Chapter 2

Neuronal model with Exponential Distributed Delay: Analysis and Simulation study

2.1 Introduction

Computational neuroscience is a fast developing area which aims to provide understanding of neuronal information processing (Dayan and Abbott, 2003; Koch, 1999; Koch, 1997; Koch et al., 1995). For gaining insight into the biophysical mechanism, many mathematical neuronal models have been proposed (Gabbiani and Koch, 1998; Gardiner, 1986). One of the widely studied models is non-leaky integrate and fire (NLIF) model which gives Inter-Spike Interval (ISI) distribution when the membrane potential governed by stochastic differential equation (SDE) with constant drift reaches a threshold (Koch, 1999). This problem can be viewed as a first passage time (FPT) problem having solution expressible in terms of an inverse Gaussian distribution. In a more realistic model known as Leaky integrate and fire (LIF) model,
the associated SDE follows Ornstein-Uhlenbeck (OU) process (Ditlevsen and Lansky, 2005). For this model, the FPT is expressible in terms of parabolic cylindrical function (Ditlevsen and Lansky, 2005). In these models, the rate of change of membrane potential depends only on the current value of their potential and thus the dynamics is governed by a Markov process.

The need for introduction of time delay in neuronal model has attracted the attention of several researchers (Masoller et al., 2008; Martinez and Segundo, 1983; Pakdaman et al., 1996; MacDonald, 1978; Holden, 1976; Liao et al., 2004; Tank and Hopfield, 1987). Martinez and Segundo (1983) have experimentally studied the effect of time delay feedback on pacemaker neuron in the stretch receptor of crayfish. They showed that delay incorporated is quite influential and small changes led to different outcomes. Further development of their work has been done by Pakdaman et al. (1996). In their paper they have increased the time delay and hypothesized that as the firing rate increases rapidly there is less neuronal variability and hence effects the overall behavior of a single neuron. Baldi and Atiya (1994) have investigated the effect of delay on the neural dynamics of oscillatory properties in neural networks. The authors have compared their numerical findings with theoretical results as well and have proven that both are almost same. Hodgkin-Huxley model incorporating time delayed feedback with additive noise source has been studied by Masoller et al. (2008) in their paper. MacDonald (1978) emphasizes that on account of
the spatial structure, there is a time delay of the order one second when the chemical constituents cross from one region to another. Further Liao et al. (2004) notes that propagation delays are encountered because of various pathways having axons of variable sizes. Holden (1976) points out that in avian binaural audition a delay of the order 10-100 msec is incurred. Tank and Hopfield (1987) also discuss several neurobiological mechanisms known to generate propagation, synaptic, action potential and response based time delays. Accordingly, it is important to incorporate such a delay in the model. Mar et al. (1999) have suggested that the inclusion of such lags in the form of distributed lag by having some spread around its mean value. These delays yield an integro-differential equation with memory kernel. The motivation of such a formulation is also provided by generalized theory of Brownian motion, which necessitates the inclusion of a delay kernel when the time scale of fluctuations becomes comparable to that of macroscopic time scale (Haken, 1977; Sullivan and Konishi, 1986). It may be pointed that several investigations have been carried out incorporating time delays in Hopfield model (Baldi and Atiya, 1994; Belair, 1993; Gopalsamy and He, 1994). The mathematical model due to Caianiello and Luca (1996) assume neuronal equation governed by distributed memory kernel. DeVries and Principe (1992) also proposed a model with a local positive feedback convolution. Gopalsamy and Leung (1997) extended the framework of Hopfield model with thresholds which are modeled by integro-differential equation (Gopalsamy and Leung, 1997).
We propose to analyze the effect of exponential memory kernel on the stochastic dynamics of membrane potential. Based on the study of a large number of simulated sample paths, one can examine several issues of interest including the FPT distribution when the membrane potential reaches a threshold $V_{th}$ (Koch et al., 1995). A useful measure of distance between pdfs in the form of Jensen-Shannon divergence based on Kullback-Leibler (KL) measure is used to study the deviation of the pdf of proposed model from that of the LIF model. This measure of deviation can usefully be employed to provide a selection criterion between our model in relation to LIF model. The coefficient of variation (CV) as well as the auto-correlation function (ACF) of the spike counts have also been evaluated for the model.

