Differences in the subthreshold dynamics of leaky integrate-and-fire and Hodgkin-Huxley neuron models

Dominic I. Standage and Thomas P. Trappenberg
Faculty of Computer Science
Dalhousie University
Halifax, NS, B3H 1W5, Canada
E-mail: {standage, tt}@cs.dal.ca

Abstract— **Many spiking neuron models have been proposed over the last decades with varying computational complexity and abstraction from biological neurons. Among the few studies that have compared spiking models, little emphasis has been given to the formal description of calibration methods in tuning model parameters. We give an example of calibrating a leaky integrate-and-fire neuron with the first-spike time of a Hodgkin-Huxley neuron. We further demonstrate how model parameters can be tuned to minimize subthreshold differences in membrane potential. This example emphasizes the dependencies of calibration methods on other experimental parameters, complicating detailed comparisons of spiking models.**

I. INTRODUCTION

Models of spiking neurons are increasingly important to the investigation of spike-time dependent brain mechanisms and the dynamics of cell assemblies. Many spiking models have been proposed, and Izhikevich [1] has recently provided a summary and discussion of a number of these model neurons. Most network investigations use leaky integrate-and-fire (LIF) neurons [2], [3], but little emphasis has been given to their relation to conductance-based models. While many investigations are not crucially dependent on the choice of neuron model, the response of LIF and Hodgkin-Huxley (HH) nodes to stochastic input has been shown to differ [4], and divergent network behaviour has also been mentioned [5].

We investigate sub-threshold differences between standard HH and LIF models. These models are fundamentally different, but there are good reasons why LIF nodes provide a functional approximation of HH nodes and a good description of spike-time dependent information processing in the brain. Prior to the opening of ion channels leading to spike generation, neurons are essentially leaky integrators, and the rapid opening of these channels lends further support to the use of LIF neurons. Additionally, the spike form is stereotypical, so it doesn't contribute to information transmission. The principle task in using LIF nodes, then, is choosing parameters that facilitate particular features of corresponding conductance-based neurons.

One approach to making LIF nodes better approximate conductance-based models is to allow for a dynamic time-scale parameter in the LIF model [6]. Another is to replace their constant threshold with a variable threshold [7]. Here, we keep this scale parameter constant for each trial, adjusting its magnitude for different input signals. We thus tune the time constant of an LIF neuron such that LIF and HH models spike at the same time in response to the same input. We show that this time constant and the time course of the subthreshold dynamic depend on the specific amplitude and waveform of the input stimulus, and that an adjustment to the form of the input stimulus can be used to reduce sub-threshold differences between LIF and HH nodes.

The focus of this paper is to demonstrate that adjustments to model parameters are necessary if spiking models are to be compared. Our simple input types (step and alpha functions) serve to demonstrate the susceptibility of these nodes to changes in input, stressing the need for calibrating conditions in comparative studies.

II. THE MODELS

The baseline model to which we compare the LIF model is the standard Hodgkin-Huxley model given by the four coupled differential equations [8]

$$C\frac{\mathrm{d}V}{\mathrm{d}t} = -g_{\mathrm{K}}n^4(V - E_{\mathrm{K}}) - g_{\mathrm{Na}}m^3h(V - E_{\mathrm{Na}})$$
$$-g_{\mathrm{L}}(V - E_{\mathrm{L}}) + CI_{\mathrm{ext}}^{\mathrm{HH}}(t) \qquad (1)$$

$$\tau_{\mathrm{n}}\frac{\mathrm{d}n}{\mathrm{d}t} = -[n - n_0(V)] \qquad (2)$$

$$\tau_{\mathrm{m}}\frac{\mathrm{d}m}{\mathrm{d}t} = -[m - m_0(V)] \qquad (3)$$

$$\tau_{\mathrm{h}}\frac{\mathrm{d}h}{\mathrm{d}t} = -[h - h_0(V)], \qquad (4)$$

where C is the capacitance of the membrane, $g_i, i \in \{\mathrm{K}, \mathrm{Na}, \mathrm{L}\}$ are conductance parameters for the different ion channels, and E_i are the corresponding equilibrium potentials. The variables n, m, and h describe the opening and closing of the voltage dependent channels. We use the standard parameters derived by Hodgkin and Huxley to simulate the action potential of the giant axon of a squid [8], $g_{\mathrm{K}} = 36, g_{\mathrm{Na}} = 120, g_{\mathrm{L}} = 0.3, E_{\mathrm{K}} = -12, E_{\mathrm{Na}} = 115, E_{\mathrm{L}} = 10.613$. Note that normalization sets the resting potential of the membrane to 0 ($u_{\mathrm{res}} \approx 0$).

