Integrate-and-Fire Models for Fast-Spiking Interneurons

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Abstract

We systematically reduce a conductance-based model of a fast-spiking interneuron
to integrate-and-fire (IF) models of different level of simplicity. The most complex
IF model that we consider contains all the dynamics of the full model outside of the
spike; in the simplest IF model, dynamics are governed solely by a nonlinear function
of the membrane potential. The behavior of the IF models are compared to those of
the full model under various input scenarios, including random current input and the
application of constant bias currents. The reduced model performs suprisingly well for
a realistic, rapidly varying current.

1 Introduction

Detailed conductance-based neuron models can reproduce electrophysiological measurements to a high degree of accuracy, but because of their intrinsic complexity these models are usually difficult to analyze. For this reason, simple phenomenological spiking neuron models, such as the integrate-and-fire (IF) model, are highly popular and have been used to study aspects of neural coding and network dynamics. Although these idealized models capture many features of complex models, derivations of the models are usually ad hoc or non-existent. Thus, some remain somewhat skeptical about generalizations made in studies that use IF models.

In order to illustrate the type of conditions that must hold to obtain quantitatively accurate IF models, we perform a step-by-step reduction of a conductance-based model for fast-spiking (FS) cortical interneurons [2] to IF models of varying degrees of simplicity. We then compare the behavior of the reduced models to that of the detailed conductance-based model during constant current application and random current input with zero mean.

Below, we give brief descriptions of the FS model and the ideas involved in the reduction, as well as a brief comparison of the models.

2 The conductance-based FS interneuron model

The conductance-based model that we consider is a model for fast-spiking cortical interneurons proposed by Erisir and coworkers [2].[1] The model neuron consists of a single compartment with a fast sodium current (I_{Na}), a fast and a slow potassium currents ($I_{\text{K}v3}$ and $I_{\text{K}v1}$) and leak current I_l:

$$C\,\frac{\mathrm{d}V}{\mathrm{d}t} = -[\,I_{\text{Na}} + I_{\text{K}v1} + I_{\text{K}v3} + I_l\,] + I_{\text{ext}}(t) \tag{1}$$

where

$$
\begin{aligned}
I_{\text{Na}} &= g_{\text{Na}}\ m^3\ h\ (V - E_{\text{Na}})\ , \\
I_{\text{K}v1} &= g_{\text{K}v1}\ n_1^4\ (V - E_{\text{K}})\ , \\
I_{\text{K}v3} &= g_{\text{K}v3}\ n_3^2\ (V - E_{\text{K}})\ , \\
I_l &= g_l\ (V - E_l).
\end{aligned}
\tag{2}
$$

The gating variables m, h, n_1 or n_3 follow the usual Hodgkin-Huxley formalism.

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[1] All parameters are as set by Erisir et al. except for the leak conductance. We use $g_l = 0.25\,\text{mS/cm}^2$ (instead of $1.25\,\text{mS/cm}^2$). This yields the passive membrane time constant that is closer to that measured in FS cells *in vitro*.

3 Reduction of full FS model to IF models

Step 1: A multi-current IF model

The shape of action potentials in the FS model is always roughly the same, independently of how the spike is initiated. Furthermore, after every down-stroke of spikes, gating variables in this model achieve surprisingly characteristic values. Therefore, instead of calculating the shape of action potentials, as soon as a spike is triggered at a threshold voltage, we simply restart calculations after the down-stroke of the spike, resetting the membrane potential and the gating variables to their characteristic post-spike values. We fix the threshold at $V_{\mathrm{thr}} = -40\,\mathrm{mV}$ and the membrane potential reset value at $V_{\mathrm{reset}} = -85\,\mathrm{mV}$. The spike width is $\delta_{\mathrm{refr}} = 1.7\,\mathrm{ms}$. We adjust the reset values of the gating variables to match those when the neuron is firing at about $40\,\mathrm{Hz}$: $m_{\mathrm{reset}} = 0.0$, $h_{\mathrm{reset}} = 0.16$, $n_{1,\mathrm{reset}} = 0.874$, and $n_{3,\mathrm{reset}} = 0.2$.

