

# Subthreshold dynamics of Hodgkin-Huxley and Izhikevich spiking neuron models

Matthew D. Boardman  
Faculty of Computer Science  
Dalhousie University  
Matt.Boardman@dal.ca

## Abstract

*We compare the subthreshold dynamics of the conductance-based Hodgkin-Huxley neuron model commonly used for accurate biological modelling, with those of the computationally simpler model proposed by E.M. Izhikevich for inclusion in large neural network simulations. We find that both models deliver similar results under a variety of inputs, with the maximal membrane potential difference less than 1 mV for a step input of 10, and nearly an order of magnitude lower for an alpha input. We also find that both models exhibit a low sensitivity to high frequency noise.*

*This paper is also available at <http://www.cs.dal.ca/~boardman>.*

## 1. Introduction

The Hodgkin-Huxley spiking neuron model [1] has long been a standard reference to the shape of the membrane potential curve generated by a real, biological neuron such as those found in the mammalian cortex. However, the number of calculations required to implement this model are prohibitively expensive in simulations with a large number of neurons.

In [4], E.M. Izhikevich proposed a model (hereafter referred to as the Izhikevich model) requiring approximately two orders of magnitude fewer calculations for implementation, which allowed the model to easily be used in simulations with a large number of neurons. Despite its apparent relative simplicity, the model retained the flexibility to model the behaviour of many observed types of spiking neurons [2],[4].

In this paper, we briefly investigate differences between these two models, concentrating primarily on the dynamics prior to reaching the voltage threshold required to create a spike. We compare the subthreshold behaviour with model parameters that generate similar inter-spike frequencies, resting potential and maximum spike potential, then calibrate these models to ensure a matching threshold voltage  $\vartheta$  and sensitivity to applied current  $I_{ext}(t)$ . Since the threshold membrane potential  $\vartheta$  of both models can vary with time depending on prior behaviour, we allow the models to quiesce from initial conditions to the resting potential for 100 ms prior to applying external current.

### 1.1. Hodgkin-Huxley Model

The conductance-based, biologically accurate Hodgkin-Huxley model first proposed in 1954 in [1] has the following analytical form, restated from [6]:

$$C \frac{dv}{dt} = -g_K n^4 (v - e_K) - g_{Na} m^3 h (v - e_{Na}) - g_L (v - e_L) + I_{ext} \quad (1)$$

$$\tau_n \frac{dn}{dt} = -[n - n_0(v)] \quad (2)$$

$$\tau_m \frac{dm}{dt} = -[m - m_0(v)] \quad (3)$$

$$\tau_h \frac{dh}{dt} = -[h - h_0(v)] \quad (4)$$

where  $v(t)$  represents the membrane potential, and  $n(t)$ ,  $m(t)$  and  $h(t)$  are dimensionless vari-

ables which simulate the opening and closing of potassium (K), sodium (Na) and static (L) ion channels.

Parameters for the Hodgkin-Huxley model were chosen to match with [1], which were determined empirically to model the giant axon of a squid, however the resting membrane potential was changed to  $-70$  mV, a reasonable resting potential for a biological neuron, in order to graphically match the resting potential of the Izhikevich model with the parameters chosen below and so to better compare the shape of the curves. In addition, we used the simplified alpha and beta functions better suited to matrix implementations in MatLab, as detailed in [6].

## 1.2. Izhikevich Model

The model proposed by E.M. Izhikevich in [4] has the following analytical form:

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I_{\text{ext}} \quad (5)$$

$$\frac{du}{dt} = a(bv - u) \quad (6)$$

with the auxiliary after-spike reset:

$$\text{if } v \geq 30 \text{ mV, then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \quad (7)$$

where  $v(t)$  represents the membrane potential, and  $u(t)$  represents membrane recovery [4]. Initially the values for the parameters  $a$ ,  $b$ ,  $c$  and  $d$  were chosen to represent a typical “fast spiking” cortical neuron:  $a=0.19$ ,  $b=0.2$ ,  $c=-80$  mV and  $d=8$ . These parameters resulted in matching inter-spike frequency, resting membrane potential and maximum spike voltage, however the threshold voltages of the two models, and the time each model required to reach the threshold voltage, did not match. The models therefore needed further calibration in order to better compare the subthreshold dynamics, detailed in the next section.

## 2. Calibration of Model Parameters

Due to the spike reset in Equation 6, analytical solutions to the Izhikevich model may become quite difficult. Numerical solutions are therefore preferred, and in this paper we use the Euler method for numerical integration for both models, using the small step value  $\Delta t = 0.0001$  ms, or 0.1 ns, to retain high accuracy. The Hodgkin-Huxley model was more sensitive to the time step value, presumably due to the larger number of calculations in the algorithm.

