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Small-signal Neural Models and its Application to determining Model Parameters

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Abstract—This paper introduces the use of the concept of small signal analysis, commonly used in circuit design, for understanding neural models. We show that neural models, varying in complexity from Hodgkin-Huxley to Integrate and fire have similar small signal models when their corresponding differential equations are close to the same bifurcation with respect to input current. The small signal model allows circuit designers to intuitively understand the behavior of complicated differential equations in a simple way. We use small-signal models for deriving parameters for a simple neural model (like resonate and fire) from a more complicated but biophysically relevant one like Morris-Lecar. We show similarity in the sub threshold behavior of the simple and complicated model when they are close to a Hopf bifurcation and a Saddle-node bifurcation. Hence, this is useful to correctly tune simple neural models for large scale cortical simulations.

I. NEURAL MODELS AND PARAMETER EXTRACTION

Neural models of varying complexity are used by neuroscientists for understanding detailed channel dynamics as well as computational principles in the brain. The Hodgkin-Huxley model [1] is typically used by biologists to model detailed kinetics of ion-channels. However, the earliest such neuron model introduced in the early fifties consisted of a set of four dimensional differential equations with around twenty tunable parameters. Using such a complicated model is a numerically intractable for large scale neural simulations trying to mimic a human cortex. Also, finding the correct set of parameters for a desired behavior is very tedious.

Hence, computational neuroscientists have developed simpler models like integrate and fire or resonate and fire [2] which capture some of the essential properties of the more realistic models but are numerically efficient. However, finding the correct parameters for the simpler neural model to match its properties with the complicated model is not necessarily an easy task; this requires solving an over determined problem since the number of parameters in the complicated model is much more than that in the simpler one. In this paper, we present a method for solving this problem using the concept of small-signal analysis that is a workhorse for the circuit designer. This concept can also be used for tuning silicon neurons like in [3]. Therefore, this work provides a framework for correctly tuning neuron parameters enabling large scale (hardware or software) neural simulations. This approach to parameter tuning is shown in Fig. 1.

In circuit design, small-signal analysis involves linearizing a non-linear element around its operating point to generate a circuit comprising linear circuit elements. A similar concept

Fig. 1: **Small signal model:** Actual biology, complicated ion-channel models like Hodgkin-Huxley and simple neural models like Integrate and fire can be reduced to similar small signal models if they are operating close to the same bifurcation. This similarity can be used to obtain the parameters of the simple model from the bio-physically realistic one.

has been used earlier in chapter 10 of [4] to intuitively understand the behavior of Hodgkin-Huxley channel models. We generalize that method for arbitrary neural models and also apply the same principle to translate parameters across different models. In [5], transformations are applied to the input stimulus to make the sub threshold behavior of integrate and fire neurons and Hodgkin-Huxley neurons similar. Instead of modifying the input, we choose parameters optimally to match the sub threshold behaviors of the two models. Thus there is no need to know the type of stimulus a priori.

II. SMALL SIGNAL NEURAL MODELS

To describe the concept of small signal neural models, we start with a general set of differential equations given by:

$$\begin{aligned}\dot{V} &= f(V, \bar{n}, \bar{\alpha}) \\ \dot{\bar{n}} &= g(V, \bar{n}, \bar{\alpha})\end{aligned}\quad (1)$$

where V represents the membrane voltage, $\bar{n}$ represents a vector of gating variables and $\bar{\alpha}$ is a vector of parameters. Now considering a small current stimulus, δi , is incident on the membrane, we can find its small signal impedance by taking derivatives of (1) to get:

$$\begin{aligned}\delta i &= Df_V \delta V + Df_{\bar{n}} \delta \bar{n} \\ \delta \dot{\bar{n}} &= Dg_V \delta v + Dg_{\bar{n}} \delta \bar{n}\end{aligned}\quad (2)$$

where Df and Dg are the Jacobian matrices consisting of partial derivatives for the functions f and g respectively evaluated at the equilibrium. Finally, applying the concept of Laplace transforms to (2), we get:

$$\delta i = (Df_V + Df_{\bar{n}} Dg_V [sI - Dg_{\bar{n}}]^{-1}) \delta V \quad (3)$$

Fig. 2: **Bifurcations in Morris-Lecar:** The Morris-Lecar model can be tuned to exhibit both the (a) Hopf and (b) Saddle-node bifurcations at low input currents.

where I is the identity matrix.

