

Emergence of power law behavior in threshold based neuron model with stochastic membrane decay constant

Saket Kumar Choudhary

Abstract— A new phenomenon to obtain the power-law behavior in neuronal properties for a threshold based neuron model is proposed. Membrane decay constant in leaky integrate-and-fire neuron model is considered to be a stochastic process which results a new model, the LIFSD neuron model (leaky integrate-and-fire neuron model with stochastic membrane decay constant). Two neuronal activities, namely, stationary state membrane potential and ISI (inter-spike-interval) distribution for the LIFSD model is investigated. In order to obtain the stationary state membrane potential, Fokker-Planck equation (FPE) with reflecting boundary condition, associated with LIFSD neuron model is solved which results the power-law behavior. ISI distribution depicts the power-law behavior during Monte Carlo simulation based study of proposed model. To mathematically complete LIFSD model, explicit expressions for membrane potential and its first two moments; mean and variance for membrane potential are also calculated.

The LIFSD neuron model is found capable to generate the power law behavior for stationary state membrane potential distribution and ISI distribution. However a number of other neuronal activities are still left to investigate in context of the power law behavior. These findings suggest the robustness of proposed model for input-output relationship prediction and also prove that the development of the net membrane potential and the spiking activity in the single neuron are due to the aggregate effort of group of ions and molecules.

Keywords— Fokker Planck Equation, Inter-Spike-Interval distribution, Neuron Model, Power Law, Stochastic Differential Process, Stochastic Process.

I. INTRODUCTION

Power law behavior is the characteristic feature for investigating many body systems [16], [25]. An attribute X with probability distribution proportional to $X^{-\alpha}$; $\alpha > 1$ is characterized by power-law [10]. It has a wide range of application like earth-quake, fragmentation, laser cooling, economics, animal behavior, etc. [10], [16]. A number of physiological and experimental studies focused on neuronal dynamics have suggested emergence of the power law behavior at microscopic and macroscopic level such as neuronal avalanches [4], inter-spike-interval distribution [6], power spectral density for the membrane potential [24],

adaption processes in spiking [26], etc. Replication of these experimental findings via mathematical model is one of the prime issues in theoretical neuroscience. Sharma and Karmeshu [33], Karmeshu and Sharma [18] have theoretically obtained the power-law behavior for ISI distribution in threshold based neurons (LIF model and IF model). Pettersen et al [25] has noticed the power law behavior in power spectral density for membrane potential distribution. These investigations [18], [25], [33] are focused for group behavior of neuron and suggest that emergence of the power-law behavior in neuronal activities are due to group effect. An ensemble of homogeneous and/or heterogeneous neuron results the power-law behavior when they “group together and fire together” [18]. Generation of the power law behavior in neuronal activities for single threshold based neuron model is still an unanswered prominent question [5], [25].

Mathematical modeling for single neuron model requires focus on computational issues like neuronal activity, neuronal dynamics and information processing etc [1], [5], [13], [19]. Neuron receives random synaptic input from other neurons and from external environment. These inputs generate fluctuation in membrane potential and make it capable to process information in terms of variable spiking pattern [13], [31]. Abbott and Dayan [1] have suggested that membrane conductance changes due to generation of an output spike. Mears et al [20] has measured coupling strength (conductance) among β -cells and noticed that temperature play a crucial role in its time dependent behavior. Engel et al [15] has investigated time dependent behavior of conductance's for stellate and pyramidal neurons obtained from rat entorhinal cortex. Schmid et al [32] has studied conductance fluctuation in terms of random gating behavior of ion channels. Verechtchaguina et al [37] has modeled conductance fluctuation in Resonate-and-fire neuron via Langevin equation. On account of factors related to random behavior of ion channels, varying concentration of ions and molecules (neurotransmitters) inside-outside soma (cell body) and membrane temperature fluctuation; membrane conductance can be regarded as a fluctuating entity [2], [13], [14], [28], [36]. In this article, we investigate neuronal activities of single threshold based neuron model with fluctuating membrane conductance in terms of power-law behavior. Membrane decay constant in LIF neuron model can be assumed to be a

Saket Kumar Choudhary is with the Impel Labs. Pvt. Ltd. Bengaluru, India. (phone: +91-8296486927; e-mail: saket_au@rediffmail.com; saket_53_scs@jnu.ac.in; saket@impel.io).

stochastic process due to aforementioned reasons which results the LIFSD model.

The article is organized into seven sections. After a brief introduction in Section I, next Section II deals with mathematical formulation of LIFSD neuron model. Stochastic evolution of membrane potential in LIFSD model is discussed in section III. This section also includes computations related to explicit expressions for first two moments of membrane potential. Section IV discusses stationary state probability distribution of membrane potential which reflects the power law behavior in its limiting conditions. Section V deals with Monte Carlo simulation based investigation of LIFSD model. Here LIFSD neuron model is found capable to generate ISI distribution patterns with the power-law behavior. Section VI includes detailed discussion regarding assumptions. The last section VII gives the conclusion.

