UDC 612.822:53.096:576.32/.36

L. WANG[1], S. LIU[1], J. ZHANG[2], AND Y. ZENG[2]

TEMPERATURE-DEPENDENT TRANSITIONS OF BURST FIRING PATTERNS IN A MODEL PYRAMIDAL NEURON

Received March 6, 2012

Environmental temperature exerts significant influences on neuronal firing and information encodings. Concepts on the mechanisms of the respective effects are still elusive and controversial. In our study, we examined the effect of temperature on firing patterns in a model cortical pyramidal neuron. It was found that a variety of firing patterns is obtained under different temperatures. In addition, the transition modes between these firing patterns display a clear periodic bifurcation phenomenon when the temperature varies within a certain range. Several typical bifurcation modes were found, in particular period-doubling bifurcation and period-adding bifurcation.

Keywords: temperature; model cortical pyramidal neuron, interspike interval (ISI), periodic bifurcation, firing patterns.

INTRODUCTION

The activities of neurons are mainly manifested in their electrical behaviors. The respective kinds of behavior are commonly represented as potential differences between the inside and outside of neurons, which are also termed as the membrane potential (MP); action potentials (APs) are the most important form of changes in the latter. Except for the intrinsic mechanisms, such as the distribution of ion channels [1, 2], morphology of the neuron [3, 4], and permeability of the neuronal membrane [5, 6], other factors, such as types of external stimuli [7, 8], noise (internal or external) [9, 10], and temperature [11, 12], can all contribute to the electrical responsiveness of neurons.

As an unignorable factor in the neural systems, temperature can exert crucial influences on the functional properties of neurons. Variation in temperature can lead to changes in the basic properties of excitable cells, e.g., the MP, input resistance, shape and amplitude of APs, and propagation of the latter [13]. Earlier documents have shown that the permeability ratio between sodium and potassium is temperature-dependent, and this ratio in gastroesophageal giant neurons of a marine mollusc may rise with increased temperature [14] but decreases in cat spinal motoneurons under rapid local temperature changes [15]. In addition, different kinds of animals may behave dissimilarly under a certain temperature; some animals are mostly activated at higher temperatures [16], while others may incline to be activated at lower temperatures [17].

Temperature dependences in the nervous system were subjected to intense research because of their physiological significance and dynamical complexity. For instance, Yang and Jia [18] studied the effect of temperature on neuronal spontaneous AP trains and concluded that the increase in patch temperature could lead to a decrease in the mean open rates of sodium and potassium channels of a Hodgkin–Huxley (HH) neuron, and the mean duration of spikes also decreased. Thompson et al. [19] investigated the temperature-dependent intrinsic membrane properties and synaptic potentials in guinea pig *CA1* hippocampal pyramidal neurons. They concluded that reductions in temperature, e.g., by 5 to 10°C from the normal, can significantly change the intrinsic and synaptic characteristics of these neurons, and adaptation of spiking of hippocampal *CA1* neurons during a prolonged depolarizing stimulus can be enhanced at low temperatures. Some researchers examined the effects of temperature on the neuron firing patterns using computational approaches. For example, Du et al. [12] analyzed firing behaviors of a cold receptor neuron in a conductance-based model using computer simulation; these authors used ISI distance as a measure for neuronal information encoding, to characterize the

---

[1] South China University of Technology, Guangzhou, China.
[2] Biomedical Engineering Center, Beijing University of Technology, Beijing, China.
Correspondence should be addressed to Shenquan Liu
(e-mail: mashqliu@scut.edu.cn) or Yanjun Zeng (e-mail: yjzeng@bjut.edu.cn).

effects of temperature in the mentioned model neuron. Their simulation results showed that neuronal spike sequences of cold receptor neurons are more strongly affected by noise under low temperatures, while the impacts are relatively small at high temperatures. Yuan et al. [20] studied the impact of environmental temperature on spike properties of an HH neuron subjected to direct current stimulation and concluded that changes of neuronal burst spiking with variation of environmental temperature are realized due to shifts in the environment-dependent spiking threshold.

Based on these valuable and instructive studies, we examined the influence of temperature on neuronal burst firing behavior and its transition modes in a model pyramidal neuron. Numerical results of this study not only illustrate the important role of temperature in the generation and switching of various burst firing patterns, but also give us specific transition modes from which we can clearly see how these firing patterns change from one type to another.

MODEL AND METHODS

The model we investigated is that of a cortical pyramidal neuron simplified to two compartments (soma and dendrite). We used the mathematical expression of the two-compartment model [21]. The somatic compartment included only the channels necessary for spike generation (Na^+ and K^+), while the dendritic compartment included a slow potassium and a persistent sodium current (Fig. 1A). Although simplified, as compared with some other models including more types of ion channels [4, 22-24], this minimized two-compartment model can successfully capture the phenomenon of complex bursting, i.e., a typical firing behavior of cortical pyramidal neurons [21]. The neuronal MPs follow the equations below.

The model descriptions of this pyramidal neuron are as follows:

$$\begin{aligned} C_m \frac{dV_s}{dt} &= -g_{Na} m^3 h (V_s - E_{Na}) - g_K n^4 (V_s - E_K) - \\ &\quad - g_{Leak}(V_s - E_{Leak}) - \frac{g_c}{p}(V_s - V_d) + I_{soma}, \\ C_m \frac{dV_d}{dt} &= -g_{NaP} m_\infty{}^3 (V_d - E_{Na}) - g_{KS} q (V_d - E_K) - \\ &\quad - g_{Leak}(V_d - E_{Leak}) - \frac{g_c}{1-p}(V_d - V_s) + I_{dendrite}, \end{aligned} \tag{1}$$