To clarify the concept, we shall next apply this principle to a complicated model and a simple model and use the resulting small signal models for parameter translation. Since the neural properties depend on the bifurcation the model undergoes, we shall consider both the bifurcations of codimension I - Hopf and Saddle-node. As an example of a bio-physically realistic model, we choose the Morris-Lecar model [6] which can be tuned to exhibit both the bifurcations. We choose the resonate and fire (raf) model and the quadratic integrate and fire (qif) model as the simplest models that capture the properties of the neural models close to a Hopf and a Saddle-node bifurcation respectively.

The Morris-Lecar model is given by the following equations:

$$\begin{aligned}
 C\dot{V} &= \overline{G_{Ca}}m_{ss}(V)(E_{Ca} - V) - \overline{G_K}W(V - E_K) \\
 &\quad - \overline{G_L}(V - E_L) + i \\
 \dot{W} &= \frac{(w_{ss}(V) - W)}{\tau_W(V)} \\
 m_{ss}(V) &= \frac{1}{2} \left\{ 1 + \tanh \left[\frac{V - V_1}{V_2} \right] \right\} \\
 w_{ss}(V) &= \frac{1}{2} \left\{ 1 + \tanh \left[\frac{V - V_3}{V_4} \right] \right\} \\
 \tau_W(V) &= gain / \cosh \left[\frac{V - V_3}{2V_4} \right]
 \end{aligned} \tag{4}$$

In the rest of the paper we use the units of mV for voltages, ms for time, pA for current, nS for conductances and we assume the membrane capacitance is 1 pF. Figure 2 plots the bifurcation diagrams for the two cases. The parameter set for Fig. 2(a) is $E_{Ca} = 100$, $E_L = -50$, $E_K = -70$, $\overline{G_{Ca}} = 1.1$, $\overline{G_L} = .5$, $\overline{G_K} = 2$, $V_1 = -1$, $V_2 = 15$, $V_3 = 0$, $V_4 = 30$, $gain = 5$. The major difference in the parameters for the case in Fig. 2(b) is that potassium activation is steeper and occurs at a higher membrane voltage quantified by $V_3 = 10$, $V_4 = 30$, $gain = 3$. To derive the small signal impedance for the Morris-Lecar model, we again assume that a small current stimulus is incident on the membrane (as in (2)) to get:

$$\begin{aligned}
 \delta i &= (\delta i_{Ca} + \delta i_K + \overline{G_L}\delta V) \\
 \delta i_{Ca} &= (\overline{G_{Ca}}m_{ss} + \overline{G_{Ca}}\frac{dm_{ss}}{dV}(V - E_{Ca}))\delta V = G_{Ca}\delta V
 \end{aligned}$$

Fig. 3: Small signal membrane impedance for (a) the Morris-Lecar model, (b) the resonate and fire model and (c) the quadratic integrate and fire model.

$$\begin{aligned}
 \delta i_K &= \overline{G_K}W\delta V + \overline{G_K}(V - E_K)\delta W \\
 &= G_K\delta V + \overline{G_K}(V - E_K)\delta W
 \end{aligned} \tag{5}$$

Thus we see that the calcium and the leak channels directly contribute conductances to the membrane impedance while the potassium channel provides an impedance that depends on δW . To get the exact impedance, we use the Laplace transform on the equation for the gating variable W to get:

$$s\delta W = p\delta V - \frac{1}{\tau_W}\delta W \tag{6}$$

where $p = -\frac{w_{ss}}{\tau_W^2}\frac{d\tau}{dV} + \frac{1}{\tau_W}\frac{dw_{ss}}{dV} + \frac{W}{\tau_W^2}\frac{d\tau_W}{dV}$. Combining equations (5) and (6) we get:

