IJMLNCE JOURNAL

International Journal of Machine Learning and Networked Collaborative Engineering

Journal Homepage: http://www.mlnce.net/home/index.html

DOI : https://doi.org/10.30991/IJMLNCE.2019v03i02.004

Information Processing in GLIF Neuron Model with Noisy Conductance

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Abstract

In this article, we investigate the generalized leaky integrate-and-fire (GLIF) neuron model with stochastic synaptic conductance. A neuron remains connected with other neuron via dendrites and axons at synapse, which can be treated as an electrical capacitor. Dendrites carry electro-chemical signals from input neuron to synapse whereas axons are responsible for their transmission form synapse to other neurons. Concentration of these electro-chemicals in synapse varies during entire time period. We investigate the effect of varying concentration of electro-chemicals at synapse in a single neuron model. Concentration variation of electro-chemicals at synapse is incorporated as noise in GLIF model. Excitatory and inhibitory synaptic conductance of neuron in GLIF is assumed as stochastic entities driven by Gaussian White noise. Stationary state membrane potential distribution for the proposed model is computed with reflecting boundary conditions, which is noticed as geometrically distributed. In order to investigate spiking activity and information encoding mechanism, an extensive simulation based study has been carried out. Temporal encoding technique is used to analyze the encoding mechanism. It is noticed that ISI distribution has higher variance with respect to excitatory input than inhibitory input. ISI distribution also exhibits the power-law behavior for electro-chemical balance situation.

Keywords

Colour Noise,

Conductance,

GLIF Model,

GIF Model,

ISI Distribution,

Stochastic,

Decay Constant

1. Introduction

Neuron processes information in form of action potential (spike) and transmits in sequence of spikes [11, 16]. These spike sequence exhibit the highest scale of variability in their patterns. Variability in spike

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sequence contains encoded information which transmits to other neurons or part of body [11, 16, 19]. A number of measurements have suggested the reliability of encoded information into variable spike sequences. Neurotransmitters, which are responsible for membrane potential fluctuation, can be categorized in two classes: namely, excitatory neuro-transmitters and inhibitory neuro-transmitters [4, 6, 22]. Excitatory neurotransmitter increases the membrane potential whereas inhibitory neurotransmitter decreases the membrane potential value. Random arrival of these neurotransmitters causes fluctuation in net potential value; which also affect the spiking activity and generates variability in spiking pattern [4, 6]. Potential value contributed by these neurotransmitters can be classified as excitatory potential and inhibitory potential and their arrival pattern has been modeled via Poisson process i.e. arrivals are independent of each other [10, 19, 23].

Lapicque has introduced the integrate-and-fire (IF model) neuron model which is also the first mathematical model of neuron [1, 25]. In IF model, it is assumed that a neuron receives potential in form of neurotransmitters from other neurons and external world in form of input, which increases its membrane potential and at a fixed potential value (threshold), it emits collected neurotransmitters and generate an action potential. Leaky Integrate-and-Fire (LIF) neuron model is an extension of IF model, where membrane decay constant (β) has been incorporated [1, 14, 25]. Mathematical representation for rate of change of membrane potential in LIF model can be given as below.

$$\frac{dV}{dt} = -\beta V(t) + I(t) \tag{1}$$

Here $I(t)$ is the time dependent input stimulus. Many researchers have modeled $I(t)$ in different ways viz. constant value, periodic value, stochastic value driven by Gaussian white noise, *etc*. A number of researcher have assumed $I(t)$ as a sum of current due to excitatory neurotransmitter and inhibitory neurotransmitter [2, 3, 22] i.e. $I(t)$ can be replaced via

$$I(t) = G_e(V_e - V)S_e + G_i(V_i - V)S_i \tag{2}$$

Here, G_e and G_i are excitatory and inhibitory synaptic conductance, S_e and S_i are excitatory and inhibitory synaptic strengths. Substitution $I(t)$ of from Eq. (2) to IF model and LIF model transform them into Generalize Integrate-and-Fire (GIF) and Generalized Leaky-Integrate-and-Fire (GLIF) neuron models [2, 3, 28]. In this article, we investigate spiking activity, information processing mechanism and stationary state membrane potential for GLIF model with stochastic synaptic conductance.

The article is structured in 6 sections. After a brief introduction about IF model, spiking variability in section 1, Section 2 deals with the formulation of GLIF model. Here stochastic synaptic conductance has been used to model the assumption. Section 3 deals with mathematical computation of GLIF model and stationary state membrane potential for GLIF neuron model is computed. Information processing mechanism into GLIF model is investigated in next section 4. Here, a detailed simulation based study is performed to compute ISI distribution. Discussion related to model and findings has is elaborated in section 5. Finally, the last section contains conclusions and future scope for the study.

