Dynamic Neural Networks for Sensorimotor Control

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Abstract— **This is preliminary work in the investigation of crayfish sensorimotor coordination mechanisms. A previously-characterized model of the slowly-adapting stretch receptor organ (SAO) is being extended and incorporated into a simulation of the motor control circuit, including the involved motoneurons, muscles, and interneurons. It is well known that the responses of the SAO to both muscle stretch and synaptic input are complex and nonlinear. The significance of this for overall operation of the sensorimotor system is unclear. We present preliminary results of the action of the SAO in this context.**

Keywords—**Synaptic coding, transient analysis, muscles, neuromuscular stimulation, dynamics, nonlinear systems, biophysics.**

Introduction

The primary purpose of this work is to expose some of the functionality represented in the neural components of a motor control system. Additionally, it is our goal to understand system recovery from unexpected external perturbations.

The model we have chosen incorporates a single muscle with a single embedded slowly adapting stretch receptor organ (SAO). As this host muscle is perturbed, the SAO will modify its output spike train with respect to the muscle's extension. This, likewise, will possibly force a change in the activity of the motor control circuit and thus the muscle's stretch. Additionally, the SAO's discharge may be altered in response to changes in its inhibitory synaptic input. When studying the error recovery of the system, we hope to determine that its behavior is stable with respect to small perturbations the host muscle. These perturbations may represent opposing muscle tension, external stimuli, etc.

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This is a preliminary report describing the models and results obtained to date.

Methods

We summarize each part of the model (muscle, SAO dendrites, SAO soma/axon) in turn, and then discuss some issues stemming from the simulation algorithms used.

SAO Response to Muscle Stretch

A model to determine the stretch-related dendritic current in the SAO whose host muscle is subject to stress was developed from physiological experiments by Swerup and Rydqvist [6]. It involves a model of the muscle tension/stretch relationship and the receptor current dependency on stretch.

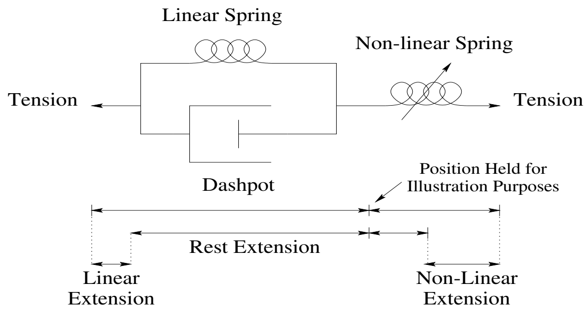

Fig. 1. Muscle Model

The muscle model consists of two components in series: a non-linear spring and a linear spring connected in parallel to a dashpot, otherwise known as a Voigt element. This can be seen in Figure 1.

The extension of the muscle is

$$\epsilon = \epsilon_1 + \epsilon_2 \tag{1}$$

where ϵ_1 is the extension of the Voigt element and ϵ_2 is the extension of the non-linear spring. For the muscle to be in a static state, the force gradient across the joining point of the two components must be zero.

Hence, the tension across either component must be equal to the tension across the muscle as a whole. To state this mathematically, the non-linear spring extension relates to tension by

$$\sigma_m = k_2\,\epsilon_2^{n+1} \tag{2}$$

where k_2 is the non-linear spring coefficient and n is the non-linear power coefficient. The linear element's tension is

$$\sigma_m = k_1\,\epsilon_1 + B\,\frac{\mathrm{d}\epsilon_1}{\mathrm{dt}} \tag{3}$$

where k_1 and B are the spring and dashpot coefficients. Since the tension of the two components of the muscle must equal, it follows that

$$\sigma_m = k_1\,\epsilon_1 + B\,\frac{\mathrm{d}\epsilon_1}{\mathrm{dt}} = k_2\,\epsilon_2^{n+1} \tag{4}$$

To determine the extension as a function of the overall extension, (1) is solved for ϵ_1 and substituted into (4)

$$k_1\,(\epsilon - \epsilon_2) + B\,\frac{\mathrm{d}(\epsilon - \epsilon_2)}{\mathrm{dt}} = k_2\,\epsilon_2^{n+1} \tag{5}$$

Finally, solving for $\mathrm{d}\epsilon_2/\mathrm{dt}$:

$$\frac{d\epsilon_2}{dt} = \frac{k_1\,\epsilon - k_1\,\epsilon_2 - k_2\,\epsilon_2^{n+1}}{B} + \frac{\mathrm{d}\epsilon}{\mathrm{dt}} \tag{6}$$

Where ϵ and $\mathrm{d}\epsilon/\mathrm{dt}$ are inputs. Once the ϵ_2 is known for a point in time, the tension of the muscle can be found by using (3).