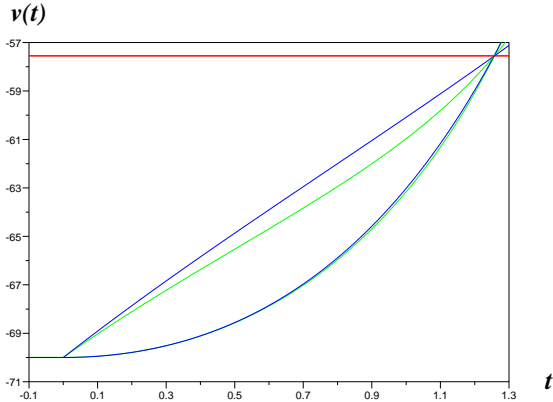
This step value was used for all cases other than rough, initial calibration. Comparison of the curves in Figure 1 with those using a step value of  $\Delta t = 0.001$  ms, or 1 ns, an order of magnitude higher, yielded a maximum difference less than 0.01 mV, or approximately 1% of the maximum difference between the models under a step input current as shown in Figure 2.

It was also found that both models require a significant rest time before input is applied, in order to balance the internal parameters to find an appropriate resting membrane potential. A 100 ms period prior to applying the external current was given for this purpose.

Threshold voltages for both models were found using the numerical method from [5], in which the external current is incrementally reduced from a high value until the current is no longer sufficient to generate a spike: the maximum membrane potential for this input current was then taken to be the threshold voltage  $\vartheta$ .

Further calibration was necessary in order for the threshold voltage  $\vartheta$  of the two models to match and to occur at the same time with the same input. Rather than adjusting model parameters as in [5] section 3, a scalar value  $a_{\text{ext}}$  was applied to the externally applied current in Equation 5 as in [5] section 4. This scalar was then incrementally adjusted to  $a_{\text{ext}}=1.6379$ , or approximately 60%, until the threshold voltages of both models matched, at  $\vartheta^{HH} = \vartheta^{IZ} = -57.55$  mV as shown in Figure 1.

This scalar  $a_{\text{ext}}$  adjusted the sensitivity of the



**Figure 1.** Calibration of Izhikevich (blue, darker) and Hodgkin-Huxley (green, lighter) models for step input of 10 (upper two curves) and alpha input (lower two curves), both applied from  $t = 0$ , to the threshold voltage (red, upper horizontal line) of  $\vartheta^{HH} = \vartheta^{IZ} = -57.55$  mV. The time constant  $\tau$  for the alpha input was chosen such that the time to reach the threshold voltage coincides exactly with that required for the step input, in order to better compare the shape of the resulting curves. In both cases, the threshold voltage was reached at  $t = 1.256$  ms.

Izhikevich model to external current such that the threshold voltages of the two models matched, however, even with the same external current the threshold voltage was reached at different times. A second scalar  $t_s$  was therefore applied to slightly compress the time scale for the Izhikevich model, by approximately 30%.

As a result of these changes, the inter-spike frequencies no longer matched. However, the subthreshold behaviour matched much more closely, and this is what we concentrate on in this paper. This same method would therefore not be appropriate for higher level comparisons of the spiking frequencies, for example.

To confirm that the use of these two scalars is appropriate in our case, model parameters  $a$  and  $b$  were adjusted to  $a=0.3$  and  $b=0.234$  so that the resulting model roughly matched the curve in Figure 1. Although the results were close to the curve found by adjusting the  $a_{\text{ext}}$  and  $t_s$  scalars, it was found that adjusting these two parameters at once was computationally expensive, since the two parameters  $a$  and  $b$  are interdependent resulting in a two-dimensional search space. Thus this

simplification is appropriate in our case for examining the subthreshold dynamics. These adjusted model values were not used in further calculations however, because it was found that further fine tuning of the parameter values would be necessary in order to make the curves visually match in plots such as Figure 1 and Figure 2.

### 3. Discussion and Conclusion

Three types of external input were applied starting from time  $t = 0$ . The first type was a step input with magnitudes of either 10 or 100 (in the following plots, a value of 10 is used). The second type was an alpha function input with magnitude 10 of the following form:

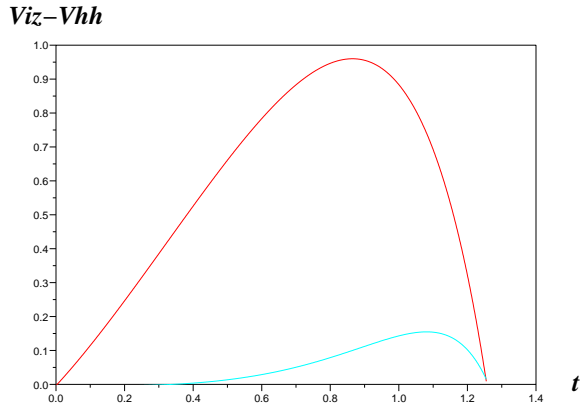
$$I_{\text{ext}}(t) = I_{\text{max}} t e^{t/\tau_\alpha} \quad (8)$$

where  $\tau_\alpha=1.6$  ms was chosen such that the resulting curves of the membrane potential reached the threshold voltage at the same time as with the step input, for better comparison of the shape of each curve. The third input type was a similar alpha function, but with some introduced high frequency noise with uniform distribution, introduced in the form of a scalar adjustment with a maximum modification to the input current of  $\pm 50\%$ . For this random noise to be consistent across both models, the models were calculated simultaneously across the time range for all time step values.

