How to switch from standing to walking

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Introduction and Background

All animals behavior is characterized by the movement of the body and by its response to sensory stimuli. The nervous system shows great variability in the processing of sensory information and thus also in its response to such information. Here, we used an insect model system, the femur-tibia joint control system of the stick insect, to investigate how the nervous system switches between two different motor outputs, despite having the same sensory input. For our simulation we tried to combine the physical structure of the nervous system with the activity of nerve cells and the required computation within the nervous system.

For switching between the two behaviors (standing and walking), the nervous system has to toggle from static joint control during standing to movement control of the limbs when the animal starts to walk. This is exemplified by the response of the femur-tibia extensor motoneurons to rampwise elongation of the femoral chordotonal organ (fCO). The fCO is the only proprioceptor which measures the position of the femur-tibia joint and the velocity of movements in this joint. During standing, a resistance reflex (RR) is generated (Fig. 1 top). In contrast, during walking the same stimulus causes a reflex reversal, the “active reaction” (AR) (Fig. 1 bottom). It is assumed that changes on the interneuronal level are responsible for the reversal of the motor output (Driesang & Büschges, 1996).

We used a computer simulation based on the known network structure (Fig. 2, an extension of Sauer, et al., 1996) to test this hypothesis with a brute force algorithm. We systematically altered the strength of identified nonspiking interneuronal pathways (Büschges, 1990; Stein & Sauer, 1998) known to process velocity and position information from the fCO.

