SPIKING NEURONS AND INFORMATION TRANSMISSION

A Dissertation submitted to the
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of

MASTER OF TECHNOLOGY
IN
COMPUTER SCIENCE AND TECHNOLOGY

BY
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This is to certify that the dissertation entitled "**SPIKING NEURONS AND INFORMATION TRANSMISSION**" being submitted by Mr. **Vineet Kumar Dubey** to the School of Computer and Systems Sciences, **Jawaharlal Nehru University**, New Delhi, in partial fulfillment of the requirements for the award of the degree of **Master of Technology** in **Computer Science and Technology**, is a record of bonafide work carried out by him under the supervision of Prof. Karmeshu.

This work has not been submitted in part or full to any university or institution for the award of any other degree or diploma.

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DECLARATION

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Dedicated to

My Parents

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ABSTRACT

The most important and complex organ in any living being is brain. The complex behavior of brain has always overwhelmed researchers, psychologists, and scientists. They are trying to draft its behavior right from its evolution but due to complexity lying in its behavior led to little success till today in this area. On the similar lines, we have put our concentration on the most basic unit of the brain. Spikes are generated whenever the potential activated due to stimulus of neuron reaches threshold value. Conceptual application of Information theory, Monte-Carlo technique to the inter spike interval distribution led to some exciting facts of brain and its behavioral aspects.

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List of Abbreviations

IF	Integrate and Fire
ODE	Ordinary Differential Equation
H-H	Hodgkin-Huxley
OUP	Ornstein-Uhlenbeck Process
FPT	First Passage Time
PDF	Probability Density Function
ISI	Inter Spike Interval
LIF	Leaky Integrate and Fire
IF-FHN	Integrate and Fire Fitzhung-Nagumo
SDE	Stochastic Differential Equation
WN	White Noise
CV	Coefficient of Variation

Chapter1

Introduction

Understanding of brain and nervous system is a fast emerging interdisciplinary area. How do electrical and chemical signals in brain represent and process information is the ultimate goal of computational neuroscience. Sejnowski [21] in the foreword of computational neuroscience notes “Computational neuroscience is an approach to understanding the information content of neural signals by modeling the nervous system at many different structural scales, including the biophysical, the circuit and the system levels. Computer simulations of neurons and neural networks are complementary to traditional techniques in neuroscience”.

Computational models are being increasingly employed to provide insight into the neuronal mechanisms which informs the basis for information processing to the brain. Becker [1] discusses the three levels

1. Sensory coding and perpetual processing
2. High level memory systems
3. Representations that guide actions.

In the context of information processing by brain, one of the great success in the initial stages of information processing is its realization that the brain can be modeled as a communication channel and thus the information theoretic framework as developed by C. E. Shannon [18] is applicable. This realization led to application of information theory in neuroscience.

The main goal of computational neuroscience is to develop computational models that may reveal the function of tissue. Sejnowski, Koch and Churchland [20] emphasize the need for minimal models which can reproduce the basic properties. This in turn will throw light on the computational constraints which governs the design of nervous system. The study of nervous system can be undertaken at several levels ranging from a single neuron to several neurons which group together. The number of neurons in human brain is 10^{12} and the number of synapse is 10^{15} which suggest that each neuron on an average has 10^{3} synapses. For the purpose of illustration we show in figure (1.1), the three parts dendrite tree, soma and axon which comprise a neuron.

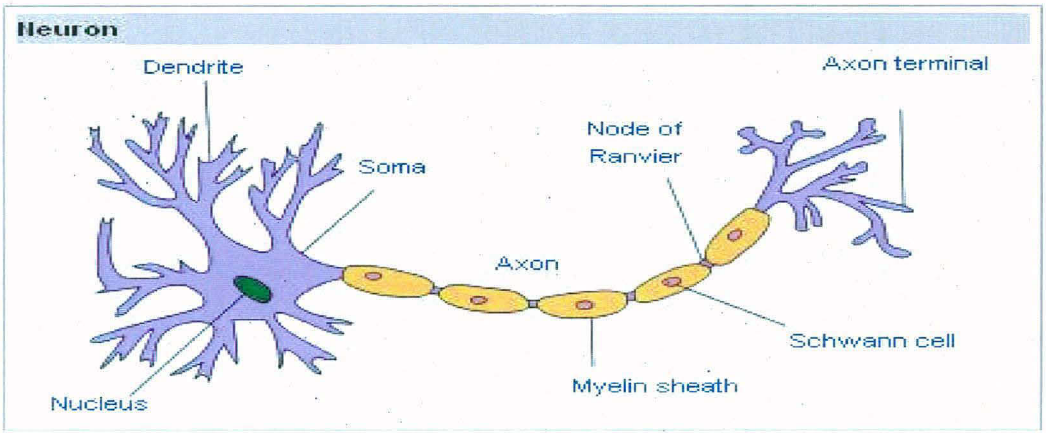

Figure 1.1:Structure of Neuron (Source: http://en.wikipedia.org/wiki/Neuron)

The field of computational neuroscience can be regarded as an interdisciplinary field which requires interface between neuroscience, computational techniques and stochastic methods. Computational neuroscience requires detailed understanding of stochastic dynamics at molecular level, cellular level etc.[22]. Accordingly the fundamental description of a single neuron can be obtained in terms of ion channel. There are several models which accounts for such a description. The notable are well known Hodgkin-Huxley model which is governed by four coupled nonlinear differential equations [15,21]. These equations depict periodic behavior which mimics the spiking neuron pattern. Though this model has provided considerable insight into neuronal behavior, it is difficult to visualize its behavior in four dimensional phase space. Other models viz. Fitz-Hugh Nagumo, Morris-Lecar are based on two variable ODEs and require two dimensional phase space for their description[2]. They also show bifurcation and exhibit transitions from quiescent to periodic behavior like Hodgkin-Huxley model. In view of presence of non linearity and stochasticity, these models are intractable and therefore another class of models, described by single stochastic variable are in vogue and they are referred to as IF model which exhibits discontinuous behavior because of existence of threshold value of the membrane potential As membrane potential reaches the threshold value a spike is generated [14]. Thereafter the potential is again reset at the initial value and the membrane potential evolves till it again reaches the threshold value resulting in generation of another spike. This process continues resulting in generation of inter-spike interval statistics. In contrast to other models, IF model are piece-wise linear having discontinuous flow. The stochastic differential equation in these cases is modeled as Ornstein-Uhlenbeck process (OUP) and the associated ISI (inter spike interval) distribution is obtained as first passage time distribution. Recently Deco and Schurmann [3,4,5] have employed IF model based on OUP driven by Poisson input to gain insight into information processing mechanism. To this end they employed information theoretic framework [4,5] using the concept of entropy and mutual information. In the following section, we briefly outline the information theoretic framework.

The understanding of biophysical mechanism responsible for generating neuronal activity is fairly well understood [2], these authors points out that the detailed descriptions involving several neurons may lead to a large number of coupled differential equations governing, interconnected networks. It is found that mathematical models for single neuron based on electric circuit theory are useful for providing insight into the single neuronal dynamics.

Entropy: Discrete and Continous Random Variables

The foundation of information theory was laid down by Claude Shannon in 1948 [18] in the context of communication theory. Shannon was interested in two issues pertaining to

- What is the ultimate achievable data compression?
- What is the ultimate achievable rate of transmission of Information?

These questions led to the development of information theory through the classical paper "A Mathematical Theory of Communication" by Shannon [18].

For the two above mentioned questions, Shannon introduced entropy, mutual information and channel capacity etc. The contribution of Shannon provided a measure of uncertainty in the form of entropy. It is important to note that information theory deals with the surprisal element not the semantic aspect.

Shannon considered the random variable X associated with random experiment which assumes values say$\{x_1, x_2, x_{3,\ldots}, x_n\}$ with corresponding probability distribution

$$P = \{p_1, p_2, p_3, \ldots, p_n\}$$

We have,

$$P_k = P(X = x_k), \qquad k=1, 2, 3, \ldots, n$$

Such that,

$$\sum_k p_k = 1, \quad 0 \le p_k \le 1. \tag{1.1}$$

Shannon introduced a set of axioms and proved that the information associated with the event($X=x_k$) is $-\log p_k$. We have

$$I(x_k) = \log\frac{1}{p_k} = -\log p_k \tag{1.2}$$

It is easy to see that for a 'certain' outcome, there is no surprise and

$I(X_k)=0$ for $p_k=1$.

Entropy

The amount of average information is given by

$$H(X) = H(p_1, p_2, p_3 \ldots. p_n)$$

$$= -\sum_{k=1}^{n} p_k \log p_k \tag{1.3}$$

Shannon called this expression as entropy as it is similar to entropy being used in statistical mechanism in physics [9].

We take $0\log0=0$. This implies that entropy remain unchanged if we introduce some impossible events in the scheme.

It would be useful to know that the maximum entropy in (1.3) is equal to log n, where $p_1=p_2=p_3 \ldots .=p_n=\frac{1}{n}$.

