

A Biological Plausible Generalized Leaky Integrate-and-Fire Neuron Model

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Abstract— This study introduces a new Generalized Leaky Integrate-and-Fire (GLIF) neuron model. Unlike Normal Leaky Integrate-and-Fire (NLIF) models, the leaking resistor in the GLIF model equation is assumed to be variable, and an additional term would have the bias current added to the model equation in order to improve the accuracy. Adjusting the parameters defined for the leaking resistor and bias current, a GLIF model could be accurately matched to any Hodgkin-Huxley (HH) model and be able to reproduce plausible biological neuron behaviors.

I. INTRODUCTION

The spiking neuron model has become an essential computational unit in the third generation of artificial neural networks, commonly referred to as Artificial Spiking Neural Network (ASNN) [1]. Spiking neuron models as the key computing unit in ASNN, were well reviewed in [2-4], ranging from the most complicated and yet most biologically plausible models to the simplest models. However, the challenge still remains in finding a spiking neuron model which combines both computational efficiency and biological accuracy.

The Hodgkin-Huxley (HH) model is the most popular model known to biologists [5]. This HH model is a set of Ordinary Differential Equations (ODE) which describe the dynamics of cell membrane potential and ion transportations of a neuron. The parameters are estimated by analyzing the ionic current data gathered from the voltage clamped experiments on the giant axon neuron of a squid [6, 7]. Although the HH model has been proven to be most accurate in reproducing the neuro-electrical activities of biological neurons, its applications in ASNN are still rare, due to its computational complexity.

Researchers interested in building large scale ASNNs also proposed another category of neuron models which are simpler than the more intricate neuron models, yet could still reproduce some of the basic features found in biological neurons. Such kind of neuron models are usually referred to as “phenomenal models” [8]. One of the most commonly used models is called the Leaky Integrate-and-Fire (LIF) model [9], which treat the neuron as a passive capacitor connected by a linear leaky resistor. The LIF model is seen as

a valuable tool for analyzing key neuron properties because of the way it models one of the key features of a neuron’s membrane: the membrane’s conductance. Also, the ODE-based model can be solved analytically, thus providing intuitive insight to the biological neuron activities [10].

The LIF model is considered as a one-dimensional model since there is only one state variable in its ODE. Two-dimensional models such as the FitzHugh-Nagumo model [11], the Morris-Lecar model [12], the Izhikevich model [13] as well as the Adaptive Exponential Integrate-and-Fire model [14] introduce additional state variables in their ODEs to mimic the more complicated neuro-electrical features. However, two- or more dimensional models are more computationally taxing and are close to impossible to be solved analytically in contrast to their one-dimensional counterparts.

In this study, we propose a design model of a new Generalized LIF (GLIF) by innovative modifications of the Normal Leaky Integrate-and-Fire (NLIF) model. The ODE of the GLIF model is one-dimensional in complexity so that it could be solved analytically, while its computational requirements are amenable to minimization.

II. MODEL DEFINITION

The following equations define the newly developed GLIF model, which is a modification of the NLIF model:

$$C_m \frac{du(t)}{dt} = i_s(t) - u(t) \cdot g_{\text{kern}}(t - t^f) + i_{\text{kern}}(t - t^f), \quad (1)$$

where u is the membrane voltage of a neuron, C_m is the membrane capacitance, and t^f is the most recent firing time as defined by:

$$t^f : u(t^f) = u_{\text{th}} \text{ and } \left. \frac{du}{dt} \right|_{t^f} > 0. \quad (2)$$

Function g_{kern} in (1) describes the trajectory of the overall membrane conductance after each output fires; while function i_{kern} describes the trajectory of the post-fire overall ionic current.

Stimulation of this model is expressed as a summation of currents from all synapses connected to this neuron, denoted by i_s in (1). The firing time of this neuron as defined by (2) is updated when the membrane voltage crosses a threshold u_{th} .

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Immediately after each output fire, a new t^f is used to calculate g_{kern} and i_{kern} . The time interval $t - t^f$ is referred to as the survival time, i.e., the length in which the neuron stays quiescent since the last time it fired.

We assume that the kernel functions could be described through summation terms of a set of functions g_j as follows:

$$\begin{aligned} g_{\text{kern}}(t) &= g_0 + \sum_j g_j(t) \\ i_{\text{kern}}(t) &= \sum_j E_j g_j(t), \end{aligned} \quad (3)$$

where g_0 is the constant leaking conductance when the neuron is quiet, g_j are bell-shaped functions which could fit the trajectories of conductance for each ion-channels during an action potential, and E_j are the resting potentials for those channels. The bell-shaped curves g_j as used here are the derivatives of generalized sigmoid functions Γ_j , which are formulated as follows:

$$\Gamma_j(t) = \frac{A_j}{1 + e^{-(t-\mu_j)/l_j}} + k_j t, \quad (4)$$

$$g_j(t) = \frac{d\Gamma_j}{dt} = \frac{A_j}{l_j} \frac{e^{-(t-\mu_j)/l_j}}{[1 + e^{-(t-\mu_j)/l_j}]^2} + k_j, \quad (5)$$

where A_j , μ_j , l_j , and k_j are empirical parameters controlling the shape and location of the bell curve, which need to be fitted to the experimental ionic current data.

