A Numerical Study of the Bistability of a Mathematical Model of Leech Oscillator Interneurons: The Transient Current Pulse Condition for Inducing the Switch from a Periodic Spiking State to a Chaotic Spiking State

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Abstract

This article reports the results of a numerical simulation of the bistability of a mathematical model of leech oscillator interneurons that is described by a system of nonlinear ordinary differential equations. The study examines the bistability of a periodic spiking state and a chaotic spiking state that was reported previously under certain parameter conditions of this model, and it conducts a numerical simulation to clarify the transient current pulse condition for inducing the switch from a periodic spiking state to a chaotic spiking state. The transient current pulse is injected at different phases of a periodic spiking oscillation. The results of numerical simulation suggest that a depolarizing current pulse can induce the switch. The maximum value ($I_{\text{app, max}}$) and minimum value ($I_{\text{app, min}}$) of the current pulse amplitude that induces the switch are revealed at each phase of a periodic spiking oscillation. In addition, the range of amplitude that can induce the switch (defined as $I_{\text{app, max}} - I_{\text{app, min}} + 1$) is revealed at each phase of a periodic spiking oscillation. Correlations between $I_{\text{app, min}}$ and $I_{\text{app, max}}$, between $I_{\text{app, min}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$, and between $I_{\text{app, max}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$ are revealed.
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1 Introduction

Mathematical models of leech oscillator interneurons (e.g., models that have been reported previously [1–3]) are examples of nonlinear dynamical systems in neurobiophysics. These models are all described by systems of nonlinear ordinary differential equations (ODEs) based on the Hodgkin–Huxley formalism, simulate the interneurons’ membrane potential oscillation, and exhibit various types of dynamical states, including as a silent state, a spiking state, and a bursting state. One difference between these models [1–3] is the number of state variables (i.e., the dimension) of the models (this difference derives from the difference in pharmacological conditions). Under certain pharmacological conditions, the leech oscillator interneuron model is described by a 14-dimensional [1] or 5-dimensional [2] model, and exhibits bistability of a bursting state and a silent state. Under a different pharmacological condition, the model is described by a 3-dimensional model [3], and it exhibits bistability of two different types of spiking states. Interestingly, this 3-dimensional model exhibits a chaotic spiking state under a certain parameter condition [3]. Moreover, this chaotic spiking state can coexist with a periodic spiking state (i.e., there is bistability of a periodic spiking state and a chaotic spiking state) [3]. Findings of a previous study of the 5-dimensional model suggested that one can observe the switch from a bursting state to a silent state by injecting a certain transient current pulse, and they demonstrated the dependence of the switch on the phase and amplitude of the current pulse [2]. Based on this previous report, for better understanding of the bistability of the 3-dimensional model, it is important to reveal the dependence of the switch on the phase and amplitude of the current pulse between different dynamical states (e.g., the switch from a periodic spiking state to a chaotic spiking state). However, this has not been investigated as yet. This study carries out a numerical simulation of the 3-dimensional model to provide detailed clarification of the current pulse condition for inducing the switch from a periodic spiking state to a chaotic spiking state.

2 The 3-Dimensional Mathematical Model of Leech Oscillator Interneurons

The mathematical model examined in this study is described by a system of three-coupled nonlinear ODEs:
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\[ \frac{dV}{dt} = \frac{1}{C} \left( I - I_{Na}(V,h_{Na}) - I_{K2}(V,m_{K2}) - I_L(V) \right) \quad (1) \]

\[ \frac{dm_{K2}}{dt} = \frac{1}{\tau_{K2}} \left( f_{-83,(0.018-0.025361)}(V) - m_{K2} \right) \quad (2) \]

\[ \frac{dh_{Na}}{dt} = \frac{1}{\tau_{Na}} \left( f_{500,0.0333}(V) - h_{Na} \right) \quad (3) \]

where \( V \) (the membrane potential of leech oscillator interneurons), \( m_{K2} \) (the gating variable of activation of the persistent potassium conductance), and \( h_{Na} \) (the gating variable of inactivation of the transient sodium conductance) are state variables; \( t \) (s) is time; \( C \) (= 0.5 nF) is the membrane capacitance; \( \tau_{K2} \) (= 0.25 s) and \( \tau_{Na} \) (= 0.0405 s) are the time constants of \( m_{K2} \) and \( h_{Na} \), respectively; \( I \) (nA) (a transient current pulse) is a system parameter (detailed explanations are given in the results section); \( f_{A,B}(V) \) is a Boltzman function (i.e., \( f_{A,B}(V) = \frac{1}{1 + e^{(A-B)/C}} \)); and