This can be easily seen as follows.

$$\text{Max } H(X) = -\sum_{k=1}^{n} p_k \log p_k \qquad (1.4)$$

Such that,

$$\sum p_k = 1 \qquad (1.5)$$

We construct Lagrangian

$$L(p_1, \ldots\ldots p_n) = -\sum p_k \log p_k - (\lambda - 1)(\sum p_k - 1) \qquad (1.6)$$

where λ is Lagrange's undetermined multiplier.

Differentiating (4) w.r.t. p_k we have,

$$\frac{\partial L}{\partial p_k} = -\log p_k - 1 - (\lambda - 1) = 0$$

$$or \quad p_k = e^{-\lambda}$$

Noting that,

$$\Sigma\, p_k = 1, \text{ we get } p_1 = p_2 = \ldots p_n = \frac{1}{\text{n}}$$

Using this, we get

$$Max\ H(X) = \log n$$

This means that when all outcomes are equally, we get the maximum entropy.

Differential entropy of continuous Random variable

It is important to note that the entropy for a continuous random variable with pdf f(x) does not take the form $-\int f(x)\ln f(x)dx$ analogous to discrete random variable. To understand the reason for this we closely refer to the both by [8]. Treating the continuous random variable X as the limiting form of discrete random variable, we write

$$p_k \approx f(x_k)\Delta x$$

Hence

$$H(X) = -\lim_{\Delta x \to \infty} \Sigma \log f(x)\Delta x$$
$$= \int f(x)\ln f(x)dx - \lim_{\Delta x \to \infty} (\log \Delta x)\int f(x)dx$$

It may be noted that in the limit $\Delta x \to 0$ the last term on r.h.s. tends to infinity which makes the entropy of continuous random variable infinitely large [8].

A pertinent question is:"How does one reconcile this discrepancy?" One can get rid of this by taking difference between entropies of two probability distribution viz. $f_X(x)$ *and* $f_Y(y)$ [10] of random variables X and Y.

We find

$$\lim_{n \to \infty}[H(X_n) - H(Y_n)] = h(X) - h(Y) \quad (1.7)$$

Where the differential entropies h(X) and h(Y) are defined as

$$h(X) = -\int f_X(x)\log f_X(x)dx \quad (1.8)$$

$$h(Y) = -\int f_Y(y)\log f_Y(y)dy \quad (1.9)$$

These differential entropies (8), (9) have forms analogous to the entropies of discrete random variables. Using the concept of differential entropies, Kligr and Folger [10] defined Boltzmann information Transmission.

Mutual Information

Consider discrete random variable X and Y which are join distribution with probability distribution

$$p_{ij} = p(x_i, y_j) = p(X = x_i, Y = y_j), \quad i = 1, 2, \ldots, n \quad \text{j}=1, 2, \ldots, m \tag{1.10}$$

The marginal distribution for random variables X and Y are given as

$$p(x_i) = p_i = p(X = x_i) = \sum_j p_{ij} \tag{1.11}$$

Similarly,

$$q(y_j) = q_j = \sum_j p_{ij}$$

If X and Y are independently distributed, then

$$p_{ij} = p_i p_j$$

The joint entropy of random variable X and Y is defined as

$$H(X,Y) = -\sum_i \sum_j p(x_i, y_j) \log p(x_i, y_j) \tag{1.12}$$

For independent random variables

$$H(X,Y) = H(X) + H(Y)$$

Conditional Entropy

If one considers X as an input and Y as output of stochastic system, then H (X|Y) represents the uncertainty about X after the output Y is observed.

In terms of conditional probability distribution, we define

$$H(X|Y = y_j) = -\sum_i \sum_j p(x_i|y_j) \log p(x_i|y_j) \tag{1.13}$$

Summering over all y_j with corresponding, probability q (y_j) of realization, we get

$$\begin{aligned} H(X|Y) &= -\sum_j q(y_j) H(X|y_j) \\ &= -\sum_j \sum_i q(y_j) p(x_i|y_j) \log p(x_i|y_j) \\ &= -\sum_i \sum_j p(x_i, y_j) \log p(x_i|y_j) \end{aligned}$$

In a similar manner, we can define

$$H(Y|X) = -\sum_i \sum_j p(x_i|y_j) \log q(y_j|x_i) \tag{1.14}$$

Shannon defined a measure of dependence between X and y as mutual information given as

$$\begin{aligned} I(X,Y) &= H(X) - H(X/Y) \\ &= \sum_i \sum_j p_{ij} \log \frac{p_{ij}}{p_i . q_j} \end{aligned} \tag{1.15}$$

It can be seen that

$$I(X;Y) \geq 0 \;\; and \;\; I(X;Y) = I(Y;X)$$

The mutual information I(X : Y) can be rewritten as

$$I(X,Y) = H(X) + H(Y) - H(X/Y) \tag{1.16}$$

Shannon used the concept of mutual information to define the notion of channel capacity as [9, 18].

$$C = \arg_{p(x)} \;\; \max I(X;Y)$$

Continuously random variable jointly distributed

For correlated random variables X and Y with joint pdf f(x,y),the mutual information is defined in terms of differential entropies as [8].

$$I(X;Y) = \iint f_{X,Y}(x,y) \log\left(\frac{f_{X,Y}(x,y)}{f_X(x) f_Y(y)}\right) \quad (1.17)$$

Following Kligr and Folger [10], (1.17) is an appropriate form for information transmission given by

$$-\int f_X(x) \log f_X(x) dx - \int f_Y(y) \log f_Y(y) dy + \iint f(x,y) \log f(x,y) dx dy \quad (1.18)$$

This is also the expression form for mutual information similar to (1.17).

Electrical Model of Neuron

Koch [14] in his classic book on "Biophysics of Computation" observed that Neuroscientist have discovered the principles in the design and operation of nervous system. In other words the brain receives sensory signals which get encoded into various physical /biophysical variables like membrane potential, neural firing rate etc.

The membrane potential is a biophysical variable in the nervous system which fulfills certain desired requirements for information processing system [22].

Electrical Properties of Nerve Cell

We give below the basic requirement to be fulfilled by a physical variable in the information processing context. Koch [11, 13] notes

1. It must operate at high speeds.
2. It must have a rich repertoire of computational primitives with the ability to implement a variety of linear and nonlinear, high gain, operations.
3. It must interface with the physical world in sense of being able to represent sensory input pattern accurately and translated the result of the computations into action that is motor output.

Koch argues as to why membrane potential fulfills the required features. Membrane potential performs neuronal operations at a rapid rate in the brain.

It is well established that the basic neuronal model consist of a resistance and capacitance i.e. RC circuit gives in figure (1.2).

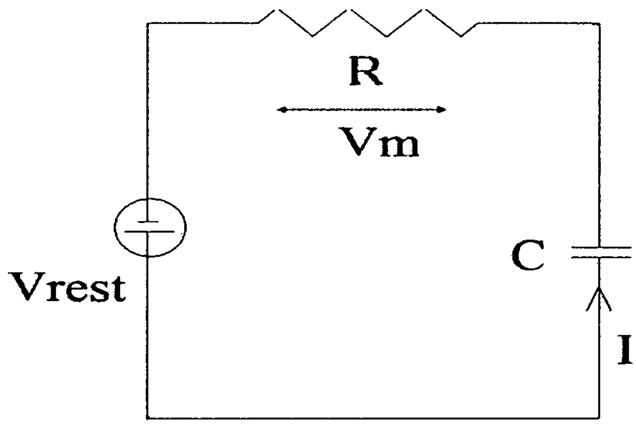

Figure 1.2: Neuronal circuit representation

$$Q = C_m V_m$$

$$Ic = \frac{dQ}{dt} = C\,\frac{dVm}{dt}$$

Applying Kirchhoff's law, we get

$$\frac{dV_m}{dt} = -\frac{V_m}{RC} + \frac{V_{rest}}{RC} + \frac{I_c}{C} \tag{1.19}$$

where Q,R,C,V_m and I_c represents, Charge collected on membrane, membrane resistance, membrane capacitance, membrane potential and current flow due to ions respectively.

Chapter2

Dynamic Models of Neural System

The development of mathematical models of neuronal system is vastly limited due to the present state of the available knowledge about the brain. Rabinovich et.al. [16] argue that the level of mathematical analysis will not be at the same level of sophistication as for other physical and electronic systems. This is due to the fact that our understanding of the brain is generally at the phenomenon level. The best one can do is to construct phenomenon models. It is known that input through synapses on dendrite tree are received which may or may not result in generation of spike. The underlying mechanisms are nonlinear. Thus nonlinear modeling approaches are useful in the study of nervous systems, for understanding the dynamics of neurons, it is better to develop phenomenological models as neurons are fairly complex entities [22]..

2.1 Hodgkin-Huxley Model

The fundamental contribution in the model building exercise has been due to Hodgkin and Huxley (1952). Their model referred to as Hodgkin and Huxley model is formulated as a system of four coupled ODEs and can be regarded as principal tool for computational neuroscience [16].

