

# The Electrical Properties of Dendritic Spines and the Temporal Filtering Properties of Neurons<sup>1,2</sup>

Evan Haskell<sup>a,3</sup> Gary J. Rose<sup>b</sup>

<sup>a</sup>*University of Utah, Department of Mathematics, Salt Lake City, Utah  
haskell@math.utah.edu*

<sup>b</sup>*University of Utah, Department of Biology, Salt Lake City, Utah  
gary.rose@m.cc.utah.edu*

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## Abstract

How neurons transform information is a fundamental issue in understanding the the neural control of behavior. The electrosensory system of the weakly electric fish, *Eigenmannia*, is well suited for studying cellular mechanisms of sensory coding and filtering. Filtering characteristics of neurons in the dorsal torus of *Eigenmannia* are correlated with the density of dendritic spines. We develop a model of the interaction between the spine and soma. This model exhibits the temporal filtering properties of spiny neurons in responding to the Electric Organ Discharge and Jamming Avoidance Response signals. As well, the model indicates how these neurons are able to have PSP amplitudes that are independent of the polarization level of the cell.

*Key words:* spine, electrosensory, electrolocation, temporal filtering, electric fish

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## 1 Context: Jamming Avoidance Response of the Weakly Electric Fish

How neurons transform information is a fundamental issue in understanding the relationship between neurons and behavior. In many cases, behavioral studies can provide insight into general features of these transformations. An example is electrolocation associated jamming avoidance behavior of weakly electric fish, *Eigenmannia*. The weakly electric fish electrolocates by way of an electric organ discharge (EOD). When two electric fish come into contact there can be a detrimental interference between the EODs resulting in modulations of phase and amplitude that can interfere with the ability to electrolocate.

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<sup>1</sup> For consideration of presentation at CNS03

<sup>2</sup> alternate title: From Spine to Behavior

<sup>3</sup> Corresponding Author

As such, the weakly electric fish is endowed with the ability to adjust the frequency of its EOD in what is known as the jamming avoidance response (JAR). The JAR of the weakly electric fish is greatest for modulations or “beat rates” of 3-8 Hz. Beat rates can be of most interference to the fish’s ability to electrolocate. Beat rates of more than 20 Hz do not impair the ability to electrolocate and hence elicit little to no JAR from the fish. During a JAR both fish alter their EODs. The fish with the lower frequency lowers its EOD and the other raises its EOD frequency. In doing so, the beat rate is increased to values that have little or no effect on electrolocation. A neural correlate of these behavioral findings is that neurons in the midbrain act as filters of temporal patterns of input. Inspired by this behavior and the role played by spiny neurons in the dorsal torus semicircularis of the weakly electric fish in filtering input from the electrosensory lateral line lobe, a simple model of spine-soma interaction is presented.

## 2 Model

In this abstract, we present a simple passive model of spine-soma interaction. The premise of this model is that synaptic events occur on a dendritic spine. The unitary event is filtered by the spine creating a current into the soma. The focus is placed on the electrical properties of a single spine-head which is meant to be representative of the average spine-head. In order to maintain this focus, somatic responses are considered to be independent of the dendritic location of the spine-head. Hence, the resulting current flow into the soma from the spine can be thought of as the effective, or average, current from a population of spines.

The soma and spine are both modeled as leaky integrators. That is, they are each treated as separate isopotential compartments. The equations governing the evolution of the spine voltage,  $V_{sp}(t)$ , and the soma voltage,  $V_{so}(t)$ , when the spine receives a normalized source current,  $I_{source}(t)$ , are:

$$\begin{aligned}\frac{dV_{sp}}{dt} &= -\frac{1}{\tau}(V_{sp} - \mathcal{E}_{sp}) + I_{source}(t) \\ \frac{dV_{so}}{dt} &= -\frac{1}{\sigma}(V_{so} - \mathcal{E}_{so}) + \frac{1}{c_{so}}I_{neck}(t) - I_h(t)\end{aligned}$$

where,  $\tau$  and  $\sigma$  are resting membrane time constants for the spine and soma respectively,  $\mathcal{E}_{sp}, \mathcal{E}_{so}$  are leakage reversal potentials and  $c_{so}$  is the membrane capacitance of the soma.  $I_h(t)$  is a normalized hyperpolarizing current that may be injected into the soma. This current is included for later exposition of the implications of this model and comparison to recordings from spiny neurons in the dorsal torus of the weakly electric fish.  $I_{neck}(t)$  is the current flowing

