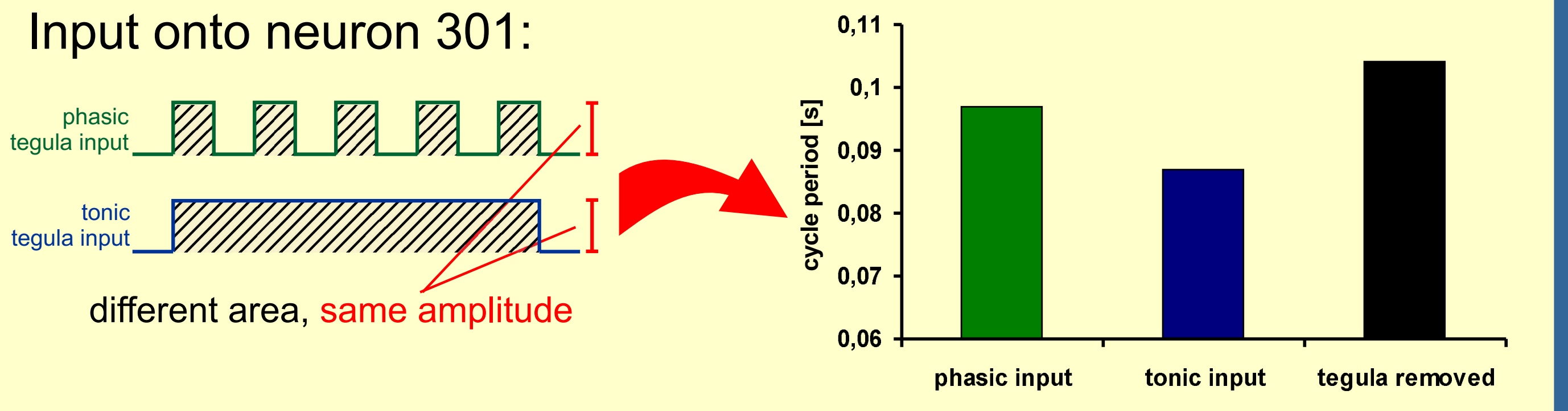

Fig. 8 shows that not only a phasic reset of 301, but also a tonic excitation was sufficient to speed up the rhythm.

Conclusions

- ➔ Our model network of the locust flight oscillator exhibited the key characteristics of the biological rhythm generator.
- ➔ It thus appears as an adequate platform for analyzing the function of sensory feedback, namely tegula and strech receptor inputs.
- ➔ Implementing tegula feedback accelerated the wingbeat rhythm, which validates the transfer function we used to implement tegula feedback.
- ➔ Acceleration of the wingbeat rhythm was already observed when tegula feedback impinged on just interneuron 301.
- ➔ Tegula feedback provides a tonic excitatory component, but also needs a phasic excitation of interneurons to produce the proper motor output.

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