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Non-periodic responses of the Izhikevich neuron model to periodic inputs

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Abstract: In the field of neuroscience, it is widely acknowledged that neurons exhibit periodic, quasi-periodic, and chaotic responses to periodic inputs. In this study, we evaluated the responses of the Izhikevich neuron model stimulated by sinusoidal inputs. First, we analyzed the dynamical behavior of the Izhikevich neuron model to the sinusoidal inputs in the state space and found two types of responses: periodic and non-periodic. Next, we obtained the domains of the periodic and non-periodic responses on the frequency–amplitude plane of the sinusoidal inputs by evaluating the diversity index of the inter-spike intervals. Finally, we analyzed the responses of the Izhikevich neuron model using the stroboscopic plot. Consequently, we clarified that a periodic response is a limit cycle and an irregular response is a torus, which implies that the irregular responses of the Izhikevich neuron model stimulated by sinusoidal inputs are quasi-periodic responses.

Key Words: Izhikevich neuron model, quasi-periodicity, diversity index of inter-spike intervals, stroboscopic plot

1. Introduction

The responses of a single neuron stimulated by sinusoidal inputs have been investigated experimentally, and the results have clarified that a neuron exhibits periodic, quasi-periodic, and chaotic responses to periodic inputs. One of the effective methods for identifying the types of neural responses is the stroboscopic plot: state points are sampled on a phase plane at several phases of a periodic input. For example, Hayashi et al. [1] investigated the chaotic responses of *Onchidium* giant neurons to sinusoidal inputs. Using the stroboscopic plot, they found that the state points on the attractor were mixed by the baker's transformation, which has an important mechanism for producing chaotic behavior: an attractor is stretched at some phases and folded at others. Aihara et al. [2] examined squid giant axons stimulated by sinusoidal inputs. Using the stroboscopic plot, they observed that periodic, quasi-periodic, and chaotic responses occurred.

The responses observed in real neurons have also been observed in mathematical neuron models. For example, Aihara et al. [3] investigated the responses of the Hodgkin–Huxley model [4] stimulated

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by the sinusoidal inputs and reproduced the complex behavior observed in the squid giant axons. The Hodgkin–Huxley model comprises four ordinary differential equations and can reproduce various spike patterns that are observed in a real neuron. However, although it is one of the most important mathematical neuron models, the Hodgkin–Huxley model is computationally intensive.

Consequently, computationally simple models have been proposed. For example, the Izhikevich neuron model [5] is a computationally simple mathematical neuron model consisting of two ordinary differential equations. Further, it has been confirmed that the model can reproduce various spike patterns observed in real neurons. Farokhniaee et al. [6] studied the responses of the Izhikevich neuron model to sinusoidal inputs from the viewpoint of n:m mode-locked states, where a neuron fires n action potentials per m cycles of sinusoidal inputs. The domains of various n:m mode-locked states were obtained on the frequency-amplitude planes. However, it is also important to investigate whether other irregular responses, such as chaotic or quasi-periodic responses can be observed when the Izhikevich neurons are stimulated by periodic inputs.

In this study, we used the Izhikevich neuron model with the parameter set of a regular spiking (RS) neuron and analyzed the responses to sinusoidal inputs. First, we analyzed the dynamical behavior in the phase plane of the Izhikevich neuron model stimulated by the sinusoidal inputs. Consequently, we discovered that both periodic and non-periodic responses exist. Second, we analyzed the responses of the Izhikevich neuron model by using the diversity index of inter-spike intervals (ISIs) to distinguish between the periodic and irregular responses. Numerical experiments showed that the domains of both periodic responses and non-periodic responses exist on the frequency–amplitude plane of sinusoidal inputs. Third, we investigated the responses using the stroboscopic plot to observe the state points at phases of the sinusoidal inputs. We found that a periodic response is a limit cycle and a non-periodic response is a torus, which indicates that the irregular responses of the Izhikevich neuron model stimulated by sinusoidal inputs are quasi-periodic responses.

2. The Izhikevich Neuron Model

The Izhikevich neuron model [5] is defined by the following two ordinary differential equations:

$$\begin{cases} \dot{v} = 0.04v^2 + 5v + 140 - u + I(t), \\ \dot{u} = a(bv - u). \end{cases}$$
(1)

In Eq. (1), v represents the membrane potential of a neuron and u represents the recovery variable, which describes the activation of K⁺ ionic currents and the inactivation of Na⁺ ionic currents and gives negative feedback to v; a and b are dimensionless parameters. When $v \ge 30$ [mV], the neuron fires, and both v and u are reset by $v \leftarrow c$ and $u \leftarrow u+d$, where c and d are dimensionless parameters. With a proper parameter set, the Izhikevich neuron model can reproduce various spike patterns [5]. In Eq. (1), I(t) is a time-dependent external input and comprises two terms: the constant term I_{DC} and the periodic term I_{AC} :

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

where A is the amplitude and T is the period of the periodic input.