The chapter is organized as follows. Section 2 discusses the proposed model with exponential delay kernel. Analysis of the model is performed in section 3. This section also contains the computation of Autocorrelation function (ACF) of membrane potential and the associated power spectral density (PSD). In both the cases, we find damped oscillatory behavior which is absent in LIF model. The coefficient of variation (CV) with respect to time is also evaluated in this section. Section 4 is concerned with the study of FPT which is based on extensive numerical simulations of the SDEs. It also gives the computation of Jensen-Shannon divergence between the ISI distributions obtained for LIF model and the proposed model. We also study the behavior of CV with respect to varying $\eta$ and show unique changes in CV when
the noise intensity parameter is changed. The last section contains the conclusion.

2.2 The Model with Distributed Delay

The rate of change in membrane potential is assumed to be affected by the past values of the potential, thus accounting for memory effects. When the membrane potential of the neuron at the cell body crosses the threshold $V_{th}$, the neuron produces an action potential or spike for negligible duration and resets its potential to $V_{reset}$ (Koch, 1997). The time elapsed between two such consecutive spikes defines an inter-spike interval (ISI). The spiking time is viewed as FPT when $V(t)$ reaches the threshold $V_{th}$ such that

$$ T = \inf \{ t \geq 0, V(t) > V_{th} | V(0) = V_{0} < V_{th} \} \quad (2.2.1) $$

The evolution of the membrane potential in the proposed model is governed by

$$ \frac{dV}{dt} = -\beta \int_{0}^{t} K(t - \tau) V(\tau) d\tau + \mu + \sigma_{\xi} \xi(t), \quad V(t = 0) = V_{0} \quad (2.2.2) $$

which is a stochastic integro-differential equation (SIDE) with $K(t)$ is the delay kernel. Here $\beta^{-1}$ is the time constant associated with the integrated effect of membrane potential dissipation and $\mu$ is the drift parameter. $\xi(t)$ represents Gaussian white noise with intensity $\sigma_{\xi}$. The correlation structure of $\xi(t)$ is given as

$$ E[\xi(t)] = 0 \quad and \quad E[\xi(t_{1})\xi(t_{2})] = \delta(t_{1} - t_{2}) \quad (2.2.3) $$
2.2.1 Exponential delay kernel

Manwani and Koch (1999) and Koch (1999) pointed out that in voltage dependent channels, a small excitatory signal leads to depolarization followed by hyperpolarization. Erchova et al. (2004) have observed the oscillatory properties of CA1 pyramidal cells in the vicinity of firing threshold. These authors have also suggested a LCR framework to analyze the membrane potential in terms of second order differential equation. It may be underlined that the model (2) yields similar second order stochastic differential equation for the LCR circuit, when the kernel is of exponential type. We investigate the model in detail with exponential delay kernel, i.e.

\[ K(t) = \eta e^{-\eta t}, \quad (2.2.4) \]

where \( \eta \) is the memory time constant associated with the membrane potential dissipation. From Eq. (2.2.2), we get

\[ \frac{dV}{dt} = -\beta \int_{0}^{t} \eta e^{-\eta(t-\tau)} V(\tau) d\tau + \mu + \sigma \xi(t), \quad V(t = 0) = V_0 \quad (2.2.5) \]

By extending the state space, we transform the non-Markovian process to a Markovian process and thus the model can be expressed in terms of coupled SDEs. Writing

\[ X(t) = \int_{0}^{t} \eta e^{-\eta(t-\tau)} V(\tau) d\tau \quad (2.2.6) \]
Eq.(4.2.15) yields the system of coupled SDEs given as

\[
dV(t) = (-\beta X(t) + \mu)dt + \sigma \xi dW_\xi(t), \quad V(t = 0) = V_0
\]
\[
dX(t) = -\eta X(t)dt + \eta V(t)dt, \quad X(t = 0) = 0 \tag{2.2.7}
\]