2. Generalized Leaky Integrate-and-Fire Neuorn Model

Driving After more than 50 years of Lapicque's IF model, Stein has proposed GIF model where input stimulus is modeled as a sum of pre-synaptic excitatory and inhibitory currents [2, 3, 28]. Furthermore, Stein has assumed the arrivals of pre-synaptic current as a Poisson process and investigated information processing in terms of neuronal firing rate [27]. Wilbur and Rinzel [29] have investigated Stein's Generalized IF model only for excitatory neurotransmitters. They have measured multiple parameters like firing rate, calculation time etc. which is important for physiological point of view. Wilbur and Rinzel [29] have also investigated the inter-spike-interval distribution (ISI distribution). Tuckwell [26] has studied the firing rate of GLIF model with excitatory current and inhibitory current, both, and noticed a fine agreement in firing rate with existing experimental data. Richardson and Gerstner [20] have studied GLIF model with stochastic synaptic conductance. They have modeled synaptic conductance via Ornstein-Uhlenbeck process and have computed voltage distribution, conductance distribution, ISI distribution etc. Lansky [17] has assumed evolution of membrane potential in GLIF model as a diffusive process and computed ISI distribution. He [17] has also computed the cumulative ISI distribution for exponentially distributed excitatory and inhibitory neurotransmitters. Hurby [13] has studied GLIF model with realistic synaptic potential and noticed bursting period, quiescence period, spiking rate and spike frequency. In order to avoid membrane potential fluctuations, Goriset. al. [12] modeled spike generation in GLIF model as a Poisson process and investigated response distribution with excitatory neurotransmitters. This model [12] is found comparatively more suitable for visual sensory neurons. Teeter et. al. [24] has applied unsupervised methods with GLIF neuron to classify cell types in mammalian neocortex. Choudhary et. al. [4], Choudhary and Solanki [6] has modeled membrane potential contribution due to excitatory neurotransmitters and inhibitory neurotransmitters via hypo-exponential distribute delay kernel in distributed delay framework (DDF) of threshold based neuron model. Their model is capable to generate different kinds of spiking patterns as reported in multiple literatures. Uni-modal, bi-modal, multi-modal etc. kind of ISI distribution patterns has been noticed in their investigation [4, 6]. DDF provides a way to capture the effect of past values of membrane potential over its present evolution so that variability in spiking pattern can be explained in better way [7]. Stationary state membrane potential distribution of LIF model in DDF exhibit no change under the change of delay kernel functions and statistically remains constant which is noticed as Gaussian distributed [6, 7].

3. Stationary State Probability Distribution in GLIF Model

Substitution of $I(t)$ from Eq. (2) to Eq. (1) yields [2, 3]

$$\frac{dV}{dt} = -\beta V(t) + G_e(V_e - V)S_e + G_i(V_i - V)S_i \tag{3}$$

Here V_e and V_i are initial value of excitatory potential and inhibitory potential. Further simplification of Eq. (3) results into GLIF as

$$\tau_m \frac{dV}{dt} = -(V - V_0) + G_e(V_e - V)S_e + G_i(V_i - V)S_i \tag{4}$$

τ_m is membrane resistance. It is noticed in multiple literature that electrical properties of membrane changes after each spike so that synaptic conductance also changes [20]. Thus, excitatory and inhibitory synaptic conductance G_e and G_i can be assumed to be a time dependent entities so that Eq. (4) can be rewritten as

$$\tau_m \frac{dV}{dt} = -(V - V_0) + G_e(t)(V_e - V)S_e + G_i(t)(V_i - V)S_i \tag{5}$$

Following Richardosn and Gerstener [20], $G_e(t)$ and $G_i(t)$ are assumed to be stochastic entities. In forgoing study, we are modeling these two entities driven by Gaussian white noise i.e. $G_e(t) = \bar{G}_e + \xi_e(t)$ and $G_i(t) = \bar{G}_i + \xi_i(t)$ [5, 9, 23]. Here $\bar{G}_e$ and $\bar{G}_i$ are mean value of excitatory and inhibitory synaptic conductance. $\xi_e(t)$ and $\xi_i(t)$ are mutually exclusive Wiener processes driven by Gaussian white noise with intensity , $<\sigma_e>=0$, $<\sigma_i>=0$,respectively, i.e. $<\xi_e(t)\xi_i(t)>=0$, $<\xi_e(t)>=0$, $<\xi_i(t)>=0$, $<\xi_e(t_1)\xi_e(t_2)>=\frac{\sigma_e^2}{2}$ and $<\xi_i(t_1)\xi_i(t_2)>=\frac{\sigma_i^2}{2}$. Thus Eq. (5) simplifies as

$$\tau_m \frac{dV}{dt} = -(V - V_0) + (\bar{G}_e + \sigma_e dW_e(t))(V_e - V)S_e + (\bar{G}_i + \sigma_i dW_i(t))(V_i - V)S_i \tag{6}$$

Further simplification of Eq. (6) results into

$$dV = -(AV - B)dt + \left(\frac{\sigma_e S_e (V - V_e)}{\tau_m} dW_e \right) + \left(\frac{\sigma_e S_e (V - V_i)}{\tau_m} dW_i \right) \quad (7)$$

Here, $A = \dfrac{1 + \bar{G}_e S_e + \bar{G}_i S_i}{\tau_m}$ and $B = \dfrac{V_0 + \bar{G}_e V_e S_e + \bar{G}_i V_i S_i}{\tau_m}$

Let $p(V,t)$ be the spatial probability distribution corresponding to the membrane potential $V(t)$ described by Eq (7), then its associated Fokker-Planck equation can be given as