In this study, we set (a, b, c, d) = (0.02, 0.2, -65, 8), which corresponds to an RS neuron [5]. The model was numerically calculated by using the Euler method with the interval h = 0.01 [ms]. The firing time $t_{\rm F}$ is defined by the following linear interpolation when the membrane potential v(t + h) is above 30 [mV] [7]:

$$t_{\rm F} = t + \frac{30 - v(t)}{v(t+h) - v(t)}h$$
(3)

3. Numerical Experiments

3.1 Phase Planes

Figure 1 shows an example of the trajectories of the periodic and irregular responses. In Fig. 1, the states of $0 \le t < 5,000$ [ms] are omitted as transient states and the states of $5,000 \le t \le 5,600$ [ms]



Fig. 1. Trajectories of the Izhikevich neuron model stimulated by sinusoidal inputs. (a) A periodic response (A = 7.5 and T = 200 [ms]) and (b) an irregular response (A = 2.5 and T = 200 [ms]).

are plotted. Figure 1(a) is the response when A = 7.5 and T = 200 [ms]. The trajectory is closed and nine spikes exist in the trajectory; thus, the response is period nine. Figure 1(b) is the response when A = 2.5 and T = 200 [ms]. The trajectory is not closed, which indicates that the response is not periodic but non-periodic. In Fig. 1(a), the *v*-nullcline intersects with the *u*-nullcline if the sinusoidal input takes the minimum value $(I(t) = I_{DC} - A)$. By contrast, in Fig. 1(b), the *v*-nullcline never intersects with the *u*-nullcline. When the amplitude A = 6, the *v*-nullcline is tangential to the *u*-nullcline at the minimum value of I(t). These characteristics could play a crucial role in producing the irregular responses of the Izhikevich neuron model stimulated by the sinusoidal inputs.

3.2 The Diversity Index of Inter-Spike Intervals

In Sec. 3.1, we showed that a qualitative difference exists in the behavior of the Izhikevich neuron model stimulated by the sinusoidal inputs. In this section, we introduce a quantitative index to investigate the relationship between the responses and the sinusoidal inputs. Specifically, we use the diversity index of ISIs [8] to evaluate the response of the Izhikevich neuron model. Let us define the *i*th firing time of the membrane potential v as t_i . Then, we obtain the *i*th ISI as $s_i = t_{i+1} - t_i$. The diversity index of ISIs is defined as R = M/N, where M is the number of different types of ISIs and N is the total number of ISIs [8]. When the responses are irregular, M is close to N. Therefore, R is



Fig. 2. Diversity indices of ISIs when the amplitude A and the period T are changed.

close to unity for a sufficiently large N. When the responses are periodic, M is significantly smaller than N. Therefore, R is close to zero for a sufficiently large N. Thus, R is larger than zero and less than or equal to unity. In this study, if the *i*th and *j*th ISIs are equal to two decimal places, we define them to be the same.

We set $I_{DC} = 10$ and changed the amplitude A over the range of $0 \le A \le 10$ in increments of 0.1, and the period T over the range of $1 \le T \le 2,000$ [ms] in increments of unity. Spikes of $0 \le t < 5,000$ [ms] were omitted as transient states, and spikes of $5,000 \le t \le 15,000$ [ms] were used to calculate the diversity indices of ISIs.

Figure 2 shows the diversity indices of ISIs. The horizontal and vertical axes represent the period T and the amplitude A of Eq. (2), respectively. The color bar represents the diversity indices of ISIs. In Fig. 2, the region where the diversity indices of ISIs are close to zero corresponds to the periodic responses and the region where the diversity indices of ISIs are close to unity corresponds to the irregular responses. When the period T is relatively small and the amplitudes are less than six, the responses are periodic. As T increases, the boundary between the periodic responses and irregular responses to the amplitude of approximately A = 6.