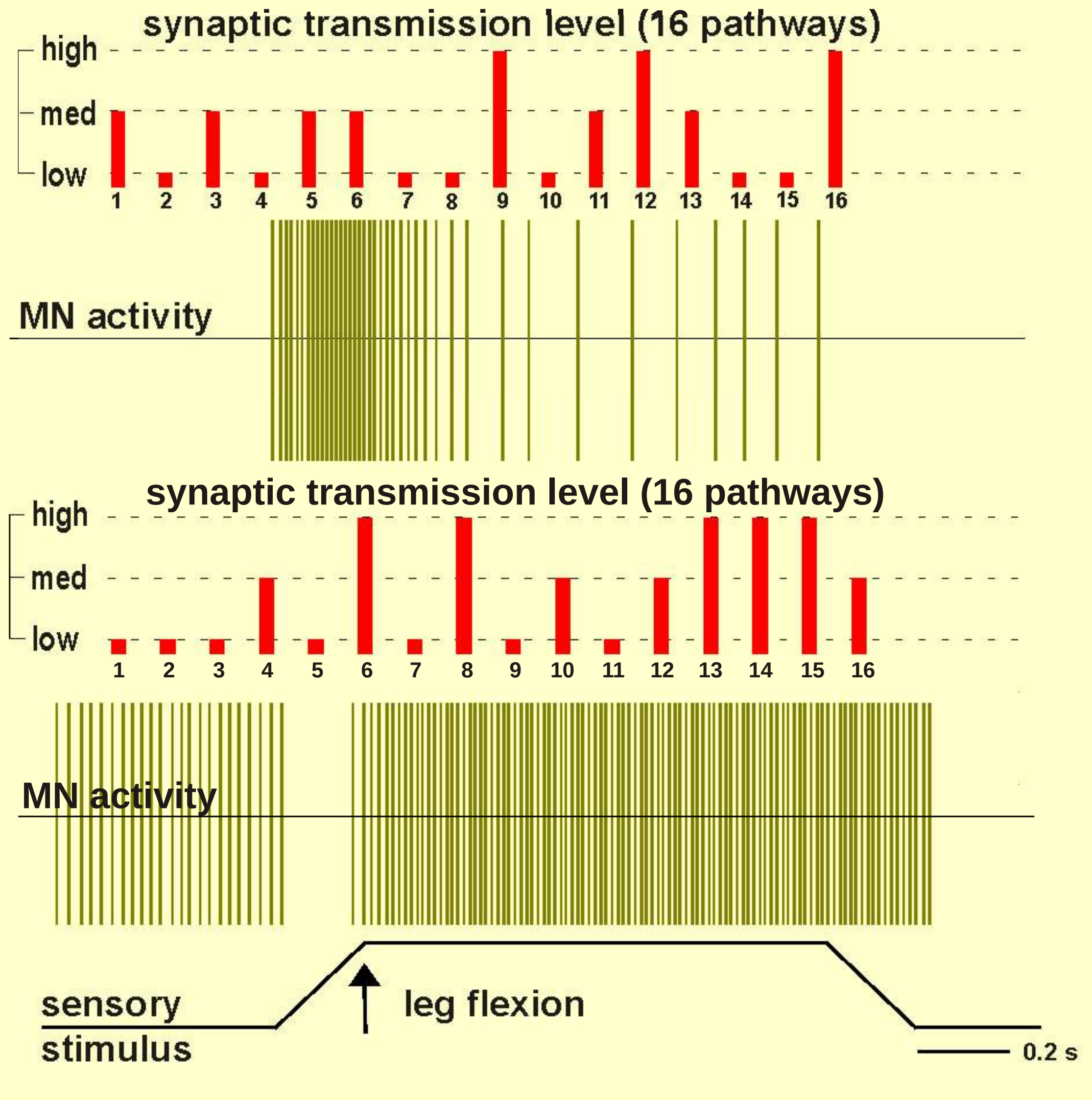


Fig.1: Different motor outputs. MN: Motorneuron. Red bars indicate synaptic transmission levels of interneuronal pathways.

Materials and Methods

In the femur-tibia joint fCO information is processed by identified nonspiking interneurons. These interneurons receive monosynaptic excitatory inputs from fCO afferents and polysynaptic inhibition from spiking interneurons. 10 excitatory and 6 inhibitory types of interneurons synapse on the extensor motoneuron (MN).

We used Hodgkin & Huxley model cells in the simulation environment *madSim* to model this network. We specifically altered the pathway transmission levels between identified interneurons and the motoneuron (red arrow in Fig.2) to test whether this was sufficient to change the motor output from standing to walking.

