Characterising Information Correlation in a Stochastic Izhikevich Neuron*

Zhijun Yang, Vaibhav Gandhi, Mehmet Karamanoglu
Department of Design Engineering and Mathematics
School of Science and Technology, Middlesex University
London NW4 4BT, UK
{Z.Yang, V.Gandhi, M.Karamanoglu}@mdx.ac.uk

Bruce Graham
Division of Computer Science and Mathematics
School of Natural Sciences, Stirling University
Stirling FK9 4LA, UK
b.graham@cs.stir.ac.uk

***Abstract*—The Izhikevich spiking neuron model is a relatively new mathematical framework which is able to represent many observed spiking neuron behaviors, excitatory or inhibitory, by simply adjusting a set of four model parameters. This model is deterministic in nature and has achieved wide applications in analytical and numerical analysis of biological neurons due largely to its biological plausibility and computational efficiency. In this work we present a stochastic version of the Izhikevich neuron, and measure its performance in transmitting information in a range of biological frequencies. The work reveals that the deterministic Izhikevich model has a wide information transmission range and is generally better in transmitting information than its stochastic counterpart.**

Keywords—Izhikevich neuron; Information content; Mutual information; Probability; Correlation

I. Introduction

A decade ago E.M. Izhikevich presented a novel spiking neuronal model which is able to mimic a single *in vivo* or *in vitro* biological neuron in generating ample spiking patterns [1]. This model combines the feature of biological plausibility of the classical Hodgkin-Huxley model with the feature of computational efficiency of the simple integrate-and-fire model. It can simulate many observed neuron behaviors by simply tuning a set of four model parameters. Nowadays the Izhikevich neuron model has been used in many works in computational neuroscience to simulate the brain functions like visual [2], auditory [3], tactile [4] and cortical [5] signal processing, and to mimic the dynamical behaviors of the large-scale neocortical neuronal networks [6] and their associated properties like categorization and decision-making [7]. The significance of this neuronal model, in terms of its abstraction and ability to provide detailed ionic level simulation, has been well recognized [8].

Neurons communicate with each other through release of neurotransmitters at synapses, which is driven by spikes (or action potentials). In neuroscience the information conveyed by neurons is described in two approaches, i.e., the mean firing rate of the stimulus spike train carries information, or the precise timing of the spikes carries information. For whichever approach it would be interesting to know how much information could be retained in the output spike train of a neuron in terms of the corresponding input spike train. In information theoretic analysis, the information transmitted between the stimuli to and outputs of a neuron can be expressed in terms of the interspike interval (ISI) distributions of the relative spike trains. Mathematical operations based on these distributions give measurements of the reliability and variability (corresponding to the entropy and conditional entropy, respectively) of the neuron responses with respect to different stimuli. The shared information between the input and output of a spiking neuron can thus be computed as the mutual information (MI) representing the information transmission capability of that neuron. This method, namely the direct method of maximum likelihood estimation [9], has been used to measure the information transmitted through an integrate-and-firing neuron [10], and an MNTB neuron with the calyx of Held synapse [11].

Although the dynamics of a single Izhikevich neuron has been well studied [12], its performance on information transmission is rarely explored. In this work, we first present a stochastic version of the Izhikevich neuron model, and then we use the information theoretic analysis method to characterize the information flowing through the neuron in the form of the input and output spike trains.

II. Methods

In this section the spiking neuron model and the method for measuring information transmission are introduced. The original Izhikevich model is presented which is followed by its stochastic version. The direct method of maximum likelihood estimation of the input and output spike train probabilistic distributions and computing of mutual information is also given.

A. The Izhikevich Spiking Neuron Model

The Izhikevich spiking neuron [1] is expressed by the following nonlinear ordinary differential equations.

$$V^{'} = 0.04V^2 + 5V + 140 - u + I \qquad (1)$$

This work was supported in part by a UK BBSRC grant to BPG, and a grant of the National Science Foundation of China 61073118.

$$u' = a(bV - u) \quad (2)$$

After the spike reaches its apex (*+30mV*), the membrane potential and the recovery variable are reset according to the following equation,

$$\text{if} \quad V \geq 30mV, \quad \text{then} \quad V \leftarrow c, \quad u \leftarrow u + d \quad (3)$$

where V is the membrane potential of the neuron, u is the recovery variable and I is the synaptic input current. By choosing different values for the model parameters *[a, b, c, d]*, the neuron can generate different spiking patterns. In this study the neuron is an excitatory one with the parameters *[a,b,c,d]=[0.02, 0.2, -65, 8]*. With this configuration of model parameters the neuron delivers regular spikes upon a constant input current [12]. This original Izhikevich neuron is a deterministic model as it issues the same output spike train when it is stimulated by a same, repeated input spike train.