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial V}\{-(AV - B)p\} + \frac{1}{2}\left(\frac{\sigma_e^2 S_e^2 + \sigma_i^2 S_i^2}{\tau_m^2} \right) \frac{\partial^2}{\partial V^2}(V^2 p) \quad (8)$$

The probability current-flux $J(V,t)$ associated with Eq. (8) takes the form

$$J(V,t) = (AV - B)p + \frac{1}{2}\left(\frac{\sigma_e^2 S_e^2 + \sigma_i^2 S_i^2}{\tau_m^2} \right) \frac{\partial}{\partial V}(V^2 p) \quad (9)$$

In order to obtain stationary state probability distribution of membrane potential with reflecting boundaries

$$J(V,t) = 0 \quad (10)$$

Simultaneous use of Eq. (9) and Eq. (10) results

$$(AV - B)p + \frac{1}{2}\left(\frac{\sigma_e^2 S_e^2 + \sigma_i^2 S_i^2}{\tau_m^2} \right) \frac{\partial}{\partial V}(V^2 p) = 0 \quad (11)$$

Further simplification of Eq. (11) results

$$V^2 \frac{\partial p}{\partial V} = -\left(\frac{2A}{T^2} + 2 \right) V + \frac{2B}{T^2} \quad (12)$$

Here $\left(\dfrac{\sigma_e^2 S_e^2 + \sigma_i^2 S_i^2}{\tau_m^2} \right) = \zeta$ Integration of Eq. (12) with reflecting boundary conditions results

$$p = V^{-\omega} e^{-\beta / V} \quad (13)$$

Here, $2\left(\dfrac{A}{\zeta^2} + 1 \right) = \omega$ and $\dfrac{2B}{\zeta^2} = \beta$. When V is very large as compared to β i.e. $\dfrac{\beta}{V} \to 0$ then Eq. (13) takes the form becomes

$$p = KV^{-\omega} \quad (14)$$

Here K is a constant value.

4. Infomation Processing in GLIF Model

In order to investigate the information processing mechanism in the GLIF model with proposed stochastic conductance, an extensive simulation based study is performed. We apply Monte-Carlo numerical simulation technique to investigate associated stochastic differential equation in the proposed GLIF model.

There are a number of numerical simulation methods are proposed in literature, we apply Euler-Maruyama (EM) scheme in the simulation study [15]. Following EM scheme, the time duration T for membrane potential evolution is divided into n equally spaced sub-intervals $[0,t_1]$, $[t_1,t_2]$,..., $[t_{n-1},t_n]$, each sub-interval has size $h=T/n$ which is also known as step size. According to Eq. (7), let V_i be the membrane potential at time $t=t_i$ then the membrane potential at successive time $t=t_{i+1}$ becomes

$$V_{i+1}=Vi-\left(AV-B\right)h+\left(\frac{\sigma_e S_e(V-V_e)}{\tau_m}dW_e\right)\sqrt{\xi_{ei}}+\left(\frac{\sigma_e S_e(V-V_i)}{\tau_m}dW_i\right)\sqrt{\xi_{ii}} \qquad (15)$$

for $i=1,2,...,n$, with initial values $V_0=0$, $X_0=0$ and $Y_0=0$. ξ_{ei} and ξ_{ii} are independent identically distributed standard Gaussian variates.