In terms of membrane potential V and variables m, h and n representing activation and inactivation of the ionic conductance's [16] present Hodgkin and Huxley model as

$$C_m \frac{dV}{dt} = G_{leak}(V_{leak} - V) + G_{Na} m^3 h (V_{Na} - V) + G_K n^4 (V_K - V) + I_{app}$$

$$\tau_m \frac{dm}{dt} = m_\infty(V) - m;$$

$$\tau_h \frac{dh}{dt} = h_\infty(V) - h;$$

$$\tau_n \frac{d.m}{dt} = n_\infty(V) - n;$$

where m_∞, h_∞, n_∞ represent the steady state values of the conductance variables. Here I(t) denotes the external current. Further Robinovich et.al. [16] pointout that inclusion of other ionic currents make model more realistic. Several variants of Hodgkin and Huxley model have been proposed in the literature. Hodgkin Huxley model describes the electrical potential through potassium and sodium activation variables, n(t) and m(t) respectively, and sodium inactivation variable h(t).

2.2 Morris-Lecar Model

Morris-Lecar (1981) proposed a model with two variables such that it is capable of potential generation .The model can be described as

$$\frac{dv}{dt} = g_L[(v_L - v(t)] + n(t) g_n [v_n - v(t)] + g_m m_\infty \left(\frac{dv}{dt}\right)[v_m - v(t)] + I$$

$$\frac{dn}{dt} = \lambda(v(t))[n_\infty(v(t)) - n(t)]$$

$$m_\infty(v) = \frac{1}{2}\left(1 + \tanh \frac{v - v_m}{v_m^0}\right)$$

$$n_\infty(v) = \frac{1}{2}\left(1 + \tanh \frac{v - v_n}{v_n^0}\right)$$

$$\lambda(v) = \Phi_n \cosh \frac{v - v_n}{2 v_n^0}$$

where $v(t)$ is the membrane potential, $n(t)$ describes the recovery activity of a calcium Current and I is an external current.

2.3 <u>Fitzhugh Nagumo Model</u>

Rabinovich et.al. [16] has discussed several neural models. We describe briefly Fitzhugh-Nagumo model which exhibits oscillating spiking neural dynamics. The differential equations are

$$\frac{dx}{dt} = \mu x - cx^3 - y + I$$
$$\frac{dy}{dt} = x + by - a$$

where x(t) is the membrane potential, and y(t)describes the dynamics of fast currents, I is an external current. The parameter values a, b, and c are constants and can be adjusted to allow spiking neuron. So for we have discussed deterministic models. How do we incorporate noise in deterministic selling? We briefly discuss a commonly adopted approach for associating SDE with deterministic model.

2.4 <u>Stochastic Differential equation: Study of noise effects</u>

A pertinent question is related to study of noise in dynamical system is its inclusion in order to fix our ideas let us consider a deterministic system given by the differential equation

$$\frac{dX(t)}{dt} = a(X,t)$$

In presence of noise, this differential equation gets modifies to

$$\frac{dX(t)}{dt} = a(X,t) + noise$$

How does one incorporate noise? It is customary to identify 'noise' as white noise ξ(t) which can be interpreted as a formal derivative Wiener process {W(t)}.Physically, it means that the time scale of fluctuations is much smaller in relation to macroscopic time scale.

Mathematically we can write

$$dW(t)=W(t+dt)-W(t)= \xi(t)dt$$

[6].

The Wiener process is a solution of the Fokker plank equation

$$\frac{\partial}{\partial t} p(w,t/w_0,t_0) = -\frac{1}{2}\frac{\partial^2}{\partial w^2} p(w,t/w_0,t_0)$$

with initial condition

$$\lim_{t \to t_0} p(w,t/w_0,t_0) = \delta(w-w_0)$$

The solution of Fokker plank equation is given as

$$p(w,t/w_0,t_0) = \frac{1}{\sqrt{2\pi(t-t_0)}} \exp\left[-\frac{(w-w_0)^2}{2(t-t_0)}\right]$$

Wiener process represents a Gaussian Such that

$$E[W(t)]=W_0 \text{ and } E[(W(t))-W_0]=(t-t_0)$$

Without loss of generality, we take $t_0=0$ and $w_0=0$.

Gardiner [6] gives an intuitive interpretation by pointing out that the variance of wiener process tends to infinity as $t \to \infty$. This means the sample paths are highly variable. The sample paths of wiener process are continuous but not differentiable.

The Wiener process satisfies the following [19].

1. $\{W(t), 0 \le t < \infty\}$ has stationary independent increases.

2. W (t) for t>0 has Gaussian distribution.

Noting that $Var[W(t)] = t$,

One can express

$$W(t) = X\sqrt{t}$$

where $X \sim N(0,1)$.

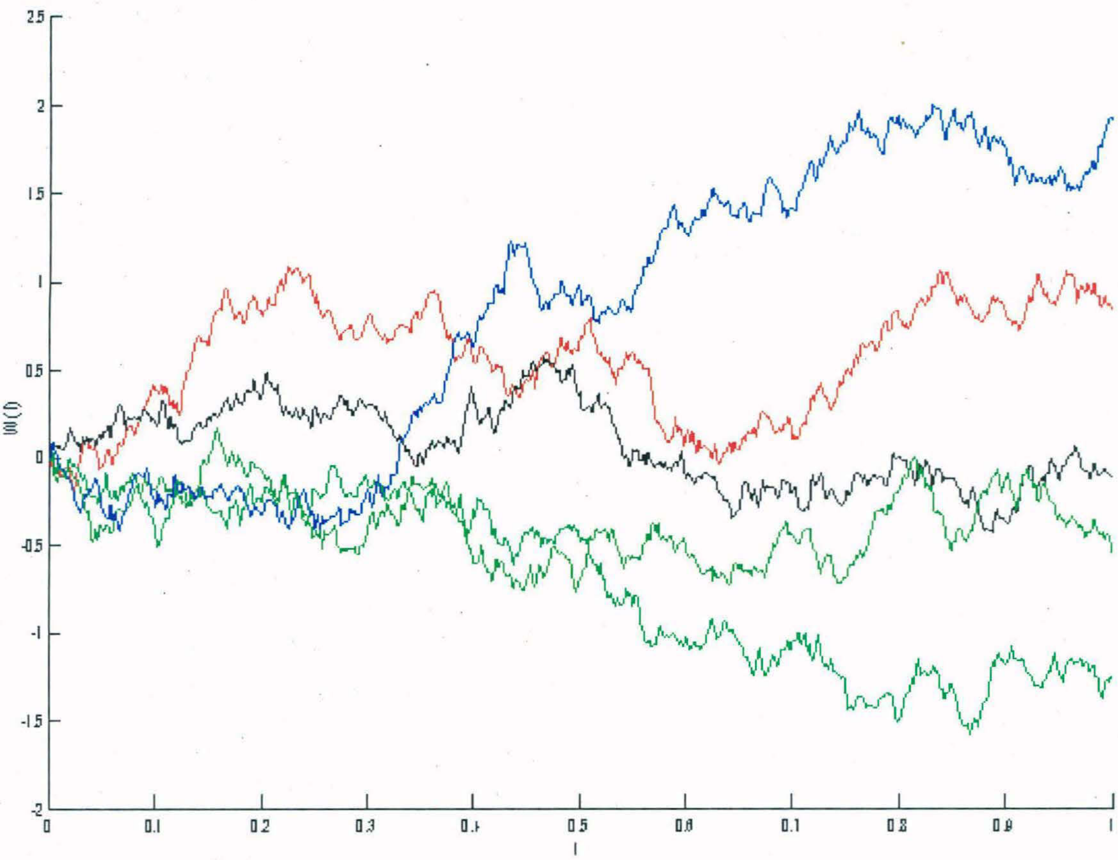

Figure 2.1: Wiener process

2.5 Neuronal models with Stochastic Noise in H-H Model

Recently a number of papers have considered the effect on noise on the dynamics of Hodgkin-Huxley model. The electrophysiological activity has been formed to exhibit stochastic characteristics. Tuckwell reported the stochastic effects on Hodgkin-Huxley model neurons in the vicinity of bifurcation to periodic firing, noise will small magnitude can silence a neuron Tuckwell and Jost() point out the emergence of a new phenomenon called as inverse stochastic resonance.

Tuckwell and Jost [23] formulated Hodgkin-Huxley equations with additive current noise having the form

$$dX_1 = f_1(X)dt + \frac{\sigma}{C}dW$$

$$dX_2 = f_2(X)dt = \left[\alpha_n(X_1)(1-X_2) - \beta_n(X_1)X_2\right]dt$$

$$dX_3 = f_3(X)dt = \left[\alpha_m(X_1)(1-X_3) - \beta_m(X_1)X_3\right]dt$$

$$dX_4 = f_4(X)dt = \left[\alpha_h(X_1)(1-X_4) - \beta_h(X_1)X_4\right]dt$$

where, $$f_1(X) = \frac{(\mu + \bar{g}_k X_2^4(V_K - X_1) + \bar{g}_{Na} X_3^4 X_4(V_{Na} - X_1) + g_L(V_L - X_1))dt)}{C}$$

These authors define $X_1(t)=V(t_1),\ldots, n$.

These notation used by Tuckwell and Jost [23]is slightly different. The term $\frac{\sigma}{C}dW(t)$ represent stochastic noise which renders the variables $X_i(t), i=1,\ldots.4$, stochastic. Here dW(t) represents Wiener increment process which will be discussed in next chapter.