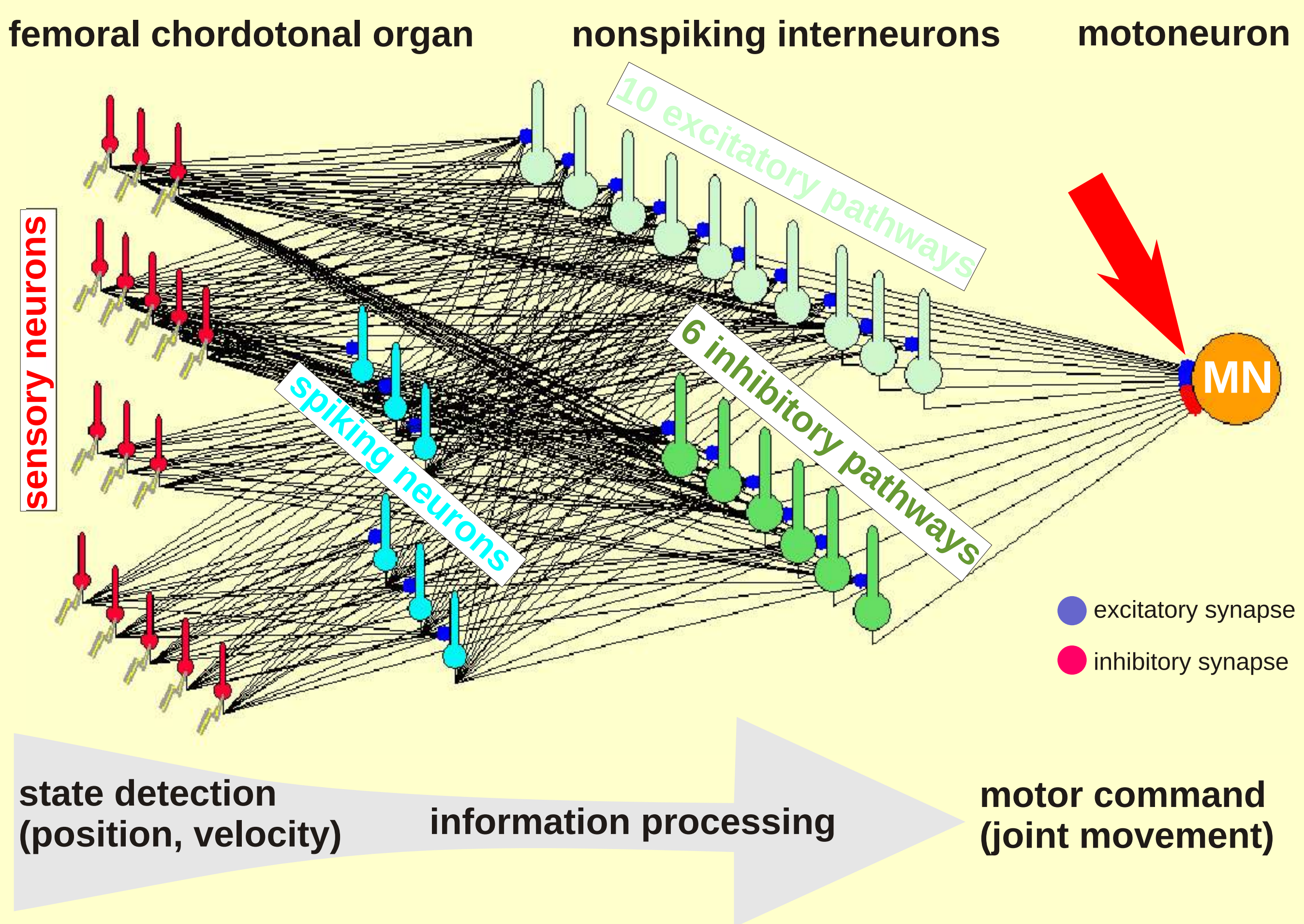


Fig.2: Simulated femur-tibia control system with direction of information flow. Small arrows: current injections.

Results

Brute force recombination reveals that specific combinations of synaptic strengths are sufficient to switch from standing to walking

- ➡ database: 43,046,721 motor outputs
- ➡ analysis: resemblance with electrophysiological data