We choose the HH model as an example of a conductance-based model, treating it as the baseline for neuronal behavior. We recognise that the model is an approximation of real neuronal behavior, and that more advanced models have been proposed that include the effects of additional ion channels [9]. Furthermore, the HH model can be simplified, as the voltage dependence of the variables n_0 and m_0 show similar characteristics and can be combined [10], [11], [9].

The HH model is compared to the LIF model, described in three steps

1) Subthreshold leaky integrator:

$$\tau_{\mathrm{m}} \frac{\mathrm{d}u(t)}{\mathrm{d}t} = -u(t) + I_{\mathrm{ext}}^{\mathrm{IF}}(t). \tag{5}$$

2) Firing Threshold: the firing time t^{f} is given by a constant delay (t^{c}) after the potential crosses the firing threshold ϑ:

$$u(t^{\mathrm{f}} - t^{\mathrm{c}}) = \vartheta. \tag{6}$$

3) Refractory time and reset: the membrane potential is reset to a value u_{res} after a fixed absolute refractory time t^{R}

$$u(t^{\mathrm{f}} - t^{\mathrm{c}} + t^{\mathrm{R}}) = u_{\mathrm{res}}. \tag{7}$$

Due to its apparent simplicity, the LIF model is common in computational studies of spiking neurons. Unfortunately, steps 2 and 3 must be coded with conditional statements unless their effect is altered so they may be described with continuous functions in the form of a differential equations. Solving differential eqn. (5) with conditional eqns. (6) and (7) can only be integrated piecewise due to non-differentiable points in the model at $t^{\mathrm{f}} - t^{\mathrm{c}}$ and $t^{\mathrm{f}} - t^{\mathrm{c}} + t^{\mathrm{R}}$. In contrast, ODE solvers can be applied directly to the HH equations. We use numerical solutions for the HH equations and analytical solutions for the subthreshold dynamics eqn. (5) of LIF nodes. Another advantage of the HH model is that parameters may be given physical meaning and assigned measurable values.

III. CALIBRATING CONDITIONS: INPUT SIGNALS AND FIRING TIME

While it is clear that the HH and LIF models are inherently different, we ask how they may be compared. The models have thus to be calibrated so their features are equivalent under equivalent conditions. In this study, we choose parameters in the LIF model such that the time of its first spike matches that of the HH model following sufficient external stimulus. We calibrate the models on their first spikes to provide a simple example of possible calibration methods. Matching the firing times in a spike train provides a more challenging problem.

There is no firing threshold in HH nodes. Their sub-threshold dynamic models that of biological neurons [12] and any perceived threshold is variable. The HH 'firing threshold' then, is not a constant, and depends on sub-threshold dynamics consistent with biological neurons [12]. To match the firing times of HH and LIF nodes, we first approximate a firing threshold for the HH model for step and alpha input (from an initial membrane potential of 0). We apply a series of inputs of decreasing amplitude a_{ext} to the HH node. The maximum value of V elicited by the maximum amplitude of input *in*sufficient to cause a spike is considered the threshold (ϑ^{HH}). For each input type, this approximate threshold is used as the firing threshold of the LIF node in subsequent experiments ($\vartheta^{\mathrm{IF}} = \vartheta^{\mathrm{HH}}$).

The membrane time constant τ_m must be determined such that in response to the same input, the LIF node crosses the firing threshold at the same time as the HH node. The differential equation for the LIF subthreshold dynamic (eqn. (5)) can be solved analytically for specific input functions. For a step input function with amplitude a_{ext},

$$I_{\mathrm{ext}}^{\Theta} = a_{\mathrm{ext}}\Theta(t_{\mathrm{on}}), \tag{8}$$

this is given by

$$u(t) = u_{\mathrm{res}} + a_{\mathrm{ext}} * (1 - e^{\frac{-t+t_{\mathrm{on}}}{\tau}}). \tag{9}$$