through the spine neck from the spine head to the soma and is proportional to the difference between the spine and soma potentials,

$$I_{neck}(t) = -\frac{1}{R_{neck}}(V_{so}(t) - V_{sp}(t))$$

where  $R_{neck}$  is the spine-neck resistance. For convenience in presentation, we define the time constant  $\rho = c_{so}R_{neck}$ . When the membrane potential of the soma exceeds a threshold voltage,  $V_{th}$ , it is said to emit an action potential and returns to a reset potential,  $V_{reset}$ , after a refractory period,  $\tau_{ref}$ .

### 3 Demonstration of the Model

Many properties of the model given here can be computed analytically or simulated very efficiently. In this section we will explore some of the basic properties and implications of our model. As well, a comparison between the temporal filtering properties of the model and spiny neurons in the dorsal torus of the electric fish in responding to sensory signals is shown.

A first natural question to ask is to find the response of the soma to an unitary event arriving at the spine. This impulse response function for the soma membrane potential at rest to an unitary event arriving at time  $t = T$ ,  $I_{source} = A\delta(t - T)$ , is for  $t > T$ :

$$V_{so}(t) = \frac{\rho\mathcal{E}_{so} + \sigma\mathcal{E}_{sp} - \sigma\rho I_h}{\rho + \sigma} + \frac{\tau\sigma}{\tau\rho + \tau\sigma - \sigma\rho}\tau A \left( e^{-\frac{t-T}{\tau}} - e^{-\frac{\rho+\sigma}{\rho\sigma}(t-T)} \right). \quad (1)$$

An example of the impulse response function is shown in figure 1a. The relatively large spine-neck resistance,  $R_{neck}$  requires the response of the spine to be much larger than the soma potential in order to elicit a current flow into the soma. In this manner, a conductance modulation at the spine due to an unitary event is transformed into a current injection to the soma. In the plot of  $V_{so}$ , the solid and dashed lines correspond to no hyperpolarizing current,  $I_h = 0$ , and a small  $I_h$  being injected into the soma, respectively.

If an unitary event were to arrive at the soma thus modulating a conductance, a larger PSP would be expected for a larger hyperpolarizing current,  $I_h$ . This is due to the greater amplification of the conductance event resulting from the more hyperpolarized state of the neuron. However, PSPs in dorsal torus spiny neurons resulting from stimulation by the lateral lemniscus (LL) have the same size regardless of  $I_h$  (3). Note that both curves in the figure reach their peak response at the same time,  $t_{peak}$ , and have the same peak change in membrane potential  $\Delta v_{peak}$ , regardless of the level of hyperpolarizing current,  $I_h$ . This

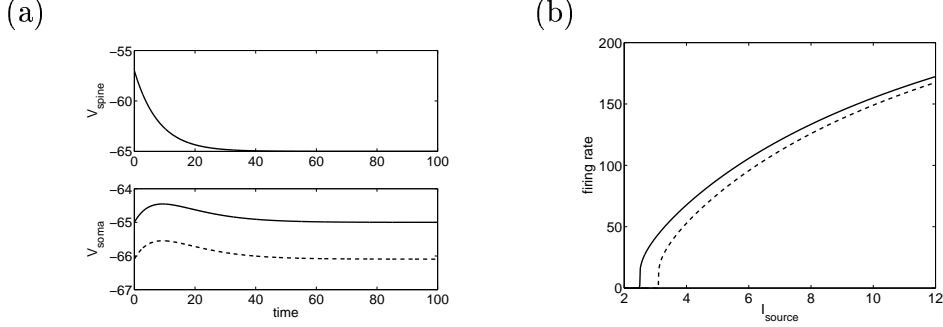


Fig. 1. **RESPONSE PROPERTIES OF THE MODEL CELL:** Examples of (a) the response to an unitary synaptic event and (b) the resulting firing rate of the neuron to a constant current applied to the spine for the model presented. The solid and dashed lines refer to  $I_h = 0$  and a small  $I_h$ . In panel a, note that the peak response of  $V_{so}$  for both curves is at  $t_{peak} = 9.3161ms$  and have the same peak response  $\Delta v_{peak} = .5461mV$  (both values calculated analytically).

can be seen from expressions for  $t_{peak}$  and  $\Delta v_{peak}$  computed analytically from equation (1) (not shown). Since the model spine-head membrane potential  $V_{sp}$  is independent of the soma membrane potential  $V_{so}$ , an unitary event will have the same effect on the spine-head independent of  $I_h$ . Thus, the PSP amplitude in the soma is also independent of the hyperpolarization level of the soma. Hence, from this model we can implicate a plausible role played by the spine in the neural response seen by spiny neurons to LL stimulation.