As noted above, these SDEs correspond to second order differential equations similar to LCR circuit. Eq.(2.2.7) represents a Markovian process and the associated Fokker-Planck equation (FPE) for the joint pdf \(p(V,X,t)\) for the stochastic process \(\{V(t), X(t)\}\), reads as

\[
\frac{\partial p(V,X,t)}{\partial t} = -\frac{\partial}{\partial V} [(-\beta X + \mu)p] + \frac{\partial}{\partial X} [\eta Xp] + \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial V^2}, \tag{2.2.8}
\]

with initial conditions

\[
p(V,X,0) = \delta(V - V_0)\delta(X). \tag{2.2.9}
\]

The associated backward equation yields the FPT of the dynamical evolution of the membrane potential whose analytical solution is difficult to obtain. Accordingly, for examining the effect of distributed delay, one is required to go in for simulation based investigations (Gerstein and Mandlebrot, 1964; La'nsky' and La'nska', 1994; La'nsky', 1984; Ricciardi and Sacerdote, 1979; Stein, 1965; Svirskis and Rinzel, 2000).

\section{2.3 Analysis of the model}

Noting that (4.2.15) is linear and driven by Gaussian white noise process (Gardiner, 1986; Karmeshu, 1997), the solution can be expressed as
\[ V(t) = \chi(t) + \int_0^t G(t - s)F(s)ds, \]  
(2.3.1)

where \( G(t) \) represents the Green’s function, given by

\[ G(t) = \frac{e^{-\eta t^2}}{2\gamma} \left[ \eta \sin\left(\frac{\gamma t}{2}\right) + \gamma \cos\left(\frac{\gamma t}{2}\right) \right], \]  
(2.3.2)

The deterministic part \( \chi(t) \) in Eq. (2.3.1) is

\[ \chi(t) = V_0 G(t) + \frac{\mu}{\beta} \left[ 1 + G(t) - \frac{e^{-\eta t^2}}{2\gamma} \left[ 2\beta \sin\left(\frac{\gamma t}{2}\right) \right] \right], \]  
(2.3.3)

where

\[ \gamma = \sqrt{4\eta\beta - \eta^2} \]  
(2.3.4)

In view of Gaussian noise source, the pdf of \( V(t) \) will be a Gaussian process and thus can be characterized by the first two moments only. Using Eqs. (2.3.1), (2.3.2) and (2.3.3), the first moment of the membrane potential is

\[ E[V(t)] = \chi(t) \]  
(2.3.5)

The mean evolution of the membrane potential for different values of \( \eta \) is shown in Fig 2.1. For lower values of \( \eta \), the mean evolution of the potential depicts damped oscillatory behavior and settles to equilibrium value. For large \( \eta \), the model converges to the LIF model and \( E[V(t)] \) does not show any oscillatory pattern.

In terms of
Figure 2.1: Mean evolution of membrane potential v/s time (\( \beta = 1s^{-1} \), \( V_0 = 0.01V \) and \( \mu = 1Vs^{-1} \))

\[
U(t) = V(t) - E[V(t)]
\]  

(2.3.6)

Eqs. (2.3.1) and (2.3.5) yields

\[
U(t) = \int_0^t G(t-s)F(s)ds
\]  

(2.3.7)

For obtaining the time-dependent variance \( (\sigma_V^2(t)) \) of the membrane potential \( V(t) \), we note
\[ E[U^2(t)] = E[(V(t) - E[V(t)])^2] \]

\[ \sigma_V^2(t) = \int_0^t \int_0^t G(t - s_1) G(t - s_2) E[F(s_1)F(s_2)] ds_1 ds_2 \]

\[ = \int_0^t \int_0^t G(t - s_1) G(t - s_2) \left[ \sigma^2 \delta(s_1 - s_2) \right] ds_1 ds_2 \quad (2.3.8) \]

It is easy to see that

\[ \sigma_V^2(t) = \sigma^2 A(t) \quad (2.3.9) \]

where

\[ A(t) = \int_0^t \int_0^t G(t - s_1) G(t - s_2) \left[ \delta(s_1 - s_2) \right] ds_1 ds_2 \quad (2.3.10) \]