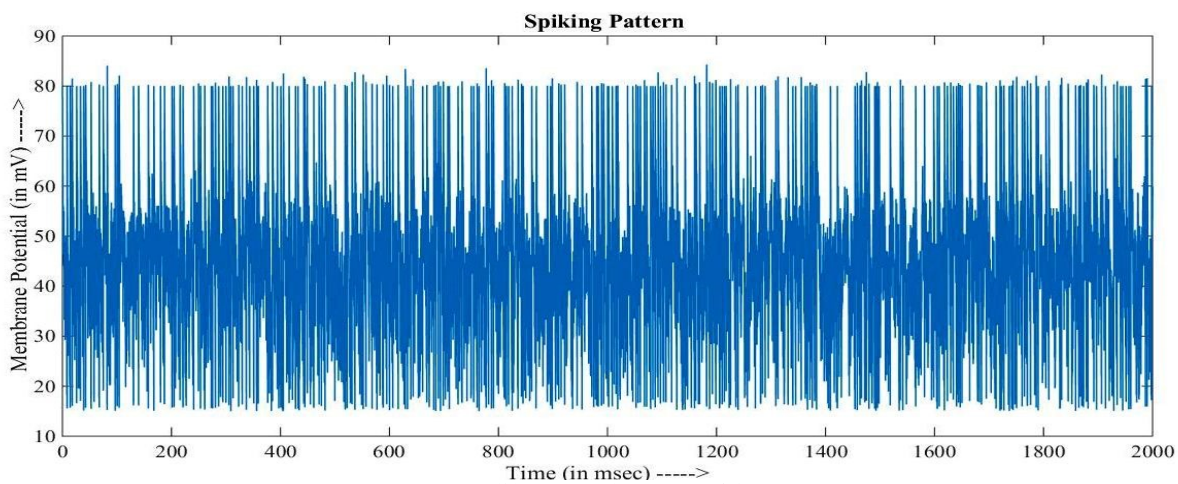

Fig. 1: Spiking Pattern in GLIF Model

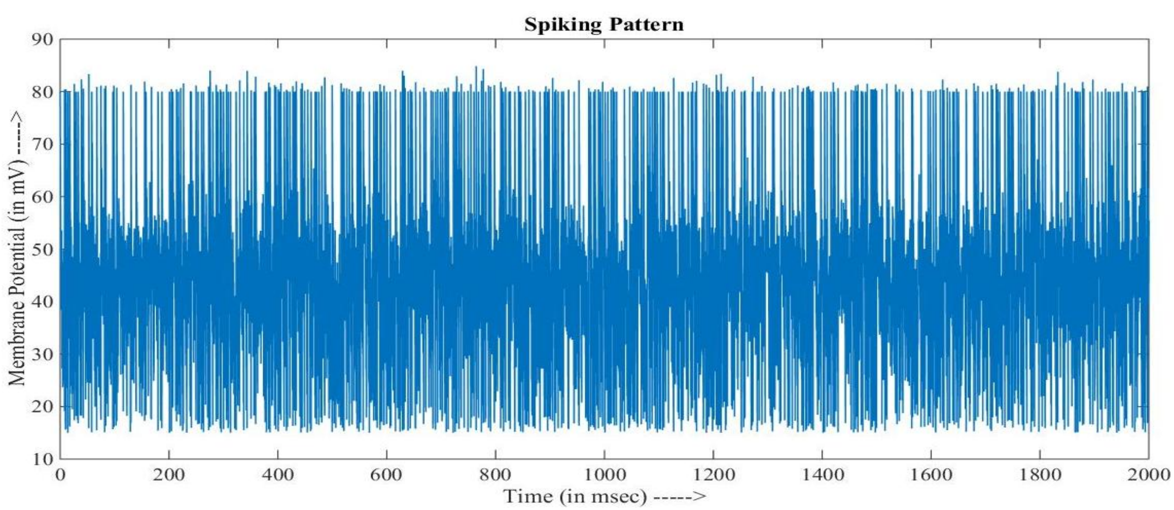

Fig. 2 : Spiking Pattern in GLIF Model

Neuron encodes information in two ways, namely, rate encoding scheme and temporal encoding scheme [19, 22, 23]. We apply temporal encoding scheme to investigate information processing mechanism in the GLIF model. Neuron uses time interval between two consecutive spikes to encode information in rate encoding scheme. The probability distribution of this time intervals is known as inter-spike-interval (ISI) distribution. In order investigation information processing mechanism in GLIF model, spiking pattern of the propose model, for different combination of parameters, is investigated. For similar combination of parameter values, ISI distribution of the model is also studied. Combination of parameter values is given in Table 1. Spiking pattern for the GLIF model is shown in Fig 1. to Fig 5 whereas Fig 6 to Fig 10 illustrates ISI distribution for the GLIF model with parameter combinations given in Table 1. We use τ , V_0 , $V_{threshold}$, V_{reset} , V_E^0 and V_I^0 as a constant throughout the simulation study. Their values are 1, -80, -15, -80, -15 and -75, respectively. We varied rest of six parameter values as given in the following Table1.