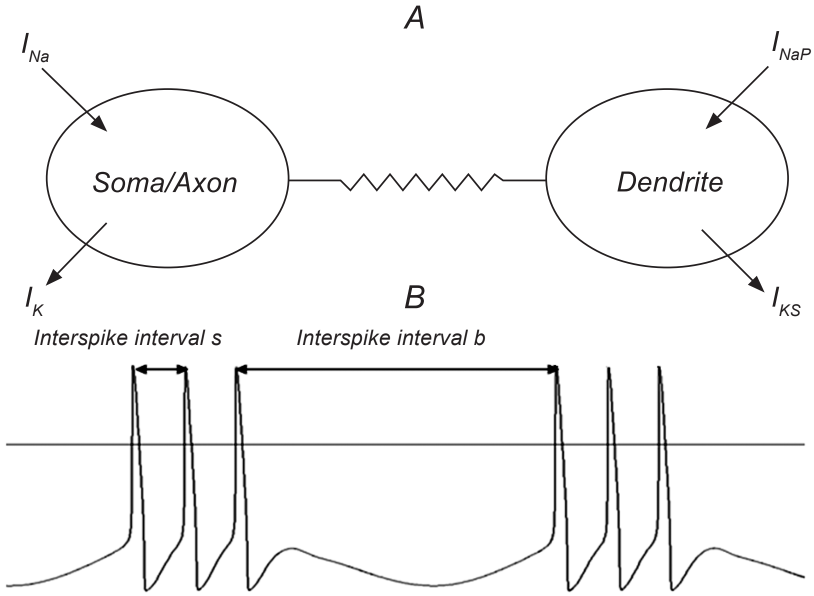
where I_{soma} and $I_{dendrite}$ are current injections to the compartments. The voltage-dependent gating variables are described using standard HH formalism.

$$\frac{dx}{dt} = \phi_x \frac{x_\infty(V) - x}{\tau_x(V,T)} \; (x = m,h,n,q), \tag{2}$$

$$I_y = g_y(T) a^m b^n (V - V_y)(x = m,h,n,q), \tag{3}$$

In Eq. (2), T is the environmental temperature, $\tau_x(V,T)$ is the function of V and T, and x is the activation and inactivation variable, like a and b in Eq. (3). In Eq. (3), $g_y(T)$ is the maximum channel conductance, and V_y is the equilibrium potential.

In order to take into account the impacts of



F i g. 1. Scheme of a two-compartment model of a cortical pyramidal neuron (A) and schematic diagram of interspike intervals (ISIs) in neuronal spike trains (B). Interspike interval *s* denotes the ISI between adjacent spikes within a burst, while an ISI *b* denotes the ISI between adjacent bursts.

Р и с. 1. Схема двокомпартментної моделі кортикального пірамідного нейрона (*А*) та схематична діаграма міжімпульсних інтервалів у нейронних імпульсних послідовностях (*B*).

temperature on firing behaviors of the pyramidal neuron, the following nonlinear relations between temperature and $g_y(T)$, $\tau_x(V,T)$, were introduced (similarly to [20]). This kind of nonlinear relationship was previously used [12, 25, 26], but with different base of the exponential-type function.

$$g_y(T) = g_y \exp(\frac{T - T_0}{T_G}), \tag{4}$$

$$\tau_x(V,T) = \tau_x(V) \exp(-\frac{T - T_0}{T_r}). \tag{5}$$

As in [20], Eqs. (4) and (5) are used to simulate the impact of temperature on neuronal firing activities. These two effects can be manifested by the fact that with increase in temperature the ion conductance would increase, while the time constant of the ion channel gating variable would decrease. The T_G and T_r are the specified temperature values, with which environmental temperature can affect the ion conductances and time constants of the channel gating variables [20], and T_0 is the temperature under which electrophysiological experiments on neurons were conducted. According to the literature on pyramidal neuron experiments [27-29], we chose $T_0 = 35$ °C. Other parameters and expressions contained in this model are as follows:

$\alpha_m = -0.1(V_s + 31)/(\exp(-0.1(V_s + 31)) - 1)$,
$\beta_m = 4\exp(-(V_s + 56)/18)$,
$\alpha_h = 0.07(\exp(-(V_s + 47)/20)$,
$\beta_h = 1/(\exp(-0.1(V_s + 17)/ + 1)$,
$\alpha_n = -0.01(V_s + 34)/(\exp(-0.1(V_s + 34)) - 1)$,
$\beta_n = 0.125\exp(-(V_s + 44)/80)$,
$m_\infty = 1/(1+\exp(-(V_d + 57.7)/ 7.7))$,
$q_\infty = 1/(1+\exp(-(V_d + 35)/ 6.5))$,
$\tau_q = 200/(\exp(-(V_d + 55)/ 30) + \exp((V_d + 55)/ 30)$.

The basic value of the membrane capacitance is $C_m = 1\mu F/cm^2$. The asymmetry between the areas of two compartments is taken into account in the parameter p = somatic area/total area, which has a base value of $p = 0.15$ [21]. The coupling conductance is $g_c = 1 mS/cm^2$. The initial temperature scaling factors are $\phi_m = 10.0$ and $\phi_h = \phi_n = 3.33$; these three parameters are kept as constants during our simulations, and they are used to characterize the amplitude of temperature affecting each gating variable. The ion conductances are $g_{Leak} = 0.18$, $g_{NaP} = 0.12$, $g_{KS} = 0.7$, $g_{Na} = 55$, and $g_K = 20$ mS/cm², while the equilibrium potentials are $E_{Leak} = -65$, $E_{Na} = 55$, and $E_K = -90 (mV)$.