The effect of including noise in Hodgkin-Huxley model enhances the complexity in the sense that the first order and second order moment equations results in fourteen coupled nonlinear differential equations .in order to have a feel of the complexity of the problem, we reproduce the equation as obtained by Tuckwell and Jost [23].

Mean Evolution Equation

Denoting by $m_i(t)=E[X_i(t)], i=1,2,3,4$, we have

$$\frac{dm_1}{dt} = \frac{1}{c}[\mu + \bar{g}_k m_2^4 (V_k - m_1) + \bar{g}_{Na} m_3^3 m_4 (V_{Na} - m_1) + g_L (V_L - m_1)$$

$$- 4\bar{g}_K m_2^3 C_{12} - 3\bar{g}_{Na} m_3^2 m_4 C_{13} - \bar{g}_{Na} m_3^3 C_{14} + 6\bar{g}_K m_2^2 (V_K - m_1) C_{22}$$

$$+ 3\bar{g}_{Na} m_3 m_4 (V_{Na} - m_1) C_{33} + 3\bar{g}_{Na} m_3^2 (V_{Na} - m_1) C_{34}]$$

$$\frac{dm_2}{dt} = \alpha_n(m_1)(1-m_2) - \beta_n(m_1)m_2 + \frac{1}{2}(\alpha_n''(m_1)(1-m_2) - \beta_n''(m_1)m_2)C_{11} - (\alpha_n'(m_1) + \beta_n'(m_1))C_{12}$$

$$\frac{dm_3}{dt} = \alpha_m(m_1)(1-m_3) - \beta_m(m_1)m_3 + \frac{1}{2}(\alpha_n''(m_1)(1-m_3) - \beta_n''(m_1)m_3)C_{11} - (\alpha_m'(m_1) + \beta_n'(m_1))C_{13}$$

$$\frac{dm_4}{dt} = \alpha_h(m_1)(1-m_4) - \beta_h(m_1)m_4 + \frac{1}{2}(\alpha_h''(m_1)(1-m_4) - \beta_h''(m_1)m_4)C_{11} - (\alpha_h'(m_1) + \beta_h'(m_1))C_{14}$$

Variance Evolution Equations

Denoting by $C_{ij}(t)=E[X_i(t)\ X_j(t)]$, we have

$$\frac{dC_{ii}}{dt} = 2\sum_{i=1}^{4}\left\{\frac{\partial f_i}{\partial x_l}\right\}_m C_{ii} + \sum_{k=1}^{4}\left\{g_{ik}^2\right\}_m$$

$$\frac{dC_{11}}{dt} = -\frac{2}{C}\left[\bar{g}_k\, m_2^4 + \bar{g}_{Na}\, m_3^3 m_4 + \bar{g}_L\right] C_{11} + \frac{8}{C}\bar{g}_k\, m_2^3 (V_k - m_1) C_{12}$$

$$+\frac{6}{C}\bar{g}_{Na}\, m_3^2 m_4 (V_{Na} - m_1) C_{13} + \frac{2}{C}\bar{g}_{Na}\, m_3^3 (V_{Na} - m_1) C_{14} + \left(\frac{\sigma}{C}\right)^2$$

$$\frac{dC_{22}}{dt} = 2\left[(\alpha_n^{'}(m_1)(1-m_2) - \beta_n^{'}(m_1)m_2)C_{12} - (\alpha_n(m_1) + \beta_n(m_1))C_{22}\right]$$

$$\frac{dC_{33}}{dt} = 2\left[(\alpha_m^{'}(m_1)(1-m_3) - \beta_m^{'}(m_1)m_3)C_{13} - (\alpha_m(m_1) + \beta_n(m_1))C_{33}\right]$$

$$\frac{dC_{44}}{dt} = 2\left[(\alpha_h^{'}(m_1)(1-m_4) - \beta_h^{'}(m_1)m_4)C_{14} - (\alpha_h(m_1) + \beta_h(m_1))C_{44}\right]$$

In a similar manner, Tuckwell and Jost [23] have obtained evolution of covariance equations. Therefore in order to study the evolution of first order and second order dynamics of stochastic HH model, one is required to solve fourteen coupled nonlinear equations. Our purpose to discuss this is to highlight that analytical study of stochastic nonlinear systems is quite complex. Therefore, we resort to Monte-Carlo simulation of such systems. The above mentioned models are generic in the sense that they can yield the spiking neurons. We describe below another class of models which are widely used. When the membrane potential reaches the threshold, a spike is generated.

Integrate and Fire model: Spiking Neurons

The spiking neuron experimental data which is often collected in neurophysiology is about the arrival timing of action potential. Denoting by t_i the time corresponding to the arrival of the i^{th} spike, we get a time series $\{t_1, t_2, t_3, \ldots\}$ of discrete events. As pointed in Gabbani and Koch [11, 13], temporal coding of information in spiking patterns is useful in encoding of stimulus, such that the characteristics of neural code are closely linked to randomness in neuronal firing.

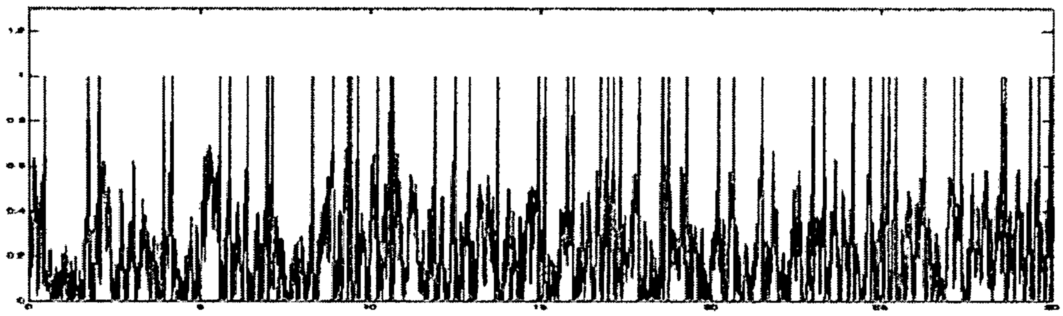

Figure 2.2: Spikes

This class of models captures basic biophysical properties of nerve cells viz. refractoriness, spike trains, information transmission [11, 13]. We discuss two types of models:

1) Perfect Integrate and Fire Neuron
2) Leaky Integrate and Fire Neuron

1. Perfect IF model

The stochastic dynamics of membrane potential is given by

$$dV(t) = \mu(t) + \sigma dW(t), \quad V(t=0) = V_0$$

where W(t) is Wiener process. Here μ represents drift which is defined in terms of excitatory and inhibitory rates. The parameter σ denotes the strength of fluctuations. In order that the membrane potential reaches the threshold with probability one, the drift parameter $\mu > 0$.

In order to obtain the Inter spike interval (ISI) distribution, we are required to compute the first passage time distribution (FPT) for the membrane potential to reach the threshold.

Mathematically, FPT is defined as

$$T = \inf\{t \geq 0 \; ; \; V(t) > V_{th}, \; \mathrm{V(0)<V_{th}}\}$$

It is important to note that for this model, the explicit form of FPT is known in terms of inverse Gaussian distribution i.e.

$$f(t) = \frac{V_{th} - V_0}{\sqrt{2\pi\sigma^2 t^3}} \exp\left[-\frac{(V_{th} - V_0 - \mu t)^2}{2\sigma^2 t}\right], \quad t > 0$$

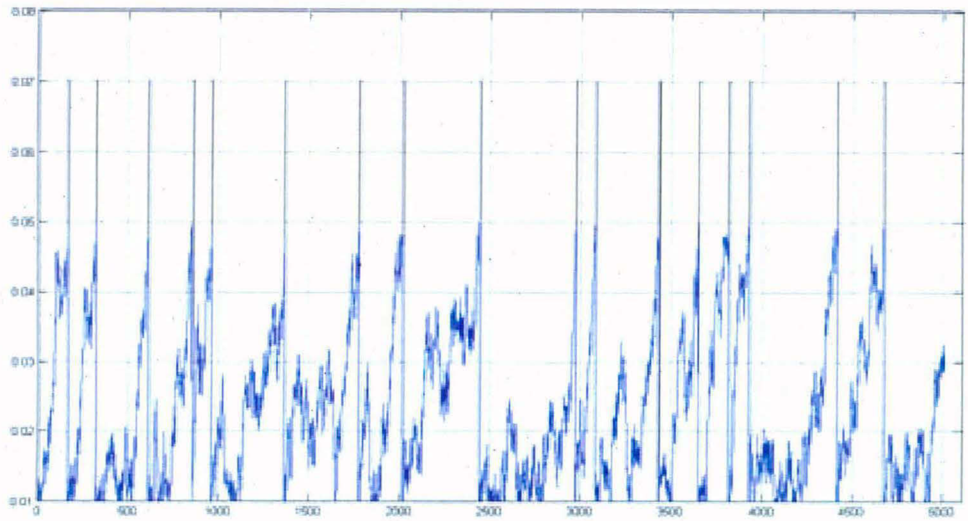

Figure2.3: FPT- Monte-Carlo simulation of membrane potential

2. Leaky Integrate and Fire Model

As early as 1907 Lapicque attempted to model membrane potential in terms of an RC circuit. The model reads as

$$\frac{dV}{dt} = -\frac{V}{\tau} + \mu + \sigma\xi(t), \quad V(t=0) = V_0$$

where τ denotes the time constant $(RC)^{-1}$. Hence ξ (t) is the white noise and μ represents the deterministic part of current. Mathematically the stochastic variate V(t) satisfies Ornstein-Unlenbeck process expressible as solution of SDE

$$dV = \left(-\frac{V}{\tau} + \mu\right)dt + \sigma\, dw(t)$$

The analytical solution for problem is not known in the literature. We have to resort to Monte-Carlo simulation.