Using Eq. (2.3.2), we evaluate the double integral in Eq. (2.3.10) to yield

\[ A(t) = \left( \frac{\eta^2 + \gamma^2}{8\gamma^2} \right) \left[ \frac{1 - e^{-\eta t}}{\eta} + \frac{e^{-\eta t} \cos(\gamma t + 3\theta) - \cos(3\theta)}{\sqrt{\eta^2 + \gamma^2}} \right] \quad (2.3.11) \]

where

\[ \theta = \cos^{-1} \left( \frac{\eta}{\sqrt{\eta^2 + \gamma^2}} \right) \quad (2.3.12) \]

The description of the membrane potential is governed by Gaussian process having

\[ E[V(t)] = \chi(t) \quad \text{and} \quad \sigma_V^2(t) \]. Accordingly, the knowledge of the first two moments of membrane potential yields the pdf as

\[ p(V, t : V_0) = \frac{1}{\sqrt{2\pi\sigma^2 V(t)}} \exp \left[ -\frac{(V - \chi(t))^2}{2\sigma^2 V(t)} \right], \quad -\infty < V(t) < +\infty \quad (2.3.13) \]
The pdfs of $V(t)$ for two different time epochs are depicted in Fig 2.2.

The membrane potential reaches the equilibrium in the limit of large time i.e. $t \to \infty$ with equilibrium values of the first two moments

$$E[V(\infty)] = \chi(\infty) = \frac{\mu}{\beta}.$$  \hspace{1cm} (2.3.14)

$$\sigma^2_V(\infty) = \sigma^2_\xi A(\infty).$$  \hspace{1cm} (2.3.15)
where

\[ A(\infty) = \left( \frac{\eta^2 + \gamma_0^2}{8\gamma_0^2} \right) \left[ \frac{1}{\eta} - \frac{\cos(3\theta)}{\sqrt{\eta^2 + \gamma_0^2}} \right] \]  

(2.3.16)

The evolution of the first two moments of \( V(t) \) depict different behaviors depending on the parameter \( \gamma = \sqrt{4\eta^2 - \eta_0^2} \). We consider three cases when \( \beta > \eta/4, \beta < \eta/4 \) and \( \beta = \eta/4 \).

**Case 1: \( \beta > \eta/4 \):**

For this case the Green's function is given by Eq. (2.3.2), and the first and second moments are given by Eqs. (2.3.3), (2.3.9) and (2.3.11).

**Case 2: \( \beta < \eta/4 \):**

The Green's function for \( \xi = \sqrt{\eta^2 - 4\eta\beta} \) reads as

\[ G(t) = \frac{e^{-\eta t/2}}{2\xi} \left[ \eta \sinh\left(\frac{\xi t}{2}\right) + \xi \cosh\left(\frac{\xi t}{2}\right) \right]; \]  

(2.3.17)

It is easy to see that the first two moments are

\[ \chi(t) = V_0 G(t) + \frac{\mu}{\beta} \left\{ 1 + G(t) - \frac{e^{-\eta t/2}}{2\xi} \left[ 2\beta \sinh\left(\frac{\xi t}{2}\right) \right] \right\} \]  

(2.3.18)

\[ \sigma_V^2(t) = \frac{e^2}{\xi} \left( \frac{\eta^2 - \xi^2}{-8\xi^2} \right) \left[ 1 + (1 - e^{-\eta t}) \frac{1}{(\eta^2 - \xi^2)} \left\{ -e^{\eta t} (A + B + C) \right\} \right]; \]  

(2.3.19)

where

\[ A = (\xi^3 + 3\eta^2\xi) \sinh(\xi t), \quad B = (\eta^3 + 3\xi^2\eta) \cosh(\xi t), \quad C = \eta^3 + 3\eta^2 \xi \]  

(2.3.20)
Case 3: $\beta = \eta/4$

The Green's function is

$$G(t) = \frac{e^{-\frac{\eta t^2}{2}}}{\sqrt{2\pi}} \left[ 1 + \frac{\eta t}{2} \right]; \quad (2.3.21)$$

and the first two moments of the membrane potential distribution are

$$x(t) = V_0 G(t) + \frac{\mu}{\beta} \left[ 1 + G(t) - \frac{e^{-\frac{\eta t^2}{2} \beta t}}{2} \right], \quad (2.3.22)$$

$$\sigma^2_x(t) = \sigma^2_x \left( \frac{5}{8\eta} \right) \left[ 1 - e^{-\eta t} \left( 1 + \frac{3\eta t}{5} + \frac{\eta^2 t^2}{10} \right) \right] \quad (2.3.23)$$

