2023 RISP International Workshop on Nonlinear Circuits, Communications and Signal Processing (RISP NCSP 2023), Feb. 28 - Mar. 3, 2023

Periodic Input Leads an Izhikevich Neuron to Induce both Periodic and Irregular Responses

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Abstract

Electrophysiological experiments have clarified the properties of a single neuron, and mathematical neuron models that reproduce neuronal dynamics have been proposed. One of such models is the Izhikevich neuron model, which can reproduce various spike patterns with a remarkable computational efficiency. In this study, we computationally stimulated the Izhikevich neuron model with sinusoidal forcing. Evaluation of responses focusing on interspike intervals (ISIs) identified both periodic and irregular responses. The results also showed that the coefficient of variation of periodic responses was higher than that of irregular responses and that both activities were subject to modulation.

1. Introduction

Among the most important goals in the field of neuroscience is to clarify the mechanism of information processing by the brain. A way of reaching the goal is investigation of nonlinear dynamics of a single neuron, the fundamental component of the brain. Physiological experiments and mathematical modeling have worked together. Hayashi et al. [1] stimulated *Onchidium*'s giant neurons with sinusoidal current and identified chaotic responses. Aihara et al. [2] stimulated *Doryteuthis bleekeri*'s giant axons with sinusoidal input and identified periodic, quasi-periodic, and chaotic responses.

Computational neuroscience holds numerical experiments and analyses of mathematical neuron models. For example, Hodgkin and Huxley examined the electrophysiological properties of a neuron and formulated them as ordinary differential equations, later called the Hodgkin–Huxley model, for the first time [3]. Aihara et al. [4] observed that a periodically forced Hodgkin–Huxley model induced periodic, quasi-periodic, and chaotic responses. Although the Hodgkin–Huxley model has electrophysiologically meaningful parameters and can reproduce various spike patterns, it is computationally intensive on account of high dimensionality and unsuitable for large-scale simulations. Consequently, simpler neuron models have been proposed, among which is the Izhikevich neuron model [5]. The Izhikevich neuron model can reproduce as many kinds of neuronal activities as the Hodgkin–Huxley model does when it is much less computationally intensive.

Farokhniaee and Large [6] stimulated the Izhikevich neuron model with sinusoidal forcing and investigated mode–locking behavior. Nobukawa et al. [7, 8] examined responses of the Izhikevich neuron model to weak sinusoidal inputs. We have already studied the activities of regular spiking [9, 10], fast spiking [11], intrinsically bursting [12], and chattering [12] neurons of the Izhikevich neuron model and compared the four neuron types from the viewpoint of ISIs [13, 14]. However, much remains to be studied on other types of neurons.

In the present study, we evaluated responses of a low-threshold spiking (LTS) neuron of a periodically forced Izhikevich neuron model with three measures quantifying ISIs: the diversity index [15, 16], the coefficient of variation, and the local variation [17, 18].

2. The Izhikevich Neuron Model

The Izhikevich neuron model is a reduced variant of the Hodgkin–Huxley model and defined as follows:

$$\begin{cases} \dfrac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I(t) \\ \dfrac{du}{dt} = a(bv - u) \end{cases} \tag{1}$$

with the reset process after firing described as follows:

$$\text{when } v \geq 30 \text{ [mV]}, \quad \text{then} \begin{cases} v \leftarrow c \\ u \leftarrow u + d, \end{cases} \tag{2}$$

where v is the membrane potential and u is the recovery variable that gives negative feedback to v which represents the activation of K^+ ionic currents and inactivation of Na^+ ionic currents; t is time in milliseconds; a, b, c, and, d are dimensionless parameters to determine neuron types; $I(t)$ is time-dependent external forcing. The parameter set for an LTS neuron, the object of this study, is shown in Table 1.