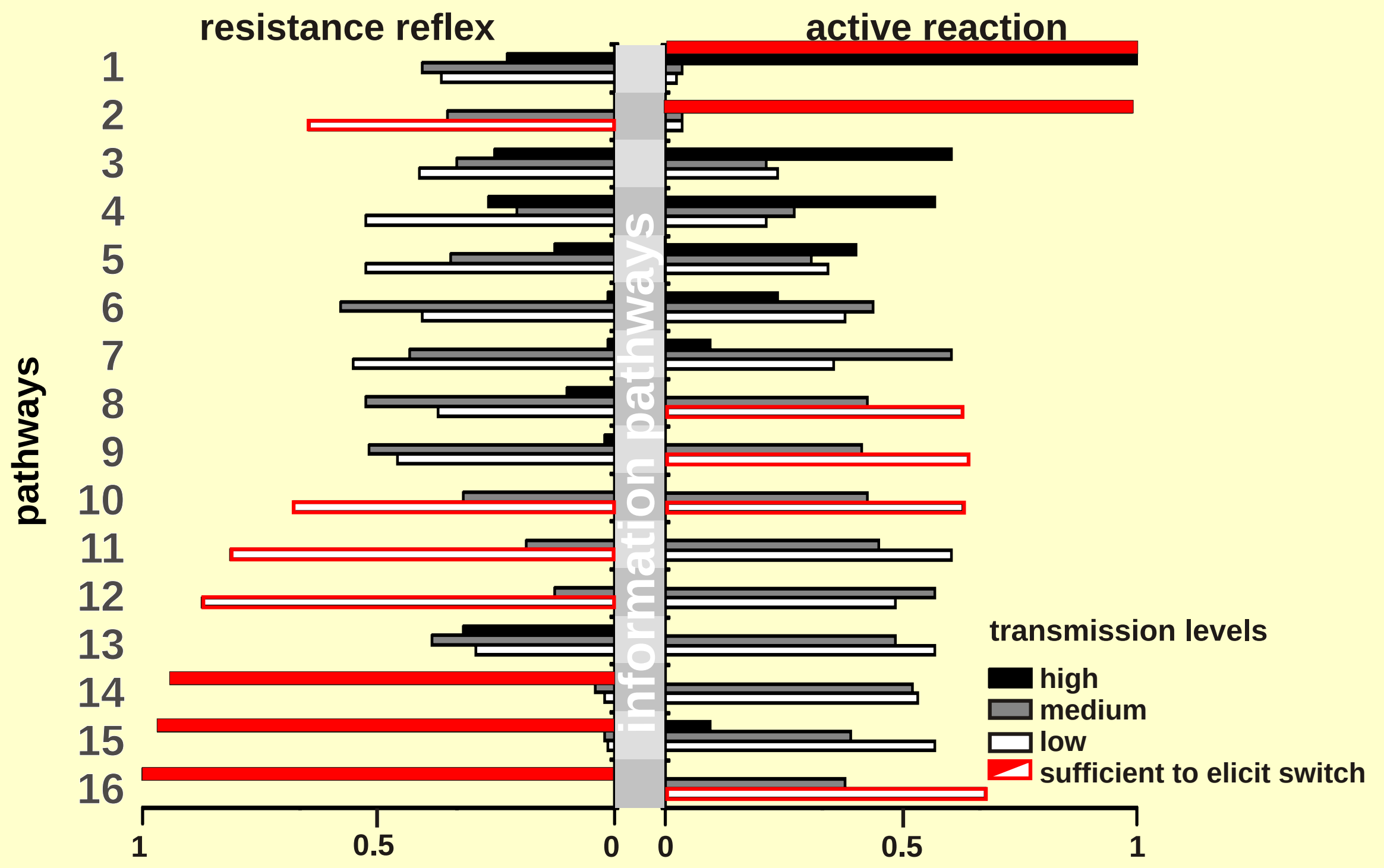
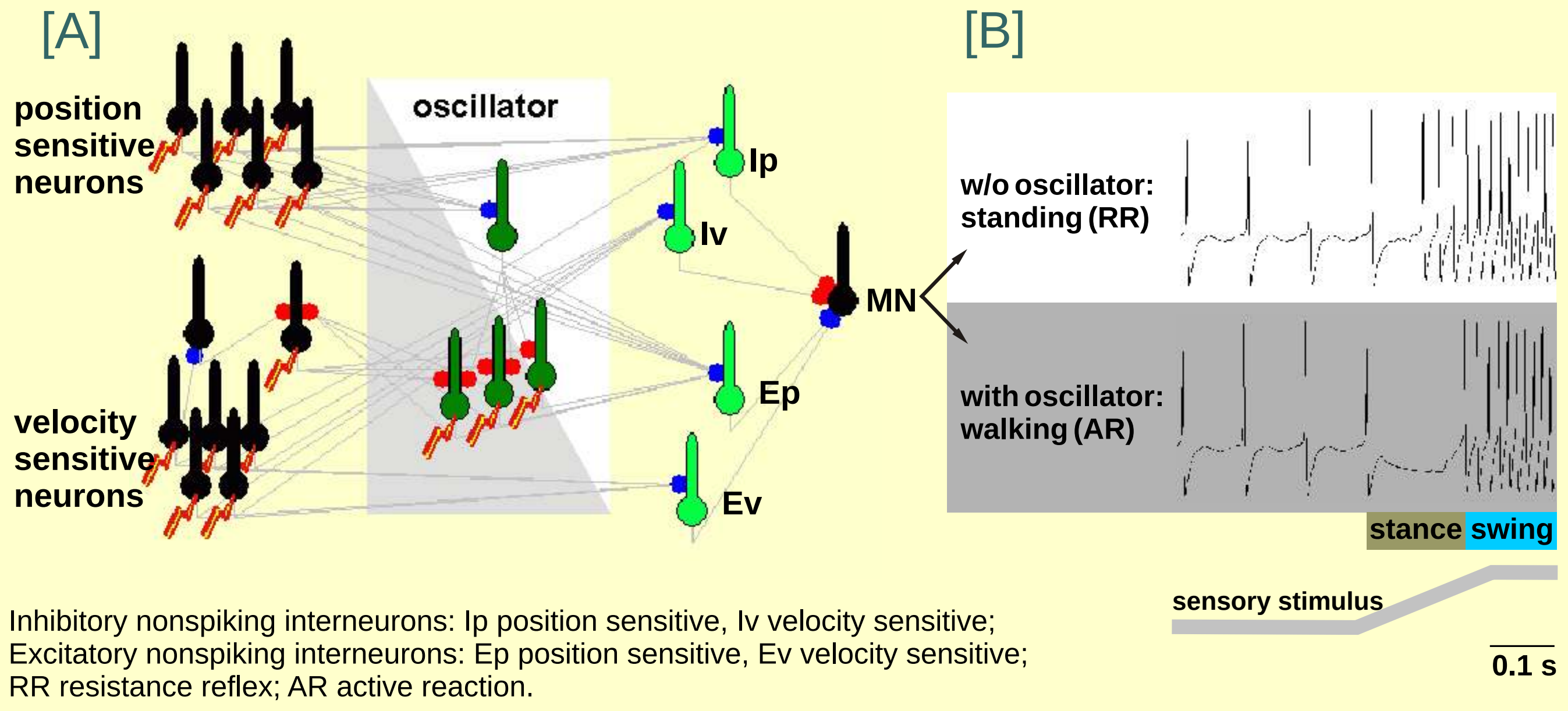


Fig. 3: Normalized occurrence of synaptic transmission levels reveals preferences for synaptic strengths during resistance reflex and active reaction (Straub et al., 2004).