Chapter3

Information Transmission in Spiking Neurons

Introduction

Deco and Schurmann [3,4,5] have discussed information theoretic framework for measuring information transmission as mutual information when an external stimulus is applied.

From the timing of spikes, how can one reliable encode the input stimuli. Deco and Schurmann [3,4,5] asked the question of coding strategy for discrimination of input signals by single neuron.

Representing the shot noise process by a Poisson stream cdf events with mean rate λ such that the number of events at time t is

$$P_n(t) = \frac{e^{-\lambda t}(\lambda t)^n}{n!}, \qquad n = 0,1,2,...$$

The corresponding entropy is given by

$$\begin{aligned} Hin &= -\sum_{n=0}^{\infty} pn(t) \ln pn(t) \\ &= -\sum_{n=0}^{\infty} \frac{e^{-\lambda t}(\lambda t)^n}{n!} [-\lambda t + n \ln \lambda t - \ln(n!)], \qquad n = 0,1,2,... \end{aligned}$$

Taking time precision ε such that $\lambda\varepsilon << 1$, we find the entropy per spike of input train [3,4,5] is

$$H_{in}=(\lambda)[1-\ln(\lambda\varepsilon)]$$

It is also well known that for Poisson arrivals with rate λ, the inter arrival time is given by the probability density function

$$f(t) = \lambda e^{-\lambda t}, \lambda \geq 0$$

where λ^{-1} is mean time interval.

Computation of mutual information

The input spike is governed by realizations of a homogeneous Poisson process S(t) such that

$$s(t) = \frac{dS(t)}{dt} = \sum_i \delta(t - t_i)$$

Here $\{t_1, t_2,.., t_n\}$ are the time epoch of the input spike train.

In LIF model, the membrane potential is reset to its resting potential .This makes the output train independent of input train. Denoting the output train $\{t_0', t_1', ..., t_n',...\}$.

Such that $$O(t) = \sum_k \delta(t - t_k')$$

We now compute the mutual information between the input and output spike train per unit time i.e.

$$I(S(t):O(t)) = I(\{t_0, t_1, ...\}:\{t_0', t_1', ...\})$$

In order to compute this quantity, Deco and Schurmann consider spike times in the time interval $[t^{'}, t^{'} + T]$ such that $t^{'}$ can be regarded as the last output spike. Further the measurement of input spike s should be connected from $t^{'}$. Denoting by the mean rate of output spikes as $R = \frac{1}{E[T^{'}]}$;

$$I(S(t) : O(t)) = R.I(\{t_0, t_1, ...\} : T^{'})$$

which simplifies to

$$I(\{t_0, t_1, ...\} : T^{'}) = H(T^{1}) - H(T^{'} / t_{0,} t_{1,} ...)$$

where $H(T^{1})$ and $H(T^{'} / t_{0,} t_{1,} ...)$ represent entropy and conditional entropies respectively.

Deco and Schurmann assume that the distribution of random variable T' is also given by

$$p(T') = \mathrm{R} e^{-RT'}$$

Such that

$$H_{max}(T') = R[1-(R\varepsilon)]$$

Accordingly, Loss of information is found to be

$$L = \frac{H_{in} - I_{io}}{H_{in}}$$

Deco-Schrumann's Model: Monte-Carlo Based Study

The SDE associated with Deco-Schrumann's Model [3,4,5] is as follows

$$dV = (-\frac{V}{\tau} + \mu)dt + \sigma dW(t) + wdS(t)$$

where the first two term on right hand side correspond to the well known LIF Model. The last terms corresponds to the input stimuli represented as homogeneous Poisson process having rate λ.

As discussed in previous chapter, the analytical solution of this model is not available. Accordingly we have to resort to Monte-Carlo simulation of SDE.

The numerical procedure involves the discretization of the model using Euler Murayama scheme [7].

$$V((n+1)h) = V(nh)\left(1 - \frac{h}{\tau}\right) + \mu h + \sigma\sqrt{h}Z_n + w\Delta S(nh)$$

where h is the time step size and Z_n is standard Gaussian variate and

$$\Delta S(nh) = \int_{nh}^{(n+1)h} \sum_i \delta(nh - t_i)d(nh)$$

which will give number of input spikes between nh and (n+1)h.

We thus obtain the output ISI having the probability distribution $p(T' \mid t_0, t_1, \ldots, t_i, \ldots)$.

Based on the simulation study, the probability distribution of output spike is obtained. which provide the entropy H(T') per unit of the output spikes.

The conditional entropy $H(T'|t_0,t_1,\ldots.)$ for a given realization $t_0,t_1,\ldots$ is also computed. These results will yield mutual information, maximum entropy, input entropy and loss. We have carried simulation experiments for the following parameter

$$\mu = 0.5, \frac{1}{\tau} = 0.5, \sigma = 0.2, w = 1.5$$

The step size is taken to be 0/01. The simulation runs range from t=0 to t=1000 sec.

Figure (3.1) depicts the variation of mean, variance and coefficient of variation with respect to 1/λ. In figure (3.2) we have plotted variation of maximum output entropy, Hmax with respect to 1/λ. This figure is in agreement with the numerical results given Deco and Schrumann [3, 5]. In the figure (3.3), we study variation of output spike rate with respect to λ. The mutual information in figure (3.4) is given in terms of H(X)-H(X|Y).

where $H(X)=H(T')$ and $H(X|Y)=< H(T'|t_0,t_1,\ldots) >_{t_0,t_1,\ldots}$

It may be noted that our results are not in agreement with the result of Deco and Schurmann [3, 5].

