Chaotic Oscillations in a Hodgkin-Huxley Neuron – Quantifying Similarity Estimation of Neural Responses

M. Sarangdhar and C. Kambhampati

Abstract— **Periodic stimuli are known to induce chaotic oscillations in the squid giant axon for a certain range of frequencies. This behaviour is modelled by the Hodgkin-Huxley equations when a periodic stimulus is applied. The responses resulting from chaotic neural dynamics have irregular inter-spike intervals and fluctuating amplitudes. These characteristics are absent in steady state responses of the Hodgkin-Huxley neuron which are generated using a constant current stimulus. It is known that firing time information is adequate to estimate similarity of steady state responses; however, in the presence of chaotic oscillations, similarity between neural responses cannot be estimated using firing time alone. The results discussed in this paper present a quantification of the similarity of neural responses exhibiting chaotic oscillations by using both amplitude fluctuations and firing times. We relate the similarity thus obtained between two neural responses to their respective stimuli. Identical stimuli have very similar effect on the neural dynamics and therefore, as the temporal inputs to the neuron are the same, the occurrence of identical chaotic patterns result in a high estimate of similarity for the neural responses. Estimates of similarity are compared for periodic stimuli with a range of inter-spike intervals.**

Index Terms— **chaotic oscillations, periodic stimuli, neural response comparison, chaotic dynamics, spike trains.**

I. INTRODUCTION

The non-linear dynamics of a neuron have been studied both theoretically and physiologically in recent years to extend the understanding of its underlying mechanism [1-13]. The spikes or action potentials are evoked when an external stimulus is applied to the neuron. It is thought that either the firing rate or firing time of individual spikes carries specific information of the neuronal response [14-16]. This holds for all steady state responses of a neuron when a constant current stimulus is applied. However, on injection of a periodic or sinusoidal stimulus the steady state response is no longer preserved [17-26]. The self-excited oscillations of a Hodgkin-Huxley (HH) neuron [27] may become chaotic when a sinusoidal stimulus is applied with proper choices of

Mayur Sarangdhar is currently a PhD student within the Neural, Emergent and Agent Technologies Group, Department of Computer Science, University of Hull, Hull, East-Yorkshire, HU6 7RX, UK (phone: 01482 465253; e-mail: M.Sarangdhar@ 2006.hull.ac.uk).

C. Kambhampati is currently a Reader in the Department of Computer Science, University of Hull, Hull, East-Yorkshire, HU6 7RX, UK. (e-mail: c.kambhampati@hull.ac.uk).

magnitude and frequency [20-21, 25-26]. Physiological experiments on squid giant axons [18-19] and Onchidium neurons [22] have confirmed the occurrence of chaotic oscillations. This paper quantifies the similarity estimated between neural responses exhibiting chaotic oscillations. B using the amplitude distribution and the firing times of a neural spike train to estimate similarity.

The nature of a periodic stimulus is responsible to induce chaotic oscillations in a biological neuron. Irregular inter-spike interval (ISI) and fluctuating amplitudes are the characteristics of chaotic oscillations absent in steady state responses generated by constant current stimuli. Information on stimuli similarity can be derived from neural response comparison. Firing time information is adequate to estimate similarity of steady state responses; however, in the presence of chaotic oscillations or when the amplitudes of a neural response fluctuate, amplitude and firing time collectively reflect the true dynamics of a neuron and therefore both should feature in similarity estimation [28-30]. Similarity estimation is based on the principle of relative coincidences without coincidences by chance [31-32]. The amplitudes a neural response exhibiting these chaotic oscillations fit a Normal distribution and it is possible to determine amplitude coincidences using the properties of Normal distribution. Similarity between these responses can be estimated by a composite similarity measure based on amplitude and firing time coincidences. Results show that similarity based on this composite approach is mathematically realisable than similarity based on firing times or amplitudes alone. It is observed that similar periodic stimuli induce similar chaotic patterns in the neural responses and therefore the resulting neural responses have a high degree of similarity. The effect of distinct periodic stimuli is evident in the dissimilar chaotic patterns displayed in the responses. It can be derived from these results that chaotic responses with high similarity originate from very similar periodic stimuli. This agrees in principle that initial representation of a neural response is unique to the stimulus [9, 33].