Step 2a,b: Single-variable IF models

Because dynamics of m are fast relative to the membrane time constant, we can replace m with its equilibrium value $m_\infty(V)$. The gating variables h and n_1 vary rather slowly, so these variables may be replaced by their average value h_{av} and $n_{1,av}$. The average does depend on the input scenario, but we take $h_{av} = 0.45$ and $n_{1,av} = 0.8$ (values for when the neuron has a firing rate of $\sim 40\,\mathrm{Hz}$) as our standard set of parameters. Following a spike, n_3 exponentially decays fairly rapidly and is close to its resting value for all but $\sim 2\,\mathrm{ms}$ interval after the spike. Therefore, (a) we can set a refractory time of $\delta_{\mathrm{refr}} = 4\,\mathrm{ms}$ and replace n_3 by its equilibrium value at rest value $n_3(V_{eq})$ or (b) we can model n_3 as exponential decaying after a spike at $\hat{t}$, $n_3 = n_{3,\mathrm{reset}} \cdot e^{(-(t-\hat{t})/\tau_{n3})}$.

These approximations yield a single-variable nonlinear IF model [2]:

$$
\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} &= -\frac{1}{C}\{g_{\mathrm{Na}}\,[m_\infty(V)]^3\,h_{av}\,(V - E_{\mathrm{Na}}) + g_{\mathrm{K}v1}\,n_{1,av}^2\,(V - E_{\mathrm{K}}) \\
&\quad + g_{\mathrm{K}v3}\,n_3^4\,(V - E_{\mathrm{K}}) + g_l\,(V - E_l) - I_{\mathrm{ext}}(t)\},
\end{aligned}
\tag{3}
$$

where n_3 is as described in option (a) as a constant or (b) as a spike-triggered exponentially decaying function. The IF model in case (b), which has explicit time-dependence, can be thought as having a variable (relative) threshold. Note that the IF models contain explicit descriptions of biophysical currents.

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[2]With further approximations, one could obtain the standard linear leaky IF model or the quadratic IF neuron [4].

4   Comparisons

To test the quality of the IF models, we compare their behavior to that of the full fast-spiking neuron model for constant current input and for uncorrelated random input current with zero mean.

The multi-current IF model gives a near-perfect fit of the time course of the membrane potential of the full fast-spiking neuron model during repetitive firing at $40\,\mathrm{Hz}$ due to constant current input. It also approximates the gain function of the full model to a high degree of accuracy over a wide frequency range. When the same random current is applied to the multi-current IF model and full model, the voltage time course of the two models is indistinguishable most of the time. The multi-current IF model does miss or add a spike occasionally but spike coincidence rates are high over a wide range of amplitudes.

For the nonlinear IF model (2a) with our standard set of parameters, we get only a fair approximation of the gain function, except that the threshold for repetitive firing is not reproduced correctly. For random input, the mean firing rates as a function of the fluctuation amplitude are not reproduced accurately except at $40\,\mathrm{Hz}$ for which parameters have been optimized (figure 1a); although the spike coincidence rate is fairly high at $40\,\mathrm{Hz}$ (figure 1b), the approximation breaks down drastically for lower or higher rates. However, the quantitative accuracy of the nonlinear IF model is salvaged by implementing the time-dependent decay of n_3 (i.e. using the variable-threshold single variable IF model (2b)) (figure 1c,d).

5   Discussion

Our reduction of a conductance-based model to IF models involves averaging over slow processes, setting very fast variables to their V-dependent equilibrium values, and approximating the dynamics other recovery variables as exponential decaying to their resting states following a spike; for related methods, see also [1, 3]. While not always rigorous, the reduction illustrates the conditions needed (assumptions made) during each step towards a simple IF model. The essential criterion of the quality of a reduction should come, from our point of view by testing the model on realistic input, i.e., a highly variable (random) current.