In the model presented here, the spine head is not endowed with the capability to spike. As such, when a constant current,  $I_{source}(t) = I_{source}$ , is applied the spine head will reach an equilibrium potential  $V_{sp,eq} = \mathcal{E}_{sp} + \frac{\tau I_{source}}{c_{sp}}$ . In turn, the soma will reach an equilibrium potential  $V_{so,eq} = \frac{\rho \mathcal{E}_{so} + \sigma V_{sp,eq} - \sigma \rho I_h}{\sigma + \rho}$  provided  $I_{source} < \frac{1}{\tau} \left( (V_{th} - \mathcal{E}_{sp}) + \frac{\rho}{\sigma} (V_{th} - \mathcal{E}_{so}) + \rho I_h \right)$  otherwise the cell fires at a constant rate,  $f$ , given by:

$$\frac{1}{f} = \frac{\rho\sigma}{\rho + \sigma} \ln \left( \frac{V_{reset} - \frac{\rho \mathcal{E}_{so} + \sigma \mathcal{E}_{sp} - \rho \sigma I_h + \sigma \tau I_{source}}{\sigma + \rho}}{V_{th} - \frac{\rho \mathcal{E}_{so} + \sigma \mathcal{E}_{sp} - \rho \sigma I_h + \sigma \tau I_{source}}{\sigma + \rho}} \right) + \tau_{ref}$$

An example of this relationship between the driving current and the firing rate of a neuron is shown in figure 1b.

Figure 2a shows the response of a spiny ampullary neuron in the dorsal torus of *Eigenmannia*. The stimulus, S, represents a sensory signal received by the electric fish. The presented stimulus is a frequency sweep from 2 to 30 Hz. We see that for low frequency sinusoidal voltages, the cell responds very smoothly, mirroring the stimulus waveform. However for high frequency input, the cell shows an attenuated response, exhibiting a low pass filtering of the input signal. The comparable performance of the model neuron is shown in figure 2b.

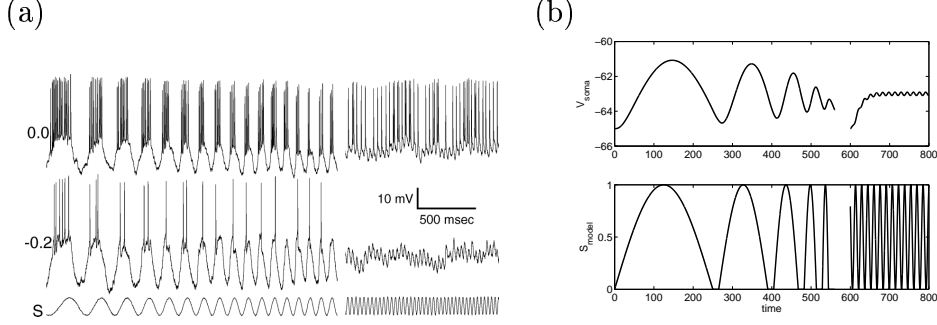


Fig. 2. **RESPONSE TO A LOW FREQUENCY SENSORY SIGNAL:** Low pass filtering by a spiny neuron in the weakly electric fish is shown in panel a. The corresponding low pass filtering of the model cell is in panel b. Panel a is reprinted with permission from (2).

$S_{model}$  is a normalized current sweep from 2 to 32 Hz. The thresholding of the soma is removed and the smooth fluctuations of the membrane potential  $V_{so}$  are shown. The model neuron shows the same low pass filtering properties. That is for the low frequency stimuli, the membrane shows a smooth fluctuation mirroring that of the stimulus. Whereas, at high frequency input, the membrane fluctuations are much reduced in amplitude. If the current,  $S_{model}$ , were injected directly into the soma of the model cell rather than into the spine-head the cell would respond to a greater range of frequencies losing much of the low pass filtering characteristics of the spiny cell (not shown).