III. PARAMETERS ESTIMATION

GLIF model could be fitted to a HH model by adjusting its parameters according to the statistical features of the HH neuron dynamics. We demonstrate here the steps to fit the GLIF model to the original HH model suggested by Hodgkin and Huxley [5] with two active ion channels. The currents in the sodium channel, the potassium channel and the linear leaky channel are as defined below:

$$\begin{aligned} i_{\text{ion}} &= g_{\text{Na}}(u - E_{\text{Na}}) + g_{\text{K}}(u - E_{\text{K}}) \\ &\quad + g_{\text{L}}(u - E_{\text{L}}) \\ g_{\text{Na}} &= \bar{g}_{\text{Na}} m^3 h \\ g_{\text{K}} &= \bar{g}_{\text{K}} n^4. \end{aligned} \quad (6)$$

The maximum conductance for sodium, potassium and leaking channels are found to be $\bar{g}_{\text{Na}} = 120 \text{ mS/cm}^2$, $\bar{g}_{\text{K}} = 36 \text{ mS/cm}^2$, and $g_{\text{L}} = 0.3 \text{ mS/cm}^2$, respectively. The corresponding reversal potentials adopted were $E_{\text{Na}} = 115 \text{ mV}$, $E_{\text{K}} = -12 \text{ mV}$, and $E_{\text{L}} = 10.6 \text{ mV}$.

We used one current based synapse [15] driven by Poisson spike train as the stimulation to the HH neuron. However, the synapse weights for individual input spikes were assumed to be random variable with uniform distribution. Suppose the input spike train has m spikes arriving at time instants $s^{(1)}$, $s^{(2)}$, ..., $s^{(m)}$, the connection weights will be w_1, w_2, \dots, w_m ,

individually, and the synaptic current injected to the HH neuron could be expressed as:

$$\begin{aligned} i_s(t) &= \sum_j w_j i_s^*(t - s^{(j)}) \Theta(t - s^{(j)}) \\ i_s^*(\tau) &= I_{s,\text{max}} \frac{\tau}{\tau_s} e^{-\tau/\tau_s}, \end{aligned} \quad (7)$$

where i_s^* is the shape function for a single input current spike, with maximum current $I_{s,\text{max}} = 23 \text{ }\mu\text{A/cm}$ and rising/decay time $\tau_s = 2 \text{ ms}$, and with Θ denoting a Heaviside step function.

An experiment to determine parameters in the GLIF model was designed using the following steps:

- i) Choose randomly a frequency λ_p between 1 Hz and 1 kHz.
- ii) Generate a spike train that lasts 1000 ms by a Poisson Process using λ_p as the mean rate.
- iii) Choose randomly a connection weight between 0 and 1 for each spike in the spike train.
- iv) Assign randomly a sign for each connection weight with equal positive and negative possibility.
- v) Calculate the input currents for the generated spike train by using (7).
- vi) Numerically solve the ODE in (6) for 1000 ms as in the Wolfram Mathematica computation environment.
- vii) Record membrane voltage u , gating variables m , n , and h at 0.1 ms time steps and save them onto a file.

The experiment was repeated 1000 times with different mean rates λ_p to ensure statistically reliable results.

A. Firing thresholds

Firing thresholds could be estimated by analyzing the local maxima found in the recorded membrane voltages. The bifurcation dynamic property of HH neuron separates the recorded membrane voltage peaks into two categories. We defined the peaks happened lower than 50mV as non-spiking peaks, and the voltage below which 95% of all recorded non-spiking peaks could be found as the firing threshold:

$$u_{\text{th}} : P_{\text{peaks}} \{U | U < u_{\text{th}}\} = 0.95. \quad (8)$$

The cumulative distribution function (CDF) of the probability density for the non-spiking peaks were calculated from the recordings, and the resulted threshold is $u_{\text{th}} = 4.69 \text{ mV}$.