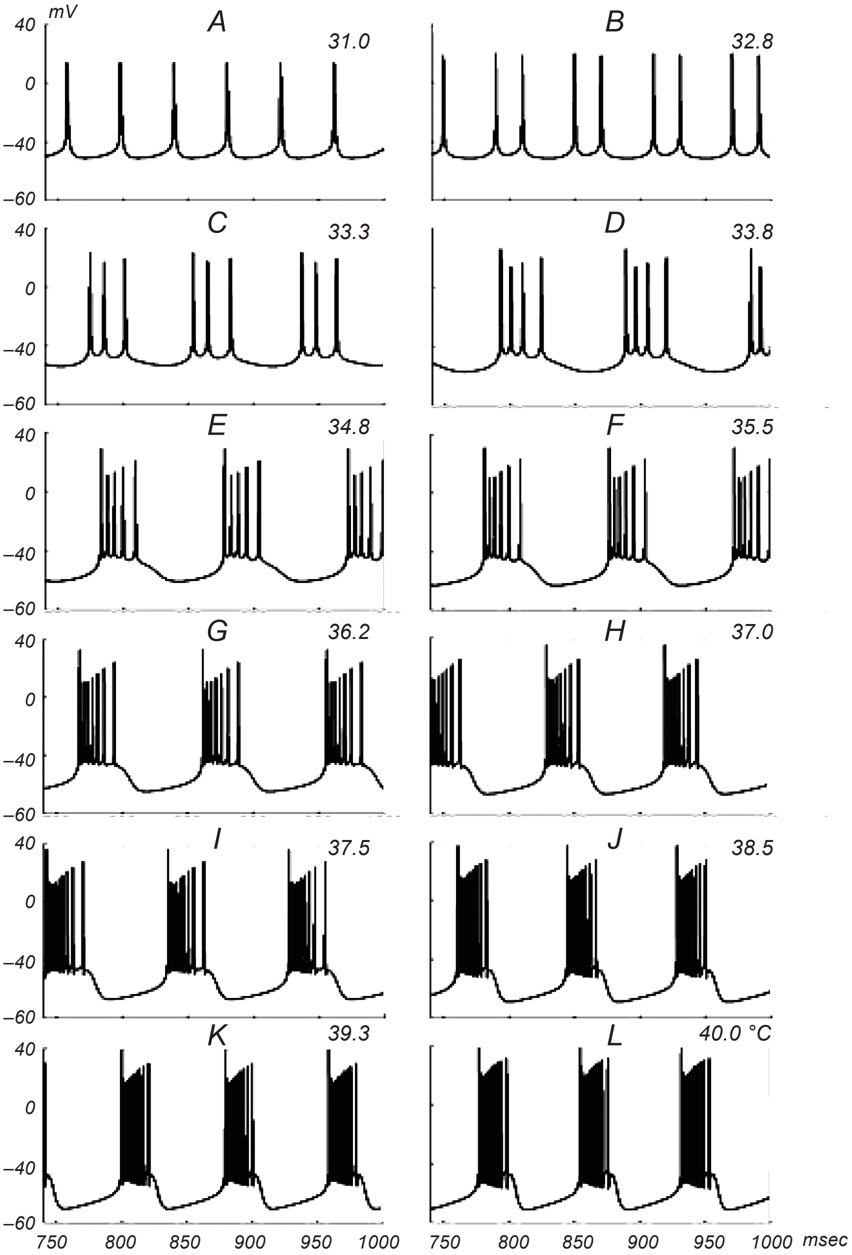
Simulations were performed using MATLAB software, and the fourth-order Runge–Kutta algorithm was employed to calculate the MP values with a time step of 0.01 msec. We only injected direct current 3.5 μA/cm² into the dendritic compartment and investigated the somatic APs in this study. In our simulation, initial values of the somatic and dendritic MP were set as –64 mV, while initial values of the other gating variables were set as 0. In order to avoid the influence of initial values, we disposed the values within a 0 to 300 msec range and analyzed the somatic AP values during a 300 to 1000 msec segment.

RESULTS

In order to characterize the transition modes between different firing patterns, we introduced such indices as interspike intervals (ISIs). The bifurcation diagram of ISIs has been widely used to describe the transition among various firing patterns [12, 25, 30-32]. The value of ISI is denoted as the time difference between adjacent peaks in spike trains, which is illustrated in Fig. 1B.

For a given neuronal spike train $\{t_1^1, t_2^1, ..., t_n^1\}$, under a parameter *Par*, we can easily get the ISI sequence $\{\Delta t_1^1, \Delta t_2^1, ..., \Delta t_N^1\}$ with the value of Par_1; here $\Delta t_i^1 = t_{i+1}^1 - t_i^1$. Thus, Par_1 corresponds to $\{\Delta t_1^1, \Delta t_2^1, ..., \Delta t_N^1\}$, while for the value of Par_2 we can also obtain an ISI sequence $\{\Delta t_1^2, \Delta t_2^2, ..., \Delta t_N^2\}$. Similarly, for the values of Par_1, Par_2, …, Par_n, we can get a total of *n* sequences of ISIs. Finally, the ISI bifurcation diagram with *Par* is plotted when we take *Par* as a variable in the horizontal axis and take the ISI sequence as a variable in the vertical axis.

Influence of Temperature on Firing Behaviors of the Pyramidal Neuron. With variation of temperature, the model pyramidal neuron exhibits a variety of firing patterns, which are demonstrated in Fig. 2A-L. From this figure, we can see that the cell shows clear period-doubling and period-adding firing phenomena. With temperature increasing from 30 to 42°C, the cell doubling bifurcates from period-1 spiking (Fig. 2A) to period-2 bursting (B), and then doubling bifurcates to period-4 bursting (data not shown). This kind of transition route is usually called period-doubling bifurcation. After a complex firing region, the period number varies from four to three (C), and the period-adding bifurcation trend (period numbers increase steadily) lasts until the period number reaches twelve (L) within this parameter region. In Fig. 3B,