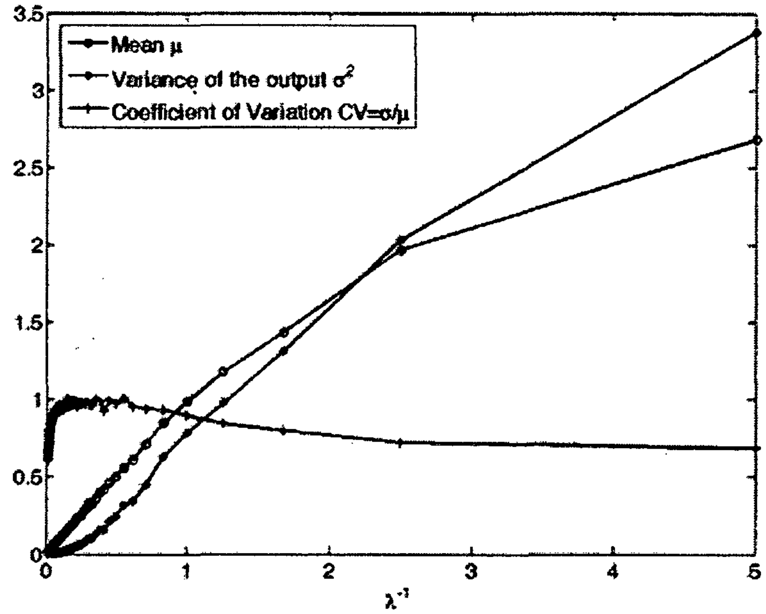

Figure 3.1: Variation of mean,variance and CV with respect varying 1/λ

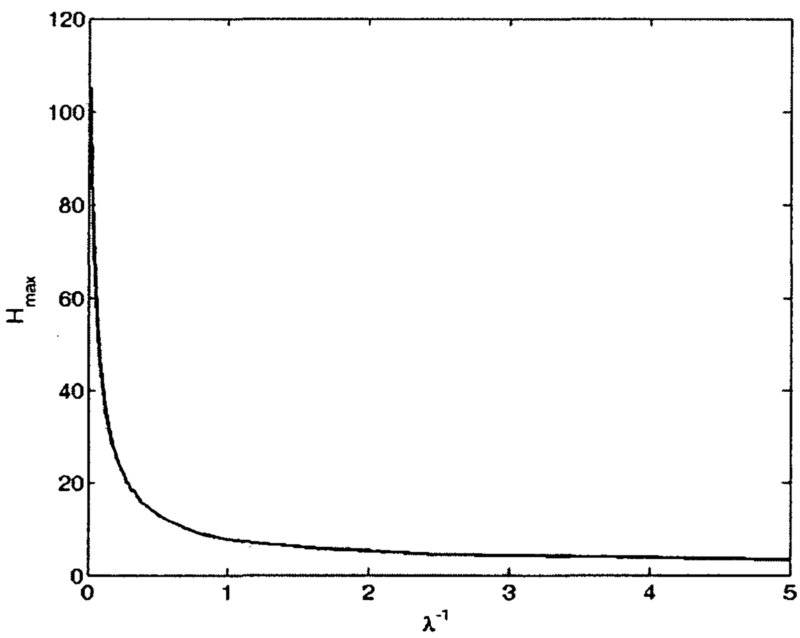

Figure 3.2: Variation in Maximum Entropy with respect varying 1/λ

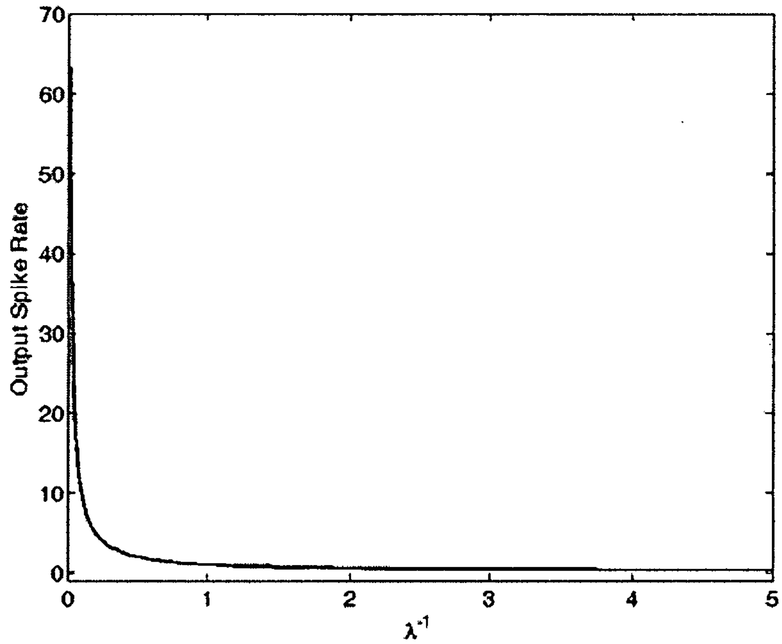

Figure 3.3: Variation in output spike rate with respect varying 1/λ

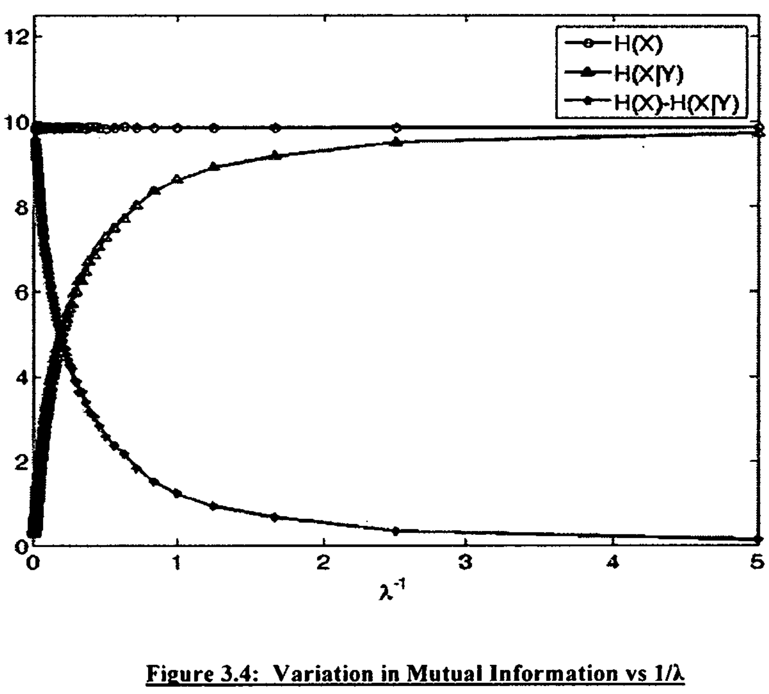

Figure 3.4: Variation in Mutual Information vs 1/λ

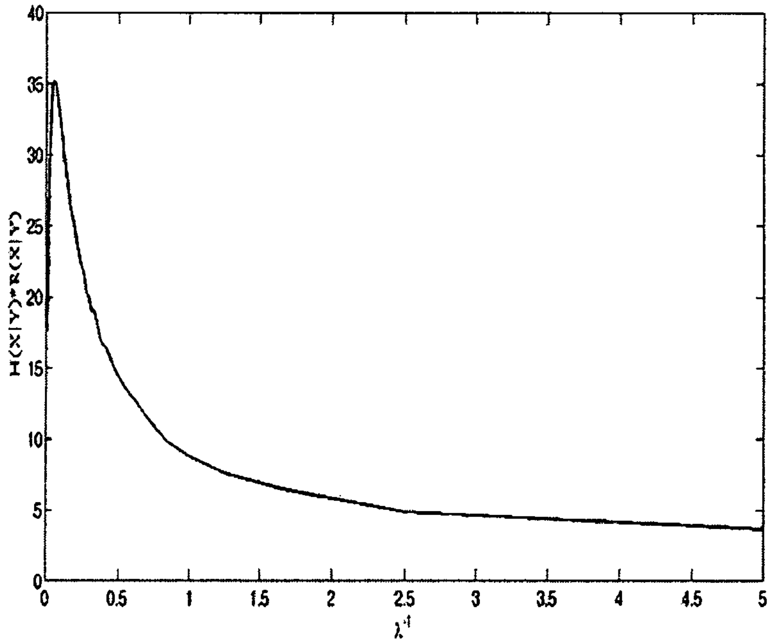

Figure 3.5: Variation of output entropy with respect to 1/λ

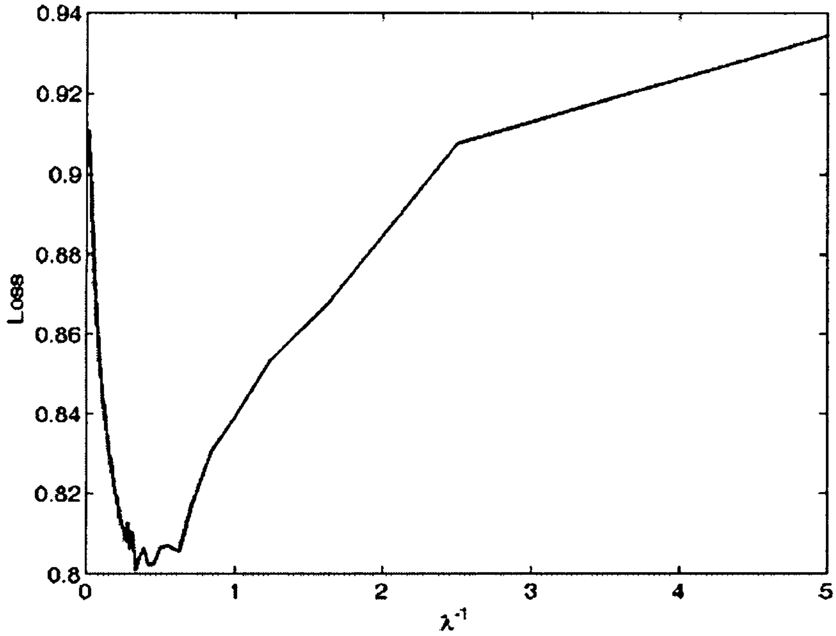

Figure 3.6: Variation in loss of information with respect varying 1/λ

Chapter 4

Effect of Variation in Drift on Information Transmission

1. Introduction

It is of interest to explore the effect of variation of drift parameter in information transmission. The drift parameter itself can vary from neuron to neuron and this investigation is of importance as large μ may push sample realization of membrane potential towards threshold affecting FPT.

Quantities of interest which needs investigation relate to output entropy, output rate, and mutual information. This analysis will also provide insight into issue related to sensitivity analysis of the model.

We consider Deco and Schrumann [3, 5] model with varying parameter μ, the model is discussed as

$$dV = (-\frac{V}{\tau} + \mu)dt + \sigma dW(t) + wdS(t) \qquad V(t=0)=V_0$$

We have carried out simulation experiments for different value of μ varying from 0.01 to 0.96 with interval of 0.05.

2. (a) Effect of increasing μ on entropy

As noted earlier, the larger values of drift parameter μ have a tendency to push membrane potential towards threshold. In other words, we can say the variability in the spiking pattern decreases resulting in reduction of entropy of the spiking neurons. This finding is also corroborated in figure (4.1) and (4.2).