B. The Stochastic Model

Since an *in vivo* neuron is unlikely to be deterministic, we modified the original Izhikevich neuron slightly by adding different levels of noise to its variables. The membrane potential and the recovery variable are both supposed to be contaminated by white Gaussian noise. The level of contamination is adjustable with the signal noise ratio (SNR) in dB. Now the stochastic version of the Izhikevich model can be written as follows.

$$V'_{SNR} = 0.04V_{SNR}^2 + 5V_{SNR} + 140 - u_{SNR} + I \quad (4)$$

$$u'_{SNR} = a(bV_{SNR} - u_{SNR}) \quad (5)$$

$$\text{if } V_{SNR} \geq 30mV, \quad \text{then} \quad V_{SNR} \leftarrow c, u_{SNR} \leftarrow u_{SNR} + d \quad (6)$$

where I is the synaptic current which can be an analogue value in the original Izhikevich neuron. Here I takes the form of spikes. V_{SNR} and u_{SNR} are the noise contaminated variables of the original Izhikevich neuron, which are represented as,

$$V_{SNR} = f(V) = AWGN(V, SNR) \quad (7)$$

$$u_{SNR} = f(u) = AWGN(u, SNR) \quad (8)$$

Here *AWGN* is a MATLAB function for adding white Gaussian noise with the relative signal to noise ratio to a signal.

C. Information Theoretic Method

Since we assume that the ISIs of the pre- and post-synaptic spike trains of an Izhikevich neuron contain information, the direct method [9] is used to characterize the extent of information content in the postsynaptic ISI with respect to an independent homogeneous Poisson spike train X as the input to the model. This involves computing the MI of pre- and post-synaptic ISIs to quantify the common information content for both input and output. Suppose the sequence of ISIs of an input spike train is $X = \{x_1, x_2, x_{3\ldots}, x_n\}$, where n is the number of the presynaptic ISIs. X represents for a Poisson process conveying temporal information. The greatest value of ISI, produced by a neuron, when a same spike train of a mean firing rate is repeatedly used to stimulate the neuron, is obtained and taken as a reference. The first percentile of this ISI value is defined as a bin resolution, whose precision can keep the information finite [9,10]. The ISI values produced by the neuron model are then discretized and distributed into the correct bins of the percentile of the greatest ISI value, hence we have the sequence of ISIs of the output spike train as $Y = \{y_1, y_2, y_3 \ldots, y_m\}$, where m is the number of postsynaptic ISIs. The probability distribution of the response *P(Y)* over a long time course can thus be estimated with the maximum likelihood direct estimation method [9]. The total entropy, *H(Y)*, in Shannon's theory [13], is a quantity measuring the amount of variability of the postsynaptic response Y to the ensemble of different inputs, without being constrained by input conditions.

$$H(Y) = -\sum_{i=1}^{100} p(y_i) \log_2 p(y_i) \quad (9)$$

where $p(y_i)$ is the probability of the ISI value y_i which fall in the i^{th} percentile with a value between y_i to y_{i+1}. The conditional entropy, $H(Y|X)$, is a quantity that measures the reliability of the postsynaptic response Y to the repeated presentations of the same inputs,

$$H(Y|X) = -\sum_{i=1}^{100} p(y_i|X) \log_2 p(y_i|X) \quad (10)$$

where $p(y_i|X)$ is the conditional probability of the model responses which fall in the i^{th} percentile, conditioned on the appearance of presynaptic stimulation sequence X. In numerical experiments, the probabilistic model was tested with different groups of Poisson spike trains with different mean frequencies. In the simulation a particular Poisson spike train of mean rate f is repeated as the input to the model for 40 times. Due to its stochastic nature the model will respond differently in its output ISI values at each time. We thus account for the reliability of a synapse conditioned on a specific input with an alternative calculation of the conditional entropy [11],

$$H(Y|X) = \frac{\sum_{j=1}^{n} (-\sum_{i=1}^{100} \hat{p}(y_i) \log_2 \hat{p}(y_i))}{n} \quad (11)$$

where n is the total number of input spikes in a spike train inducing the postsynaptic ISIs, $\hat{p}(y_i)$ is the probability of all ISI values in the 40 trials which are induced by the same input spike train and fall in the i^{th} percentile.