Activation of a relaxation oscillator triggers the switch and the transition from stance to swing phase in walking



Inhibitory nonspiking interneurons: Ip position sensitive, Iv velocity sensitive;
Excitatory nonspiking interneurons: Ep position sensitive, Ev velocity sensitive;
RR resistance reflex; AR active reaction.

Fig.4: [A] Reduced model of the femur-tibia control system; [B] Motor output

A merely position dependent transition from stance to swing phase (Bässler, 1988) could not be achieved. ➡

This was true although a negative velocity signal was used to eliminate the size of stimulus velocity (Bässler & Koch, 1989).

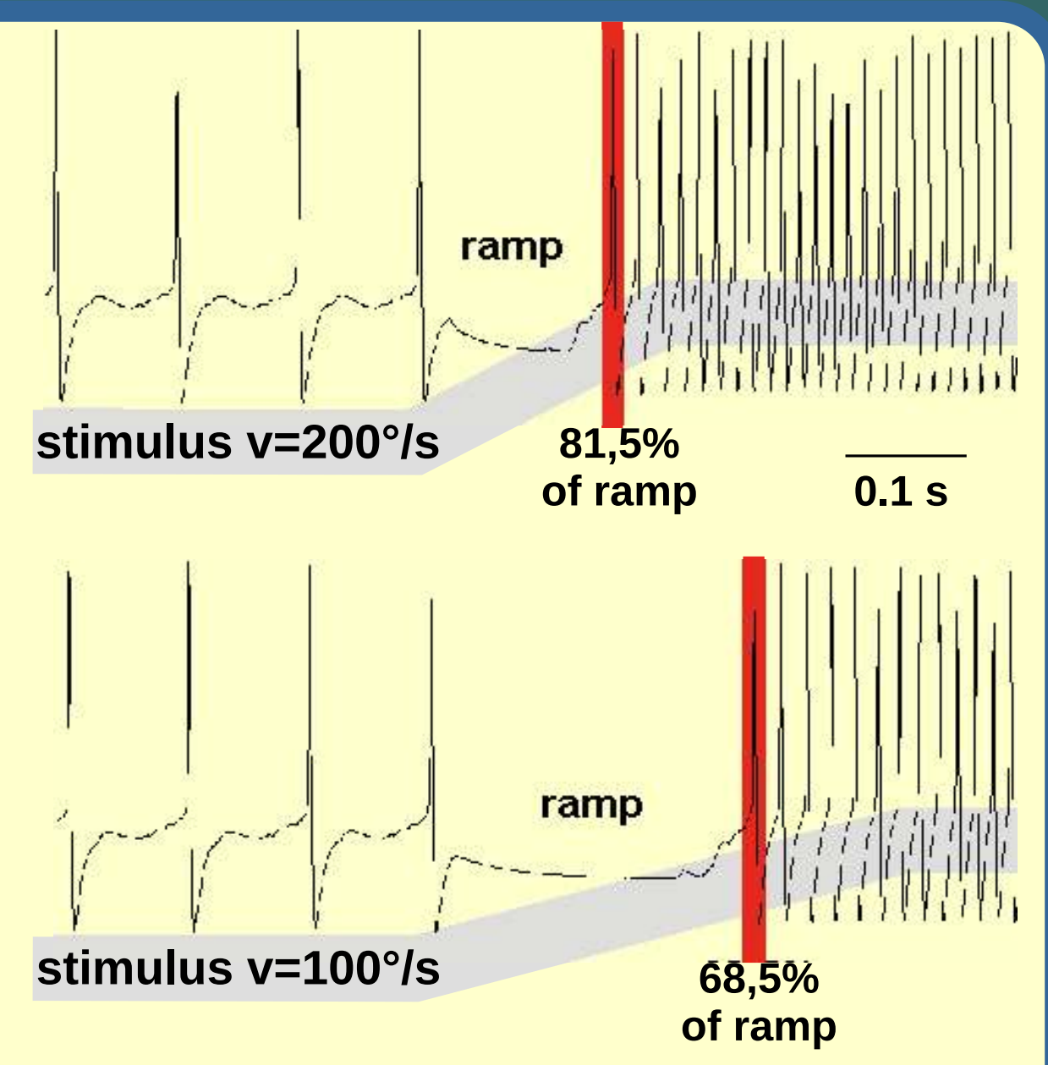


Fig.5: Motor output in the reduced model at different stimulus velocities.