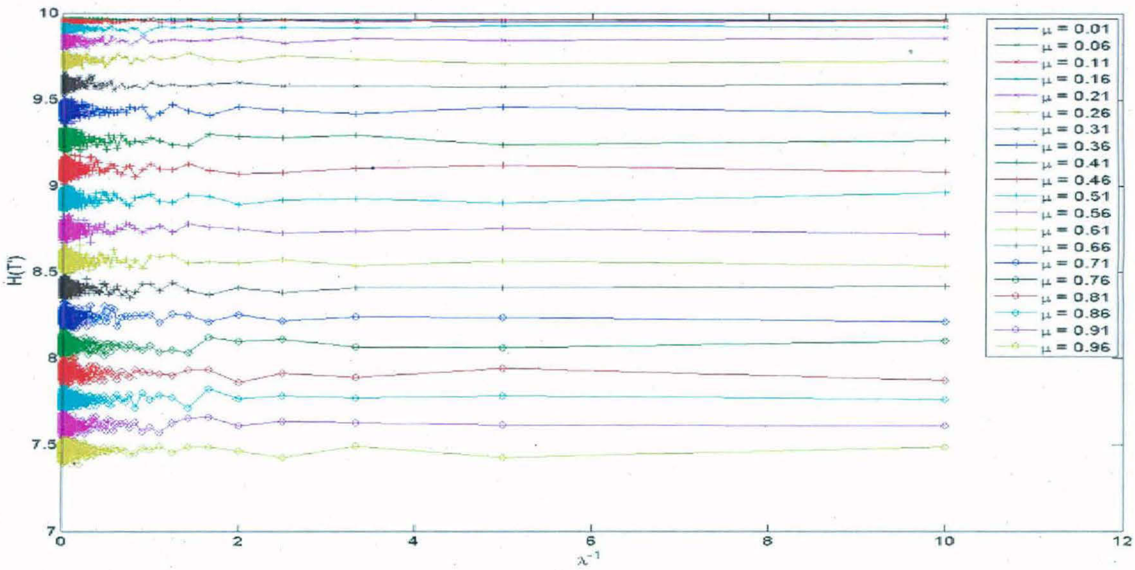

Figure 4.1: Output Entropy vs.1/λ

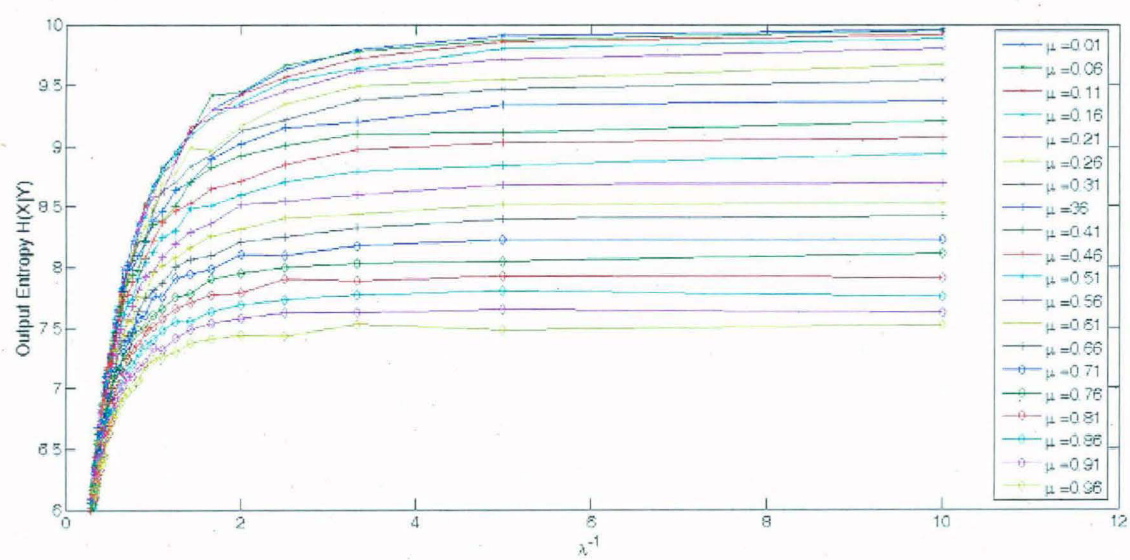

Figure 4.2: Conditional Output Entropy vs. 1/λ

(b) Effect of Variation on ISI distribution

Based on study of numerical results presented in figure (4.1) and (4.2), we expect the ISI of the model to reflect the variation of μ. we find in figure (4.3) the pdf of ISI without stimulus

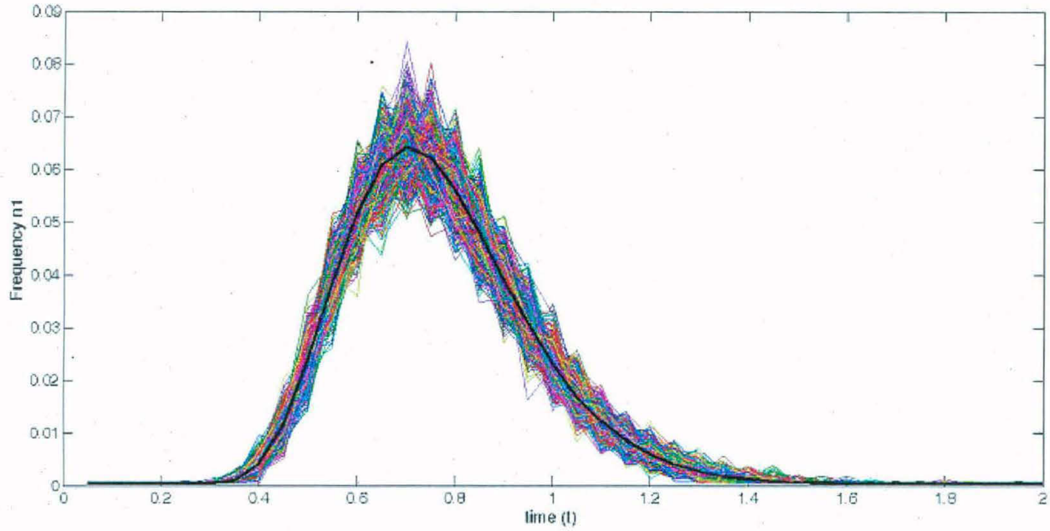

Figure 4.3: ISI distribution(without stimuli)

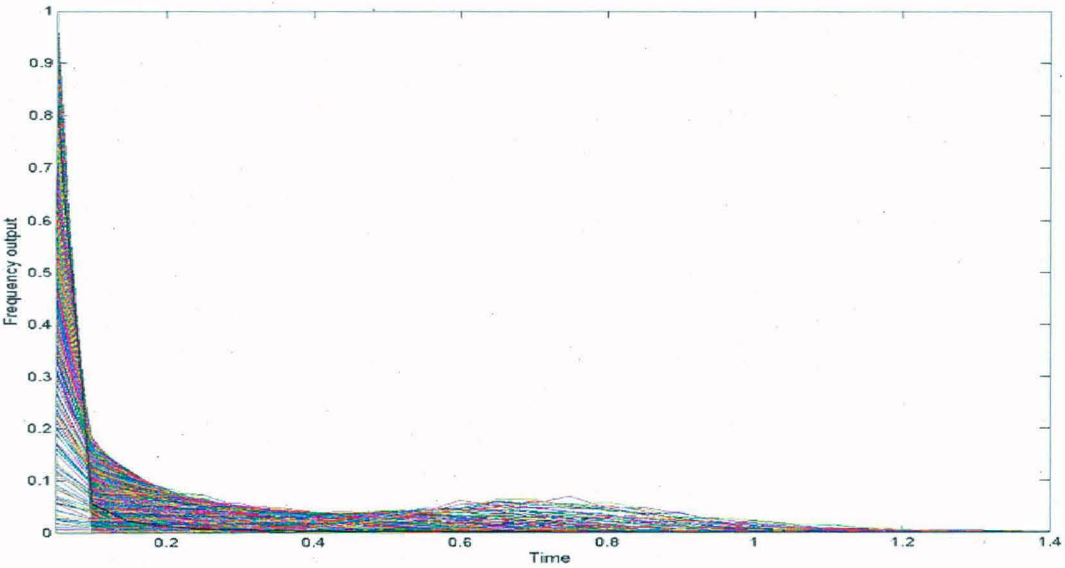

Figure 4.4: ISI distribution (with stimuli)

input has smaller width and higher model values for increasing the value of drift. The inclusion of stimuli reveals the similar behavior with shifting model values.

(c) Effect of Varying μ on CV and output rate

It is noted in figure (4.5) that the variation of output rate increases with increasing μ. In a similar manner, the coefficient of variation decreases with increasing drift parameter. Thus the relative fluctuation decreases as the parameter μ increases.