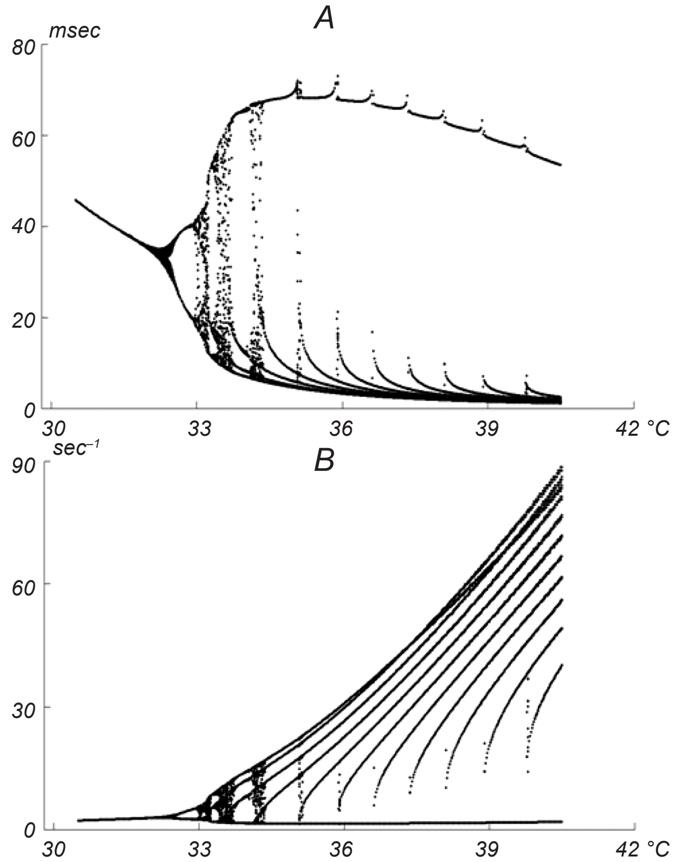


F i g. 2. Firing patterns and their transition modes observed in a model cortical pyramidal neuron with the variation of temperature (*T*). A-L) Periodic firing sequences changing with increase in the temperature (31.0, 32.8, 33.3, 33.8, 34.8, 35.5, 36.2, 37.0, 37.5, 38.5, 39.3, and 40.0°C, respectively).

Р и с. 2. Патерни розрядів та форми їх перетворень, що спостерігаються у модельному кортикальному нейроні при варіації температури (*T*).

we can observe that, with increased temperature, neuronal instantaneous firing frequency shows a clear upward trend, which indicates that high temperature gives higher firing frequency of neurons. Similar temperature-frequency curves have already been found in *Aplysia* neurons [11]. Bifurcation diagrams of ISI demonstrated in Fig. 3A also show obvious period-adding and period-doubling bifurcation phenomena between different firing patterns. Simulation results shown in Fig. 3 indicate an apparent variation rule on how temperature impacts on neuronal firing sequences in cortical pyramidal neurons.

From the model equations (1)-(5), we obtain that temperature does not affect neuronal firing frequency and ISI values directly. Temperature exerts its effect by changing the ion channel conductance [see Eq. (4)]; then, the varied ion conductances would alter the corresponding ion currents; consequently, the neuronal responsiveness and firing behavior would be influenced. In Fig. 4, we give the relation curves for the



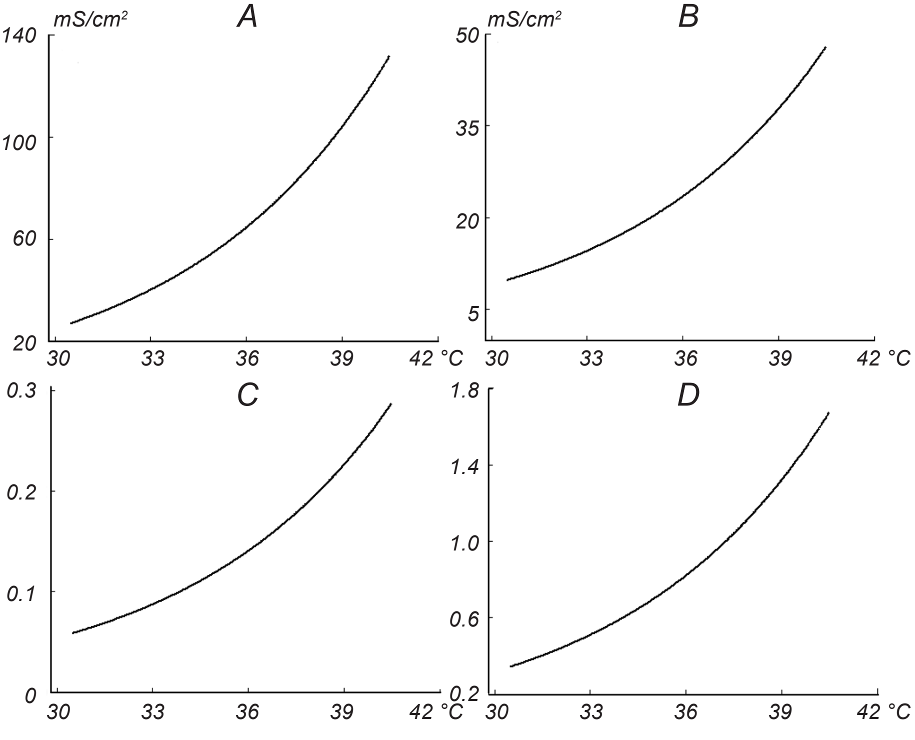
F i g. 3. Bifurcation diagrams of the ISIs, msec (A) and instantaneous firing frequency, sec^{-1} (B) with respect to the temperature, °C.

Р и с. 3. Біфуркаційні діаграми міжімпульсних інтервалів, мс (*A*) та миттєвої частоти розрядів, с (*B*) щодо температури, °C.

ion conductance with respect to temperature according to Eq. (4). The four kinds of ion conductances [$g_{Na}(T)$, $g_K(T)$, $g_{NaP}(T)$, and $g_{KS}(T)$] show an obvious positive relationship with temperature. Considering direct relations between the ion conductance and neuronal MP, we present further discussions concerning the influence of the ion conductance on neuronal firing behavior in the next section.