The mutual information *I(X;Y)* quantifying the common information between the presynaptic ISI sequence, X, and the postsynaptic ISI sequence, Y, can be described as,

$$I(X;Y) = H(Y) - H(Y|X) \quad (12)$$

III. Simulation Results

Randomly generated individual input spike trains with mean firing rates from *0.1Hz* to *100Hz* are used to stimulate the same stochastic Izhikevich neuron. The frequency range of the input spike trains covers the five biological frequency domains, i.e., delta, theta, alpha, beta and gamma rhythms. The number of spikes in a single input spike train is fixed at *1000* so the time span of spike trains of different frequencies are different. The simulation is done by using MATLAB. Each input spike train is used to stimulate a neuron repetitively for *40* times so that the entropy, conditional entropy and mutual information can be computed to characterize the correlation between the input and output spike trains. Figure *1* shows an example of the randomly generated input spike train of *20Hz* in mean firing rate and *14* in its amplitude (normalized to one in the figure), and the response of a stochastic Izhikevich neuron with *SNR=20*. It can be seen that the output spike train is much sparser compared with the input spike train as the neuron works in a fluctuation driven regime and a low amplitude is chosen for the presynaptic spikes to drive the postsynaptic action potentials.

We try to estimate the correlation between the above spike trains, i.e., the input train and its filtered output counterpart, under various conditions in our numerical experiments. In the first Monte Carlo simulation Poisson spike trains of *3* different mean firing rates, i.e., *4*, *20*, *60Hz*, are used to stimulate the neuron which has different noise levels in its activity (see Section II B). Each input spike train is used repetitively for *40* times, and the corresponding output spike train is recorded for *1000* spikes (and hence the same amount of ISIs). The entropy and conditional entropy of the neuron response, calculated based on the maximum likelihood estimated ISI distributions, are displayed in Figure *2*, according to the information theoretic method in Section II C.

It is well known that entropy is an information theoretic statistic that can be used to measure the variability of information transmission while conditional entropy measures the reliability of the transmission. For a deterministic system the conditional entropy is zero since the system generates the same outcomes upon the same inputs. The simulation shows that, when the neuron is stimulated by a theta frequency at *4* Hz, the neuron behaves somewhat regularly when it is highly noisy, with relatively weak stimuli generating small entropy and conditional entropy values. When the stimulation strength is low (here *12* or *14*), both entropy and conditional entropy values approximate zero even when the model is very noisy with the *SNR=2dB*. This observation shows that the model behaves similarly to a deterministic model without any noise under this condition, although the model is heavily noise contaminated. However, inspection of the *40* output spike trains from the noisy model when the stimulation is low in both its strength and frequencies shows that all spike trains are significantly different, as expected, in their ISIs. These contradictory observations are interesting and might reflect some hidden regular patterns which deserve a further exploration. It is observable that both entropy and conditional entropy reach their peak when SNR is around *20dB*. The model subject to different stimulations has both entropy and conditional entropy values converged and approximating the equilibrium, around *4* bits for entropy and *0* bits for conditional entropy, when the model approximates to being deterministic (high SNR).

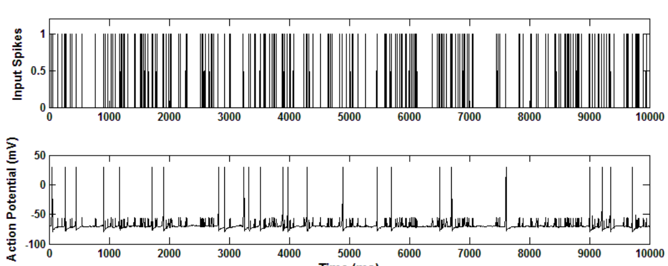

Fig. 1. An example randomly generated input spike train to a stochastic Izhikevich neuron (upper panel), the spike amplitude is *14* but here the amount is normalized to *1*. The neuron responds with a sparse spike train output (lower panel)