3.3 Stroboscopic Plot

The stroboscopic plot is effective for analyzing non-autonomous dynamical systems with periodic external force. In this method, state points are sampled at a certain phase of the periodic input. The stroboscopic plot has been adopted not only in electrophysiological experiments [1,2], but also in the analyses of mathematical models. If a finite number of state points are observed using the stroboscopic plot, an attractor is a limit cycle. The n/m synchronized oscillation is a periodic response in which a neuron fires n times during m cycles of a sinusoidal input. When the fundamental period of the n/m synchronized oscillation is equal to the product of m and the period T of a sinusoidal input of Eq. (2), m points are observed by the stroboscopic plot. If a closed curve is observed by the stroboscopic plot, the attractor is a torus, which indicates a quasi-periodic response. In the case of a chaotic response, a set of state points is stretched in the direction of the greatest instability, which leads to sensitive dependence on initial conditions; then, the set is folded onto itself, which leads to the boundedness of an attractor. Such a stretch and fold mechanism is one of the fundamental mechanisms for producing chaotic behavior.

Figure 3 shows the stroboscopic plot of a nine-period response when A = 7.5 and T = 200 [ms]. Here, the states of $0 \le t < 5,000$ [ms] are omitted as transient states, and the states of $5,000 \le t \le$



Fig. 3. Stroboscopic plot of a 9/2 synchronized response (A = 7.5 and T = 200 [ms]).



Fig. 4. Stroboscopic plot of an irregular response (A = 2.5 and T = 200 [ms]).

55,000 [ms] are plotted. The attractor is a limit cycle because two points are observed, as shown in Fig. 3. The trajectory observed in Fig. 1(a) indicates that the response is period nine. Thus, the response is 9/2 synchronized.

Figure 4 shows the stroboscopic plot of an irregular response when A = 2.5 and T = 200 [ms]. The attractor is a torus because U-shaped curves are observed, as shown in Fig. 4. The stroboscopic plot shows U-shaped curves instead of closed curves because the variables v and u are reset after the firing of a neuron in this model. The torus trajectory is a characteristic of quasi-periodic responses. Thus, the irregular response shown in Fig. 4 is not chaotic but quasi-periodic.

While examining the responses of the model with the stroboscopic plot by changing the amplitude A and the period T of the sinusoidal inputs, we found some irregular responses whose attractors were not tori. One of the examples is shown in Fig. 5. Figure 5 shows the stroboscopic plot of an irregular response when A = 1.5 and T = 180 [ms]. The U-shaped curves in the stroboscopic plot at the phases 0° , 60° , 120° , 150° , 240° , and 270° are discontinuous. The curves in the stroboscopic plot at the other phases, 30° , 90° , 180° , 210° , 300° , and 330° , are continuous.



Fig. 5. Stroboscopic plot of an irregular response (A = 1.5 and T = 180 [ms]).

4. Conclusion

In this study, we analyzed the responses of the Izhikevich neuron model stimulated by sinusoidal inputs. First, we investigated the behavior of the Izhikevich neuron model stimulated by the sinusoidal inputs on the phase plane with nullclines and found that both periodic and non-periodic responses exist. Second, we evaluated the diversity indices of ISIs by changing the amplitude and the period of the sinusoidal inputs. We found that periodic responses are induced by sinusoidal inputs with an amplitude higher than six, and irregular responses are induced by sinusoidal inputs with an amplitude less than six and with a relatively large period. Moreover, we found that the *v*-nullcline is tangential to the *u*-nullcline at the minimum value of a sinusoidal input when the amplitude is equal to six. Third, we investigated whether the state points were stretched and folded using the stroboscopic plot. Two distinct points were observed by using the stroboscopic plot of a nine-period response, which indicates that the attractor is a limit cycle. On the other hand, U-shaped curves were observed in the stroboscopic plot of an irregular response, which indicates that the irregular responses of the Izhikevich neuron model stimulated by the sinusoidal inputs are quasi-periodic rather than chaotic. Furthermore, the attractor of some irregular responses seem to be neither limit cycles nor tori.

In this study, using the diversity indices and the stroboscopic plot, we analyzed the complex and non-periodic responses of the Izhikevich neuron model stimulated by sinusoidal inputs. However, we did not find any clear evidence of the stretch and fold mechanism solely from the numerical results. One of the possible reasons for this could be due to the reset process in the Izhikevich neuron model. Thus, an important future issue is to analyze the possible chaotic responses of the Izhikevich neuron model by a more direct approach; for example, estimating Lyapunov spectra for dynamical systems with a reset process [9]. Using such an approach, we could evaluate the chaotic responses in the Izhikevich neuron model stimulated by periodic inputs and predict its complex behavior theoretically.

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