### 2.3.1 Autocorrelation function-ACF

Moreno-Bote and Parga(2006) have reported that a neuron governed by LIF model in the suprathreshold regime has an ACF with damped oscillations. Rocha et al.(2007)suggest that correlations in the spike-trains have peaks at different firing rates which exhibit damped oscillatory behavior. Bar-Gad et al.(2001) report that the bursty-type behavior of neuronal firing in globus pallidus and cerebellum is depicted with short-term peaks in ACF. A pertinent would be to examine if the computed autocorrelation function for the proposed model is in agreement with the above findings.
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To obtain the auto-correlation, $\phi(\tau)$ of the membrane potential, we write:

$$
\phi(\tau) = \int_0^t \int_0^t G(t - s_1)G(t - s_2)E[F(s_1)F(s_2)] \, ds_1 \, ds_2
$$

$$
= \phi_\xi(\tau)
$$

(2.3.24)

Using Eq.(2.2.3), $\phi(\tau)$ is given by

$$
\phi_\xi(\tau) = \frac{\alpha^2 \xi (\eta^2 + \gamma^2) e^{-\frac{\gamma^2}{2}}}{8 \gamma^2} \left[ \frac{\cos\left(\frac{\gamma \tau}{2}\right)}{\eta} - \frac{\cos\left(\frac{\gamma \tau}{2} + 30\right)}{\sqrt{\eta^2 + \gamma^2}} \right]
$$

(2.3.25)

One can easily see that Eq.(2.3.25) exhibits a decaying oscillatory ACF due to the combined effect of exponentially decaying and sinusoidal and cosine functions. It is important to write that these empirically observed patterns of ACF cannot be generated by LIF model with white noise. In contrast to LIF model, we find the proposed model with exponentially distributed delay has the ability to exhibit empirically observed pattern as depicted in Fig.2.3. This shows the versatility of the model.

### 2.3.2 Power Spectral Density

The power spectral density (psd) is the Fourier transform of Auto Correlation Function (ACF) and gives insight into the frequency domain characteristics of the neuronal signal and provides information about the prominent frequency of the system. The ACF $\phi(\tau)$ as obtained by Karmeshu et al. (2010) is given as:
**Figure 2.3:** Time variation of Autocorrelation Function for model ($\beta = 10 s^{-1}$, $\eta = 1 s^{-1}$ and $\sigma_d = 1$)

\[
\phi(\tau) = \frac{\sigma^2 \xi (\eta^2 + \gamma^2) e^{\alpha \tau}}{8 \gamma^2} \left[ \frac{\cos \left( \frac{\eta \tau}{2} \right)}{\eta} - \frac{\cos \left( \frac{\eta \tau}{2} + 30 \right)}{\sqrt{\eta^2 + \gamma^2}} \right]
\]  

(2.3.26)

The psd $S(\omega)$ is given by

\[
S(\omega) = \int_{-\infty}^{\infty} \phi(\tau)e^{-i\omega \tau} d\tau = 2 \int_{0}^{\infty} \left( \phi_d(\tau) \right) \cos(\omega \tau) d\tau
\]

which simplifies to

\[
S(\omega) = \frac{\sigma^2 \xi (\eta^2 + \gamma^2)}{2 \gamma^2 \left( \eta^2 + \gamma^2 - 4\omega^2 \right)} \left[ 8 \omega^2 \eta \left( 1 - \frac{\cos(3\theta)}{\sqrt{\eta^2 + \gamma^2}} \right) + (\eta^2 + \gamma^2 - 4\omega^2) \frac{\gamma \sin(3\theta)}{\sqrt{\eta^2 + \gamma^2}} \right]
\]  

(2.3.27)

The spectral density may depict unimodal as well as bimodal behavior depending on the choice of parameters. This aspect is depicted in Fig 2.4. It may be noted that
for $\gamma^2 > 0$, the psd is bimodal and makes a transition to unimodal for $\gamma^2 < 0$.