Effects of Ion Conductance on Neuronal Firing Patterns. The influence of temperature on neuronal firing behavior is found to be indirect in this study. From Fig. 4, we can see that the increase in temperature will lead to positive variation of the ion conductance; thus, the effects of ion conductances are discussed here.

Ion channels consisting of a large number of specific proteins are biophysical components naturally existing in the neuronal membranes. The open and closed states of these channels can play a fundamental role in the



F i g. 4. Dependences of the ion conductances with respect to the temperature *T*. A-D) $g_{Na}(T)$, $g_K(T)$, $g_{NaP}(T)$, and $g_{KS}(T)$, respectively.

Р и с. 4. Залежності іонних провідностей від температури.

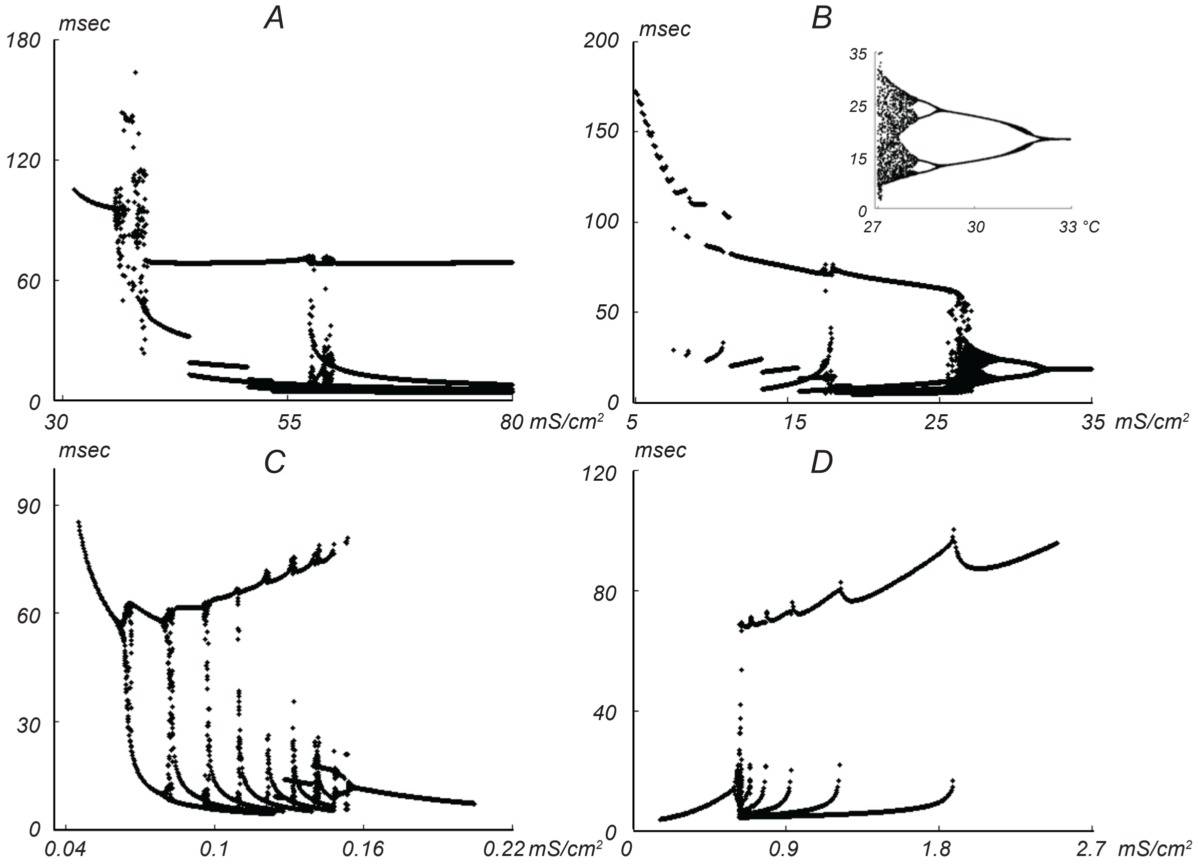


Fig. 5. Bifurcation diagrams of the ISIs with respect to the ion conductances. A-D) $g_{Na}(T)$, $g_K(T)$, $g_{NaP}(T)$, and $g_{KS}(T)$, respectively. $T = 35$°C. When considering variation of one ion conductance, the values of other ion conductances are the same as those presented in the Model and Methods paragraph.

Р и с. 5. Біфуркаційні діаграми міжімпульсних інтервалів щодо іонних провідностей.

generation of neuronal APs [33, 34]. In addition, some specific type of ion channels is thought to have critical impacts on firing properties of the neurons [21, 22, 35]. Diagrams shown in Fig. 5 are the bifurcation maps for the ISI with respect to the ion conductances of the four above-mentioned different ion channels. In Fig. 3, the variation of temperature can cause the cell to exhibit a clear periodic firing phenomenon; during this all four different ion conductances change. Thus, we cannot distinguish which ion channel(s) give(s) a primary contribution to the emergence of this periodic firing behavior. In Fig. 5A-D, we present the simulation results of the ISI bifurcation diagrams with respect to each of the four ion conductances. When investigating the effect of one ion conductance, such as $g_{Na}(T)$ in Fig. 5A, the other three ion conductances were kept invariable.