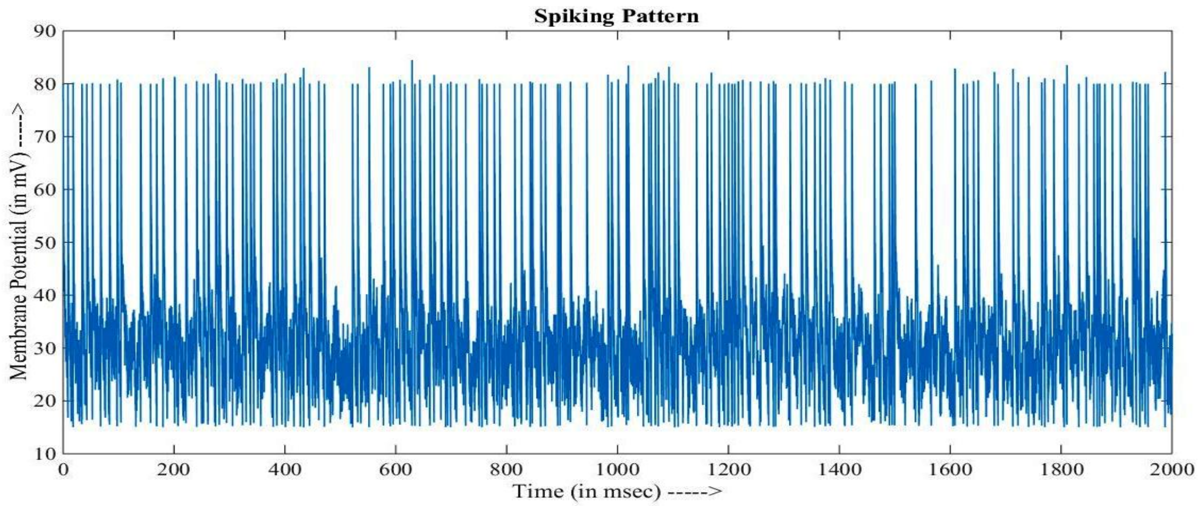

Fig. 3: Spiking Pattern in GLIF Model

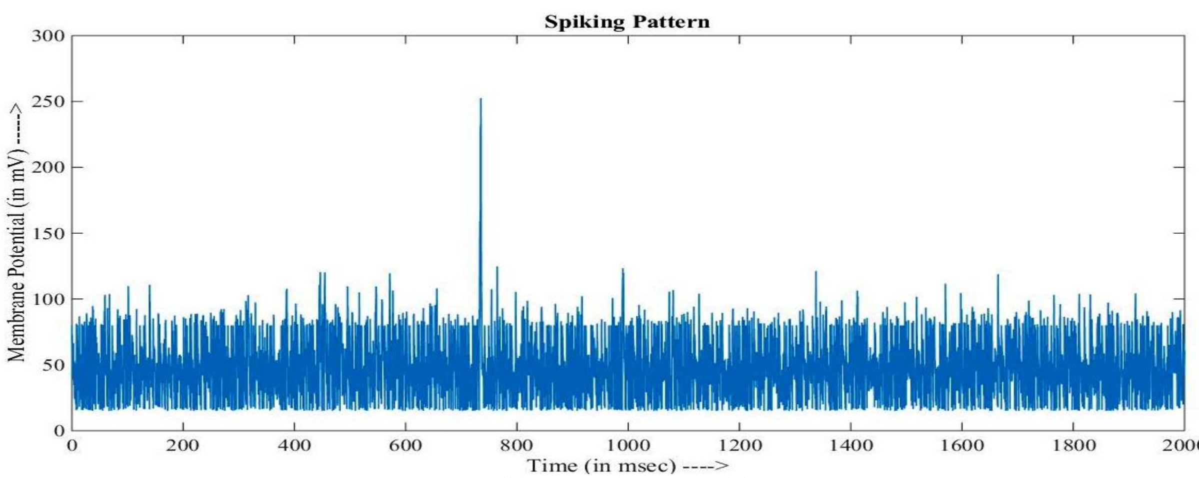

Fig. 4: Spiking Pattern in GLIF Model

Table 1: Combination of parameter values

Fig. No.	G_E	G_I	S_E	S_I	σ_E	σ_I
1, 6	0.5	0.7	1	-1.3	0.1	0.3
2, 7	0.5	0.7	1	-1.1	0.1	0.4
3, 8	0.5	0.7	1.1	-1.5	0.1	0.1
4, 9	0.5	0.7	1.1	-1.5	0.3	0.3
5, 10	0.3	0.5	1.1	-1.1	0.3	0.3