\( I_{Na}(V,h_{Na}) \), \( I_{K2}(V,m_{K2}) \), and \( I_L(V) \) are the transient sodium current, the persistent potassium current, and the leak current, respectively, which are defined as:

\[ I_{Na}(V,h_{Na}) = g_{Na} f_{-150,0.0368}(V) h_{Na} (V - E_{Na}) \quad (4) \]

\[ I_{K2}(V,m_{K2}) = g_{K2} m_{K2}^2 (V - E_K) \quad (5) \]

\[ I_L(V) = g_{L} (V - E_L) \quad (6) \]

where \( g_{Na} \) (= 200 nS), \( g_{K2} \) (= 30 nS), and \( g_{L} \) (= 8 nS) are the maximum conductances of \( I_{Na}(V,h_{Na}) \), \( I_{K2}(V,m_{K2}) \), and \( I_L(V) \), respectively; and \( E_{Na} \) (= 0.045 V), \( E_K \) (= -0.07 V), and \( E_L \) (= -0.046 V) are the reversal potentials of \( I_{Na}(V,h_{Na}) \), \( I_{K2}(V,m_{K2}) \), and \( I_L(V) \), respectively. Equations (1)–(6) are solved numerically by means of the free and open source software Scilab (http://www.scilab.org/) under the initial condition \( V = -0.0252204 \) V, \( m_{K2} = 0.115693 \), and \( h_{Na} = 0.00855340 \). Details of the equations are provided in [3].

3 Numerical Results

Figure 1 depicts the time courses of \( V \) obtained by the simulation, which starts under conditions of \( I = 0 \). Just after the onset of simulation, the model exhibits a periodic spiking state (Figure 1a and 1b). If the transient current pulse with an amplitude of 10 nA and a duration of 0.0169 s is injected into the model at \( t = 4.0705 \) s (i.e., \( I = 10 \) nA during \( t = 4.0705 \) s and \( t = (4.0705+0.0169) \) s, and \( I = 0 \) after \( t = (4.0705+0.0169) \) s), the dynamical state of the model changes from a periodic spiking state to a chaotic spiking state (Figure 1a). Conversely, if the current pulse with an amplitude of 5 nA and a duration that is the same as that in Figure 1a is injected into the model at the same timing as in Figure 1a (i.e., \( I = 5 \) nA during \( t = 4.0705 \) s and \( t = (4.0705+0.0169) \) s, and \( I = 0 \) after \( t = (4.0705+0.0169) \) s), the dynamical state of the model does not change from a periodic spiking to chaotic spiking state (Figure 1b).
To clarify in detail the current pulse condition for inducing the switch from a periodic spiking state to a chaotic spiking state, this study alters the values of the timing [i.e., phase of a periodic spiking oscillation (\(\phi\))] and amplitude (\(I_{\text{app}}\)) of the current pulse, and examines numerically whether the switch can be observed (Figure 2). Figure 2a shows the definition of \(\phi\). The simulation in Figure 2a is conducted under conditions in which \(I = 0\) at all \(t\). \(T_1 = 3.986\) s is defined as \(\phi = 0\%\), and \(T_2 = 4.155\) s is defined as \(\phi = 100\%\) [i.e., a period of a periodic spiking oscillation (= \(T_2 - T_1 = \Delta T\)) is 0.169 s] (Figure 2a). Figure 2b shows the current pulse conditions where the switch can be observed (shown as black circles), and where the switch does not occur (shown as white circles). All the simulations in Figure 2b and 2c start with \(I = 0\), and the transient current pulse with an amplitude of \(I_{\text{app}}\) and a duration of 10\% \(\Delta T\) is injected into the model at \(t = T_1 + \Delta T \times \phi\%\) (i.e., \(I = I_{\text{app}}\) (nA) during \(t = T_1 + \Delta T \times \phi\%\) and \(t = T_1 + \Delta T \times (\phi + 10)\%\), and \(I = 0\) after \(t = T_1 + \Delta T \times (\phi + 10)\%\). As shown in Figure 2b, at each \(\phi\), the switch can be induced by the current pulse whose amplitude is a positive value (i.e., the depolarizing current pulse). The maximum value (\(I_{\text{app, max}}\)) and the minimum value (\(I_{\text{app, min}}\)) of the current pulse amplitude that induces the switch are detected at each \(\phi\) (Figure 2b). When \(\phi\) is changed, \(I_{\text{app, min}}\) and \(I_{\text{app, max}}\) also change: both \(I_{\text{app, min}}\) and \(I_{\text{app, max}}\) are relatively small when \(\phi\) is between 0\%–50\% (i.e., \(\phi\) corresponds to a falling phase of a periodic spiking oscillation), whereas both values are relatively large when \(\phi\) is between 60\%–80\% (i.e., \(\phi\) corresponds to a rising phase of a periodic spiking oscillation). When \(\phi\) is changed, the range of amplitude that can induce the switch (defined as \(I_{\text{app, max}} - I_{\text{app, min}} + 1\)) also changes: the range is relatively small when \(\phi\) is between 0–50\%, whereas the range is relatively large when \(\phi\) is between 60\%–80\%. (Figure 2c).