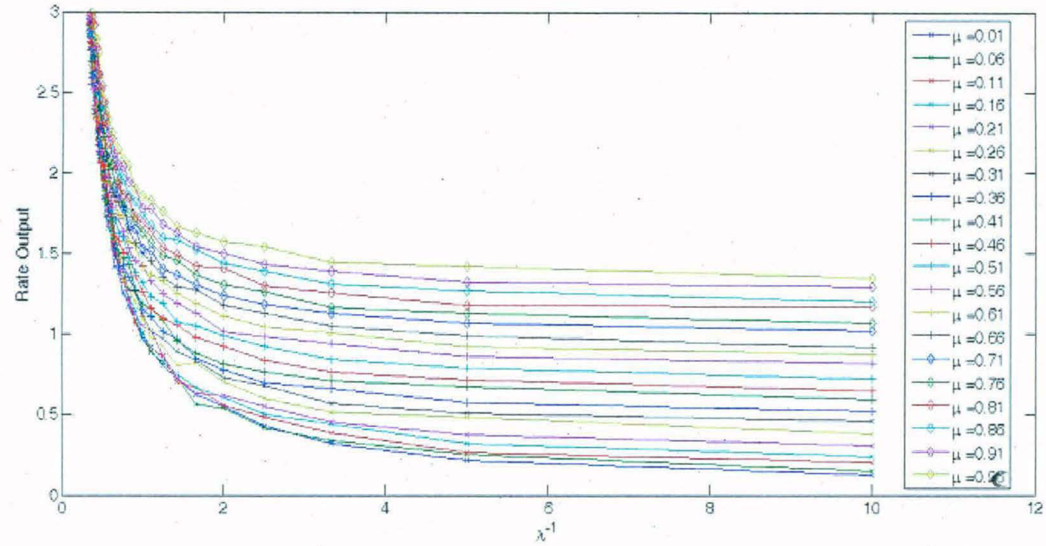

Figure 4.5: Rate of output spike vs. 1/λ

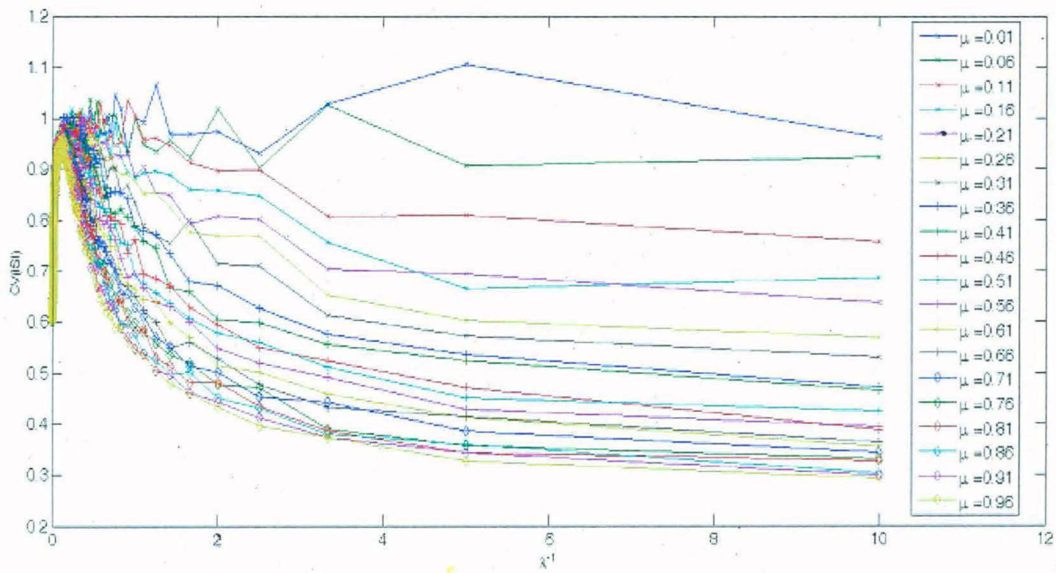

Figure 4.6: Variation of CV vs. 1/λ

3. Effect of variation of drift as Mutual Information

This investigation would provide the effect of μ on information transmission. It is found from figure (4.7) that for a given value of 1/λ, the mutual information decreases as we increase μ. This investigation is high for lower value of μ. This is an interesting contribution of the study.

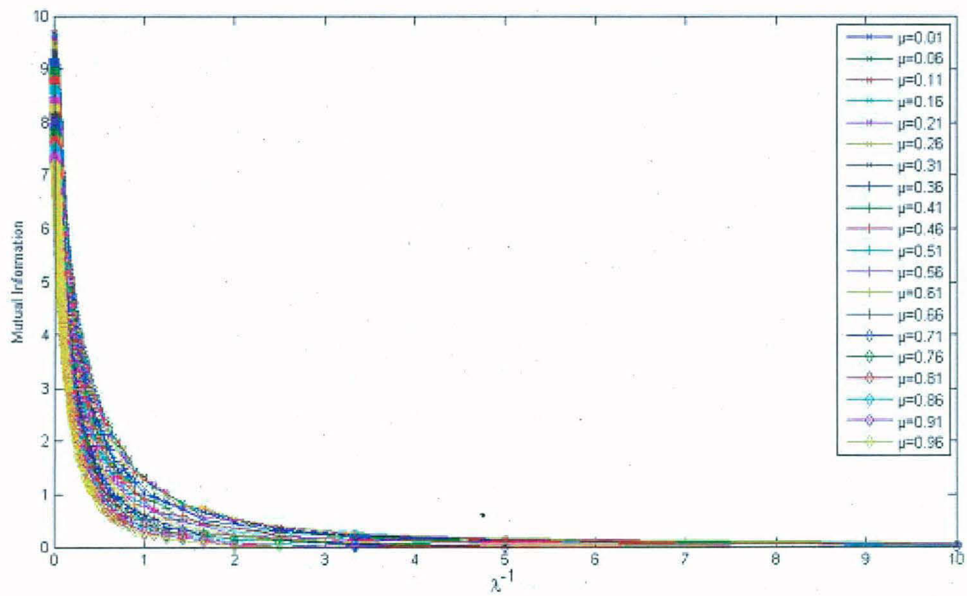

Figure4.7: Variation of Mutual Information vs. 1/λ

Chapter 5

Conclusion

We have adapted Deco-Schurmann's [3, 5] framework for study of information transmission in neuronal system under different environment. The drift parameter is likely to vary from neuron to neuron and its variation can affect the amount of information transmission. Such a study is also useful from sensitivity analysis of the model.

The framework which we have adopted is easily generalizable when one or more parameters of the model are varied. It would be useful to study the effect of stochastic drift parameter (when subject to random fluctuations) on information transfer. Mathematically, the problem would have two noise sources intrinsic to the neuronal system in addition to stochastic stimuli. The time scale fluctuations of drift stochasticity is likely to play an important role.

References:

1. Becker S., "Modelling the mind: From circuits to systems" Chapter 2 in "New Directions in Statistical Signal Processing: From Systems to brain", Haykin S. et.al. MIT Press, 2005.
2. Dayan P and Abbott L.F "Theoretical Neuroscience- Computational and Mathematical Modeling of neural system" MIT Press, 2001.
3. Deco G.et al., "Stochastic dynamics as a principle of brain function", Progress in Neurobiology, 88, 2009.
4. Deco G., Schürmann B., "Information dynamics: foundations and applications", Springer-Verlag, 2001.
5. Deco G. and Schürmann B., "Information Transmission and Temporal Code in Central Spiking Neurons", Phys. Rev. Lett. 79, 4697–4700, 1997.
6. Gardiner C.W., "Handbook of stochastic methods", 2ed. Springer, 1997.
7. Glasserman P., "Monte Carlo methods in financial engineering", Springer, 2004.
8. Haykin Simon S. "Neural networks and learning machines", Vol. 10, 3rd Edition, PHI, 2008.
9. Karmeshu (Ed.), "Entropy measures, maximum entropy principle and emerging applications", Springer-Verlag, 2003.
10. Klir G. J., Folger T. A., "Fuzzy sets, uncertainty, and information", PHI, 1988.

11. Koch C , Gabbiani F., "Principles of spike train analysis", Methods in neuronal modeling, MIT Press, 1998.

12. Koch C, Segev I, "Methods in neuronal modeling: From Ions to Networks". MIT Press, 1998.

13. Koch C et.al, "Feature extraction by burst-like spike patterns in multiple sensory maps", The Journal of Neuroscience, 1998.

14. Koch C, "Biophysics of computation" Oxford University Press, 1999.

15. N. Ernst, M. Stefan, "A Generalized Linear Integrate-and-Fire Neural Model Produces Diverse Spiking Behaviors", MIT Press, Vol. 21, No. 3,704-718,2009.

16. Rabinovich et.al. "Dynamical principles in Neuroscience", Review of Modern Phys. APS, 78, 1213–1265, 2006.

17. Rolls E.T., Deco G., "The Noisy Brain: Stochastic Dynamics as a Principle of Brain Function", Oxford University Press, 2010.

18. Shanon C. E., "A Mathematical Theory of Communication", Bell System Technical Journal, Vol. 27, October, 1948.

19. Stallings W., "High-speed networks: TCP/IP and ATM design principles", PHI, 1998.

20. Sejnowski T J, Koch C and Churchland P S, "Computational Neuroscience", Science, New Series, Vol. 241, No. 4871, 1299-1306 (1988).

21. Salinas E and Sejnowski T J, "Integrate-and-Fire Neuron driven by Correlated Stochastic input", Neural Computation, Vol.14, 2111-2155, 2002.

22. Tuckwell H.C and Feng J, "A Theoretical Overview from Computational Neuroscience-A Comprehensive Approach", Ed: Feng .J, CRC Press LLC, 2004.

23. Tuckwell HC , Jost J., "Moment analysis of the Hodgkin-Huxley system with additive noise", Physica A: Statistical Mechanics and its Applications, Elsevier , 2009.