

THE ENCODING OF INPUT CURRENTS BY MOTONEURONES IN RELATION TO NEURONAL MODELLING

M.F. Vieira ^{1,2} and A.F. Kohn ¹

¹ Universidade de São Paulo
Neuroscience Program &
Biomedical Engineering Laboratory
Escola Politécnica, Brasil
andfkohn@leb.usp.br

² Universidade Federal de Goiás, Brasil

Introduction

Several coding stages occur in the nervous system when an internal decision is reached to enact a certain movement. The desired movement is coded into spike trains of a large number of neurons in prefrontal, premotor and supplementary motor cortices as well as in other areas such as the basal ganglia and cerebellum. These spike trains can be assembled in a column vector $\underline{x}(t)$, each element representing one neuron's spike train. Another coding stage translates all those spike trains into the spike trains of neurons in the primary motor cortex, which we assemble in vector $\underline{y}(t)$. This vector is next encoded (through direct and indirect pathways) as vector $\underline{z}(t)$ containing the spike trains of motoneurons from several (K) motoneuron pools in the spinal cord that will activate axial and limb muscles involved in the desired movement. This vector $\underline{z}(t)$ can be partitioned as $\underline{z}(t)=[\underline{z}_1(t)^T \underline{z}_2(t)^T \dots \underline{z}_{K-1}(t)^T \underline{z}_K(t)^T]^T$, where each $\underline{z}_i(t)$ is associated with a given motoneuron pool. Observing only $\underline{z}_i(t)^T$ will only give us a partial view of the coding from $\underline{y}(t)$ on $\underline{z}(t)$. Needless to say, if we only examine the spike train of one motoneuron from a given motoneuron pool even less understanding can be obtained about the general coding strategy associated with the desired movement. Nevertheless, there is an interest in studying the spike trains from single motoneurons and from the ensemble of motoneurons from a given motoneuron pool because they perform the final encoding prior to the final stage which is the decoding of the spike trains into muscle contraction. Experiments have indicated that there is a degree of matching between motoneuron and muscle fibre characteristics [e.g., Kernell, 1990]. These are interesting to analyse both in terms of theoretical studies of information transmission or dynamical systems in neuromuscular structures as well as in terms of neuronal modelling. The degree of matching of motoneuronal spike trains and muscle response found in nature has to be mimicked by any "good" models of motoneurons and muscle. In this work we briefly review a few findings from the literature that point to an "optimal" matching between spike trains/motoneuronal dynamics and muscle contraction. From these data we extract relations between motoneurone spike trains and resulting muscle fibre contraction in different types of movement. These should serve as standards in the validation of motoneuron and muscle models. Spike trains from an improved motoneuron model developed by the authors are analysed in terms of the matching with muscle mechanical behaviour.

Some experimental results described in the literature

In fast movements, for example, changing a joint angle from ϕ_1 to ϕ_2 as fast as possible, the target muscle must overcome the inertia of the limb segment and hence it should generate a peak of force with a short time delay. This may be achieved by a nonlinear property of muscle fibres called the "catch property" [Burke et al, 1976], whereby a very short interspike interval

at the start of a spike train causes a fast rising force. Therefore, the timing of motoneuron action potentials for such a fast muscle contraction has to show a strong degree of initial adaptation. In motoneurons this indeed occurs due to the dynamics of ionic channels such as the calcium-dependent potassium channel. Additional data [Baldissera and Parmiggiani, 1975] has shown that motoneuron firing pattern with adaptation results in higher force plateaus than motoneuron with constant rate firing (for firing rates below 60 Hz). Therefore, two different performance measures suggest an optimality between motoneuron firing pattern and muscle (or muscle unit) contraction behaviour.

Muscle fibres with a slow (fast) twitch have a higher sensitivity in force production when the input firing rate is in a lower (higher) frequency range. There is a rough match between the primary firing rate range of motoneurons to constant injected current and the muscle fibre's steepest part of the tension-frequency curve [see review by McDonagh et al, 1999]. In other words, the motoneurons (types S and F) encode naturally occurring "constant" input currents into firing rate ranges that fit the preferential range in the decoding from motor fibre firing rate into contraction force.