II. STOCHASTIC LIF MODEL

It is well accepted that a neuron can be represented as an equivalent electrical RC -circuit with additional threshold constraint. Threshold constraint is associated with spiking time of the neuron i.e. when net membrane potential of neuron attains a certain value (the threshold), a spike is generated [1], [12]. LIF model is the simplest and widely accepted neuron model to analytically explain neural dynamics [1], [11], [27], [30]. It is a threshold based model where membrane conductance is defined in terms of membrane decay constant [1], [19]. LIF model with stochastic input stimulus $I(t)$ can be represented as

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

With initial condition $V(t=0) = V_0$. β is membrane decay constant. $I(t)$ is considered as a sum of mean input stimulus (μ) and Wiener process $\xi_1(t)$ with variance σ_1^2 i.e.

$$\langle \xi_1(t) \rangle = 0 \text{ and } \langle \xi_1(t_1)\xi_1(t_2) \rangle = \frac{\sigma_1^2}{2} \delta(t_1 - t_2).$$

β is assumed as a constant entity in entire literature [1], [18], [19], [30], [31], [33]. β can be assumed as a time dependent entity due reasons discussed in Section I. we can model it as a stochastic process driven Gaussian White noise, i.e. $\beta(t) = \beta_0 + \xi_2(t)$, where β_0 is mean decay constant and $\xi_2(t)$ is a Wiener process with noise intensity σ_2 , independent of $\xi_1(t)$ and satisfying

$$\langle \xi_2(t_1)\xi_2(t_2) \rangle = \frac{\sigma_2^2}{2} \delta(t_1 - t_2).$$

Incorporating time dependent $\beta(t)$ into LIF model (Eq. 1), rate of change of membrane potential results LIFSD neuron model which can be represented by following stochastic differential equation (SDE) [19]

$$\frac{dV}{dt} + (\beta_0 V(t) - \mu) + V(t)\xi_2(t) - \xi_1(t) = 0 \quad (2)$$

Eq. (2) is in Ito sense, SDE in Stratonovich sense corresponding to Eq. 2 becomes

$$\frac{dV}{dt} + (\bar{\beta}_0 V(t) - \mu) = -V(t)\xi_2(t) + \xi_1(t) \quad (3)$$

$$\text{With } \bar{\beta}_0 = \left(\beta_0 + \frac{\sigma_2^2}{2}\right).$$

Rate of change of membrane potential defined in Eq. 2 and Eq. 3 are SDEs with additive noise as well as multiplicative noise both, which make computation of explicit expression for $V(t)$, an interesting problem [16], [17], [35]. It also provides an opportunity to get insight into effects of multiplicative noise on membrane potential evolution, spiking activity and other related neuronal activities.

III. STOCHASTIC MEMBRANE POTENTIAL IN THE LIFSD NEURON MODEL

Stratonovich SDE satisfies ordinary calculus and explicit expression for membrane potential of LIFSD model defined in Eq. (3) is computed below.

Integration of Eq. 3 results membrane potential evolution process $V(t)$

$$V(t) = V_0 \exp\{-\bar{\beta}_0 t - \int_0^t \xi_2(s)ds\} + \exp\{-\bar{\beta}_0 t - \int_0^t \xi_2(s)ds\} \cdot \int_0^t (\mu + \xi_1(u)) \exp\{\bar{\beta}_0 u + \int_0^u \xi_2(s)ds\} du \quad (4)$$

Further simplification of Eq. 4 yields explicit expression for $V(t)$

$$V(t) = V_0 \exp\{-\bar{\beta}_0 t - \int_0^t \xi_2(s)ds\} + \mu \int_0^t \left\{ \exp\{-\bar{\beta}_0(t-u) - \int_0^t \xi_2(s)ds + \int_0^u \xi_2(s)ds\} \right\} du + \int_0^t \xi_1(u) \left\{ \exp\{-\bar{\beta}_0(t-u) + \int_0^t \xi_2(s)ds + \int_0^u \xi_2(s)ds\} \right\} du \quad (5)$$

Time dependent $V(t)$ given in Eq. 5 is a stochastic process due to the presence of Wiener processes. Thus, coefficient of variation becomes an important parameter to study evolution dynamics for $V(t)$ [19], [34], [35]. Time dependent coefficient of variation for $V(t)$ can be computed by its first two moments [19], [34], [35]. Next subsections III-A and III-B deal with computation of explicit expressions for first moment and the second moment of $V(t)$, respectively. Computation of time dependent coefficient of variation is described in subsection III-C. Fig. 1-Fig. 6 are related to stochastic evolution of membrane potential. These Figs. are shown at their appropriate place.

A. Mean Membrane Potential

Expectation of both sides of Eq. (5) results first moment of $V(t)$ i.e. mean membrane potential ($\langle V(t) \rangle$). Since $\xi_1(t)$ and $\xi_2(t)$ are mutually independent Wiener processes, expectation of Eq. 5 after some simplification results

$$\langle V(t) \rangle = V_0 \langle \exp\{-\bar{\beta}_0 t - \int_0^t \xi_2(s) ds\} \rangle + \mu \langle \int_0^t \exp\{-\bar{\beta}_0(t-u) - \int_0^u \xi_2(s) ds + \int_0^u \xi_2(s) ds\} du \rangle \quad (6)$$

Following Balakrishnan [3] and Soong [35], further simplification of Eq. 6 results explicit expression for mean membrane potential

$$\langle V(t) \rangle = V_0 \exp\left\{-\left(\bar{\beta}_0 t + \frac{\sigma_2^2 t^2}{2}\right)\right\} + \mu \int_0^t \exp\left\{-\bar{\beta}_0(t-u) + \frac{\sigma_2^2}{2}(t-u)^2\right\} du \quad (7)$$

Fig. 1 depicts evolution of membrane potential for an ensemble of neurons (red color line), mean of numerically expression of mean membrane potential (blue color line) line. An ensemble of 100000 are simulated with Monte Carlo simulation strategy as stated in Section V. For the sake of simplicity of figure, evolution of membrane potential of only 50 ensembles is shown (in red color line). Ensembles are numerically in sub-threshold regime with 0.7 mV threshold value whereas no threshold is applied in plot of explicit expression (blue color line) [12], [11], [33], [34]. This figure includes the evolution of stochastic membrane potential for initial 10 msec.