The multi-current IF model yields excellent quantitative agreement with the full FS model. However, while it is easy to implement and rapid to simulate, it is difficult to

analyze mathematically. The single variable nonlinear IF model exhibits qualitatively similar behavior to the full model, but it appears that a variable (spike-triggered time-dependent) threshold is required to quantitatively reproduce activity of the full model.

The relative simplicity of fast-spiking neurons allows the formulation of simple yet quantitatively accurate IF models. Fast-spiking interneurons show little adaptation and most of the complications caused by slow ionic processes that are more prevalent in other neurons are avoided. These aspects would not be well captured by typical IF models (see however integrate-and-fire-or-burst model by Smith etal [5]).

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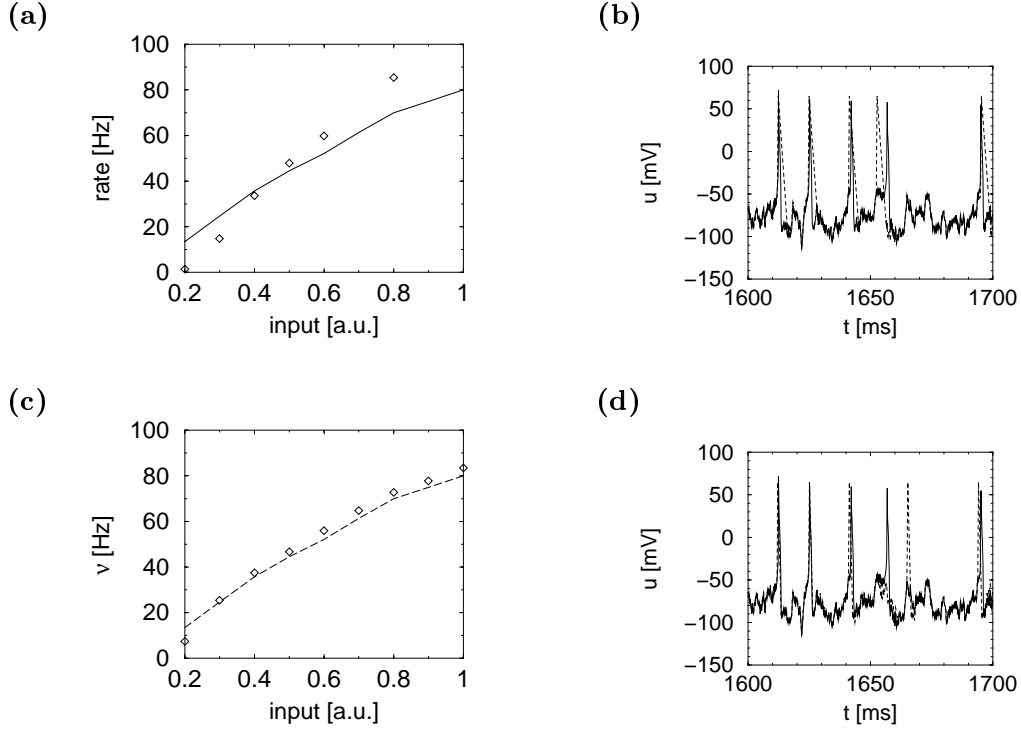
(a) **(b)**

(c) **(d)**

Figure 1: Random input. a) The mean firing rate of the full fast-spiking neuron model (solid line) compared to that of the nonlinear integrate-and-fire model (diamonds) as a function of the amplitude of the input fluctuations. b) The spike train of the nonlinear integrate-and-fire model compared to that of the full fast-spiking neuron model (mean firing rate $\sim$ 40Hz). The integrate-and-fire model fires an extra spike at about $t = 1652$ ms but misses the spike that occurs about 4 ms later. For this input scenario, about 87 percent of the spike times are correct within ± 2 ms. (c) and (d) are the same as above, but for a model with the spike-triggered time-dependence on n_3.