Table 1: The parameters a, b, c, and d, and input current $I(t)$ of an LTS neuron.

a	b	c	d	$I(t)$
0.02	0.25	-65	2	10

Here, the external forcing $I(t)$ is composed of direct current I_{DC} and alternating current $I_{AC} = A \sin \frac{2\pi}{T} t$, defined as follows:

$$I(t) = I_{DC} + I_{AC} = I_{DC} + A \sin \frac{2\pi}{T} t, \tag{3}$$

where T and A represent the period and the amplitude of the sinusoidal forcing, respectively. We examined the effect of the period T and the amplitude A of the sinusoidal input on responses.

In this study, we adopted the Euler method with the interval of $h = 0.01$ to numerically calculate the Izhikevich neuron model. To estimate firing time t_F more accurately, we applied the linear interpolation by the following equation:

$$t_{\mathrm{F}} = t + \frac{30 - v(t)}{v(t+h) - v(t)} h, \tag{4}$$

where t satisfies $v(t) < 30$ and $v(t+h) \geq 30$. Although the Runge–Kutta method can solve differential equations more accurately, the Euler method with linear interpolation can estimate sufficiently accurate firing times with fewer computations [19]. In the following numerical experiments, we omitted spike sequences in $0 < t \leq 5,000$ and used those in $5,000 < t \leq 15,000$ in order that we eliminated transient states.

3. ISI Measures

Three measures are used for analyses on responses: the diversity index D [15, 16], the coefficient of variation C_v, and the local variation L_v [17, 18].

3.1 Diversity Index

The diversity index D is defined as follows [15, 16]:

$$D = \frac{M}{N}, \tag{5}$$

where M is the number of different values of ISIs and N is the total number of ISIs. Assume that N is sufficiently large. In this study, if two ISIs are equal up to six decimal places, we define them to be the same. In the case of periodic activities, M is a limited number and significantly smaller than N, which leads to D close to zero. On the contrary, chaotic activities result in D close to unity because neuron fires at irregular intervals and M is close to N. Thus, D can evaluate regularity/irregularity of neuronal activities.

3.2 Coefficient of Variation

The unbiased variance σ^2 of ISIs is given by

$$\sigma^2 = \frac{1}{N-1} \sum_{i=1}^{N} (s_i - \bar{s})^2, \tag{6}$$

where s_i is the i-th ISI and $\bar{s} = \frac{1}{N} \sum_{i=1}^{N} s_i$ is the average ISI.

The coefficient of variation C_v is defined as the ratio of the standard deviation σ to the mean $\bar{s}$ of ISIs:

$$C_v = \frac{\sigma}{\bar{s}}. \tag{7}$$

If all the ISIs are the same, $C_v = 0$. On the other hand, $C_v \to 1$ for a spike sequence following a Poisson distribution. A higher C_v represents a more irregular activity.

3.3 Local Variation

The local variation L_v is defined as follows [17, 18]:

$$L_v = \frac{1}{N-1} \sum_{i=1}^{N-1} \frac{3(s_i - s_{i+1})^2}{(s_i + s_{i+1})^2}. \tag{8}$$

The *three* in the summands is taken so that $L_v \to 1$ when ISIs are Poison sequence. If all the ISIs are the same, $L_v = 0$.

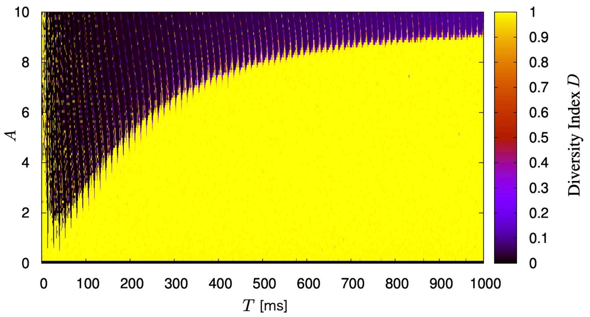
The diversity index D reflects only distribution of ISIs and insensitive to the actual differences between ISIs, to which C_v and L_v are subject. The coefficient of variation C_v is highly sensitive to fluctuation of firing rate, reflects only distribution of ISIs, and represents the global variability of spike sequences. On the other hand, the local variation L_v is subject to temporal order of ISIs and represents the intrinsic spiking characteristics independently of fluctuation of firing rate. When a neuron is globally modulated and its spike sequence seems to be locally periodic in appearance, C_v takes a large values while L_v takes a lower value. Thus, L_v can eliminate the effect of firing rate modulation and evaluate intrinsic characteristics.