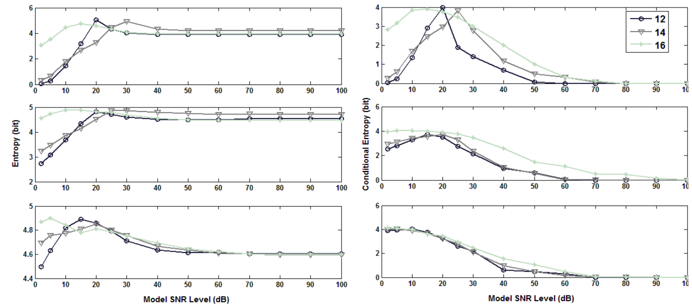

Fig. 2. Entropy (left column) and conditional entropy (right column) curves for a stochastic Izhikevich model with different noise levels (shown on the horizontal axis) subject to stimulation of *3* different random input spike trains with the mean firing rate of *4Hz* (top row), *20Hz* (middle row) and *60Hz* (bottom row). The input stimulation strength is *12*, *14* and *16*, respectively, as shown in the legend.

The model stimulated by higher input frequencies at *20* and *60* Hz performs similarly except that the entropy and conditional entropy values are still finite in very noisy conditions (low SNR).

The mutual information of the input and output spike trains, which can be used to characterize the common information in both input and output, or the correlation of both sides, is shown in Figure 3. The simulation shows that the common information content increases when the model noise level decreases. When the mean rate of input spike trains drops in both theta and beta frequencies (top and middle panels) the strongest spike trains could carry marginally more information for a very noisy model. When the noise level decreases, the strongest input spike trains carry less information than the other two types of input spike trains with weaker strength. When the model becomes quasi-deterministic with very low noise levels, the information content becomes flat around 4 bits, and the distinction between the strength of the inputs becomes minimal.

For input spike trains of gamma frequency (above *40* Hz, bottom panel), it seems that the strength of input spike trains makes no difference on information transmission efficiency.

We repeat our numeric experiments to investigate the information transmission performance of the stochastic Izhikevich model with respect to different stimulation frequencies. The stochastic Izhikevich neuron models with different noise levels at SNR=*5, 20, 80*dB were run upon input spike trains of average rates in the range from *0.1*Hz to *10*Hz, corresponding to the common delta and theta rhythms of the brain neuron. The input spike strength is fixed at *14* for this experiment. The entropy and conditional entropy of the neuron responses are shown in Figure *4*.

When the model is very noisy, the entropy and conditional entropy keep almost unchanged when the mean firing rate of input spike trains is increased, which means that little information is reliably transmitted. When the noise level is decreased from *5* to *20* dB SNR, both entropy and conditional entropy decrease with the increase of the mean firing rate of the input spike trains. In the delta rhythm range, with the increase of the stimulation frequency the information transmitted from the input to the output of the neuron gradually decreases while the transmission reliability gradually increases. In the theta rhythm range, little information is transmitted in a reliable way. When the neuron approximates its deterministic state as the noise level

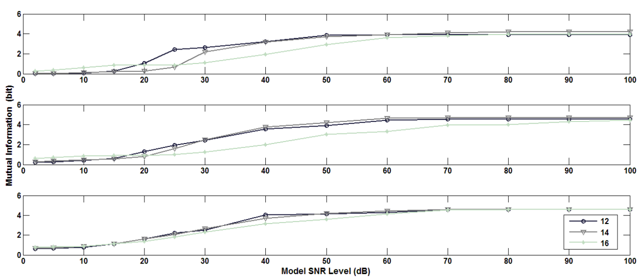

Fig. 3. Mutual information curves for the stochastic Izhikevich neuron with different noise levels subject to stimulation of *3* different random input spike trains with the mean firing rate of *4*Hz (top panel), 20Hz (middle panel) and *60*Hz (bottom panel). The input stimulation strength is *12*, *14* and *16*, respectively, as shown in the legend.