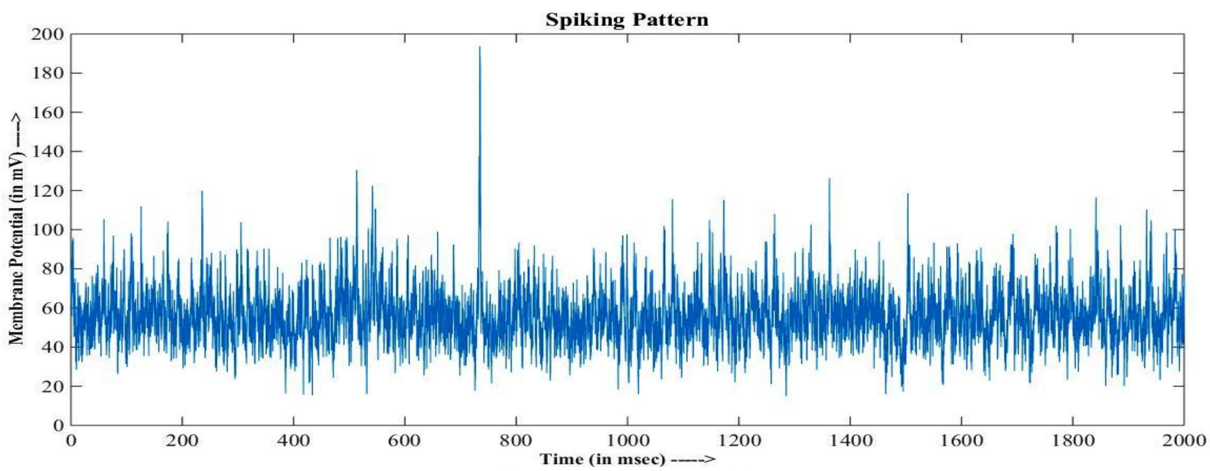

Fig. 5: Spiking Pattern in GLIF Model

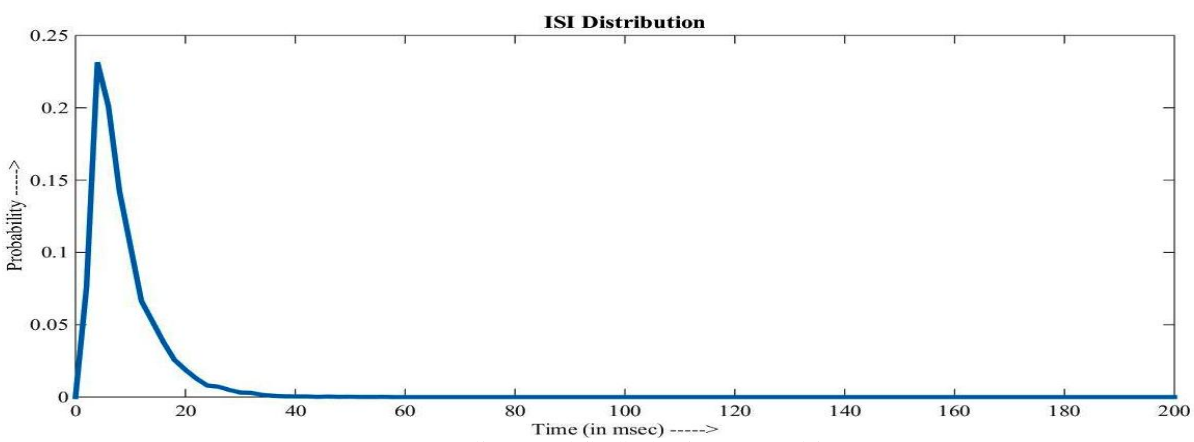

Fig. 6: Inter-Spike-Interval distribution for GLIF Model

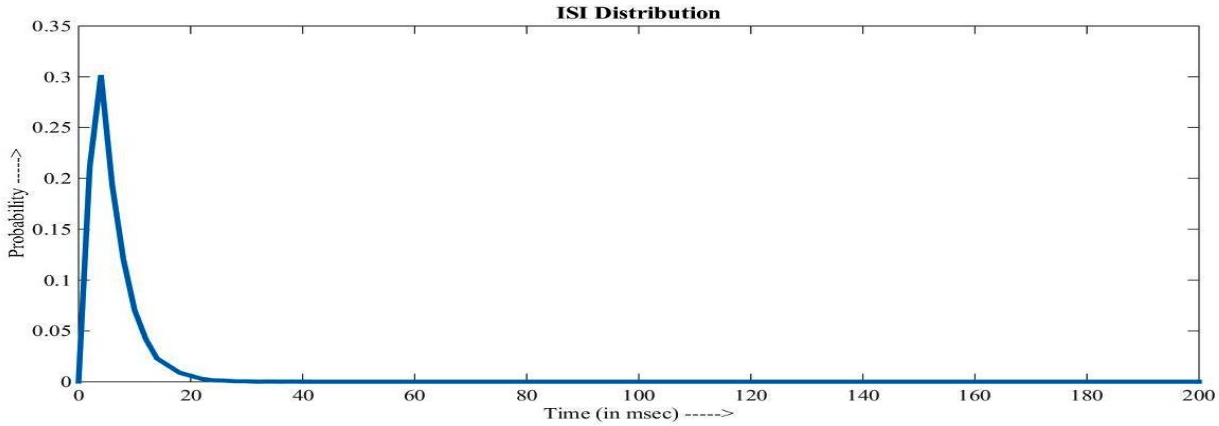

Fig. 7: Inter-Spike-Interval distribution for GLIF Model

Fig 1 to Fig 3 represent bursting nature in spiking pattern. This pattern is occurring due to small value of inhibitory input. When the value of inhibitory input (arrival rate and noise) is smaller, GLIF neuron achieves threshold value in quicker time as shown in Fig 1 and Fig 2. Further increment in inhibitory input as compared with excitatory input, the GLIF neuron exhibits noisy behavior in spiking pattern as shown in Fig 3. Here, inhibitory input moves neuron to opposite direction from firing threshold thus results into more random behavior in spiking pattern. Fig 4 and Fig 5 contains less spikes due to the further increase in inhibitory input than excitatory. Thus, it is noticed that inhibitory input (electro-chemicals) contributes to net membrane potential so that it move away from firing threshold. Fig 6 to Fig 10 represents ISI distribution for spiking activities of the GLIF neuron as shown in Fig 1 to Fig 5. Spiking patterns in Fig 1 to Fig 5 are shown only for initial 2000 msec time period whereas ISI distribution is obtained for 10000000 msec time duration. It is well illustrated in Fig 6 to Fig 9 that increase in inhibitory input leads GLIF neuron not to spike where as excitatory input enforces membrane potential to threshold value. This behavior of excitatory and inhibitory electro-chemicals increases the firing time of GLIF neuron so that the variance in ISI distribution increases. Fig 10 exhibits a situation when arrivals of excitatory and inhibitory inputs are approximately similar so that spiking rate of GLIF model reduces which decreases the spiking activity and increases the inter-spike-interval time duration. Fig 11 represents the ISI distribution on (shown in Fig 10) on Log-log scale. A straight line with slope 1.7102 is fitted on the scattered ISI distribution. Increase in the variance of the ISI time is due to the reason that electro-chemicals, working as a memory element, exhibits time dependent behavior.