For the dendritic current, the tension is used to find the stretch-sensitive ion channels' open probability P_o:

$$P_o = \frac{1}{1 + K_b\,e^{-s(\sigma_m/m)^q}} \tag{7}$$

where K_b, s, m, and q are defined in Appendix II. This open probability is related to current by

$$I_s = P_o \cdot g_{smax} \cdot (V_m - V_{srev}) \tag{8}$$

where g_{smax} is the maximum stretch activated conductance and V_{srev} is the reversal potential for the ion channels.

SAO Membrane Potential

Current from stretch-sensitive dendritic ion channels (I_s) was incorporated into a model originally developed by Edman and collaborators [2] and modified by Stiber *et al.* [5]:

$$\begin{aligned} C_m\,\frac{\mathrm{dV_m}}{\mathrm{dt}} &= -(I_{\mathrm{Na}} + I_{\mathrm{K}} + I_{L,\mathrm{Na}} \\ &\quad + I_{L,\mathrm{K}} + I_{L,\mathrm{Cl}} + I_p \\ &\quad + I_s + I_{\mathrm{syn}}) \end{aligned} \tag{9}$$

where the terms on the right side are the various ionic currents (see Appendix I for their detailed equations).

Numerical Methods

At this stage of model development and implementation, we want to know if the resulting model approximates real neuron behavior. We have chosen to compare the simulation's output with the observations of Buño *et al.* [1]. They studied SAO responses to step-like changes in muscle stretch with and without added Gaussian jitter.

Model equations were integrated using the LSODAR integration algorithm from ODEPACK [3], which allows for easy spike detection (every other time $V_m = 0$, for example). LSODAR's variable step size/variable order nature required careful consideration of approaches to generating the input extension waveforms. All inputs must act like waveforms continuous through their second derivatives, and must be produced by functions which make no assumption regarding monotonically increasing time (as LSODAR may reduce its step size, resulting in a call "backwards in time").

To produce a second derivative-continuous step, log-sigmoid functions were used in place of the discontinuity. This works well except for points near the sigmoid curves' asymptotes. At these points, the exponential terms exceed machine capacity. To overcome this, their calculated values were replaced with the asymptotic values when the error was negligible.

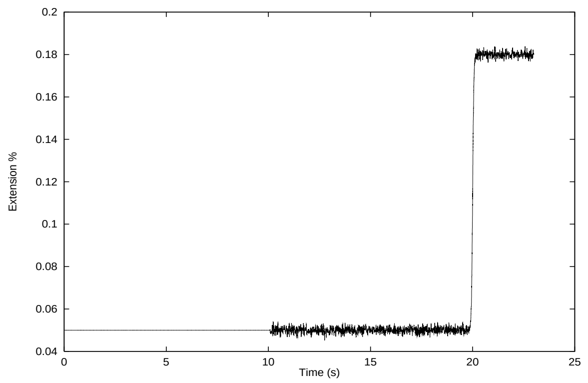

Fig. 2. Example of smoothed step and 1% noise

Any noise added must also be continuous through the second derivative *and repeatable*. Hence, Gaussian offsets generated by calls to a random number generator were insufficient. To create an approximation to Gaussian band-limited noise, a discretely sampled Gaussian noise waveform was generated for the required time span. This was low-pass filtered to remove all frequencies above 50Hz (to match the experiments). A piecewise cubic spline fit [7] was then performed in Octave [4] on the filtered noise to produce coefficients allowing repeatable, smooth interpolation during integration.