$$\delta i = (G_{Ca} + \overline{G_L} + G_K)\delta V + \frac{\delta V}{\frac{s}{q} + \frac{1}{q\tau_W}} = G\delta V + \frac{\delta V}{\frac{s}{q} + \frac{1}{q\tau_W}} \tag{7}$$

where $q = p\overline{G_K}(V - E_K)$. We see that the potassium channel contributes a conductance G_K and an inductance $L = 1/q$ with series resistance $R_L = 1/q\tau_W$. All these impedances are evaluated with V and W at their equilibrium values. These small signal impedances are presented in table I for the two parameter sets mentioned earlier with $i=23.7$ and 7.85 for the Hopf and Saddle-node cases respectively. Figure 3(a) plots this small signal model.

In both the cases, the leak and the potassium channel contribute positive conductances while the calcium channel provides a negative conductance due to positive feedback. In the case of the Saddle-node, the value of R_L is around ten times larger than $1/G$. Hence, we can intuitively understand that in this case the branch containing the inductance

TABLE I: Small signal impedances for Morris-Lecar model

Parameter	Hopf	Saddle-node
G	0.02	0.15
L	4.83	28.59
R_L	1.03	19.5

will conduct negligible current and can be neglected. Hence, the membrane impedance can be closely approximated by a combination of a resistance and a shunt capacitance. In the other case though, R_L is smaller than $1/G$ implying that the inductive branch conducts significant current. It is well known in circuit theory that the parallel combination of a capacitor and a lossy inductor acts as a band pass filter with a certain resonant frequency. Hence, we can intuitively predict that the neural model in this case has all the properties of the resonator as described in [2].

We now consider two different simpler models that capture the properties of the differential equations close to the two different bifurcations. First, we consider the raf model given by:

$$\begin{aligned}\dot{V} &= \omega n + bV + i \\ \dot{n} &= bn - \omega V\end{aligned}$$

$$\text{If } V = V_{thresh}, V \leftarrow V_{rst}, n \leftarrow n_{rst} \text{ for } t_{rst} \text{ ms.} \quad (8)$$

Applying the earlier concepts, we can derive the small signal impedance for this model as:

$$\delta i = -b\delta V - \frac{\omega^2 \delta V}{b - s} \quad (9)$$

which is shown in Fig. 3(b). The circuit elements in this schematic are exactly the same as the ones in 3(a) validating the fact that the raf model is indeed a good approximation to neural models close to a Hopf bifurcation.

Next, we consider the qif model given by:

$$\dot{V} = aV(V - V_{thresh}) + i$$

$$\text{If } V = V_{thresh}, V \leftarrow V_{rst} \text{ for } t_{rst} \text{ ms.} \quad (10)$$

whose small signal model is given by:

$$\delta i = aV_{thresh}\delta V \quad (11)$$

Thus the small signal impedance for the qif model is similar to that of the Morris-Lecar model close to the Saddle-node bifurcation. It should be noted that the leaky integrate and fire model [2] also has a similar small-signal impedance; the qif model however provides a better approximation to the spike timing since it models the nonlinearity of the differential equation close to a Saddle-node bifurcation. All of these models however behave as an integrator and show excitability for inputs that arrive close in time.

III. PARAMETER TRANSLATION AND SUB-THRESHOLD BEHAVIOR

In this section, we shall derive the parameters of the raf and qif models so that their sub-threshold dynamics match that of the appropriately biased Morris-Lecar model. In the first case, we see that the original 11 parameters of the Morris-Lecar model have been reduced to 3 effective parameters for the sub-threshold behavior: q , τ_W and G while the raf model has 2 parameters: b and ω . But it can be seen by comparing Fig. 3(a) and (b) that a direct translation of parameters by matching coefficients is not possible. Here, we can use our

knowledge of circuit theory and convert the series inductor-resistor combination into a parallel combination which has a similar impedance and quality factor (Q) close to the resonance frequency. The equations governing this transformation [7] are:

$$\omega_0 = \frac{1}{\sqrt{L_s C}}, Q = \frac{\omega_0 L_s}{R_s}, R_p = R_s(1 + Q^2), L_p = L_s(1 + \frac{1}{Q^2}) \quad (12)$$

where X_p and X_s are the parallel and series impedances respectively. Applying this transformation to the Morris-Lecar model, we get:

$$Q = \frac{\sqrt{L}}{R_L}, L_p = L + R_L^2, R_p = R_L + \frac{L}{R_L} \quad (13)$$