4. Results

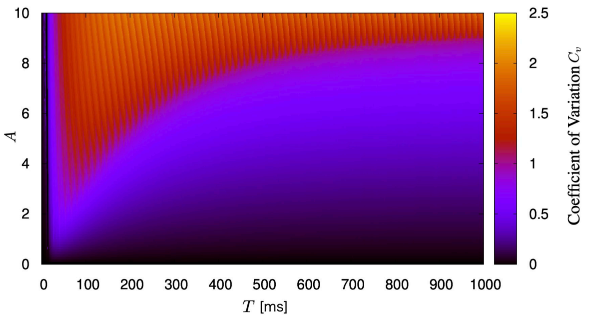
Figure 1 shows the period–amplitude planes of the measures, where the horizontal and the vertical axes represent the period and the amplitude of sinusoidal forcing, respectively, and the color bar represents values of the measures. The diversity index D indicates that there exist two domains: periodic responses (a black or purple region) and irregular responses (a yellow region) (See Fig. 1(a)). As A increases from zero to 10, the diversity index of ISIs noticeably changes. This implies that the phase transition from irregular response to periodic response occurs as A increases.

Figure 1(b) shows that smaller values of D correspond to larger values of C_v and that larger values of D correspond to smaller values of C_v. Thus, periodic spike sequence comprises a pattern of highly uneven ISIs. In an irregular spike sequence, ISIs differ slightly.

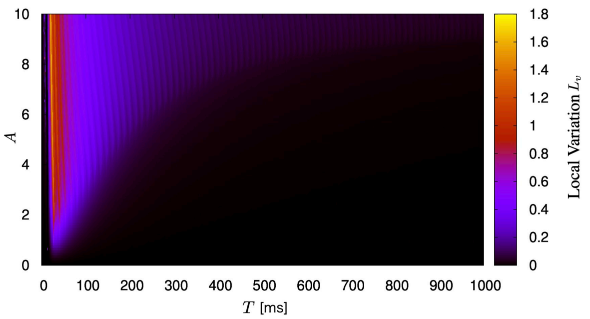
In Fig. 1(c), the values of L_v corresponding to periodic responses and corresponding to irregular responses are approximately zero in most parts although the former is slightly larger than the latter. Thus, both periodic and irregular responses are modulated by sinusoidal forcing. An exception is the region around $T = 30$, where the values of L_v are approximately equal to or larger than unity. This implies that activities are free from modulation in the region.



(a) The diversity index D



(b) The coefficient of variation C_v



(c) The local variation L_v

Figure 1: Measures of ISIs from of a periodically forced Izhikevich neuron model with parameters of an LTS neuron.

5. Conclusions

With the diversity index, the coefficient of variation, and the local variation, all of which quantify ISIs, we evaluated spike sequences of an LTS neuron of the Izhikevich neuron model in response to sinusoidal forcing. Evaluation of the diversity index shows that both periodic and irregular activities are induced depending on the period and the amplitude of sinusoidal input. Negative correlation between the diversity index and the coefficient of variation implies that periodic responses comprise repetition of a train of spikes with highly diverse ISIs and that irregular responses are much less diverse while same intervals are rarely repeated. For both periodic and irregular activities, the local variation takes low values, which indicates that modulation by sinusoidal forcing have an effect on activities regardless of periodicity or irregularity. However, when the period of sinusoidal forcing is close to 30, the local variation can be significantly high, indicating weak modulation effect.

Acknowledgment

The research of H. T. was partially supported by JSPS KAKENHI Grant Number JP22J12396. The research of T. I. was partially supported by JSPS KAKENHI Grant Numbers JP20H00596, JP21H03514, and JP22K18419.

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