By observing four bifurcation maps in Fig. 5, we can find the transition rule of neuronal firing patterns (ISI bifurcation diagrams) with respect to $g_{NaP}(T)$ and $g_{KS}(T)$. The latter are more evident than those of $g_{Na}(T)$ and $g_K(T)$. In Fig. 5C, D, we can clearly see the periodic bifurcation phenomena with increase in the corresponding ion conductance; this transition rule is comparable to that corresponding to the ISI diagram in Fig. 3A. The relation between the temperature and ion conductance shows a positive correlation. Moreover, earlier documents have confirmed that I_{NaP} (persistent sodium current) and I_{KS} (slow potassium current) play some crucial roles in the generation of various neuronal firing behaviors, and the variation in these two currents can induce the firing patterns to switch from one type to another [1, 2, 6, 21]. Thus, the explicit transition rules with the varied ion conductance in

Fig. 5C, D are understandable. Yet, the transition rules induced by the perturbation of $g_{Na}(T)$ and $g_K(T)$ are rather complex, as shown in Fig. 5A, B. Although a period-doubling bifurcation phenomenon can be observed when $g_K(T)$ varies within a small region (see insert in Fig. 5B), the whole transition mode when $g_K(T)$ changes within a larger region is complex. This needs further investigation in future works.

DISCUSSION

The environment in which neurons fire AP sequences is changeable rather than invariable, and the varied temperature may exhibit certain impacts on the neuronal excitability. An earlier study [36] demonstrated that the neuronal spike threshold shows a transient increase when temperature increases steadily and shows an opposite variation when temperature decreases. Experiments on hypothalamic tissue slices showed that temperature exert certain impact on the neuronal MP and inward currents [37]. Moreover, there are still some studies showing that temperature can affect synaptic transmission among neurons [38, 39], the voltage-sensitive conductances [40], and the output of neural circuits [41]. Thus, elucidation of the possible role that temperature plays in the generation of different firing patterns can facilitate our understanding of how temperature might affect neuronal firing behavior.

Spiking and bursting are the most commonly observed firing behaviors in neural systems where they play important roles in signal processing and information encoding. Many models generating these two typical firing patterns were subjected to intense research due to their physiological significance and dynamical complexity [2, 12, 25, 35]. The transition have modes between different spiking and bursting patterns also attracted interest from many researchers [42-44]. Fast/slow bifurcation analysis is the most frequently used approach to study the bifurcation structure contained in the transition between different firing patterns. For example, Tsaneva-Atanasova et al. [43, 44] utilized this approach to investigate the bursting patterns in endocrine cells. Duan et al. [42] applied two-parameter bifurcation analysis to neuronal firing activities in the Chay model using this approach. In addition to the fast/slow analysis approach, the bifurcation diagram of ISI is another commonly used method, which can describe the transition among various firing patterns to some extent [12, 25, 30]. In our study, the ISI diagram is used to analyze the transition between different spiking and bursting patterns induced by variations of the temperature and ion conductances.

Based on a cortical pyramidal neuron model and ISI bifurcation diagrams, the effects of environmental temperature on neuronal firing behaviors are discussed in our paper using a computational approach. From the analysis of numerical results presented in our study, we can see that pyramidal neurons, which perform functional roles in the reliable signaling and synaptic plasticity, can exhibit numerous firing patterns when temperature varies within a certain region. Bifurcation diagrams of the ISIs can give more intuitive results on how these different firing patterns switch from one type to another. The periodic bifurcation phenomenon consisting in the ISI diagrams may inspire us to study the potential roles of temperature in the firing pattern transitions in pyramidal neurons. Temperature changes did not affect the neuronal firing frequency and ISI directly in our model, while temperature can directly influence the ion conductance [see Eqs. (4) and (5)]. We further examined the influence of the ion conductances on neuronal firing behaviors. Simulation results in Fig. 5 clearly show that periodic firing phenomena can be obtained when $g_{NaP}(T)$ and $g_{KS}(T)$ vary, but the variation of $g_{Na}(T)$ and $g_K(T)$ produces rather complex bifurcation phenomena, even though period-doubling bifurcation emerges when $g_K(T)$ was changed within narrow limits. One possible reason for the distinction between the ISI bifurcation diagrams in Fig. 3 and Fig. 5 is that the periodic bifurcation phenomenon of ISI in Fig. 3 is induced by increased temperature. From Fig. 4 we get that the changes in temperature can cause variation of all the four ion conductances. So, the periodic bifurcation phenomenon of ISI demonstrated in Fig. 3A is induced by the variation of all four ion conductances simultaneously, while Fig. 5 shows how the ISI bifurcation diagrams change when one ion conductance varies alone, while the other three are kept invariable. Another possible reason is that some ion channels are more temperature-sensitive than others [45-47], which may be the cause of the difference of ISI bifurcation diagrams with respect to the ion conductance (this is shown in Fig. 5A-D).

It is worth noting that we have mainly investigated the effect of temperature on neuronal firing behaviors and the transition modes between the latter in a model pyramidal neuron in our study, while some factors other than temperature may also contribute to the formation of numerous firing patterns. These factors are external stimulation, noise (internal or external), neuronal morphology, etc. These factors deserve more attention in future studies. In addition, since the activities of the brain are largely represented as collective behavior of numerous neurons, investigating the firing properties of a single neuron is the first step to explore how the brain works. Future studies will examine dynamic behavior of large neural networks, which contain many neurons with various firing properties [48, 49]. Finally, the fast/slow approach can also be used to analyze the exact bifurcation structures consisting in the transition modes demonstrated in this study.

Л. Ван[1]*, Ш. Лю*[1]*, Д. Жан*[2]*, Я. Зен*[2]

ЗАЛЕЖНІ ВІД ТЕМПЕРАТУРИ ПЕРЕТВОРЕННЯ ПАТЕРНІВ ПАЧКОВИХ РОЗРЯДІВ У МОДЕЛЬНОМУ ПІРАМІДНОМУ НЕЙРОНІ

[1] Південнокитайський технологічний університет, Гуанчжоу (Китай).
[2] Біомедичний інженерний центр, Пекінський технологічний університет (Китай).