Similarly for the raf model, we get:

$$Q = \frac{\omega}{-b}, R_p = -\frac{b}{\omega^2} - \frac{1}{b}, L_p = \frac{1}{\omega^2} + \frac{b^2}{\omega^4} \quad (14)$$

Since the Q for the Morris-Lecar model is greater than 2, we can further approximate the raf model impedances to get:

$$R_p \approx -\frac{1}{b}, L_p \approx \frac{1}{\omega^2} \quad (15)$$

Now, we can compare the two models to get the parameters as follows:

$$\omega = \frac{1}{\sqrt{L + R_L^2}}, b = -\frac{G + R_L/(R_L^2 + L)}{2} \quad (16)$$

This process can be justified since the neuron is most excitable and likely to fire spikes for inputs with frequency close to is resonance frequency. In most cases, spike timing is the important metric which should be closely approximated if the behavior of the two models are similar near resonance.

Next, we derive the parameters for the Saddle-node case. This situation is simpler and we can directly compare the two small signal impedance models to get:

$$G = aV_{thresh} \quad (17)$$

where V_{thresh} is approximated by subjecting the neuron to increasing current pulses and noting the largest membrane voltage excursion without a spike being fired.

We shall discuss determining the other parameters related to spike generation in the next section. We now compare the sub-threshold responses of the two models when it is subject to a train of random synaptic inputs. The EPSC is approximated by a current pulse of width 2 ms whose amplitude follows a uniform random distribution between 0 and 2 pA. Figure 4 plots the comparison between Morris-Lecar and (a) raf and (b) qif models. We can see that the sub-threshold responses are reasonably matched in both cases.

IV. SPIKE TIMING PREDICTIONS

The major use of the simple neuron models is utilizing these for large scale network simulations. For many simulations, the timing of the spikes are considered as an important metric which codes information or is responsible for learning algorithms like Spike Timing Dependent Plasticity. Hence, we

Fig. 4: **Sub-threshold dynamics:** A comparison of the sub-threshold dynamics of the Morris-Lecar model with (a) raf and (b) qif models. The synaptic inputs are approximated by 2 ms wide current pulses whose amplitudes follow an uniform distribution between 0 and 2 pA. The raf and qif waveforms are shifted so that their equilibrium membrane voltages match that of the Morris-Lecar model enabling an easier comparison.

next briefly explore the ability of the simpler models, tuned using small-signal analysis, in predicting spike timing. We arbitrarily set $V_{rst} = -V_{thresh}$ and choose t_{rst} such that both models take the same time to reach steady state after firing a spike. Figure 5 compares the spike responses for the Morris-Lecar model with (a) raf and (b) qif models when they are subjected to a stream of random synaptic inputs with EPSC amplitudes drawn from a random distribution varying from 0 to 3.5 pA. We see that there is a close correspondence in the generated spikes in both cases. However, there are some errors which are related to the reset mechanism and threshold estimation (threshold voltage actually corresponds to a manifold, i.e. it depends on the other variables). We are currently exploring better ways to approximate these aspects.

V. CONCLUSION

In this paper, we have developed a method for using small-signal analysis, a tool well-known to circuit designers, for studying neural excitability. The small signal impedance models for the neuron membrane provides insight into its behavior as an integrator or a resonator. We also use the small

Fig. 5: **Above-threshold dynamics:** A comparison of the above-threshold dynamics of the Morris-Lecar model with (a) raf and (b) qif models. The synaptic inputs are approximated by 2 ms wide current pulses whose amplitudes follow an uniform distribution between 0 and 3.5 pA. The waveforms are shifted for better viewing.

signal models to translate parameters from a complicated but realistic neuron model to a simple but computationally efficient one such that their sub-threshold behaviors are similar. This translation from a large set of parameters to a very small one is enabled by using circuit theory approximations.

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