In this paper, Hodgkin-Huxley (HH) neural responses generated by varying the Inter-Spike-Interval (ISI) of periodic stimuli are compared to estimate similarity. It is observed that estimating similarity of neural responses exhibiting chaotic dynamics requires knowledge of both firing times and amplitude distribution. A comparison of similarities estimated by a) an approach considering firing times alone and b) an approach based on firing times and amplitude distribution shows that fluctuations induced by periodic stimuli are differentiated better by considering

amplitude distribution in addition to firing time information. This paper quantifies the similarity thus estimated and it is observed that it is approximately equal to the percentage number of absolute coincidences. Absolute coincidences are the number of spikes that coincide with respect to both firing times and amplitudes with a pre-defined precision δ.

II. NEURONAL MODEL AND SYNAPSE

A. The neuron model

The computational model and stimulus for an HH neuron is replicated from [15]. The differential equations of the model are the result of non-linear interactions between the membrane voltage V and the gating variables m, h and n for Na^+ and K^+ and Cl^-.

$$C\frac{dv}{dt} = \left.\begin{array}{l} -g_{Na}m^3 h(V-V_{Na}) - g_K n^4 (V-V_K) \\ -g_L(V-V_L) + I_i \end{array}\right\} \quad (1)$$

$$\left.\begin{array}{l} \frac{dm}{dt} = -(\alpha_m + \beta_m)m + \alpha_m \\ \frac{dh}{dt} = -(\alpha_h + \beta_h)h + \alpha_h \\ \frac{dn}{dt} = -(\alpha_n + \beta_n)n + \alpha_n \end{array}\right\} \quad (2)$$

$$\left.\begin{array}{l} \alpha_m = 0.1(V+40)/[1-e^{-(V+40)/10}] \\ \alpha_h = 0.07e^{-(V+65)/20} \\ \alpha_n = 0.01(V+55)/[1-e^{-(V+55)/10}] \\ \beta_m = 4e^{-(V+65)/18} \\ \beta_h = 1/[1+e^{-(V+35)/10}] \\ \beta_n = 0.125e^{-(V+65)/80} \end{array}\right\} \quad (3)$$

The variable V is the resting potential of the membrane and V_{Na}, V_K and V_L are the reversal potentials of the Na^+, K^+ channels and leakage. The values of the reversal potentials $V_{Na} = 50mV, V_K = -77mV, V_L = -54.5mV$. The conductance for the ionic channels are $g_{Na} = 120mS/cm^2$, $g_K = 36mS/cm^2$ and $g_L = 0.3mS/cm^2$. The capacitance of the membrane is $C = 1\mu F/cm^2$.

B. The synaptic current

An input spike train give by [34] is considered to generate the pulse component of the external current.

$$U_i(t) = V_a \sum_n \delta(t - t_f) \quad (4)$$

where, t_f is the firing time and is defined as

$$t_{f(n+1)} = t_{f(n)} + T \quad (5)$$

$$t_{f(1)} = 0 \quad (6)$$

T represents the ISI of the input spike train and can be varied to generate a different pulse current. The spike train is injected through a synapse to give the pulse current I_P.

$$I_P = g_{syn} \sum_n \alpha(t - t_f)(V_a - V_{syn}) \quad (7)$$

g_{syn}, V_{syn} are the conductance and reversal potential of the synapse. [32] define the $\alpha - function$ as

$$\alpha(t) = (t/\tau)e^{-t/\tau}\Theta(t), \quad (8)$$

where, τ is the time constant of the synapse and $\Theta(t)$ is the Heaviside step function. $V_a = 30mV$, $\tau_{syn} = 2ms$, $g_{syn} = 0.5mS/cm^2$ and $V_{syn} = -50mV$.