B. Kernel functions

In order to fit the GLIF kernel functions to the HH model, we searched for all the firing moments in the recorded membrane voltage, and sliced the recorded state variables m , n and h according to these firing moments. In this way, the absolute simulation time base implied in the records was converted to the survival time base. The conductance of both ion channels at each survival time step is calculated by:

$$\begin{aligned} g_{\text{Na}}[i] &= \bar{g}_{\text{Na}} m[i]^3 h[i] \\ g_{\text{K}}[i] &= \bar{g}_{\text{K}} n[i]^4. \end{aligned} \quad (9)$$

where $m[i]$, $n[i]$, and $h[i]$ indicate the values of state variables m , n , and h at the i -th survival time step $\tau[i]$.

The membrane voltage and channel conductance were grouped into sequential survival time intervals:

$$[\tau_0, \tau_1), [\tau_1, \tau_2), \dots, [\tau_q - 1, \tau_q). \quad (10)$$

The mean values and standard variances were calculated for each group of u , g_{Na} , and g_{K} , while the mean values of g_{Na} and g_{K} are numerically integrated and used to fit the Functions Γ_{Na} and Γ_{K} as stated in (4) using Minimum Mean Square Error (MMSE) method. The resulting parameters for Γ_{Na} and Γ_{K} are listed in Table I.

TABLE I. FITTING PARAMETERS FOR THE KERNEL FUNCTIONS

Function	A_i (mS·ms/cm ²)	l_i (ms)	μ_i (ms)	k_i (ms)
Γ_{Na}	35.88	0.3180	2.128	0.0115
Γ_{K}	39.53	0.7889	3.837	0.3118

These fittings are reliable with Sum Squared Error being 34.91 and 63.65; adjusted R-square being 0.9977 and 0.9983; Root Mean Square Error being 0.7386 and 0.9972 for functions Γ_{Na} and Γ_{K} , respectively.

The variable conductance and bias current function needed in (1) could then be defined in the following way:

$$\begin{aligned} g_{\text{kern}}(\tau) &= g_0 + \frac{d\Gamma_{\text{Na}}}{d\tau} + \frac{d\Gamma_{\text{K}}}{d\tau} \\ i_{\text{kern}}(\tau) &= \frac{d\Gamma_{\text{Na}}}{d\tau} E_{\text{Na}} + \frac{d\Gamma_{\text{K}}}{d\tau} E_{\text{K}}, \end{aligned} \quad (11)$$

where $E_{\text{Na}} = 115$ mV, $E_{\text{K}} = -12$ mV and $E_{\text{L}} = 10.6$ mV are reversal potentials, the same as those found in the HH model. The constant leaky conductance is set to $g_0 = 0.1961$ mS/cm² so that bias current i_{kern} diminish when the neuron is quiet (at large τ value)

IV. MODEL ACCURACY

Accuracy is a measurement that estimates the reliability for a neuron model to reproduce the behavior of a biological neuron. In this study, we used the Missed Fire Rate (MFR) and the Accidental Fire Rate (AFR) as indicators of a neuron model's accuracy.

Using the same spike train to stimulate both the HH model and the GLIF model, most of the output spikes found in HH model could be matched to the output spikes from GLIF model, with the spiking time difference limited to a small tolerance ϵ . Spikes in HH model with no matched spikes found in GLIF model are marked as Missed Fires (MF), while spikes in GLIF model without any matched spikes found in HH model are marked as Accidental Fires (AF). The error rate

of MF and AF could be calculated as follows:

$$\begin{aligned} \text{MFR} &= \frac{N_{\text{MF}}}{N_{\text{match}}} \\ \text{AFR} &= \frac{N_{\text{AF}}}{N_{\text{match}}}, \end{aligned} \quad (12)$$

where N_{MF} is the number of MFs, N_{AF} is the number of AFs and N_{match} is the number of matched output spike pairs in each simulation.

We have built 100 neurons using HH model and GLIF model respectively in Matlab environment on an Intel i7-2600 workstation with 4GB memory. The NLIF model with leaky resistance $R = 5.2$ k Ω ·cm² and time constant $\tau_m = 5$ ms was also implemented in the same environment for comparison.

In this experiment, 100 Poisson spike trains with mean frequency $\lambda_p = 150$ Hz and uniform lengths of 1000 ms were used as neuron inputs. The HH model was simulated at 0.02 ms step size using fourth-order Runge-Kutta (RK4) method to provide reliable outputs. The NLIF model and GLIF model were simulated by RK4 at various step sizes, with MFR and AFR calculated for each choice of step size. The spikes matching tolerance ϵ was set to 5 ms for the MFR and AFR calculation.