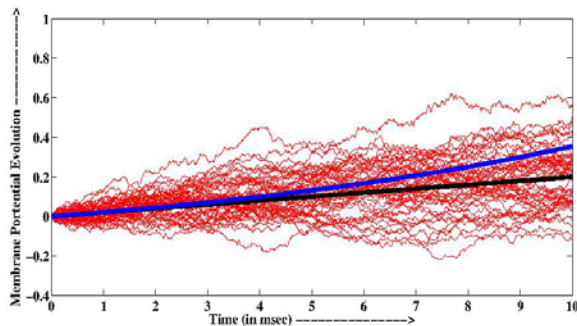


Fig. 1 Numerical simulation and plot of analytical result for mean membrane potential with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.1$.

Here, numerically computed mean and the plot of explicit expression exhibit similar evolution dynamics in initial half of the time duration but shows some difference in later half time interval. This difference is due to threshold value which is applied on evolution of ensemble of neurons but not on explicit expression and it will monotonically increase. Noise terms are also responsible to causes fluctuations in evolution of membrane potentials in ensembles whereas analytical result

monotonically increases. In this way, evolution of the mean membrane potentials obtained by numerical simulation and analytical expression are in nice agreement.

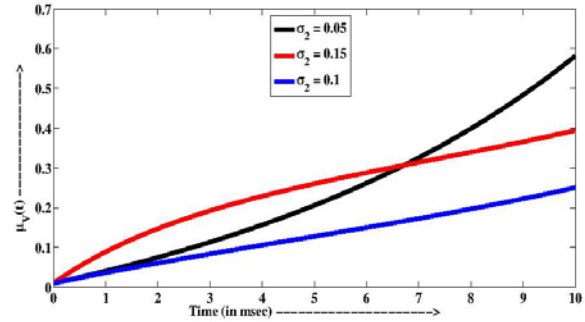


Fig. 2 Analytical results for mean membrane potential with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and different σ_2 values.

Development of mean membrane potential defined in analytical expression Eq. (7), with constant β_0 , μ , σ_1 and different values of σ_2 is shown in Fig. 2. Here, it is well illustrated that for $\sigma_2 < \beta_0$, evolution of membrane potential is due to applied input stimulus and it increases more rapidly as compared with other conditions σ_2 of values. When $\sigma_2 = \beta_0$ then behavior of LIFSD model will fluctuate between IF neuron model and LIF neuron model. In this case, membrane potential will also evolve but with comparatively lesser speed, whereas, $\sigma_2 > \beta_0$ will depicts higher fluctuations in evolution membrane potential.

B. Variance for $V(t)$

Second moment of membrane potential is known as variance. It can be computed by applying the standard formula as given in Eq. 8.

$$\sigma_V^2(t) = \langle (V(t))^2 \rangle - (\langle V(t) \rangle)^2 \quad (8)$$

Substitution for values of $V(t)$ form Eq. 5 and $\langle V(t) \rangle$ form Eq. 7 into Eq. 8 and further simplification results explicit expression for variance of $V(t)$ as below.

$$\begin{aligned} \sigma_{V(t)}^2 &= \frac{\sigma^2}{2} \int_0^t \exp\{-2\bar{\beta}_0(t-u) + \sigma_2^2(t-u)\} du \\ &+ 2\mu V_0 \int_0^t \left\{ \exp\left(\frac{\sigma_2^2}{2}(2t-u)^2\right) - \exp\left\{\frac{\sigma_2^2}{2}(u^2 - 2ut)\right\} \right\} \\ &\exp\{-\bar{\beta}_0(2t-u)\} du \end{aligned} \quad (9)$$

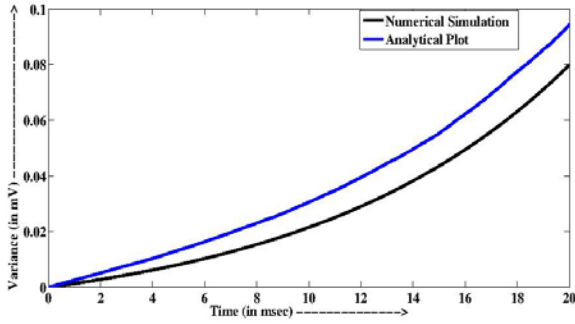


Fig. 3 Numerical simulation and plot of analytical result for variance in membrane potential with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.1$

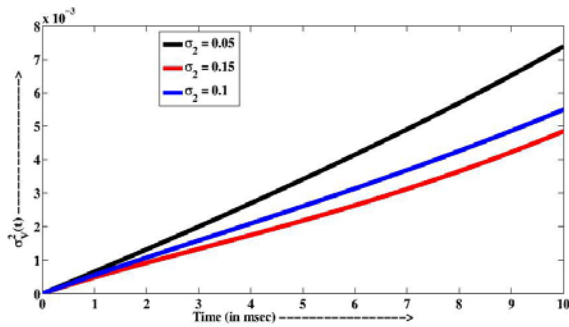


Fig. 4 Analytical results for variance in membrane potential with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and different σ_2 values.

Fig. 3 and Fig 4 represent evolution dynamics of variance of membrane potential with justifications given sub-section III-A. Fig. 3 shows variance development for initial 20 msec time duration and illustrates the matching of analytical expression of variance given by Eq. 9 with numerically observed variance of ensemble of 100000 neurons. Numerical computation of variance is carried with similar parameter values used for mean membrane potential in sub-section III-A. Fig. 4 shows stochastic evolution of analytically computed variance for different values of σ_2 with constant β_0 , μ and σ_1 . It is well illustrated that the lowest increase in variance is occurring for the highest value of $\sigma_2 (> \beta_0)$. This behavior in variance is due to the reason of stochastic membrane conductance which is responsible for more fluctuation in membrane potential evolution as compared with σ_1 .