Reasons for inaccuracy

- ➡ low firing rate (low bandwidth) of position sensitive neurons is unsuitable for signaling short stimulus ramps.
- ➡ nonlinear characteristics (summation, capacitance, voltage dependent currents) of integrate-and-fire neurons (Fig. 6).

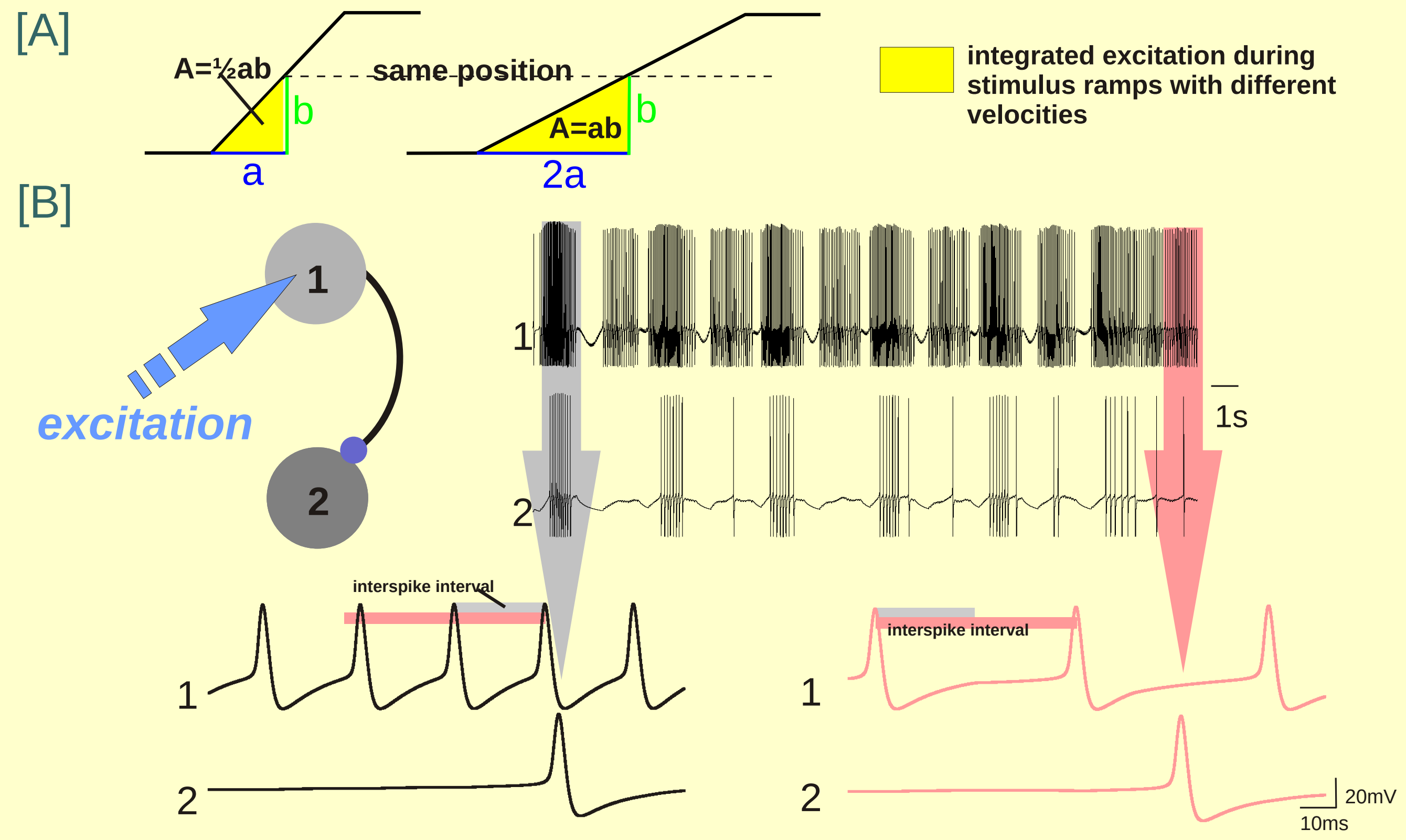


Fig.6: [A] Velocity dependent excitation of postsynaptic cell. [B] The detection of presynaptic interspike intervals is history dependent.