V. RESULTS AND DISCUSSION

The HH model, GLIF model and NLIF model were simulated by same input spike trains. A portion of the recorded membrane voltage of these three models is shown in

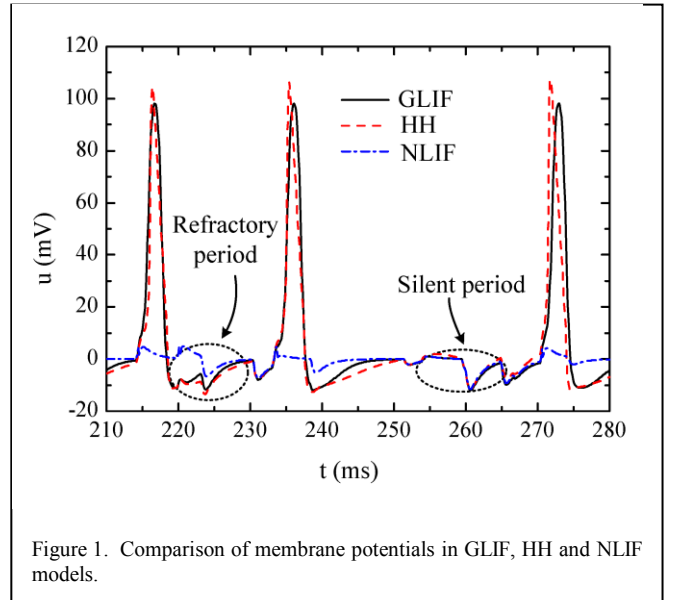


Figure 1. Comparison of membrane potentials in GLIF, HH and NLIF models.

Fig. 1. Compared to the NLIF model, the GLIF model could reproduce a much similar spike shape action potentials as the HH model. We can also observe that the membrane potentials are almost the same for these three models when the survival time is longer than 10 ms (in the so-called “silent period”), proving that the NLIF model is a good approximation when the neuron stays quiescent for long enough. Yet the membrane

voltage trajectory of NLIF model is completely different from GLIF and HH models in the post-fire region, marked as the refractory period in Fig. 1.

The accuracy measures of MFR and AFR have also been evaluated at various step sizes for both NLIF and GLIF neurons, with results plotted in Fig. 2.

It can be observed that both AFR and MFR of GLIF are much lower than those of the NLIF model, and are empirically found to be independent of the simulation step size. Comparatively, the MFR of the NLIF model increases dramatically when the simulation step size is larger than 0.4 ms, which is an indication that the numeric solving errors for NLIF model increase along with the step size. Since the computation time of RK4 method decrease exponentially while the step size increase, the possibility of selecting a larger step size for the GLIF model is seen as more competitive for large scale ASNN applications.

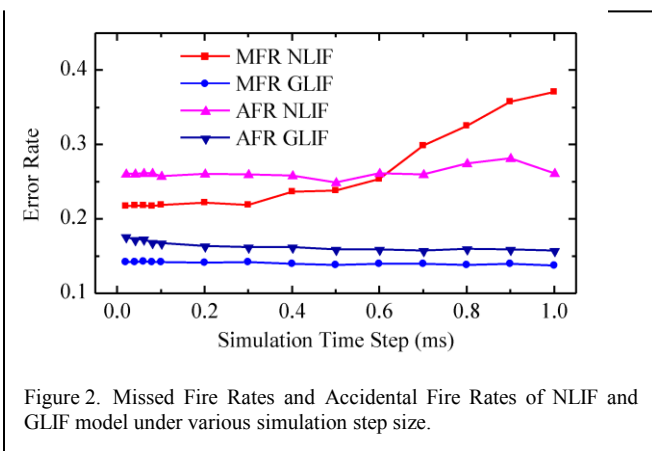


Figure 2. Missed Fire Rates and Accidental Fire Rates of NLIF and GLIF model under various simulation step size.

VI. CONCLUSION AND FUTURE WORK

Clearly the GLIF model introduced in this study could accurately simulate the dynamics of a neuron cell membrane potential if the parameters and kernel function were extracted and fitted meticulously using the statistical method we provided. Although the reference model we used to demonstrate the extracting procedure and to test the GLIF model was the HH model with two ionic channels, our GLIF model could be easily fitted to any complicated HH model with more ion channels. This last assertion can be supported simply by gathering the conductance data after each output spike, and fit those data to kernel functions for each ion channel.

The comparison of the GLIF model performance with that of the NLIF shows that our model provides much better calculation accuracy in simulating the biological neuron activity while keeping the calculation complexity to an acceptable level. Such outcomes increase the prospects of the GLIF model for its implementation in larger scale and real-time ASNNs. As we seek to reach this implementation goal, future research work will focus on building more biological plausible ASNN using the GLIF neuron model on parallel computation platforms such as the General Purpose

Graphic Process Unit (GPGPU) and FPGA devices, and applying such ASNN to resolve a multitude of real-world problems associated with pattern recognition and pattern classification, and signal processing, among other applications.

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