![Power spectral density plot](image)

**Figure 2.4**: Power spectral density for model ($\beta = 1s^{-1}$, $\eta = 1s^{-1}$ and $\sigma_x = 1$)

### 2.3.3 Coefficient of Variation

The explicit expression for the first two moments of the membrane potential yields the time dependent coefficient of variation (CV), which is used as a measure of relative fluctuations. Using Eqs. (2.3.3) and (2.3.9), we find

$$CV(t) = \frac{\sqrt{\sigma^2 \xi \left( \frac{\eta^2 + \gamma^2}{8y^2} \right)}}{V_0 G(t) + \frac{\mu}{\beta} \left( 1 + G(t) - \frac{\varepsilon}{\gamma} \left[ 2\beta \sin \left( \frac{\gamma t}{2} \right) \right] \right)} \left[ 1 - e^{-\eta t} + \frac{e^{\eta t} \cos(\gamma t + 3\delta) - \cos(3\delta)}{\sqrt{\eta^2 + \gamma^2}} \right]$$

(2.3.28)

The temporal evolution of $CV(t)$ with respect to time are depicted in Figs. 2.5, 2.6. It is to be noted that by varying $\beta$, CV varies from 120% to 50% as shown in Fig 2.5. The variation of CV with respect to $\eta$ and $\nu$ is shown in Fig. 2.6.
2.4 Numerical Simulations of FPT: ISI Distribution

The problem of finding analytical results for the first passage time problem is rather difficult. Recently, in an interesting paper, Verechtchaguina et al. (2006) extended Wiener-Rice approach based on level crossing statistics to gain some insight into FPT distribution statistics. However, it is not possible to solve FPT problem in a general setting. Hence we take recourse to simulation study based on Monte Carlo methods. There are several schemes for solving SDEs (For details see (Kloeden and Platen, 1992)). However, there are refinements of the technique due to Milstein and others (Kloeden and Platen, 1992). Further Giraudo et al. (2001) have proposed a more reliable Monte-Carlo method for the evaluation of FPT through method of
Figure 2.6: Variation of CV(t) for different $\eta(\beta = 1s^{-1}, V_0 = 0.01V, \mu = 1Vs^{-1}$ and $\sigma_\xi = 1$)

boundaries. Though several refinements have been proposed in the literature, we for the sake of this illustration consider a simple scheme based on Euler Maruyama technique as all the schemes give same qualitative features.

Using this technique Kloeden and Platen (1992), and discretizing the time interval $[0, T]$ into $n$ equal intervals of size $h = T/n$, we get

$$V((n + 1)h) = V(nh) + (-\beta X(nh) + \mu)h + \sigma_\xi \sqrt{h}\xi_n,$$

$$V(t = 0) = V_0$$

$$X((n + 1)h) = (1 - \eta h)X(nh) + \eta hV(nh),$$

$$X(t = 0) = 0 \quad (2.4.1)$$

where $\xi_1, \xi_2, ..., \xi_n$ are independent and identically distributed standard normal variates. A similar approach to compute FPT has been adopted by Lansky et al (Lansky et al., 2006).

For obtaining the FPT, we allow the sample path of the membrane potential to...
reach the threshold value $V_{th}$ where a spike is generated. Subsequently, the membrane potential is reset to its resting potential value. Repeating the procedure as outlined above, one constructs from $10^4$ sample paths the histogram which gives the ISI frequency curve shown in Fig. 2.7.

![Frequency histogram obtained from simulations for model driven by noise ($\beta = 1s^{-1}$, $\eta = 1s^{-1}$, $V_0 = 0.01V$, $\mu = 1Vs^{-1}$, $V_{th} = 1V$ and $\sigma_\xi = 1$)](image)

**Figure 2.7:** Frequency histogram obtained from simulations for model driven by noise ($\beta = 1s^{-1}$, $\eta = 1s^{-1}$, $V_0 = 0.01V$, $\mu = 1Vs^{-1}$, $V_{th} = 1V$ and $\sigma_\xi = 1$)