In addition, this study investigates correlations between \(I_{\text{app, min}}\) and \(I_{\text{app, max}}\), between \(I_{\text{app, min}}\) and \(I_{\text{app, max}} - I_{\text{app, min}} + 1\), and between \(I_{\text{app, max}}\) and \(I_{\text{app, max}} - I_{\text{app, min}} + 1\) (Figure 3). The correlation coefficients between \(I_{\text{app, min}}\) and \(I_{\text{app, max}}\) (Pearson’s correlation coefficient \(r = 0.9917, n = 11, P = 2.5311 \times 10^{-9}\)) (Figure 3a), between \(I_{\text{app, min}}\) and \(I_{\text{app, max}} - I_{\text{app, min}} + 1\) (Pearson’s correlation coefficient \(r = 0.9717, n = 11, P = 6.05511 \times 10^{-7}\)) (Figure 3b), and between \(I_{\text{app, max}}\) and \(I_{\text{app, max}} - I_{\text{app, min}} + 1\) (Pearson’s correlation coefficient \(r = 0.9940, n = 11, P = 5.69842 \times 10^{-10}\)) (Figure 3c) are all statistically significant.

4 Conclusion

This study examines the bistability of a periodic spiking state and a chaotic spiking state in a 3-dimensional mathematical model of leech oscillator interneurons [3] and reports the results of a numerical simulation of the relationship between the switch from a periodic spiking state to a chaotic spiking state by the transient current pulse and the condition of the pulse. Importantly, the study clarifies the dependence of the switch on the phase (\(\phi\)) and the amplitude (\(I_{\text{app}}\)) of the current pulse, which has not been reported previously [3]. Bistability
is also seen in mathematical models that differ from leech oscillator interneurons. In particular, our previous studies demonstrated how the switch between different dynamical states is dependent on the transient current pulse condition in mathematical models of snail RPa1 neurons [4], circadian pacemaker neurons [5], and neocortical pyramidal neurons [6]. However, the types of bistability in our previous studies (i.e., bistability of a periodic bursting state and a chaotic spiking state [4], bistability of a periodic spiking state and a depolarized steady state [5], and bistability of a periodic spiking state and a hyperpolarized steady state [6]). differ from that in the current study, which investigates the bistability of a periodic spiking state and a chaotic spiking state.

Figure 1. Time courses of $V$ of the leech oscillator interneuron model. (a) The transient current pulse (indicated by the arrow) with an amplitude of 10 nA and a duration of 0.0169 s is injected into the model at $t = 4.0705$ s. (b) The transient current pulse (indicated by the arrow) with an amplitude of 5 nA and a duration of 0.0169 s is injected into the model at $t = 4.0705$ s.
Figure 2. The dependence of the switch from a periodic spiking state to a chaotic spiking state by the transient current pulse on both the phase ($\phi$) and the amplitude ($I_{app}$) of the current pulse applied to the leech oscillator interneuron model. (a) The definition of $\phi$. (b) The dependence of the switch on $\phi$ and $I_{app}$. White circles indicate that the switch does not occur, whereas black circles indicate that the switch occurs. $I_{app,\text{min}}$ at $\phi = 0\%$ and $I_{app,\text{max}}$ at $\phi = 0\%$ are also indicated by arrows. (c) The dependence of $I_{app,\text{max}} - I_{app,\text{min}} + 1$ on $\phi$. 
Figure 3. Correlations between $I_{\text{app, min}}$ and $I_{\text{app, max}}$, between $I_{\text{app, min}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$, and between $I_{\text{app, max}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$ in the leech oscillator interneuron model. (a) The correlation between $I_{\text{app, min}}$ and $I_{\text{app, max}}$. (b) The correlation between $I_{\text{app, min}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$. (c) The correlation between $I_{\text{app, max}}$ and $I_{\text{app, max}} - I_{\text{app, min}} + 1$. 

$I_{\text{app, min}}$ (nA) $I_{\text{app, max}}$ (nA) $I_{\text{app, max}} - I_{\text{app, min}} + 1$ (nA)
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