C. Coefficient of Variation for $V(t)$

Coefficient of variation provides a measure of relative fluctuation [19], [35]. First two moments (Eq. 7 and Eq. 9) for stochastic evolution of $V(t)$ depict temporal behavior and result a time dependent coefficient of variation. The time dependent coefficient of variation for $V(t)$ can be computed as given in Eq. 9.

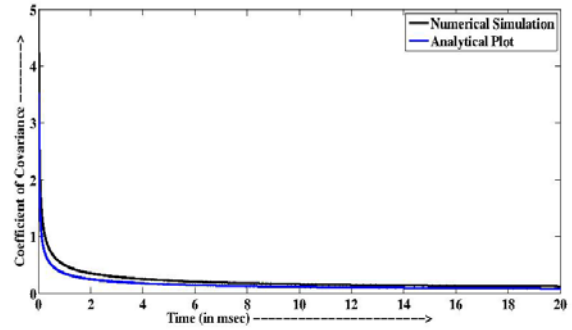


Fig. 5. Numerical simulation and plot of analytical result for coefficient of variation of membrane potential with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.1$

$$CV_{V(t)} = \frac{\sqrt{\sigma_{V(t)}^2}}{\langle V(t) \rangle} \quad (9)$$

Temporal evolution of $CV_{V(t)}$ for parameter values used in previous two sub-sections is shown in Fig. 5 and Fig. 6. Fig. 5 depicts evolution of coefficient of covariance for initial 20 msec. This Fig. shows nice agreement for $CV_{V(t)}$ in analytical result and simulation based results due to above stated reasons.

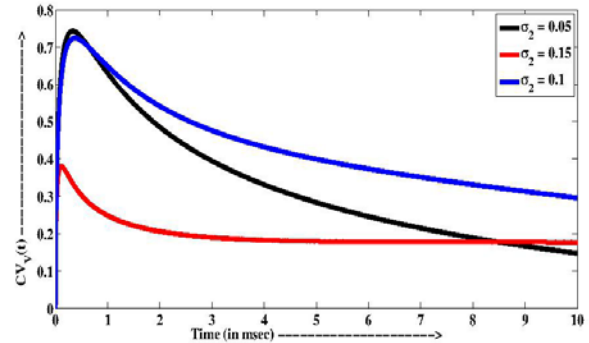


Fig. 6 Analytical results for coefficient of variation with parameter values $\beta_0 = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and different σ_2 values.

Fig. 6 represents $CV_{V(t)}$ of analytical expression for different values of. Both figures have a very small difference in their initial development for $\sigma_2 = 0.1$. This is due to the difference in initial value of the membrane potential. For Fig. 5 V_0 is taken as 0:001 mV whereas 0 mV in Fig. 6 [33], [34]. In Fig. 6, it is well illustrated that the highest value of $\sigma_2 (> \beta_0)$ depicts the lowest relative fluctuation in membrane potential. The term related to stochastic conductance in LIFSD neuron model is colored noise term, is also responsible for a large fluctuation in membrane potential development and helps neuron to reach its firing threshold in quicker time as compared with LIF neuron model. It is well illustrated in Fig. 5 and Fig. 6 that relative fluctuation of

membrane potential reduces as time progresses. This reduction in relative fluctuation of membrane potential arises due to colored noise term which generates long range dependency in LIFSD model.

IV. STATIONARY STATE MEMBRANE POTENTIAL DISTRIBUTION

Explicit expression for membrane potential for LIFSD neuron model is a stochastic process and coefficient of variation for membrane potential is a time dependent entity. Thus a natural question arises that what will be the membrane potential distribution? To this end, Fokker-Planck equation (FPE) has a great importance in investigating evolution dynamics and probability distribution of state variables defined in terms of SDEs [16]. Solution of a FPE depends on boundary conditions. Among a number of boundary conditions, reflecting boundary condition associated with sub-threshold regime of a neuron (i.e. a combination of parameter values where a neuron never emits spike for deterministic input stimulus), provides a way to get insight into the spatial probability distribution of the membrane potential [7], [8], [14]. Let $p(V, t)$ be spatial probability distribution of $V(t)$ for the LIFSD neuron model defined in Eq. 3, FPE corresponding to the LIFSD model takes the form

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial V} (\bar{\beta}_0 V - \mu) p + \frac{1}{2} \frac{\partial^2}{\partial V^2} (\sigma_1^2 + \sigma_2^2 V^2) p \quad (11)$$

With boundary conditions: $p(V, t | t = 0) = \delta(t - t_0)$; $p(V, 0) = V p(V, 0) = 0$ as $V \rightarrow \infty$.