C. The total external current

The total external current applied to the neuron is a combination of static and pulse component

$$I_i = I_S + I_P + \varepsilon \quad (9)$$

where, I_s is the static and I_p is the pulse current, ε is the random Gaussian noise with zero mean and standard deviation $\sigma = 0.025$.

It is understood that distinct sinusoidal stimuli induce different chaotic oscillations which result in dissimilar neural responses [28-30].

III. SIMILARITY ESTIMATION USING $\Gamma_{CHAOTIC}$

The similarity between neural responses exhibiting chaotic oscillations can be determined using $\Gamma_{chaotic}$. $\Gamma_{chaotic}$ estimates similarity through differences between the actual coincidences N_{pcoinc} and the expected number of coincidences $\overline{N_{pcoinc}}$ relative to the average number of spikes in the two spike trains. The similarity is normalised between 0 and 1 by a normalising factor $N_{chaotic}$.

$$\Gamma_{chaotic} = \frac{N_{pcoinc} - \overline{N_{pcoinc}}}{\frac{1}{2}(N_1 + N_2)} \frac{1}{N_{chaotic}} \quad (10)$$

where N_{pcoinc} is the number of conditional coincidences (amplitude coincidence given firing time coincidence) between the two spike trains, $\overline{N_{pcoinc}}$ is the conditional mean (average number of amplitude coincidences given firing time coincidences) and $N_{chaotic}$ is the normalising factor for chaotic oscillations. N_1 is the number of spikes in the train 1, N_2 is the number of spikes in train 2. This formulation is based on [32] where similarity based on firing times was estimated through relative number of coincidences without coincidences by chance.

Let $\aleph_1$ and $\aleph_2$ be the normal distributions for the spike trains sp_1 and sp_2 with means μ_1 and μ_2 and respective standard deviations σ_1 and σ_2. The mean probability of coincidence of any amplitude from $\aleph_2$ with an amplitude from $\aleph_1$ can be approximated using the mean of $\aleph_2$.

$$z_{mean} = \frac{\mu_2 - \mu_1}{\sigma_1} \quad (11)$$

$$\overline{z_{mean}} = p(z_{mean}) = [z_{mean}]_{from\,Z-table} - [p(\mu_1)]_{from\,Z-table} \quad (12)$$

(11) and (12) give the mean probability that an amplitude from $\aleph_2$ will lie within $\aleph_1$ and coincide with an amplitude from $\aleph_1$ The expected number of amplitude coincidences for

any two neural responses generated by periodic stimuli is therefore $\overline{z_{mean}}N_1$. If the rate of fire of sp_2 is ν and the precision for coincidence is δ, then the expected number of coincidences are given by

$$\overline{N_{pcoinc}} = 2\nu\delta N_2 \overline{z_{mean}}$$
(13)

and the normalising factor $N_{chaotic}$ normalises the estimate of similarity to a value between 0 (dissimilarity) and 1(exact match)

$$N_{chaotic} = 1 - 2\nu\delta \overline{z_{mean}}$$
(14)

Similarity on the basis of firing times alone can be determined from (10) by omitting the amplitude considerations in N_{pcoinc}, $\overline{N_{pcoinc}}$ and $N_{chaotic}$. This result is consistent with [35].

IV. RESULTS

Due to the nature of periodic stimuli and chaotic oscillations, estimating similarity between neural responses on the basis of firing times is inaccurate in view of a) false positives and b) incorrect inference about stimuli similarity. Similarity estimation is done for neural responses by varying the stimulus ISI (T) within a limit of 2ms. Stimulus is varied between 14ms-16ms (set I), 13ms-15ms (set II) and 15ms-17ms (set III) and similarity is estimated by comparing neural responses with reference responses R_{ref} for each set. The reference responses are generated by fixing the ISI(T_{ref}) for the sets at 15ms for set I, 14ms for set II and 16ms for set III. This section compares the similarity estimated by coincidence factor (Γ) and $\Gamma_{chaotic}$.