During the JAR there is a spectral mixing of the two rhythmic EOD signals. Figure 3a shows the JAR response for the weakly electric fish. The JAR current,  $S$ , shows the mixing of the two EODs. Notice that the response of the cell reflects the amplitude envelope of the signal. The corresponding JAR response of the model neuron is shown in figure 3b. Notice that the model cell also exhibits smooth membrane fluctuations mirroring the stimulus. Injecting this current straight into the soma of the model cell rather than the spine-head would result in a stronger modulation of the membrane potential reflecting the higher frequency components of the stimulus (not shown). Notice that the responses of both the spiny neuron and model neuron show a phasic delay from the input current in both figures 2 and 3.

## 4 Discussion

The model presented here shows how a spiny neuron can respond to unitary events in a manner independent of the polarization level of the soma. That is, unitary synaptics events modulating a conductance at the spine-head are transformed into current injections to the soma. As well, the model does a nice job of capturing the low pass filtering properties exhibited by spiny neurons

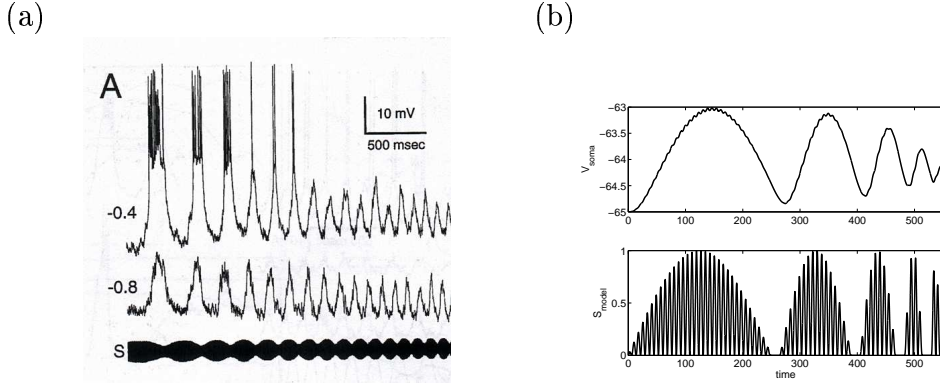


Fig. 3. **RESPONSES TO SIGNALS THAT ELICIT THE JAMMING AVOIDANCE RESPONSE:** The response to a JAR signal for a spiny neuron in weakly electric fish (panel a) and the model cell (panel b) is shown. Note that the responses mirror the low frequency envelope of the signal. Panel a is reprinted with permission from (2).

in dorsal torus of the weakly electric fish. However, this is just the beginning of a bigger story. There are other passive and active properties exhibited by some spiny neurons in the dorsal torus that are not presented in this model. As well, this model only accounts for a single spine on a single neuron.

Some of the spiny neurons in the dorsal torus exhibit synaptic depression or facilitation. That is, the response to an unitary event may be increased or decreased based on stimulation frequency independent of polarization level of the cell. As well, some of the spiny neurons exhibit active membrane properties. For example, the duration of stimulus-related EPSPs may depend on the driving force imposed on the neuron. These properties all play a role in the filtering properties of the neurons (2).

The PSPs exhibited by the spiny neurons have some variability due to the inherent noise in the system. This was not taken into account in this model. Nor was the effects of having many spines on one neuron providing many inputs to the soma. To study such a large number of spines one needs to enlist statistical methods. One such method that takes into account both intrinsic noise in the system and the large number of units is the Population Density Method (4). This method has been presented by the first author at the CNS meeting in 2000 and 2002. The population density method can be used to study both the effects of a large number of spines on one neuron; as well as, the response of a population of spiny neurons to sensory stimuli.

## References

- [1] GJ Rose, SJ Call, *Proc. Natl. Acad. Sci.* **89** (1992) 9662.
- [2] ES Fortune, GJ Rose, *J. Neurosci.* **17** (1997) 3815.
- [3] ES Fortune, GJ Rose, *J. Neurosci.* **20** (2000) 7122.
- [4] E Haskell, DQ Nykamp, D Tranchina, *Network* **12** (2001) 141.