Probability current flux $J(V, t)$ associated with above FPE becomes [16]

$$J(V, t) = (\bar{\beta}_0 V - \mu) p + \frac{1}{2} \frac{\partial}{\partial V} (\sigma_1^2 + \sigma_2^2 V^2) p \quad (12)$$

Probability current flux associated with a neuron model in its sub-threshold regime vanishes at boundaries [14], [30]. Following Frank [16], let $p_s(V)$ be stationary state membrane potential distribution for LIFSD model then Eq. 12 with reflecting boundary condition (i.e. $J(V, t) = 0$) results

$$(\bar{\beta}_0 V - \mu) p_s + \frac{1}{2} \frac{\partial}{\partial V} (\sigma_1^2 + \sigma_2^2 V^2) p_s = 0 \quad (13)$$

Integration of Eq. (13) yields $p_s(V)$ as

$$p_s(V) = K (\sigma_1^2 + \sigma_2^2 V^2)^{-\left(1 + \frac{\bar{\beta}_0}{\sigma_2^2}\right)} \cdot \exp\left\{\frac{2\mu}{\sigma_1 \sigma_2} \tan^{-1}\left(\frac{\sigma_2 V}{\sigma_1}\right)\right\} \quad (14)$$

Here K is a normalization constant and can be calculated by applying the law of conservation of probabilities [16]. For a very small σ_1 as compared with $V \exp\left\{\frac{2\mu}{\sigma_1 \sigma_2} \tan^{-1}\left(\frac{\sigma_2 V}{\sigma_1}\right)\right\}$, can be approximated by a

constant value, similarly, $\sigma_1^2 + \sigma_2^2 V^2 \approx \sigma_2^2 V^2$. Thus, stationary state membrane potential distribution ($p_s(V)$) represented by Eq. 14 can be asymptotically written as

$$p_s(V) \approx V^{-2\left(1 + \frac{\bar{\beta}_0}{\sigma_2^2}\right)} \quad (15)$$

Since $\frac{\bar{\beta}_0}{\sigma_2^2} > 0$; stationary state membrane potential distribution for LIFSD model has the power law representation as $p_s(V) \propto V^{-\alpha}$; $\alpha > 0$. This power law behavior in stationary state membrane potential distribution occurs due to aggregate effect of current noise and conductance noise terms which are white noise and color noise terms, respectively. Power spectral density for a SDE with white noise term shows delta correlated behavior whereas a SDE having a color noise term exhibits exponentially distributed behavior [3], [16]. LIFSD neuron model has both kinds of noise terms thus depicting the power-law behavior in steady state membrane potential distribution which is its actual strength as compared with other one dimensional threshold based single neuron model.

V. ISI DISTRIBUTION: SIMULATION BASED STUDY

ISI distribution provides a measure to quantify temporal information encoded by a neuron into variable spiking patterns [1], [5], [19], [26]. Investigation of ISI distribution patterns for a neuron model requires study of associated first passage time (FPT) problem i.e. study of time interval distribution when membrane potential of a neuron first time reaches to its threshold value [7], [8], [34]. Mathematically, FPT problems can be defined as [33]

$$T = \inf\{t > 0; V(0) < V_{th}, V(t) > V^{th}\} \quad (16)$$

A general solution for FPT problem associated with a neuron model is not available [1], [8], [13], [16], [11]. Its solution exists only in few special cases, e.g. analytical solution of the FPT problem corresponding to the integrate-and-fire (IF) model results inverse-Gaussian distribution whereas LIF has no explicit expression for corresponding FPT problem [18], [34]. In general, FPT problem is too complex to solve analytically and one has to look towards other investigation techniques. In foregoing analysis, the Monte-Carlo numerical simulation technique is described to investigate ISI distribution pattern for a neuron model. Euler-Maruyama numerical simulation method is applied to obtain approximate solution of FPT problem associated with LIFSD neuron model [17]. For this purpose, the time interval $[0, T]$ is divided into subintervals of equal length $h = (T - 0) / n$ as $[t_0 = 0, t_1]$, $t_1, t_2, t_3, \dots, [t_{n-1}, t_n = T]$. Membrane potential values are computed at discrete times $t_1, t_2, t_3,$

..., t_n by applying following Euler-Maruyama simulation strategy.

$$V(i+1) = V(i) + h(\mu - \beta_0 V(i)) + \sqrt{h}(\sigma_1 dW_1(i) - \sigma_2 dW_2(i)V(i)) \quad (17)$$

Here $dW_1(i)$ and $dW_2(i)$ are mutually independent Wiener processes which individually fluctuates with σ_1 and σ_2 noise intensities, respectively.

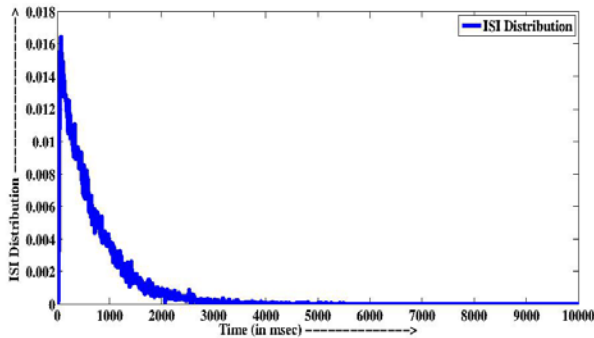


Fig. 7 ISI distribution on linear scale with parameter values $\beta = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.05$

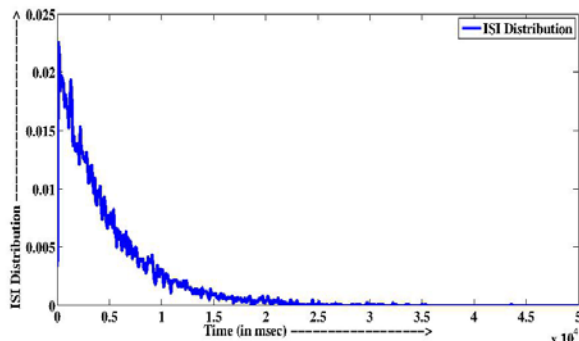


Fig. 8 ISI distribution on linear scale with parameter values $\beta = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.15$