For an alpha function input

$$I_{\mathrm{ext}}^{\alpha} = a_{\mathrm{ext}}(t - t_{\mathrm{on}})e^{\frac{-t}{\tau_{\alpha}}} \tag{10}$$

this is given by

$$u(t) = u_{\mathrm{res}} + \frac{a_{\mathrm{ext}}}{\tau}\left((\frac{t^2}{a} - \frac{2t}{a^2} + \frac{2}{a^3})e^{-\frac{t}{\tau_{\alpha}}} - \frac{2}{a^3}e^{-\frac{t}{\tau}} \right), \tag{11}$$

where

$$a = \frac{1}{\tau} - \frac{1}{\tau_{\alpha}}. \tag{12}$$

An example of the time course of the membrane potentials of the HH and LIF neurons with these adjustments is shown in Figure 1 for a step function input. The LIF node responds with a stronger initial increase in membrane potential, which is then compensated by a lower rate close to the firing threshold.
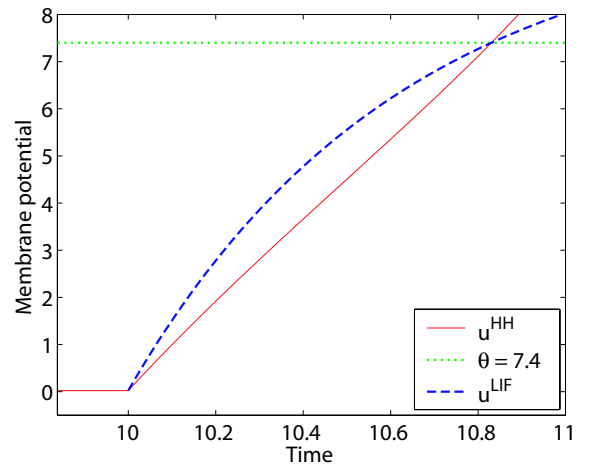

Fig. 1. The evolution of membrane potential in HH (solid line) and LIF (dashed line) model neurons in response to a constant external input $I_{\mathrm{ext}} = 10$ applied at $t = 10$ms. The firing threshold is indicated as dotted line.

The difference between the HH and LIF curves depends on details of the models and experimental settings. For step

and alpha inputs, Figure 2 shows the maximum difference between these curves for different amplitudes a_{ext}. Increasing a_{ext} reduces the difference between these curves for both input types. Because the shape of the sub-threshold curve is fundamentally different in these models (the LIF curve is convex, shown in Figure 1) reducing this difference becomes increasingly relevant as the potential approaches threshold, where the LIF node is more susceptible to noise due to its convex sub-threshold curve.
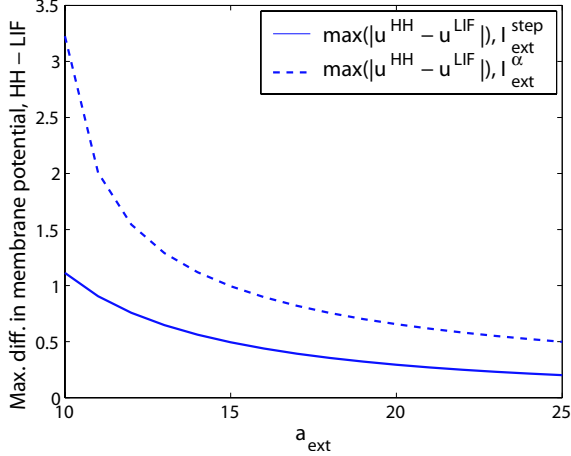
Fig. 2. Maximal difference between the subthreshold membrane potential between the HH and LIF model neurons in response to increasing amplitude of step input (solid line) and alpha function input (dashed line).

IV. REDUCING SUB-THRESHOLD DIFFERENCES BY ADJUSTMENTS TO INPUT

We have so far assumed that the form and amplitude of the input signals driving the different models should be the same for each model, but this need not be the case. One approach to finding a better correspondence between LIF and HH nodes is to modify the input each model receives. The difference curve for the membrane potential of the HH and LIF models when driven by a step function is shown in Figure 3a with a solid line. The dashed line shows the difference between the HH and LIF models if the amplitude of the LIF input is increased,

$$a_{ext}^{IF} = 10 * a_{ext}^{HH}, \qquad (13)$$

followed by recalculation of τ. This simple adjustment reduces the difference between models. Similar results can be achieved by adjusting the amplitude of the alpha function (Figure 3b.).

The difference between the models' subthreshold dynamics may be further adjusted by a time-dependent alteration to the input signal to the LIF node, or a transformation $I_{ext}^{IF} = F(I_{ext}^{HH})$ may exist to further minimize differences. This adjusted input function mimics the slower response of the HH nodes (due to the opening dynamics of the channels) by a time-delayed LIF input stimulus. Such an approach is similar to that of Stevens and Zador [6].

