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# Single neuron and network models in force control

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## ABSTRACT

The single neuron study had the goal of comparing the frequency response of two motoneuron (MN) models having similar soma dynamics but different dendritic dynamics: one had a passive dendrite and the other an active dendrite. Motoneurons with active dendrites have been described in decerebrate cats [7] in relation to the generation of a persistent inward current (PIC), bistability and plateau potentials, and are believed to occur also in humans [4]. The chosen passive-dendrite MN model was a two-compartment soma-dendrite model described in [2]. The active-dendrite MN model was based on the passive-dendrite model with the inclusion of a voltage-dependent L-type  $Ca^{++}$  channel in the dendritic compartment so that it could generate a PIC. The two models (the “passive” and “active”) were made to discharge at the same mean rate around 30/s, driven by a frequency-modulated presynaptic spike train (“the input”) of mean rate 4000/s (passive-dendrite) and 2000/s (active-dendrite) acting on the dendritic compartment. These presynaptic mean firing rates were different because in the active model the PIC that is generated in response to the synaptic drive contributes to the firing rate. The cycle histogram obtained from the instantaneous firing rate of each of the simulated MN models (“the output”) was fitted by a sine function and the gain and phase shift were computed with respect to the input modulating sine function. Note that the force generated by a motor unit associated with the motoneuron would follow the modulating frequency with no attenuation at least up to 1 Hz [1]. The frequency responses in absolute value (“gain”) were quite different in the two models: the passive-dendrite MN showed an increasing gain up to about 13 Hz and then decayed while the active-dendrite MN showed a monotonic decreasing gain of lowpass nature, with a -1 dB cutoff frequency around 0.5 Hz. The tentative functional role ascribed to a potential PIC in human motoneurons is related to the maintenance of a standing posture [6] because the resulting bistability would require very little control from the descending pathways during quiet standing. Simplistically, these pathways would be required to “turn on” the MN (make it discharge regularly) by a burst of excitatory activity, therefore, freeing the upper centers from detailed control of the motoneuron pool. On the other hand, human postural sway has about 74% of the power concentrated at low frequencies up to 0.25 Hz [8], which are due to oscillations of the center of pressure [3]. Hence, for the task of controlling quiet standing, the lowpass feature of the active-dendrite MN model seems to be well-suited, as it would attenuate higher-frequency perturbations that would increase the postural sway. At the same time, the MN would pass the low frequencies needed for the feedback to correct displacements of the center of gravity. If human motoneurons do indeed exhibit such a lowpass feature during quiet standing is an open question which suggests new directions for future research.

The second study verified how the force variability, measured by the standard deviation of an isometric maintained force, depended on the mean force value. A network of 900 motoneurons (800 type S, 50 type FR and 50 type FF), representing the MN pool that drives the soleus muscle, was driven by 100 axons, each carrying a Poisson process with a specified intensity and with an “innervation ratio” of 20% (meaning that each axon innervated a randomly-chosen subset of the motoneurons containing 20% of the MN pool). If there was no limit set to the firing rates of the MNs

in the pool, then the force standard deviation (std) showed a parabolic-like dependence on the mean force level, increasing with mean force and then decreasing as the mean force increased still further. However, if the firing rates of real MNs from humans are taken into account, then the valid part of the force std x force mean relationship is just a monotonic increasing function. This result suggests that for the soleus muscle the hypothesis of signal-dependent-noise [5] is applicable. A new investigation would be required to verify if the same is valid for the gastrocnemi muscles, as these are important synergists of the soleus in exerting plantarflexion but have a different motor unit type composition. A further step would be to study the influence of feedback from muscle spindles and Golgi tendon organs on force variability during isometric and nonisometric force and position control.

**Keywords:** persistent inward current, motoneuron models, force variability.

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