Резюме

Температура середовища істотно впливає на генерацію імпульсної активності нейроном і кодування інформації. Концепції щодо механізмів відповідних ефектів залишаються поки що незавершеними і суперечливими. У нашій роботі ми досліджували вплив температури на патерн розрядів, генерованих модельним пірамідним нейроном. Було з'ясовано, що в умовах неоднакових температур можуть формуватися різні патерни імпульсації. Крім того, поблизу переходів між цими патернами при варіації температури в певних межах виявлявся чітко виражений феномен періодичної біфуркації. Спостерігалися декілька характерних видів біфуркації, зокрема біфуркації з подвоєнням періоду та некратним зростанням останнього.

REFERENCES

1. N. Wu, A. Enomoto, S. Tanaka, et al., "Persistent sodium currents in mesencephalic neurons participate in burst generation and control of membrane excitability," *J. Neurophysiol.*, **93**, No. 5, 2710-2722 (2005).
2. R. J. Butera, J. Rinzel, and J. C. Smith, "Models of respiratory rhythm generation in the pre-Bötzinger complex. I. Bursting pacemaker neurons," *J. Neurophysiol.*, **82**, No. 1, 382-397 (1999).
3. N. Spruston, "Pyramidal neurons: dendritic structure and synaptic integration," *Nat. Rev. Neurosci.*, **9**, No. 3, 206-221 (2008).
4. Z. F. Mainen and T. J. Sejnowski, "Influence of dendritic structure on firing pattern in model neocortical neurons," *Nature*, **382**, No. 6589, 363-366 (1996).
5. R. B. Szlavik, "Strategies for improving neural signal detection using a neural-electronic interface," *IEEE Trans. Neural Syst. Rehabil. Eng.*, **11**, No. 1, 1-8 (2003).
6. L. Wang, S. Liu, J. Zhang, and Y. Zeng, "Burst firing transitions in two-compartment pyramidal neuron induced by the perturbation of membrane capacitance," *Neurol. Sci.*, **33**, No. 3, 595-604 (2012).
7. A. L. Hodgkin and A. F. Huxley, "A quantitative description of membrane current and its application to conduction and excitation in nerve," *J. Physiol.*, **117**, No. 4, 500-544 (1952).
8. M. Chiappalone, A. Vato, L. Berdondini, et al., "Network dynamics and synchronous activity in cultured cortical neurons," *Int. J. Neural Syst.*, **17**, No. 2, 87-103 (2007).
9. H. E. Plesser and W. Gerstner, "Noise in interate- and fire neurons: from stochastic input to escape rates," *Neural. Comput.*, **12**, No. 2, 367-384 (2000).
10. J. A. White, J. T. Rubinstein, and A. R. Kay, "Channel noise in neurons," *Trends Neurosci.*, **23**, No. 3, 131-137 (2000).
11. D. O. Carpenter, "Temperature effects on pacemaker generation, membrane potential, and critical firing threshold in *Aplysia* neurons," *J. Gen. Physiol.*, **50**, No. 6, 1469-1484 (1967).
12. Y. Du, Q. Lu, and R. Wang, "Using interspike intervals to quantify noise effects on spike trains in temperature encoding neurons," *Cogn. Neurodyn.*, **4**, No. 3, 199-206 (2010).
13. M. Volgushev, T. R. Vidyasagar, M. Chistiakova, et al., "Membrane properties and spike generation in rat visual cortical cells during reversible cooling," *J. Physiol.*, **522**, No. 1, 59-76 (2000).
14. A. L. Gorman and M. F. Marmor, "Temperature dependence of the sodium-potassium permeability ratio of a molluscan neuron," *J. Physiol.*, **210**, No. 4, 919-931 (1970).
15. M. R. Klee, F. K. Pierau, and D. S. Faber, "Temperature effects on resting potential and spike parameters of cat motoneurons," *Exp. Brain Res.*, **19**, No. 5, 478-492 (1974).
16. K. D. Micheva and S. J. Smith, "Strong effects of subphysiological temperature on the function and plasticity of mammalian presynaptic terminals," *J. Neurosci.*, **25**, No. 33, 7481-7488 (2005).
17. A. L. Hodgkin and B. Katz, "The effect of temperature on the electrical activity of the giant axon of the squid," *J. Physiol.*, **109**, Nos. 1/2, 240-249 (1949).
18. L. Yang and Y. Jia, "Effects of patch temperature on spontaneous action potential train due to channel fluctuations: coherence resonance," *Biosystems*, **81**, No. 3, 267-280 (2005).
19. S. M. Thompson, L. M. Masukawa, and D. A. Prince, "Temperature dependence of intrinsic membrane properties and synaptic potentials in hippocampal *CA1* neurons *in vitro*," *J. Neurosci.*, **5**, No. 3, 817-824 (1985).
20. C. Q. Yuan, T. J. Zhao, Y. Zhan, et al., "Environmental impacts on spiking properties in Hodgkin–Huxley neurons with direct current stimulus," *Chin. Phys. Lett.*, **26**, No. 11, 118701 (2009); doi: 10.1088/0256-307x/26/11/118701.
21. A. Kepecs and X. J. Wang, "Analysis of complex bursting in cortical pyramidal neuron models," *Neurocomputing*, **32/33**, 181-187 (2000).
22. J. C. Magee and M. Carruth, "Dendritic voltage-gated ion channels regulate the action potential firing mode of hippocampal *CA1* pyramidal neurons," *J. Neurophysiol.*, **82**, No. 4, 1895-1901 (1999).