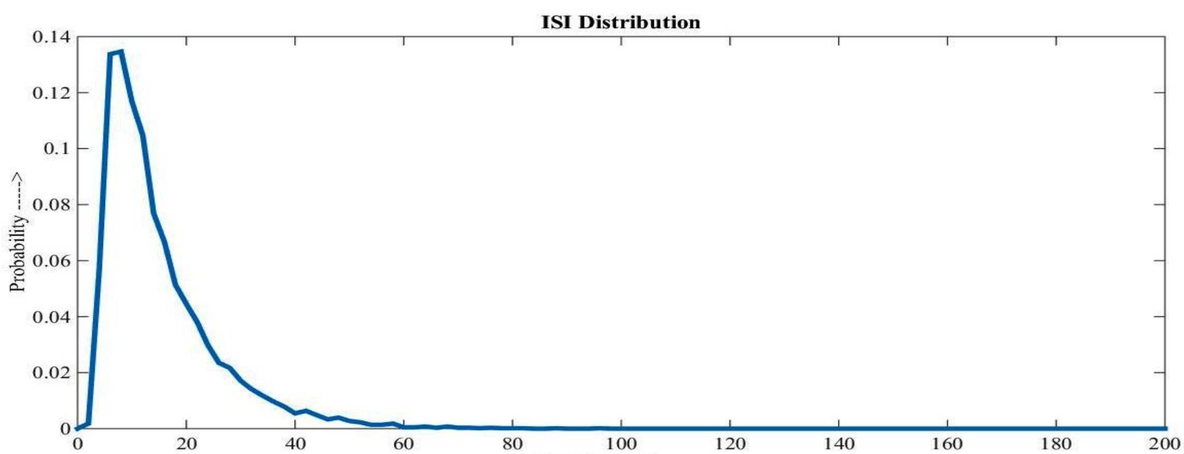

Fig. 8: Inter-Spike-Interval distribution for GLIF Model

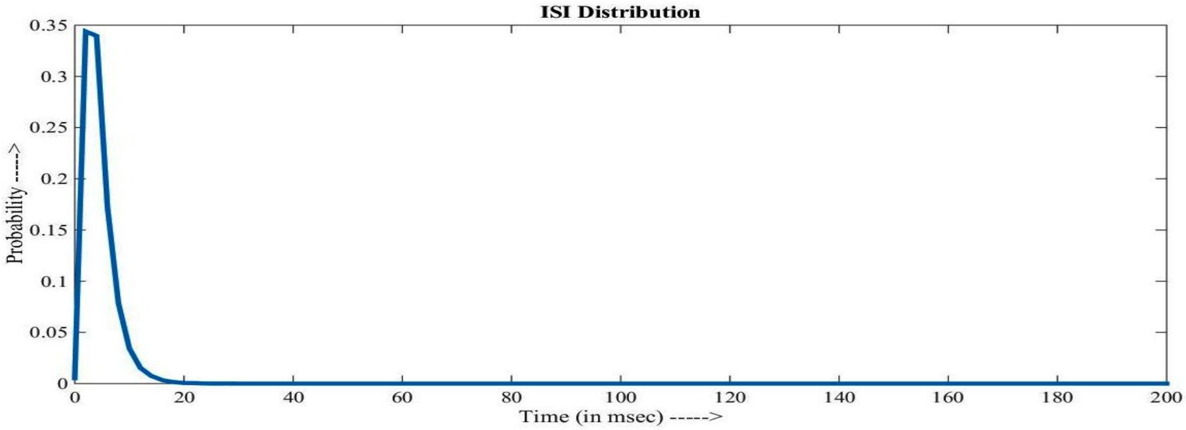

Fig. 9: Inter-Spike-Interval distribution for GLIF Model

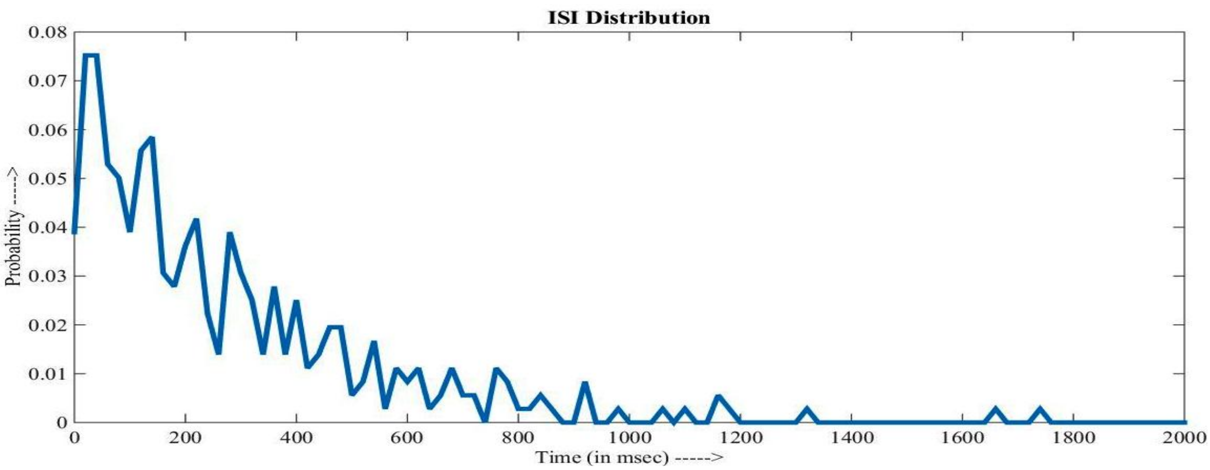

Fig. 10: Inter-Spike-Interval distribution for GLIF Model

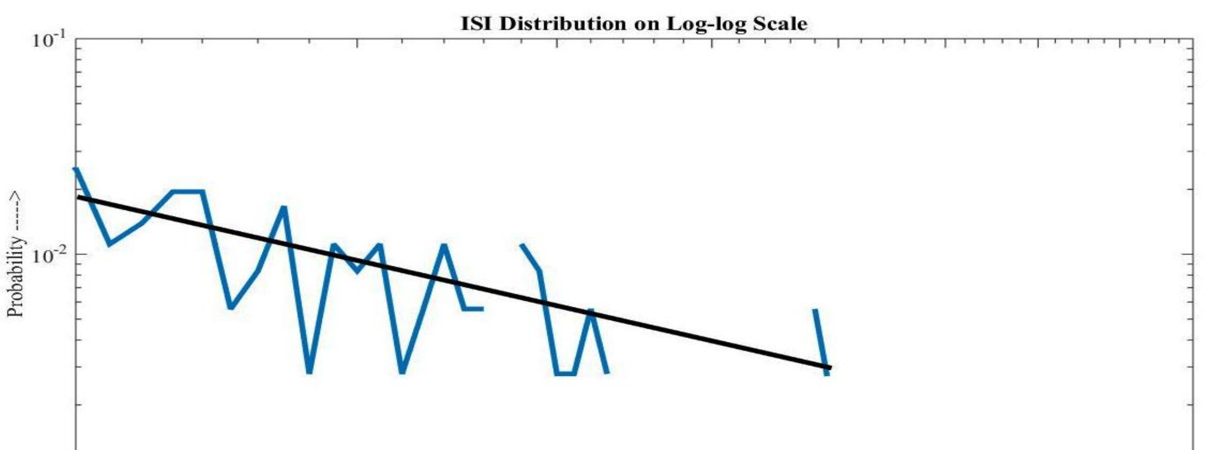

Fig. 11: Inter-Spike-Interval distribution on Log-log Scale for GLIF Model

5. Discussion

The power law is one of the prominent features for many-body problems [18]. A random variable having power-law behavior, can exhibit it in entire domain space or in a sub-domain space; which can be defined by the following generalized form [18]

$$p(x)=\begin{cases}\alpha_1(x); x\in(-\infty,a)\\ \beta x^{-\alpha}; x\in[a,b]\\ \alpha_2(x); x\in(b,\infty)\end{cases} \quad (16)$$

Here, a random variable A with an attribute x has probability distribution function $p(x)$. It has three sub-domains $(-\infty,a)$, $[a,b]$ and (b,∞). $\sigma_1(x)$ and $\sigma_2(x)$ are two different functions in two different sub-domains $(-\infty,a)$ and (b,∞). $\beta x^{-\alpha}$ is a third function in sub-domain $[a,b]$ with power-law behavior which has β as a normalization constant and $\alpha(>0)$ as a constant exponent. In this way attribute x for random variable A have three different behaviors in their three respective sub-domains as defined in Eq. (16). It is a challenging task to compute parameter values like (a,b,α) for a probability distribution. In order to obtain the value of constant exponent α as defined in Eq. (16), maximum likelihood technique provides a way to examine the power-law behavior which maximizes logarithm of probability distribution. The power law behavior can also be examined on Log-log scale scattered distribution [18]. A straight line can be fitted in sub-domain having power law behavior on scattered distributions. This line fitting also helps to examine system's attribute evolution dynamics [8, 18]. A positive slope value of fitted straight line suggests linear increase in attribute whereas negative slope depicts the linear decrease. An attribute which has constant behavior in time domain, will have a slope value 0 for fitted straight line.