A. Comparison of Γ and $\Gamma_{chaotic}$, Set I, 14ms-16ms

β represents the difference between the stimulus ISI (T) and a reference ISI T_{ref}. A positive or negative change in β indicates that neural stimuli have dissimilar ISI and their respective influence on neural dynamics is unique to the applied stimulus. The neural responses with underlying chaotic oscillations require both amplitude fluctuations and irregular firing times considered to estimate similarity. It is observed that false positive (circled) obtained by coincidence factor at $\beta = +1$ is eliminated (fig. 1). The overall similarity between pairs of neural responses is reduced in comparison with Γ due to amplitude fluctuations being considered in addition to firing time information.
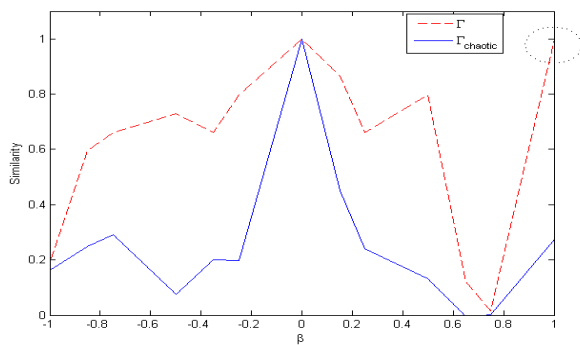

Fig.1: Similarity of neural responses generated by periodic stimuli with $14ms \leq T \leq 16ms$ and $T_{ref} = 15ms$. Γ represents the similarity estimated by coincidence factor and $\Gamma_{chaotic}$ is the similarity based on firing times and amplitudes coincidences. The incorporation of amplitude fluctuations to estimate similarity helps $\Gamma_{chaotic}$ eliminate false positive (circled) at $\beta = +1$.

Table (1) gives a clear comparison of firing time and amplitude coincidences. For $\beta = -1$, half of the neural spikes from R_{14} and R_{ref15} coincide with a precision of 2ms. However, only 20.83% of the amplitudes coincide with a precision 2mV. This is characteristic of neural responses exhibiting chaotic oscillations – a change in the stimulus reflects on the neural dynamics. Absolute coincidences are conditional coincidences i.e. number of amplitude coincidences given that corresponding firing times coincide. The number of absolute coincidences is 16.67%, which implies that out of all the neural response pairs, only 16.67% exhibit amplitude and firing time coincidences. The similarity estimated by $\Gamma_{chaotic}$ is 0.161. It appears to accurately reflect the absolute coincidences. In addition, $\Gamma_{chaotic}$ also considers coincidences by chance or expected coincidences which renders the similarity estimated by $\Gamma_{chaotic}$ unique to a pair of neural responses.

Table 1: Firing time, amplitude and absolute coincidences for various values of β in set I. $\Gamma_{chaotic}$ represents the similarity between pairs of neural responses. Firing time coincidence precision is 2ms, amplitude coincidence precision is 2mV and absolute coincidence is a conditional coincidence of amplitudes given that corresponding firing times coincide. $\Gamma_{chaotic}$ accurately calculates similarity and this can be correlated with the percentage of absolute coincidences.

β	Firing time Coincidences (%)	Amplitude Coincidences (%)	Absolute Coincidences (%)	$\Gamma_{chaotic}$
-1	50	20.83333	16.6667	0.161
	75	29.1677	25	0.2489
	79.1667	37.5	29.1667	0.2908
	83.3333	12.5	8.3333	0.0753
	79.1667	25	20.8333	0.1997
	87.5	29.1667	20.8333	0.1984
	100	100	100	1
	91.6667	50	45.8333	0.4513
	79.1667	33.3333	25	0.2392
	87.5	16.6667	16.6667	0.1312
	37.5	12.5	4.1667	0.0003
+1	100	29.1667	29.1667	0.2729

At $\beta = 0$, both stimuli have the same ISI ($T = 15ms, T_{ref} = 15ms$). All neural spikes coincide in firing times and amplitudes. The absolute coincidences confirm that the neural responses are an exact match, hence, similarity $\Gamma_{chaotic} = 1$. At $\beta = +1$, as all neural spikes show firing time coincidences, coincidence factor classifies the neural responses R_{16} and R_{ref15} as identical. This result is a false positive as indicated by the number of amplitude fluctuations. Though all neural spikes coincide with firing times, only 29.17% of amplitudes coincide, hence the absolute coincidences are 29.17%. The corresponding value of $\Gamma_{chaotic}$ is 0.2729 which is substantially lower than 1 (estimated by coincidence factor). The consideration of amplitude fluctuations in addition to firing time information successfully eliminates the false positive.