To add the noise waveform to the muscle stretch function, the two functions were blended together through another log-sigmoid envelope. This reduced the discontinuities of the introduction of noise to well below tolerances and acted as a scaling factor. As with the step function, when applicable, the log-sigmoid calculations were replaced with their asymptotic value. An example of noise added to the step function can be seen in Figure 2, where the noise's standard deviation is 1% of full muscle extension.

Analysis

At the start of simulations, the muscle was initially extended to 5% of its maximum length and the SAO allowed to adapt to stationary firing for 10 seconds. Noise was then added, and at 20s the muscle was extended to 18% and held at constant tension until its relaxation back to 5% at 40s. The transition periods of muscle extension and relaxation were 250ms.

Histograms of SAO spike count along time were generated using 1s bin widths. Comparisons of histograms with and without noise were accomplished by subtracting corresponding bins to produce difference histograms. This was substantially the same analysis performed by Buño *et al.* [1].

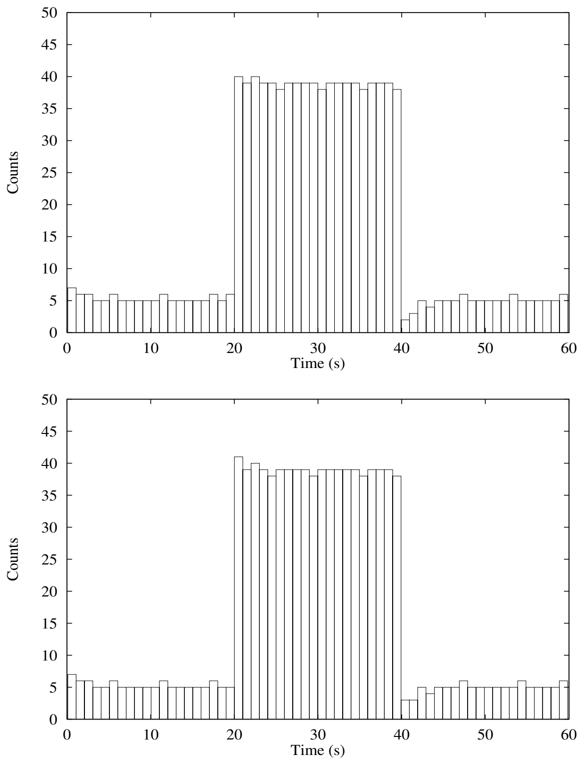

Fig. 3. SAO rate versus time histograms. The graph on the bottom contains 1% noise added at t=10 seconds.

Results

Figure 3 shows model response to muscle step extensions with (bottom) and without (top) noise. As in the living preparation, a step extension produces an overshoot in firing rate (though not as pronounced in the simulation) and subsequent adaptation, and an undershoot after a step relaxation. In this case, a low level of noise (1% of max muscle extension) had little effect (on the order of one spike per second).

When the noise level was increased to 20%, the SAO had a higher firing rate. This can be seen in Figure 4. This is consistent with Buño *et al.*'s [1] observations, but greatly reduced in magnitude.

Discussion

This paper presents a comparison of a partial sensorimotor circuit model to that observed in a living preparation. It is important to note that the parameters associated with each part of the model (corresponding to characteristics which no doubt vary among individual cells) were *not* tuned to produce results numerically equivalent to that of the living preparation. However, one major qualitative similarity — firing acceleration in response to noise — was obtained. The other major experimental result — reduction in step over and undershoot — is still under investigation. Subsequent to this work, a more complete circuit incorporating accessory cells and feedback inhibition via the SAO's prototypical synapse, flexor, flexor inhibitor, and extensor motoneurons will be assembled.