The rather slow contraction dynamics of muscle as well as the propagation delay of action potentials from the spinal cord to the muscles are partially compensated for by motoneuron properties [Baldissera et al, 1998; Matthews, 1997]. The frequency response of motoneurone instantaneous rates has a gain curve that increases with frequency and a phase response curve with phase advance [Baldissera et al, 1984]. The first property corrects partially the lowpass filtering of the muscle contraction while the second tries to compensate the phase lag caused by the finite conduction velocity of the action potential through the motoneurone axon. Hence, motoneurone models must encode sinusoidal-like current inputs to the soma into spike trains with specific frequency responses [Baldissera et al, 1984; Goroso et al, 2000]. But an important aspect has been left out of these discussions: the dendritic filtering effect. If it has a lowpass filter characteristic, with lower cutoff frequencies for distally occurring synapses, then it is clear that synaptic inputs related to voluntary commands cannot be very distal, because their effect at the initial segment would be insufficient to cause the periodic bursting at the fast oscillatory movement. Therefore, it is important to determine the frequency response from synaptic inputs occurring at a few dendritic sites to the soma.

The encoding realized by a motoneurone model and its reality

In this brief communication only a few facets of a motoneurone model spike train encoding are presented. The model is composed of several dendritic compartments and compartments for the soma and the initial segment. The soma and the initial segment are described by several ionic conductances in parallel [Vieira and Kohn, in preparation].

In very fast and forceful contractions, an important input is a current step. The resultant spike train from the model showed a very short initial interspike interval followed by a pronounced adaptation, as shown in Fig. 1 for a type FF motoneurone model. As mentioned before, the muscle will decode such a train with a "catch" property, which is relevant for the production of short rise time and large forces.

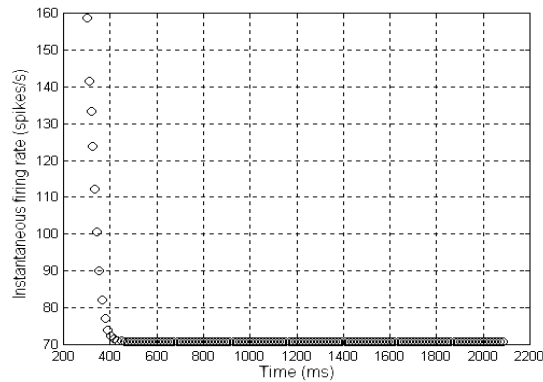


Fig. 1 – Motoneuron model instantaneous rate for a current step input.

The firing rate under steady state as a function of the current intensity is also of relevance for motoneuron-muscle function and a result obtained from the mathematical model simulation is shown in Fig. 2 for FF and FR type motoneuron models. The resultant slopes are within the range found in real motoneurons.

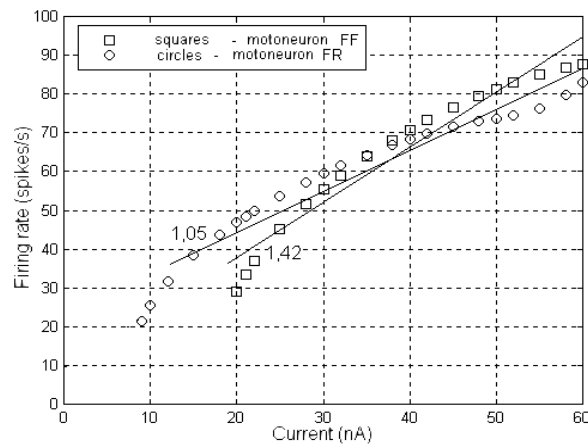


Fig. 2 – Steady state input current encoding to firing frequency for FF and FR models

The motoneuron firing rates illustrated in Fig. 2 are typically sufficient to assure a maintained fused muscular contraction. In humans it is easy to show experimentally that constant muscular contraction is associated with a nearly periodic firing pattern of each motoneurone. Further results from our model include the frequency response computed from a few places along the dendritic tree in response to sinusoidal conductance variations, the degree of nonlinearity when two nearby synapses are activated on the dendritic tree, the frequency response of the spike rate as a function of current injected in the soma. All these have been analysed in light of the encoding properties of real motoneurons and the decoding characteristics of real muscles, with the conclusion that the motoneuron models developed mimic reasonably well real motoneurons, and that the results shed further light on mechanisms responsible for the motoneurone encoding and muscle decoding correspondences found in nature.

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