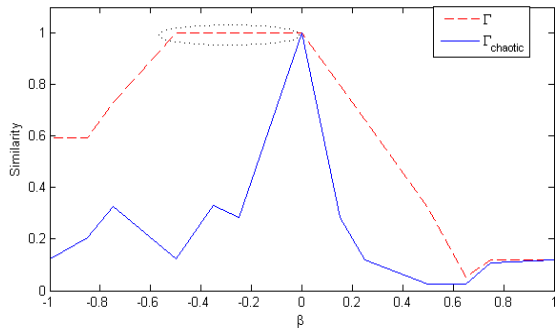### B. Comparison of Γ and $\Gamma_{chaotic}$, Set II, 13ms-15ms

Fig.2: Similarity of neural responses generated by periodic stimuli with $13ms \leq T \leq 15ms$ and $T_{ref} = 14ms$. Γ represents the similarity estimated by coincidence factor and $\Gamma_{chaotic}$ is the similarity based on firing times and amplitudes coincidences. $\Gamma_{chaotic}$ eliminates false positives (circled) between $-0.5 \leq \beta < 0$.

False positives (circled) estimated by coincidence factor, Γ, shown in fig. 2. occur for $-0.5 \leq \beta < 0$. Table 2 shows that firing time coincidences are 100% for $-0.5 \leq \beta < 0$. These pairs of neural responses are classified identical by coincidence factor. However, the corresponding amplitude coincidences are 12.5%, 33.33% and 29.17% which indicate that though the firing times coincide, the amplitude fluctuations are not identical, hence these are termed as false positives. These non-identical amplitude fluctuations are caused by the dissimilar periodic stimuli. The corresponding absolute coincidences for the false positives are 12.5%, 33.33% and 29.17%. The similarity estimated by $\Gamma_{chaotic}$ is 0.1224, 0.3302 and 0.2846 respectively which reflects the absolute coincidences. The composite consideration of irregular firing times and varying amplitudes helps differentiate neural responses and relate their dissimilarity to the stimuli.

For $\beta = 0$, the neural responses are generated by identical stimuli ($T = 14ms$ and $T_{ref} = 14ms$). Identical stimuli cause similar chaotic oscillations, hence the resulting neural responses are an exact match. This is seen in table 2 and fig. 2, at $\beta = 0$, the firing time coincidences, amplitude coincidences and the absolute coincidences are 100%. This justifies that the neural responses are an exact match and they were generated by identical stimuli, hence $\Gamma_{chaotic} = 1$. The similarity determined by $\Gamma_{chaotic}$ for other neural response pairs is also consistent in correlation with the absolute coincidences.

C. Comparison of Γ and $\Gamma_{chaotic}$, Set III, 15ms-17ms

Set III exhibits false positives (circled) for $-1 \leq \beta \leq -0.75$(fig. 3). Table 3 shows that the corresponding firing time coincidences are 100% which result in coincidence factor classifying the pair of neural responses identical. However, the amplitude coincidences are 29.17% and 20.83% indicating that the underlying oscillations are non-identical. The corresponding similarity determined by $\Gamma_{chaotic}$ is 0.2754 and 0.1992. As $\Gamma_{chaotic} \neq 1$, the neural responses are not an exact match and they were generated by dissimilar stimuli.

Table 2: Firing time, amplitude and absolute coincidences for various values of β in set II. $\Gamma_{chaotic}$ eliminates the false positives occurring for $-0.5 \leq \beta < 0$. Similarity estimated by $\Gamma_{chaotic}$ correlates to the percentage of absolute coincidences.