Parameter values used for simulation studies into this article are taken from articles [12], [11], [18], [33], [29]. Articles [12], [11], [18], [33] has suggested a fix sub-threshold value for $\beta_0 = 0.1$, $\mu = 0.3$ and $\sigma_1 = 0.01$ and these values are treated as a constant in all simulation studies. Article [29] suggested a range of conductance noise σ_2 as $[0.05, 0.15]$. The simulation study is carried out for conductance noise term with minimum value (0.05), maximum value (0.15) and its average (0.1). Two ISI distribution patterns for proposed model of our interest are shown in Fig. 7 and Fig. 8. Qualitatively both ISI distributions are uni-modal but qualitatively they have significant differences. These figures are scattered on log-log scale which are shown in Fig. 9 and Fig. 10, respectively. Fig. 7 and Fig. 8 illustrate ISI distribution for minimum and maximum values of σ_2 with other parameter values assumed to be constant. These figures

suggest that conductance noise plays a crucial role in membrane potential evolution in sub-threshold regime. For minimum value of σ_2 LIFSD neuron can take approximately 6000 msec maximum whereas for the maximum value of σ_2 this time interval is extended up to approximately 44000 msec. Here it is interesting to note that the decrease in spiking activity is with increment in σ_2 value. This increase in spiking activity is due to long range dependence of membrane potential on the colored noise term.

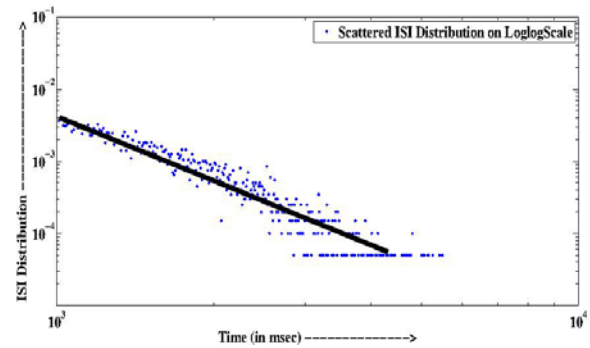


Fig. 9 Scattered ISI distribution on Log-log with parameter values $\beta = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.05$ and a straight line (in black color) with slope -0.87423 is fitted.

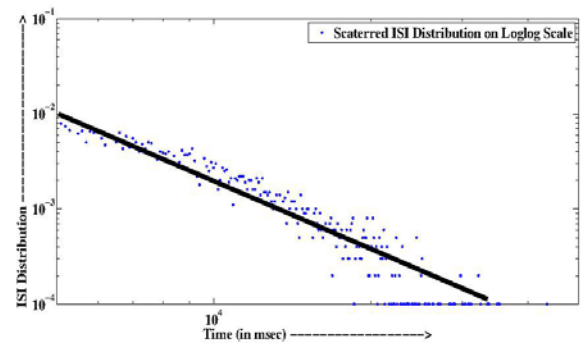


Fig. 10 Scattered ISI distribution on Log-log with parameter values $\beta = 0.1$, $\mu = 0.03$, $\sigma_1 = 0.01$ and $\sigma_2 = 0.15$ and a straight line (in black color) with slope -0.9253 is fitted.

Furthermore, ISI distribution patterns shown in Fig. 9 and Fig. 10 contain a long tail which motivates to investigate occurrence of long-tails in terms of power-law behavior [10], [23]. Fig. 9–Fig. 10 are scattered plot on log-log scale for ISI distributions shown in Fig. 7 and Fig. 8. A straight line (in black color) with negative slope is fitted on the scattered ISI distribution (blue dots) in Fig. 9 and Fig. 10 [10], [23]. Fitting a straight line in scattered ISI distribution patterns suggest about existence of the power-law behavior in its tails. In presence of a small input stimulus, ISI distributions for LIFSD neuron model depict the power law behavior due to aggregate effect of white noise and color noise term. Color noise term is also responsible for long range dependence of membrane potential which enforces a neuron to fire even in the absence of input stimulus. Thus, the LIFSD model is found capable to generate ISI distribution patterns with the power law behavior

in its long tails. A detailed discussion regarding the power-law behavior and assumption behind derivation of LIFSD neuron model is given in the next section.

VI. DISCUSSION

ISI distribution patterns corresponding to evolution of membrane potential in a noisy neuron depict right side skewed behavior with heavy tail and provides an interesting problem to investigate tail behavior specially in terms of power-law [1], [6], [15], [25]. The power-law behavior can exist in entire domain or in a sub-domain. A generalized form of the power-law distribution is given as [23]

$$p(x) = \begin{cases} \alpha_1(x); x \in (-\infty, a) \\ \beta x^{-\alpha}; x \in [a, b] \\ \alpha_2(x); x \in (b, \infty) \end{cases} \quad (18)$$

Here $p(x)$ is probability distribution of an attribute for a random variable x . $\sigma_1(x)$ and $\sigma_2(x)$ are two other functions of x . β is a normalization constant and $\alpha (> 0)$ is a constant exponent. Random variable x has the power-law behavior in sub-domain $[a, b]$ and different behaviors in two other sub-domains defined in Eq. 18. Computation for combination of parameter values (a, b, α) becomes a challenging task in such kind of probability distribution. To this end, maximum likelihood technique provides a way to examine the power-law behavior and to obtain value of α [23]. It maximizes logarithm of probability distribution and can be checked with scattered distribution on Log-log scale [23]. A straight line can be fitted on scattered distributions. Slope of a fitted straight line depicts evolution dynamics [10], [23]. Positive slope corresponds to linear increase in attribute during evolution of random variable x whereas negative slope depicts the linear decay.