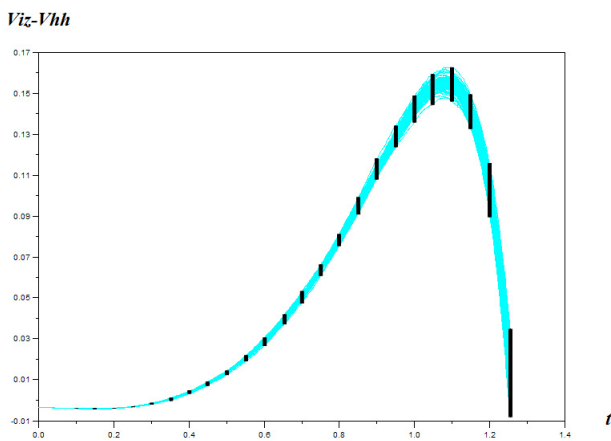
The difference between the Hodgkin-Huxley and Izhikevich models during the period from when the current is first applied to when the membrane potential reaches the threshold voltage is plotted in Figure 2.

The maximum difference between the models for the step input with magnitude 10, shown in the upper curve of Figure 2(a), was found to be approximately 0.95 mV. This is on a par with the difference obtained under similar conditions between the Hodgkin-Huxley and Integrate-And-Fire model shown in [5], in which the difference was found to be approximately 1.1 mV.

The maximum difference between the models for the alpha input with magnitude 10, shown in



(a) Step input (red, darker) and noise-free alpha input (cyan, lighter).



(b) Alpha input with 50% noise (uniform distribution) for 100 runs. Error bars show range of values at each time  $t$ .

Figure 2. Difference in subthreshold membrane potential from Izhikevich and Hodgkin-Huxley models for several dynamic inputs applied from  $t = 0$ .

the lower curve of Figure 2(a), was found to be approximately 0.15 mV. This is somewhat better than the difference obtained under similar conditions between the Hodgkin-Huxley and Integrate-And-Fire model shown in [5], in which the difference was found to be approximately 0.8 mV for a maximum input current of 15, however this difference may be partially due to a different choice of the time constant  $\tau_\alpha$ .

Both models were found to exhibit a low sensitivity to high frequency noise, as shown in Figure 2(b). Even with 50% noise, implemented

through a scalar multiplier applied to  $I_{\text{ext}}$ , the maximum variation in comparison to the alpha input alone, was approximately 0.035 mV.

Interestingly, this noisy alpha input also created small variations in the time required for the models to reach the threshold voltage, on the order of approximately  $\pm 0.01$  ms, or 10 ns, which is approximately 1% of the total subthreshold time (this is not shown in Figure 2(b) for clarity). It seems likely that the inherent noise in a stochastic system such as the many synaptic connections in a mammalian cortex would exhibit a smaller magnitude, however further investigation could determine if similar noise is one of the factors responsible for the observed fluctuations in spiking frequency in natural, biological cortical neurons, and if this is found to be the case, then further research would be needed to determine the biological cause responsible for this high frequency noise.

In conclusion, we have found that the Izhikevich model can accurately reproduce the subthreshold dynamics of a biological neuron if model parameters are carefully chosen, with significantly fewer calculations required for implementation.

## References

- [1] A.L. Hodgkin and A.F. Huxley, *A quantitative description of ion currents and its applications to conduction and excitation in nerve membranes*, Journal of Physiology, 117:500-544, 1952.
- [2] E.M. Izhikevich, *Simple Model of Spiking Networks*, IEEE Transactions on Neural Networks, Submitted, 2005.
- [3] E.M. Izhikevich, *Which Model to Use for Cortical Spiking Neurons?*, IEEE Transactions on Neural Networks (Special Issue on Temporal Coding), 15:1063-70, 2004.
- [4] E.M. Izhikevich, *Simple Model of Spiking Neurons*, IEEE Transactions on Neural Networks, 14(6):1569-72, 2003.
- [5] T.P. Trappenberg and D.I. Standage, *Differences in the subthreshold dynamics of leaky*

*integrate-and-fire and Hodgkin-Huxley neuron models*, Draft, 2004.

- [6] T.P. Trappenberg, *Fundamentals of Computational Neuroscience*, Oxford University Press, pp. 290–2, 2002.