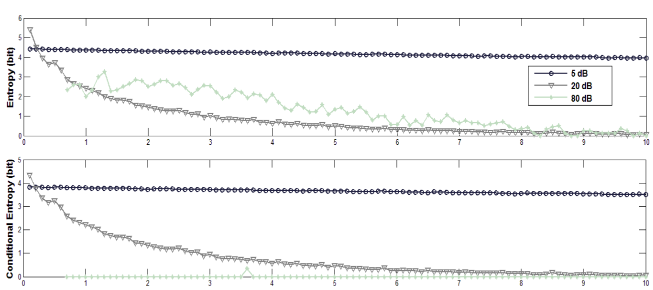

Fig. 4. The evolution of entropy (upper panel) and conditional entropy (lower panel) curves with the mean stimulation rate for the stochastic Izhikevich model with different noise levels (shown in the legend) subject to the stimulation of a fixed spike strength of *14*.

decreases for the SNR=*80*dB, in the delta rhythm range the entropy keeps at a relatively high level, and in theta range the entropy approaches zero gradually as the frequency increases, while the conditional entropy stays at zero in both rhythm ranges. This signifies that the neuron has finite information transmitted through it in the delta rhythm range, but much less information transmitted through it in the theta range.

The mutual information for the information transmission between the input and output spike trains is shown in Figure 5. It is consistent with our previous analysis that for the very noisy model the common information in both input and output terminals is almost unchanged. If the noise level in the neuron decreases a bit (in this case SNR=*20*dB), the common information is fairly high at the very low stimulation frequencies (*0.1-0.2*Hz) and decreases quickly with the increase of the stimulation frequency. For an almost deterministic model (SNR=*80*dB) the common information is high in the delta rhythm range of the input, and it gradually decreases in the theta range.

A further study on a deterministic Izhikevich neuron stimulated by a range of input spike trains with the mean firing rate from *0.1*Hz to *10*Hz, with frequency resolution of *0.1*Hz, is also done. The stimulation strength is again fixed at *14*. As in the previous tests, we stimulate the neuron with an input spike train within the specified frequency range to compute the entropy, conditional entropy and mutual information values. This process is repeated for *10* times with different random spike train inputs for statistical reliability. This is to ensure that the numeric results do not depend on a single input signal for all frequencies. The average curve of the *10* runs is shown in Figure *6* below.

The curve shown in Figure 6 can be qualitatively confirmed by the mutual information curve of a quasi-deterministic Izhikevich neuron as shown in Figure 5. At around 3 Hz, which is a delta frequency, the neuron demonstrates a peak value for mutual information. This observation implies a regular spiking Izhikevich neuron might have a wide information transmission range and its maximum information transmission capability may be in the low, delta frequency range. The output spike trains emitted by this type of neuron can be correlated with the input spike trains, and hence this sort of correlation may be carried on by the connected, descendant neurons to form a polychronous group of neurons [14], whose information transmission is studied by an accompanying work [15].

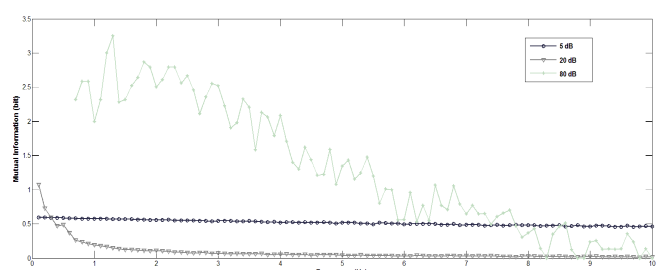

Fig. 5. Mutual information curves for the stochastic Izhikevich neuron with different noise levels subject to stimulation of different random input spike trains with the mean firing rate from *0.1* Hz to *10* Hz. The input stimulation strength is fixed at *14*.

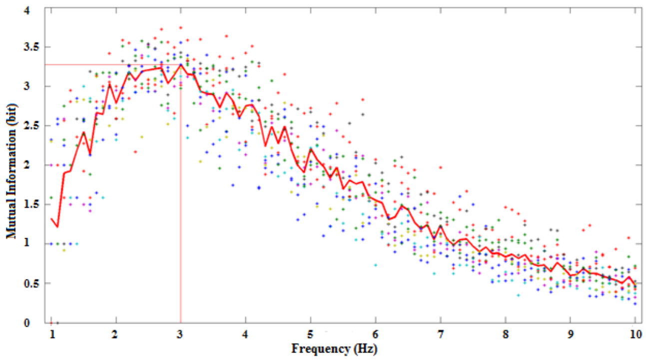

Fig. 6. The mutual information calculated based on the input and output spike trains' ISI distribution of an original, deterministic Izhikevich neuron. For each mean firing rate *10* independent, random spike trains are generated to stimulate the neuron. The corresponding *10* mutual information values are calculated and their averages are shown by a curve.