Many neuronal attributes depict power-law behavior as discussed in Section I has been replicated in mathematical formulation for ensemble of neurons [18], [33]. It is a prominent question that “can the single neuron model replicates experimental findings for power-law behavior in neuronal attributes [25], [26]?” To this end, the proposed neuron model is capable to replicate the power-law behavior for steady state membrane potential and ISI distribution patterns. The neuronal charge in LIFSD model decays very slowly in leaner order which leads to emergence of power-law behavior in steady state membrane potential distribution. This activity enables LIFSD model to process information even in the absence of external input stimulus during long time duration. Deterministic LIF model is not capable to explain sub-threshold dynamics [1], [9], [13]. In order to investigate sub-threshold dynamics of a neuron, various researchers have expanded ion channel functions in Hodgkin-Huxley model and have suggested a reduced two dimensional model as given below [9].

$$\left. \begin{aligned} C \frac{dV}{dt} &= -gV - g_l w + I_{syn}(t) \\ \tau_l \frac{dw}{dt} &= -w + V \end{aligned} \right\} \quad (19)$$

Here, g is leak conductance, g_l works as a synaptic conductance. Synaptic conductance provides a measure of strength contributed by the recovery variable w in evolution of $V(t)$. Positive value of g_l suggests negative feedback on membrane potential. Such kind of situation occurs during inactivation of sodium ion channel, calcium ion channel and activation of potassium ion channel. Similarly, activation of sodium, calcium ion channels and inactivation of potassium ion channel make g_l a negative entity, which represents the positive feedback state on membrane potential. Membrane decay constant (β) for LIF neuron model is an inverse of membrane time constant ($1/\tau$). β can be also represented in terms of leak conductance (g) and membrane capacitance (C). These equivalent representations of β results expression: $\beta = 1/\tau = g/C$. Assumption for g as a time dependent entity with constant C results β as a time dependent entity. The LIF model can be extended with time dependent assumption of g . The LIFSD model is a similar extension of LIF model where $\beta(t)$ is considered as a stochastic process driven by Gaussian white noise. The LIFSD model becomes integrate-and-fire model for $\beta(t) = 0$. In deterministic LIF model β can't be negative but in extended model $\beta(t)$ is also responsible to play the role of g_l as in Eq. 19, thus its value can be negative. The assumption of time dependent β makes the LIFSD model richer than LIF model in terms of explaining neuronal dynamics.

VII. CONCLUSION

The membrane potential evolution process and spiking activity of a neuron massively depend on other neurons and external environment which make mathematical modeling and prediction of spiking activity a too complex task. The LIFSD model is an attempt to incorporate nearly all entities responsible for membrane potential fluctuation, in term of stochastic membrane decay constant. The novelty of proposed model lies in generation of the power-law behavior for certain neuronal activities. Sharma and Karmeshu [18], [33] have been also computed the power-law behavior for ISI distribution but in case of ensemble of neuron, whereas, LIFSD neuron model is found capable to exhibit the power law for steady state membrane potential distribution and ISI distribution patterns, in case of a single neuron activity. LIFSD neuron model has certain more features in terms of adapting negative values for membrane decay constant as discussed in Section VI, which is not possible in LIF or other threshold based neuron models. Conductance noise term in LIFSD

model create a mechanism responsible for long range dependence of membrane potential so that a LIFSD neuron can emit a spike even in the absence of input stimulus. In this context the proposed model would be helpful to study neuronal dynamics in case of sleep and unconsciousness conditions. Furthermore, Neuronal information processing mostly deals with statistical information processing. In Information theory, it is assumed that variable which contains the higher variance will contain larger information. As coefficient of variation is a ratio of square root of variance and mean of the variable, larger value of mean along with the larger value of variance contains more information comparatively but reduces value of coefficient of variation [21], [22] as shown in Fig. 6. The membrane potential of LIFSD model evolves with $CV_{V(t)}$ less than 1, which is a desirable feature in time-series analysis.

As the power law behavior is a characteristic feature in study of many-body problems, LIFSD neuron model can be regarded as a fair representative of neuronal information processing system into many-body problem framework. Furthermore, application of many-body problem on to LIFSD model can help to get more insight into information processing mechanism of a neuron [10], [16].