GLIF neuron has a kind of gamma distribution for membrane potential in its stationary state with reflecting boundary conditions as shown in Eq. (13). When the membrane resistance is very small as compared to the membrane potential, ISI distribution as shown in Eq. (13), reduces to exhibit the power-law behavior, which is noticed in Eq. (14). Occurrence of the power-law behavior for stationary state membrane potential suggest the long-range dependency for electro-chemicals moving to-and-fro from the synapses.

6. Conclusion and Future Scope

We investigate the GLIF model with stochastic synaptic conductance. Noise generated via multiple kinds of electro-chemicals, molecules and ions is captured via well established Winner process. Incorporation of Wiener process into the GLIF model, turn it into a system with colored noise where noise generates huge fluctuations as it becomes multiple of current value of the state variable [16, 23]. It also provides an essential parameter for long-range dependency of the membrane potential on the information. This long range dependency behavior in information processing occurs due to the memory elements such as electro chemicals. These elements contribute to membrane potential for large time interval results the power-law behavior in stationary state membrane potential distribution and ISI distribution of the GLIF model with stochastic synaptic conductance.

We have investigated membrane potential distribution in stationary state and temporal coding technique of information processing of the neuron. It will be interesting to investigate multiple other neuro-dynamical features of the proposed GLIF model with or without DDF.

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How to Cite

Baghela1, Vishwadeepak Singh, Bharti, Sunil Kumar and Choudhary , Saket Kumar, "Information Processing in GLIF Neuron Model with Noisy Conductance",*International Journal of Machine Learning and Networked Collaborative Engineering,* Vol. 03 No. 2, 2019, pp.102-113. doi : https://doi.org/10.30991/IJMLNCE.2019v03i02.004.