Appendix

I. Permeability Model Equations

The ionic currents in (9) are defined in the following equations for the voltage-sensitive channels (I_{Na}, I_{K}), leak ($I_{L,X}$, $X = \mathrm{Na}, \mathrm{K}, \mathrm{Cl}$), and Na-K pump ($I_p$). As no synaptic inputs were presented here, $I_{\mathrm{syn}} = 0$.

$$I_{\mathrm{Na}} = A\bar{P}_{Na} m^2 h l \frac{V_m F^2}{RT} \times \frac{[\mathrm{Na}^+]_{\mathrm{o}} - [\mathrm{Na}^+]_{\mathrm{i}}\, \mathrm{e}^{\mathrm{FV_m/RT}}}{1 - e^{FV_m/RT}} \quad (10)$$

$$I_k = A\bar{P}_k n^2 r \frac{V_m F^2}{RT} \times \frac{[\mathrm{K}^+]_{\mathrm{o}} - [\mathrm{K}^+]_{\mathrm{i}}\, \mathrm{e}^{\mathrm{FV_m/RT}}}{1 - e^{FV_m/RT}} \quad (11)$$

$$I_{L,X} = AP_{L,X} \frac{V_m F^2}{RT}$$

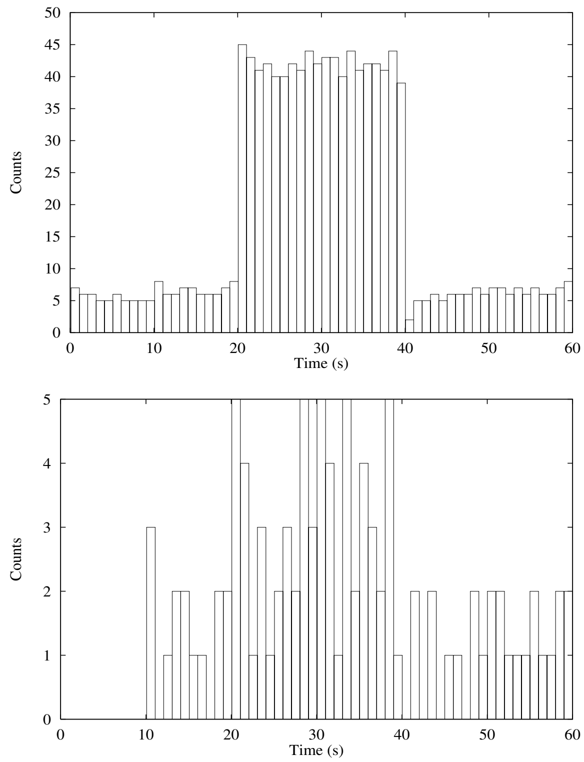

Fig. 4. Response to 20% noise. Rate versus time histogram shows response to noise (top), while the difference histogram (bottom) compares this to the noise free plot of Figure 3(top).

$$\times \frac{[X]_o - [X]_i \, e^{FV_m/RT}}{1 - e^{FV_m/RT}} \tag{12}$$

$$I_p = \frac{AF}{3} \frac{\bar{J}_{p,\mathrm{Na}}}{\left(1 + \frac{K_m}{[\mathrm{Na}^+]_\mathrm{i}}\right)^3} \tag{13}$$

$$\tag{14}$$

The gating variables' ($g = \{m, h, l, n, r\}$) kinetics are determined by

$$\mathrm{dg/dt} = (g_\infty - g)/\tau_g \tag{15}$$

$$g_\infty = \nu_g + \frac{1 - \nu_g}{1 + e^{z_g e (V_m - V_g)/kT}} \tag{16}$$

$$\tau_g = Q_g \bar{\tau}_g \bigg/ \left[e^{\frac{\delta_g z_g e}{kT}(V_m - V_g)} + e^{\frac{(\delta_g - 1) z_g e}{kT}(V_m - V_g)} \right] \tag{17}$$

$$Q_g = \left(\frac{1 - \delta_g}{\delta_g}\right)^{\delta_g} + \left(\frac{1 - \delta_g}{\delta_g}\right)^{\delta_g - 1} \tag{18}$$

Here, the asymptotic value of g is represented by g_∞. Equation (17) determines the time constant.

II. Muscle Parameters

Constant	Value	Units
k_1	400	kPa
k_2	2200	kPa
n	1.5	
B	12	kPa
k_b	106	
s	0.00277	Pa^{-1}
q	1	
m	25	
I_{smax}	-200	nA
V_{srev}	10	mV
C_m	4.3	nF
g_{leak}	0.56	μS
V_{rest}	-65	mV
V_{leak}	-65	mV

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