23. L. L. Yuan and X. Chen, "Diversity of potassium channels in neuronal dendrites," *Prog. Neurobiol.*, **78**, No. 6, 374-389 (2006).
24. S. Remy, H. Beck, and Y. Yaari, "Plasticity of voltage-gated ion channels in pyramidal cell dendrites," *Current Opin. Neurobiol.*, **20**, No. 4, 503-509 (2010).
25. S. Postnova, C. Finke, W. Jin, et al., "A computational study of the interdependencies between neuronal impulse pattern, noise effects and synchronization," *J. physiol.*, **104**, Nos. 3/4, 176-189 (2010).
26. N. G. Hyun, K. H. Hyun, K. B. Hyun, et al., "A computational model of the temperature- dependent changes in firing patterns in *Aplysia* neurons," *Korean J. Physiol. Pharmacol.*, **15**, No. 6, 371-382 (2011).
27. A. E. Metz, T. Jarsky, M. Martina, and N. Spruston, "R-type calcium channels contribute to afterdepolarization and bursting in hippocampal *CA1* pyramidal neurons," *J. Neurosci.*, **25**, No. 24, 5763-5773 (2005).
28. L. Badel, S. Lefort, R. Brette, et al., "Dynamic I-V curves are reliable predictors of naturalistic pyramidal-neuron voltage traces," *J. Neurophysiol.*, **99**, No. 2, 656-666 (2008).
29. M. H. Kole, S. Hallermann, and G. J. Stuart, "Single Ih channels in pyramidal neuron dendrites: properties, distribution, and impact on action potential output," *J. Neurosci.*, **26**, No. 6, 1677-1687 (2006).
30. A. O. Komendantov and N. I. Kononenko, "Deterministic chaos in mathematical model of pacemaker activity in bursting neurons of snail, *Helix pomatia*," *J. Theor. Biol.*, **183**, No. 2, 219-230 (1996).
31. A. O. Komendantov, C. C. Canavier, "Electrical coupling between model midbrain dopamine neurons: effects on firing pattern and synchrony," *J. Neurophysiol.*, **87**, No. 3, 1526-1541 (2002).
32. P. V. Carelli, M. B. Reyes, J. C. Sartorelli, and R. D. Pinto, "Whole cell stochastic model reproduces the irregularities found in the membrane potential of bursting neurons," *J. Neurophysiol.*, **94**, No. 2, 1169-1179 (2005).
33. G. Baranauskas, "Ionic channel function in action potential generation: current perspective," *Mol. Neurobiol.*, **35**, No. 2, 129-150 (2007).
34. C. M. Colbert and E. Pan, "Ion channel properties underlying axonal action potential initiation in pyramidal neurons," *Nat. Neurosci.*, **5**, No. 6, 533-538 (2002).
35. A. Enomoto, J. M. Han, C. F. Hsiao, et al., "Participation of sodium currents in burst generation and control of membrane excitability in mesencephalic trigeminal neurons," *J. Neurosci.*, **26**, No. 13, 3412-3422 (2006).
36. W. J. Heitler, C. S. Goodman, and C. H. Rowell, "The effects of temperature on the threshold of identified neurons in the locust," *J. Comp. Physiol.*, Ser. A, **117**, No. 2, 163-182 (1977).
37. Y. Zhao and J. A. Boulant, "Temperature effects on neuronal membrane potentials and inward currents in rat hypothalamic tissue slices," *J. Physiol.*, **564**, 245-257 (2005).
38. B. R. Johnson, J. H. Peck, and R. M. Harris-Warrick, "Temperature sensitivity of graded synaptic transmission in the lobster stomatogastric ganglion," *J. Exp. Biol.*, **156**, 267-285 (1991).
39. M. Burrows, "Effects of temperature on a central synapse between identified motor neurons in the locust," *J. Comp. Physiol.*, Ser. A, **165**, No. 5, 687-695 (1989).
40. X. J. Cao and D. Oertel, "Temperature affects voltage-sensitive conductances differentially in octopus cells of the mammalian cochlear nucleus," *J. Neurophysiol.*, **94**, No. 1, 821-832 (2005).
41. T. M. Szabo, T. Brookings, T. Preuss, and D. S. Faber, "Effects of temperature acclimation on a central neural circuit and its behavioral output," *J. Neurophysiol.*, **100**, No. 6, 2997-3008 (2008).
42. L. X. Duan, Z. Q. Yang, S. Q. Liu, and D. W. Gong, "Bursting and two-parameter bifurcation in the Chay neuronal model," *Discrete Contin. Dyn. Syst.*, Ser. B, **16**, No. 2, 445-456 (2011).
43. K. Tsaneva-Atanasova, H. M. Osinga, T. Riess, and A. Sherman, "Full system bifurcation analysis of endocrine bursting models," *J. Theor. Biol.*, **264**, No. 4, 1133-1146 (2010).
44. W. Teka, K. Tsaneva-Atanasova, R. Bertram, and J. Tabsk, "From plateau to pseudo-plateau bursting: making the transition," *Bull. Math. Biol.*, **73**, No. 6, 1292-1311 (2011).
45. J. K. Tiwari and S. K. Sikdar, "Temperature-dependent conformational changes in a voltage-gated potassium channels," *Eur. Biophys. J.*, **28**, No. 4, 338-345 (1999).
46. J. Chemin, A. Mezghrani, I. Bidaud, et al., "Temperature-dependent modulation of CaV3 T-type calcium channels by protein kinases C and A in mammalian cells," *J. Biol. Chem.*, **282**, No. 45, 32710-32718 (2007).
47. T. E. DeCoursey and W. Cherny, "Temperature dependence of voltage-gated H^+ currents in human neutrophils, rat alveolar epithelial cells, and mammalian phagocytes," *J. Gen. Physiol.*, **112**, No. 4, 503-522 (1998).
48. S. Ghosh-Dastidar and H. Adeli, "Spiking neural networks," *Int. J. Neural Syst.*, **19**, No. 4, 295-308 (2009).
49. S. Ghosh-Dastidar and H. Adeli, "A new supervised learning algorithm for multiple spiking neural networks with application in epilepsy and seizure detection," *Neural Netw.*, **22**, No. 10, 1419-1431 (2009).