● excitatory synapse

Solution

- ➡ higher afferent firing rate to improve temporal resolution.
- ➡ position detector should recognize all interspike-intervals shorter than a specific threshold value to avoid non-linearities.

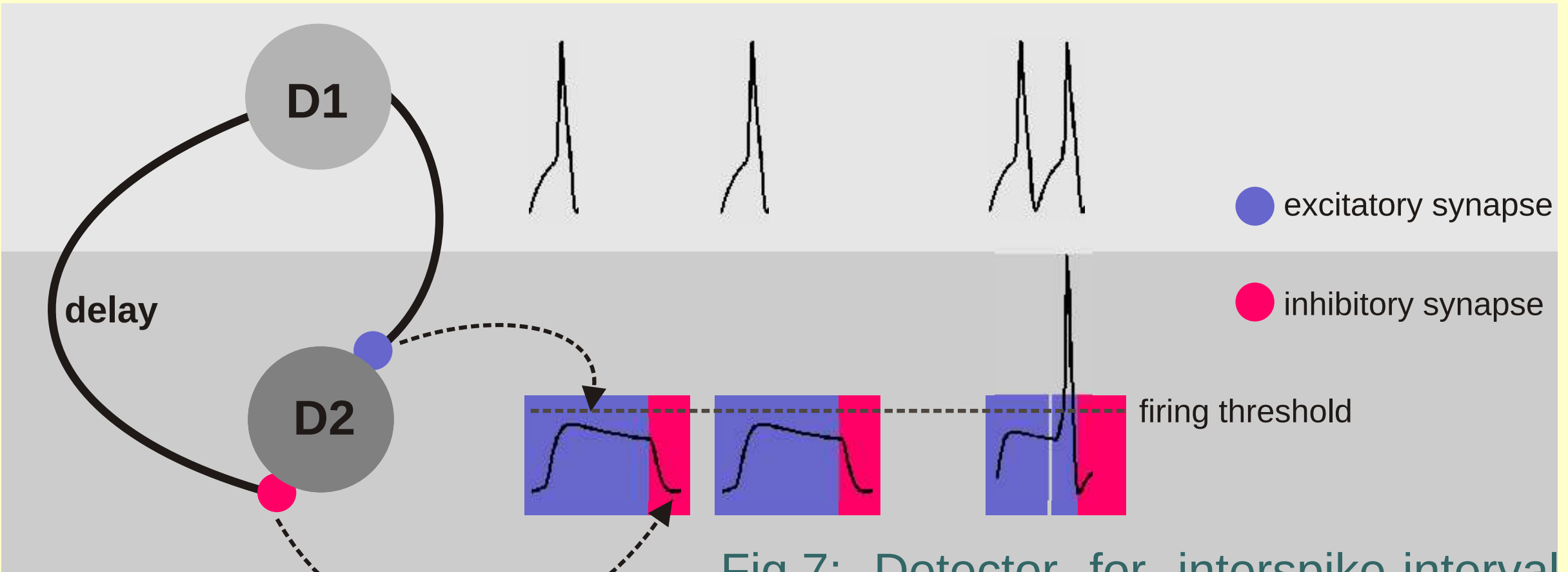


Fig.7: Detector for interspike-interval shorter than a specific value.

Improvement: this detector reduces the velocity dependent variance of position detection from 13% to 4.25%.

Conclusions

- ➡ The same neuronal network can produce two different behaviors despite having the same sensory information.
- ➡ The switch between both behaviors can be produced by specific changes in the weighting of identified parallel information pathways to the motoneuron.
- ➡ A relaxation oscillator circuit acts presynaptically to the known interneuronal pathways and causes the switch.
- ➡ For a precise position dependent transition from stance to swing phase during walking a detector for interspike-intervals and the appropriate sensory information is necessary.

Currently, we are studying a possible impact of the interspike-interval detector on presynaptic inhibition of sensory neurons.

References:
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