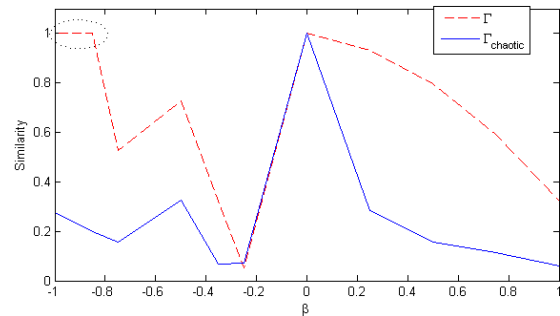| β	Firing time Coincidences (%)	Amplitude Coincidences (%)	Absolute Coincidences (%)	$\Gamma_{chaotic}$
-1	75	16.6667	12.5	0.1204
	75	25	20.8333	0.2044
	83.3333	37.5	33.3333	0.3272
	100	12.5	12.5	0.1224
	100	33.3333	33.3333	0.3302
	100	29.1667	29.1667	0.2846
	100	100	100	1
	87.5	37.5	29.1667	0.2857
	79.1667	16.6667	12.5	0.1178
	58.3333	8.3333	4.1667	0.0263
	41.6667	33.3333	4.1667	0.0243
	45.8333	45.8333	12.5	0.1075
+1	45.8333	20.8333	12.5	0.1188

Fig.3: Similarity of neural responses generated by periodic stimuli with $15ms \leq T \leq 17ms$ and $T_{ref} = 16ms$. Γ represents the similarity estimated by coincidence factor and $\Gamma_{chaotic}$ is the similarity based on firing times and amplitudes. The incorporation of amplitude fluctuations to estimate similarity helps $\Gamma_{chaotic}$ eliminate false positives (circled) for $-1 \leq \beta \leq -0.75$.

Table 3: Firing time, amplitude and absolute coincidences for various values of β in set III. The false positives determined by coincidence factor for $-1 \leq \beta \leq -0.75$ are eliminated. Similarity between neural response pairs estimtated by $\Gamma_{chaotic}$ correlates with the percentage of absolute coincidences.

β	Firing time Coincidences (%)	Amplitude Coincidences (%)	Absolute Coincidences (%)	$\Gamma_{chaotic}$
-1	100	29.1667	29.1667	0.2754
	100	20.8333	20.8333	0.1992
	70.8333	25	16.6667	0.1581
	83.3333	33.3333	33.3333	0.3243
	58.3333	12.5	8.3333	0.0666
	41.6667	12.5	8.3333	0.0704
	100	100	100	1
	95.8333	33.3333	29.1667	0.2851
	87.5	20.8333	16.6667	0.1558
	75	16.6667	12.5	0.1124
+1	58.3333	37.5	8.3333	0.0617

For $\beta = 0$, the neural responses are generated by identical stimuli ($T = 16ms$ and $T_{ref} = 16ms$). The similarity between other neural response pairs reflects their dissimilar stimuli and correlates with the absolute coincidences. For

$\beta > 0$, $\Gamma_{chaotic}$ decreases with an increase in β indicating that similarity between the neural responses decreases with an increase in the difference in the ISI of two stimuli. Any difference in the ISI of a stimulus causes a temporal change and effect on neural dynamics is evident in the dissimilarity estimated by $\Gamma_{chaotic}$.

V. CONCLUSIONS

The nature of a periodic stimulus is responsible to induce chaotic oscillations in a biological neuron. Irregular inter-spike interval (ISI) and fluctuating amplitudes are the characteristics of chaotic oscillations absent in steady state responses generated by constant current stimuli. Information on stimuli similarity can be derived from neural response comparison. Estimating similarity based on firing times (coincidence factor) alone is insufficient in view of a) false positives and b) incorrect inference about neural stimuli. Firing time information is adequate to estimate similarity of steady state responses; however, in the presence of chaotic oscillations or when the amplitudes of a neural response fluctuate, amplitude and firing time collectively reflect the true dynamics of a neuron and therefore both should feature in similarity estimation [28-30].