### 2.4.1 Numerical simulation of Coefficient of variation

The coefficient of variation (CV) is also used as a measure of variability of spiking neuronal activity. It is given as

$$CV(t) = \frac{\sqrt{\text{var}(\text{ISI})}}{\text{mean}(\text{ISI})} \quad (2.4.2)$$
The bursty-type behavior of the proposed model is confirmed from the high values of CV obtained when there is switching between bursting and nonbursting. (Koch, 1999) This transition thus depends on the time scale of the memory kernel time constant $\eta$. In Fig (2.8 and 2.9), we observe that CV as a function of $\eta$ depicts behavior pattern which changes as one changes the parameter $\sigma_\xi$. In a recent study (Moreno-Bote and Parga, 2006; Rocha et al., 2007; Bar-Gad et al., 2001) it has been reported that the autocorrelation structure of the spike count exhibits damped oscillatory behavior. Based on our simulation experiments, as shown in Fig 2.10, we find that the pattern is in agreement with the empirical findings (Moreno-Bote and Parga, 2006; Rocha et al., 2007; Bar-Gad et al., 2001).

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{cv_vs_eta.png}
\caption{Variation of CV v/s $\eta$ for different value of $\sigma(\beta = 1s^{-1}, V_0 = 0.01V, V_{th} = 1V, \mu = 1Vs^{-1}$ and $\sigma_\xi = 1$)}
\end{figure}
2.4.2 Study of JS Divergence for ISI distribution: LIF and the Proposed Model

The KL measure is the distance between two probability distributions \( P = \{p_1, p_2, \ldots, p_n\} \) and \( Q = \{q_1, q_2, \ldots, q_n\} \) where \( Q \) is the reference distribution. KL measure is asymmetric and is given by

\[
D(P\|Q) = \sum_{i=1}^{n} p_i \log \frac{p_i}{q_i}
\]  

(2.4.3)

Noting \( D(P\|Q) \neq D(Q\|P) \), another measure viz. Jensen-Shannon divergence which is symmetric. It is defined by

\[
JS(P, Q) = \frac{D(P\|Q) + D(Q\|P)}{2}
\]  

(2.4.4)

Kostal and Lansky Kostal and La’nsky’(2006) have proposed KL measure based approach to compare two ISI distributions. To this end, we use it to quantify the similarity between the proposed and the LIF model with white noise by studying the effect of \( \eta \) on the Jensen-Shannon divergence (Karmeshu, 2003). As \( \eta \) becomes
Figure 2.10: Autocorrelation function of spike counts ($\beta = 4s^{-1}$, $\eta = 0.5s^{-1}$, $V_0 = 0.01V$, $V_{th} = 0.7V$, $\mu = 1Vs^{-1}$ and $\sigma_z = 0.2$)

larger, the exponential kernel converges to Dirac-delta function and the proposed model essentially reduces to LIF model driven by white noise (Kostal and La'nsky', 2006; Tuckwell et al., 1988). This is reflected as Jensen-Shannon divergence decays to zero with increasing $\eta$ as depicted in Fig. 2.11.

2.5 Conclusion

Most of the studies pertaining to spiking neurons are based on the study of LIF model and its variants. The LIF model has been successfully employed to study various aspects of neuronal dynamics. However, there are some empirical findings corresponding to damped oscillatory behavior of ACF, bursty-type behavior observed in CV, existence of unimodal and bimodal peaks in psd etc., which cannot be explained within
LIF framework. The proposed model is a generalized one which incorporates the distributed delay kernel accounting for memory effects. LIF model can be recovered as a special case when memory kernel is represented by delta function. The advantage of the proposed model is that it has the potential to explain the empirical findings observed in respect to ACF, CV and psd. Further, the proposed model has the ability to generate different models depending upon the choice of delay kernel.

Figure 2.11: Variation of distance between proposed and LIF models ($\beta = 1s^{-1}$, $V_0 = 0.01V$, $V_{th} = 1V$, $\mu = 1Vs^{-1}$ and $\sigma_\xi = 0.2$)
Figure 2.12: Convergence of the proposed model and LIF model for large $\eta$ ($\beta = 0.55s^{-1}$, $\eta = 90s^{-1}$, $\tau^{-1} = 0.55s^{-1}$, $V_0 = 0.01V$, $\mu = 0.5Vs^{-1}$, $V_{th} = 0.7V$ and $\sigma_c = 0.4$)