IV. Conclusion

In this work we presented a stochastic version of the Izhikevich neuron, and studied its information transmission capability by using the information theoretic method. The entropy, conditional entropy and mutual information values are obtained through maximum likelihood estimation of the ISI distributions of the input and output spike trains. Our work reveals that, in general, the deterministic Izhikevich neuron has a better information transmission capability than its noisy counterpart. The information processing ability is related with the mean firing rate of the input spike trains. It is obvious, from our numerical experiments, that the input spike trains with a mean firing rate in the range of the higher delta frequencies or the lower theta frequencies may be able to stimulate the neuron more efficiently in terms of having more information content encoded in the output spike trains.

Acknowledgment

This work has been supported, in part, by a UK BBSRC grant to BPG, and a China NSFC grant 61073118. We are grateful to Aymeric Siomme's effort to introduce MATLAB parallel computing toolbox to accelerate the data processing.

References

[1] E.M. Izhikevich, "Simple model of spiking neurons," IEEE Trans. Neural Netw., 14(6) : 1569-72, 2003.

[2] H. Super, A. Romeo, "Rebound spiking as a neural mechanism for surface filling-in," Journal of Cognitive Neurosci., 23(2) : 491-501, 2011.

[3] O. Macherey, R.P. Carlyon, A.V. Wieringen, J. Wouters, "A dual-process integrator-resonator model of the electrically stimulated human auditory nerve," Journal of the Association for Research in Otolaryngology (JARO), 8(1) : 84-104, 2007.

[4] L. Patanè, S. Hellbach, A.F. Krause, P. Arena, V. Dürr, "A insect- inspired bionic sensor for tactile localization and material classification with state-dependent modulation," Frontiers in Neurorobotics, 6:8, Jan. 2012.

[5] M. Richert, J.M. Nageswaran, N. Dutt, J.L. Krichmar, "An efficient simulation environment for modeling large-scale cortical processing," Frontiers in Neuroinformatics, 5:19, Sept. 2011.

[6] E.M. Izhikevich, G.M. Edelman, "A large-scale model of mammalian thalamocortical systems, " PNAS, 105 : 3593-98, 2008.

[7] M. Beyeler, N.D. Dutt, J.L. Krichmar, "Categorization and decision-making in a neurobiologically plausible spiking network using a STDP-like learning rule," Neural Networks, 48 : 109-124, 2013.

[8] A.V.M. Herz, T. Gollisch, C.K. Machens, D. Jaeger, "Modeling single-neuron dynamics and computations: A balance of detail and abstraction" Science, 314 : 80-85, 2006.

[9] A. Zador, "Impact of synaptic unreliability on the information transmitted by spiking neurons," Journal of Neurophysiology, 79 : 1219-29, 1998.

[10] C.F. Stevens, A. Zador, "Information through a spiking neuron," In: Advances in Neural Information Processing Systems (NIPS), vol. 8, pp.75-81, MIT Press, 1996.

[11] Z. Yang, M. Hennig, M. Postlewaite, I. Forthyse, B.P. Graham, "Wide-band information transmission at calyx of Held," Neural Computation, 21, 991-1017, 2009.

[12] E.M. Izhikevich, "Dynamical systems in neuroscience: The geometry of excitability and bursting," The MIT Press, 2007.

[13] C.E. Shannon, W.Weaver, "The mathematical theory of communication" University of IllinoisPress, 1949.

[14] E.M. Izhikevich, "Polychronization: Computation with spikes," Neural Computation, 18, 245-282, 2006.

[15] L. Guo, Q. Zhu, Z. Yang, V. Gandhi, M. Karamanoglu, "Analysis of spike-based information flow in an Izhikevich network," manuscript submitted to IJCNN, Killarney, Ireland, July 2015.