The amplitudes a neural response exhibiting chaotic oscillations fit a Normal distribution and using the properties of Normal distribution, it is possible to determine amplitude coincidences. Similarity between these responses can be estimated by a composite similarity measure based on amplitude and firing time coincidences. In addition, similar periodic stimuli induce similar chaotic patterns in the neural responses and therefore the resulting neural responses have a high degree of similarity. The effect of distinct periodic stimuli is evident in the dissimilar chaotic patterns displayed in the responses. It follows that chaotic responses with high similarity originate from very similar periodic stimuli. This agrees in principle that initial representation of a neural response is unique to the stimulus [9,33].

The results show that the similarity estimated using both firing times and amplitudes can be quantified by analyzing the number of absolute coincidences. Absolute coincidences are the number of spikes that coincide with respect to both firing times and amplitudes with a pre-defined precision δ. It is observed that similarity estimated by $\Gamma_{chaotic}$ is approximately equal to the percentage number of absolute coincidences. If the number of absolute coincidences are 25%, then the similarity estimated by $\Gamma_{chaotic}$ is approximately 0.25. This quantification ensures that the estimated similarity is realistic and mathematically realizable.

REFERENCES

[1] Lundström I (1974). Mechanical Wave Propagation on Nerve Axons. Journal of Theoretical Biology, 45, 487-499.
[2] Abbott LF, Kepler TB (1990). Model Neurons: From Hodgkin Huxley to Hopfield. Statistical Mechanics of Neural Networks, Edited by Garrido L, 5-18.
[3] Hasegawa H (2000). Responses of a Hodgkin-Huxley neuron to various types of spike-train inputs. Physical Review E, Vol. 61, No. 1.
[4] Agüera y Arcas B, Fairhall AL (2003). What causes a Neuron to Spike? Neural Computation 15, 1789-1807, (2003).
[5] Agüera y Arcas B, Fairhall AL, Bialek W (2003). Computation in a Single Neuron: Hodgkin and Huxley Revisited. Neural Computation 15, 1715-1749.
[6] Fourcaud-Trocmé N, Hansel D, van Vreeswijk C, Brunel N (2003). How Spike Generation Mechanisms Determine the Neuronal Response to Fluctuating Inputs. The Journal of Neuroscience, 23(37): 11628-11640.
[7] Kepecs A, Lisman J (2003). Information encoding and computation with spikes and bursts. Network: Comput. Neural Syst. 14, 103-118.
[8] Bokil HS, Pesaran B, Andersen RA, Mitra PP (2006). A Method for Detection and Classification of Events in Neural Activity. IEEE Transactions on Biomedical Engineering, Vol. 53, No. 8.#
[9] Davies RM, Gerstein GL, Baker SN (2006). Measurement of Time-Dependent Changes in the Irregularity of Neural Spiking. Journal of Neurophysiology, 96:906-918.
[10] Diba K, Koch C, Segev I (2006). Spike Propagation in dendrites with stochastic ion channels. Journal of Computational Neuroscience 20: 77-84.
[11] Dimitrov AG, Gedeon T (2006). Effects of stimulus transformations on estimates of sensory neuron selectivity. Journal of Computational Neuroscience 20: 265-283.
[12] Izhikevich EM (2006). Polychronization: Computation with Spikes. Neural Computation 18, 245-282.
[13] Li X, Ascoli GA (2006). Computational simulation of the input-output relationship in hippocampal pyramidal cells. Journal of Computational. Neuroscience, 21:191-209.
[14] Rinzel J (1985). Excitation dynamics: insights from simplified membrane models. Theoretical Trends in Neuroscience Federal Proceedings, Vol. 44, No. 15, 2944-2946.