REFERENCES

- [1] L. F. Abbott and P. Dayan, "Theoretical Neuroscience: Computational and mathematical modeling of neural systems, Computational Neuroscience", The MIT press, 2001.
- [2] P. Achard and E. D. Schutter, "Complex parameter landscape for a complex neuron model", *PLoS Computational Biology*, 2(7) (2007) 0794-0802.
- [3] V. Balakrishnan, "Elements of Non-equilibrium Statistical Mechanics, Ane Books", India, 2008.
- [4] J. M. Beggs and D. Plenz, "Neuronal avalanches in neocortical circuits", *The Journal of Neuroscience*, 23(35), (2003) 11, 167-11, 177.
- [5] A. Borst and F. E. Theunissen, "Information theory and neural coding", *Nature Neuroscience*, 2(11), (1999) 947-957.
- [6] S. E. Boustani, O. Marre, S. Behuret, P. Baudot, P. Yger, T. Bal, A. Destexhe and Y. Fregnac, "Network-state modulation of power-law frequency-scaling in visual cortical neurons", *PloS Computational Biology*, 5(9) (2009) 1-18.
- [7] A. N. Burkitt, "A review of the integrate-and-fire neuron model: I. homogeneous synaptic input", *Biological Cybernetics*, 95(1) (2006) 1-19.
- [8] A. N. Burkitt, "A review of the integrate-and-fire neuron model: II. inhomogeneous synaptic input and network properties", *Biological Cybernetics*, 95(2) (2006) 97-112. (2006).
- [9] N. Brunel, "Modeling point neurons from Hodgkin-Huxley to integrate-and-fire. Computational modeling methods for neuroscientists, ed. by E. D. Schutter", The MIT Press, (2010) 161-186.
- [10] A. Clauset, C. R. Shalizi and M. E. J. Newman, "Power-law distributions in empirical data", *SIAM Review*, 51(4) (2009) 661-703.
- [11] S. K. Choudhary, K. Singh and V.K. Solanki, "Spiking Activity of a LIF Neuron in Distributed Delay Framework", *International Journal of Interactive Multimedia and Artificial Intelligence*, 3(7), (2016) 70-76.
- [12] S. K. Choudhary, K. Singh and S. K. Bharti, "Variability in spiking pattern of leaky integrate-and-fire neuron due to excitatory and inhibitory potentials", 2nd International Conference on Computing for Sustainable Global Development (INDIACom) (2015) 2025-2030.
- [13] A. Destexhe and M. R. Lilith "Neuronal Noise", *Computational Neuroscience*, Springer (2012).
- [14] A. Destexhe, M. Rudolph and D. Pare, "The high-conductance state of neocortical neurons in vivo", *Nature Reviews: Neuroscience* 4(7) (2013) 739-761.
- [15] A. T. Engel, L. S. Geier, A. V. M. Herz, S. Schreiber and I. Erchova, "Subthreshold membrane-potential resonance shape spike-train patterns in the entorhinal cortex", *Journal of Neurophysiology*, 100(3) (2008) 1576-1589.
- [16] T. D. Frank, "Nonlinear Fokker-Planck Equations: Fundamentals and Applications", *Springer Series in Synergetics*, Springer, 2005.
- [17] D. J. Higham, "An algorithmic introduction to numerical simulation of stochastic differential equations", *SIAM Review*, 43(3) (2001).
- [18] Karmeshu and S. K. Sharma, "Ensemble of LIF neurons with random membrane decay constant: Emergence of power-law behavior in ISI distribution", *IEEE Transactions on Nanobioscience*, 13(3) (2014) 308-314.
- [19] C. Laing and G. J. Lord, "Stochastic Methods in Neuroscience", Oxford University Press, 2010.
- [20] D. Mears, N. F. Sheppard, I. Atwater and E. Rojas, "Magnitude and modulation of pancreatic β -cell gap junction electrical conductance in situ", *The Journal of Membrane Biology*, 146 (1995) 163-176.
- [21] Z. F. Mainen and T. J. Sejnowski, "Reliability of Spike Timing in Neocortical Neurons", *Proceeding of the Joint Symposium on Neural Computation: UCSD and California Institute of Technology*, 1994.
- [22] Z. F. Mainen and T. J. Sejnowski, "Reliability of Spike Timing in Neocortical Neurons", *Science New Series*, 268(5216) (1995) 1503-1506.
- [23] M. L. Mansfield, "Numerical tools for obtaining the power-law representations of heavy-tailed datasets", *The European Physical Journal B*, 89:16 (2016) 1-13.
- [24] K. J. Miller, L. B. Sorensen, J.G. Ojemann and M. D. Nijs, "Powerlaw scaling in the brain surface electric potential", *PLoS Computational Biology*, 5(12) (2009) e1000, 609.
- [25] K. H. Pettersen, H. Linden, T. Tetzlaff and G. T. Einevoll, "Reconciling power laws in microscopic and macroscopic neural recordings", 2013.
- [26] C. Pozzorini, R. Naud, S. Mensi and W. Gerstner, "Temporal whitening by power-law adaptation in neocortical neurons", *Nature Neuroscience*, 16(7) (2013) 942-951.
- [27] B. Prthame and D. Salort, "On a voltage-conductance kinetic system for integrate & fire neural networks", *Kinetic and Related Models*, 6(4) (2013) 841864.
- [28] M. J. F. Richardson and W. Gerstner, "Synaptic shot noise and conductance fluctuations affect the membrane voltage with equal significance", *Neural Computation*, 17 (2005) 923-947.
- [29] A. Rouc, G. L. Camera, H. R. Luscher, W. Senn and S. Fusi, "Neocortical cells respond as integrate-and-fire neurons to in-vivo like input currents", *Journal of Neurophysiology*, 90 (2003) 1598-1615.
- [30] M. Rudolph and A. Destexhe, "An extended analytic expression for the membrane potential distribution of conductance-based synaptic noise", *Neural Computation*, 17 (2005) 2301-2315.
- [31] A. B. Schmerl and M. D. McDonnell, "Channel-noise induced stochastic facilitation in an auditory brain-stream neuron model", *Physical Review E*, 88: 052 (2005) 722112.
- [32] G. Schmid, I. Goychuk and P. Hanggi, "Capacitance fluctuations causing channel noise reduction in stochastic Hodgkin-Huxley systems", *Physical Biology*, 3(4) (2006) 248254.
- [33] S. K. Sharma and Karmeshu, "Power law behavior in if model with random excitatory and inhibitory rates", *IEEE Transactions on Nanobioscience*, 10(3) (2011) 172-176.
- [34] S. K. Sharma and Karmeshu, "Neuronal model with distributed delay: Emergence of unimodal and bimodal ISI distributions", *IEEE Transactions on Nanobioscience*, 12(1) (2013) 1-12.
- [35] T. T. Soong, "Random Differential Equations in Science and Engineering", Academic Press, 1973.
- [36] A. J. Trevelyan and J. Jack, "Detailed passive cable models of layer 2/3 pyramidal cells in rat visual cortex at different temperatures", *Journal of Physiology*, 539 (2002) 632-636.
- [37] T. Verechchaguina, I. M. Sokolov and L. S. Geier, "Interspike interval densities of resonate and fire neurons", *BioSystems*, 89 (2007) 63-68.