We adjust the membrane time constant as necessary to match the spike time of the HH neuron, therefore changing
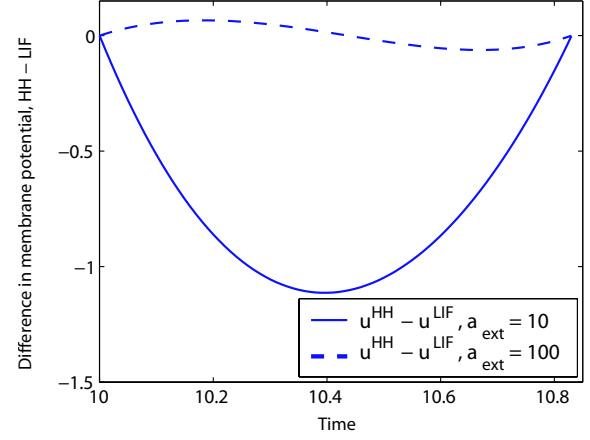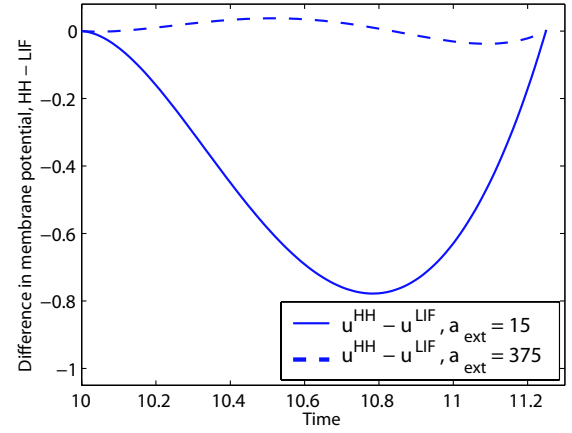

Fig. 3. Difference between the subthreshold membrane potential of HH and LIF models in response to (a) step-function input and (b) alpha function input. Solid lines are under the condition $a_{ext}^{IF} = a_{ext}^{HH}$. Dashed lines correspond to (a) $a_{ext}^{IF} = 10 * a_{ext}^{HH}$ and (b) $a_{ext}^{IF} = 25 * a_{ext}^{HH}$.

this constant for the different curves shown in Figure 3. For example, the time constant for the solid line in Figure 3a is $\tau = 0.62$, whereas $\tau = 10.84$ in the adjusted case (dashed line in Figure 3a). Similarly, in the case of the unadjusted alpha function in Figure 3b, $\tau = 0.6$, whereas $\tau = 28.32$ in the adjusted case (dashed line in Figure 3b. These adjustments serve to further demonstrate that the time constant of the LIF neuron should not be treated as the membrane time scale parameter of a biophysical neuron. Note that we still keep the time parameter constant within each trial and do not consider varying time scale parameters such as in [6].

V. Discussion and Conclusions

When comparing different models, care must be given to the specification of calibrating conditions such as the adjustment of spike times. Here we discuss only a noise-free case, but the curves in Figure 1 demonstrate that noise may influence LIF nodes more than HH nodes due to a larger buildup of potential for longer periods close to threshold. Adjustments to noise models must therefor be considered with the use of these nodes.

Differences between HH and LIF models can be minimized by transformations in their driving signals. Unfortunately, such transformations are dependent on the signals themselves. It is unknown whether a general methodology for the specification of such transformations can be found.

We have only discussed the subthreshold response for the first spike in the HH and LIF models. Further issues need consideration when comparing spike trains in different models, such as differences in refractory periods. The LIF model discussed here has an absolute refractory time, while the HH model includes a more precise approximation of the hyperpolarization dynamics. This difference further highlights the necessity of carefully chosen parameters in comparison-based studies.

Comparative studies of neuron models are important to verify that perceived discrepancies between models do not depend on un-tuned parameters, where tuning depends on the specific simulations or network behaviour under study. Comparative studies must therefor specify the methods of calibration used to create an adequate baseline for comparison. If the use of different neuron models leads to divergent experimental results following careful tuning of model parameters, further study should focus on appropriate use of models at various levels of abstraction, and on the calibration of neuron simulations under relevant experimental conditions. In this study, we compare a relatively simple conductance-based model with the LIF neuron. If LIF nodes are insufficient to reproduce network effects found with conductance models, then a mechanistic account of the phenomena under study may be found in the detail of the conductance model.

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