[15] Panzeri S, Schultz SR, Treves A, Rolls ET (1999). Correlations and the encoding of information in the nervous system. Proc. R. Soc. Lond. B 266, 1001-1012.
[16] Gabbiani F, Metzner W (1999). Encoding and Processing of Sensory Information in Neuronal Spike Trains. *The Journal of Biology*, **202**, 1267-1279.
[17] Wang XJ, Buzsáki G (1996). Gamma Oscillation by Synaptic Inhibition in a Hippocampal Interneuronal Network Model. *The The Journal of Neuroscience, 16(2)*
[18] Guttman R, Feldman L, Jakobsson E (1980). Frequency Entrainment of Squid Axon Membrane. Journal of Membrane Biology, 56, 9-18.
[19] Matsumoto G, Kim K, Ueda T, Shimada J (1980). Electrical and Computer Simulations upon the Nervous Activities of Squid Giant Axons at and around the State of Spontaneous Repetitive Firing of Action Potentials. J. Phys. Soc. Jpn., 49, 906.
[20] Aihara K, Matsumoto G, Ikegaya Y (1984). Periodic and Non-periodic Responses of a Periodically Forced Hodgkin-Huxley Oscillator. Journal of Theoretica Biology, 109, 249-269.
[21] Matsumoto G, Aihara K, Ichikawa M, Tasaki A (1984). Periodic and Nonperiodic responses of membrane potentials in squid giant axons during sinusoidal current simulations. Journal of Theoretical Neurobiology, 3, 1-14.
[22] Hayashi h, Ishizuka S, Hirakawa K (1985). Chaotic responses of the pacemaker neuron. J. Phys. Soc. Jpn., 54, 2337.
[23] Holden AV (1987). Chaos. Manchester: Manchester University Press.
[24] Hasegawa H (2008). Information conveyed by neuron populations – Firing rate, fluctuations and synchrony. Neuroquantology, Vol. 6 (2), 105-118.
[25] Kaplan D, Glass L (1995). Understanding Non Linear Dynamics. Springer, New York.
[26] Wilson HR (1999). Spikes, Decisions and Actions – The dynamical foundations of neuroscience. Oxford University Press Inc., New York.
[27] Hodgkin A, Huxley A (1952). A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.* **117**:500–544.
[28] Sarangdhar M, Kambhampati C (2008a). Spiking Neurons: Is coincidence-factor enough to compare responses with fluctuating membrane voltage? In World Congress on Engineering 2008 : The 2008 International Conference of Systems Biology and Bioengineering, London, U.K. 2-4 July 2008, Vol. 2, pp 1640-1645.
[29] Sarangdhar M, Kambhampati C (2008b). Spiking Neurons and Synaptic Stimuli: Determining the Fidelity of Coincidence-Factor in Neural Response Comparison. Engineering Letters, Volume 16 Issue 4, pp 512-517.
[30] Sarangdhar M, Kambhampati C (2009). Spiking Neurons and Synaptic Stimuli - Neural Response Comparison using Coincidence-Factor. In Advances in Electrical Engineering and

Computational Science. Edited by Gelman L, Balkan N, Ao S. Published by Springer.

[31] Joeken S, Schwegler H (1995). Predicting spike train responses in neuron models; in M.Verleysen (ed.), Proceedings of the 3rd European Symposium on Artificial Neural Networks 1995, Brussels, Belgium, April 19-21, 1995, pp 93-98.

[32] Kistler WM, Gerstner W, Leo van Hemmen J (1997). Reduction of the Hodgkin-Huxley Equations to a Single-Variable Threshold Model. Neural Computation 9: 1015-1045.

[33] Chechik G, Anderson MJ, Bar-Yosef O, Young ED, Tishby N, Nelken I (2006). Reduction of Information Redundancy in the Ascending Auditory Pathway. Neuron 51, 359-368.

[34] Park MH, Kim S (1996). Analysis of Phase Models for two Coupled Hodgkin-Huxley Neurons. *Journal of the Korean Physical Society*, **Vol. 29, No. 1**, pp. 9-16.

[35] Jolivet R, Lewis TJ, Gerstner W (2004). Generalized Integrate-and-Fire Models of Neuronal Activity Approximate Spike Trains of a Detailed Model to a High Degree of Accuracy. Journal of Neurophysiology 92: 959-976.