

BURSTING AND TWO-PARAMETER BIFURCATION IN THE CHAY NEURONAL MODEL

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ABSTRACT. In this paper, we study and classify the firing patterns in the Chay neuronal model by the fast/slow decomposition and the two-parameter bifurcations analysis. We show that the Chay neuronal model can display complex bursting oscillations, including the “fold/fold” bursting, the “Hopf/Hopf” bursting and the “Hopf/homoclinic” bursting. Furthermore, dynamical properties of different firing activities of a neuron are closely related to the bifurcation structures of the fast subsystem. Our results indicate that the codimension-2 bifurcation points and the related codimension-1 bifurcation curves of the fast-subsystem can provide crucial information to predict the existence and types of bursting with changes of parameters.

1. Introduction. Bursting is one of the most important firing activities of neuronal systems. Bursting oscillations that are observed in electrical activities of neuron membranes can give rise to different patterns of time rhythms and oscillating modes, which play an important role in the neural information processes. For example, the bursting has more highly robust to noise than to single spike [1]; bursting can encode different stimulus features into distinct spike patterns [2].

Typically, bursting in neurons can be generated from the interplay of fast currents that are responsible for spiking activity and slow currents that modulate the activities. The phenomena of bursting are seen in a wide range of neuron and

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endocrine cells, including thalamic neurons, hypothalamic neurons, pyramidal neurons in the neocortex, respiratory neurons in pre-Bötzinger complex, pituitary cells, and pancreatic β -cells [3]. In 1985, Rinzel recognized a type of bursting that exhibits a transition between a rest state and a spiking state [4]. The transition was considered to be originated from a slow variation process that modulates the fast firing activities. Since then the dynamical behavior and classifications of bursting have been studied experimentally and theoretically [5, 6]. Theoretical studies were performed mainly by investigating the detailed bifurcation structures of the fast and slow subsystems. Two important bifurcations of the fast subsystem are associated with bursting activity in the fast-slow bursting: the bifurcation of an equilibrium attractor which results to the transition from resting to repetitive spiking, and the bifurcation of the limit cycle attractor which results to the transition from spiking to resting. In 2000, a complete topological classification of bursting based on these two bifurcations was proposed by Izhikevich [7], who gives an overview of different types of bursting observed either in biological experiments or in theoretical analysis, or in both.

Bursting oscillations have been widely studied under various conditions, e.g., [7, 8, 9, 10, 11]. Shorten and Wall [9] studied the bursting oscillations and mode transitions in a Hodgkin-Huxley type model, and found a novel “fold cycle/fold cycle” bursting oscillations in the model. Perc and Marhl [10] investigated different bursting of point-point types and point-cycle types in some non-excitable cells. Belykh et al [12] showed four different scenarios for the emergence of bursting. Fan and Chay [13], Gu et al [14], and Yang et al [15, 16] considered different types of bursting in the Chay neuronal model by the fast/slow decomposition and bifurcation analysis.

Since bifurcations of fast subsystems can mark the transitions between active and quiescent states in bursting rhythms, they play a critical role in determining which types of bursting can occur in neuronal models. Guckenheimer and Tien [17] dealt with the relationship among transitions in several bursting models through bifurcations of reduced subsystems.

Bifurcation analysis can also be used to study other biological systems [18, 19]. In our previous works [15, 16, 20, 21], we have also applied the bifurcation theory and the fast/slow decomposition to study the generation and transition of bursting in the Chay and Morris-Lecar models. In these works, we developed a method to explore the bursting transition through the two-parameter bifurcation of the fast subsystem in both Chay and Morris-Lecar neuronal models, and discussed bursting types and transition modes under various bifurcation structures. In this paper, we consider two cases in the Chay neuronal model: consider the maximum of conductance of voltage-gated Ca^{2+} channel g_T^* as a control parameter, or consider the leak conductance g_L^* as the control parameter. Both of these two cases have similarly two-parameter bifurcation structures under different parameter sets. We further study the relationship between the bursting modes and the bifurcation structure of the fast subsystem in these two cases. The results show that Chay neuronal models share similar transition mechanisms of bursting when the two-parameter bifurcation structures in the corresponding fast subsystems are similar to each other. We note that this method is able to predict the type of bursting occurred in a chosen set of parameter values in neuronal models with fast-slow time scales.

The rest of this paper is organized as follows. In Section 2 we give a short description of the model and introduction of our methods. In Section 3, we will show that

different firing activities occur with the change of parameter g_I^* by the fast/slow decomposition and the two-parameter bifurcation analysis of the fast subsystem. The transition mechanisms between different firing patterns are also studied. Section 4 studies different firing activities with the change of parameter g_L^* , and the relationship between bursting modes and the two-parameter bifurcation structures of the fast subsystem. Conclusions are given in the Section 5.

2. Model and method.

2.1. Model description. The Chay model was proposed to simulate the firing patterns of pancreatic β -cells [22], and can also be used to simulate spiking/bursting and chaos behavior in real neurons.

The three-variable Chay neuronal model consists of the ‘mixed’ $\text{Na}^+ - \text{Ca}^{2+}$ current, the K^+ current, the Ca^{2+} -dependent K^+ current, and the leakage current. Let V to be the membrane potential, n the probability of opening the voltage-sensitive K^+ channel and C the intracellular concentration of Ca^{2+} ions. The model equations are given as follows:

$$\frac{dV}{dt} = g_I^* m_\infty^3 h_\infty (V_I - V) + g_{K,V}^* (V_K - V) n^4 \quad (1)$$

$$+ g_{K,C}^* \frac{C}{1+C} (V_K - V) + g_L^* (V_L - V) + I,$$

$$\frac{dn}{dt} = \frac{n_\infty - n}{\tau_n}, \quad (2)$$

$$\frac{dC}{dt} = \rho [m_\infty^3 h_\infty (V_C - V) - k_C C]. \quad (3)$$

Here m_∞ , h_∞ and n_∞ are gate variables, which have forms $y_\infty = \alpha_y / (\alpha_y + \beta_y)$ (here $y = m, n, h$, respectively), with α and β depend on V as follows:

$$\begin{aligned} \alpha_m &= 0.1(25 + V)/(1 - e^{-0.1*V-2.5}), \\ \beta_m &= 4e^{-(V+50)/18}, \\ \alpha_h &= 0.07e^{-0.05V-2.5}, \\ \beta_h &= 1/(1 + e^{-0.1V-2}), \\ \alpha_n &= 0.01(20 + V)/(1 - e^{-0.1V-2}), \\ \beta_n &= 0.125e^{-(V+30)/80}. \end{aligned}$$

The relaxation time of the voltage-gated K^+ channel is given by $\tau_n = \lambda_n(a_n + b_n)$. All other parameters are constants, with definitions and default values listed in Table 1.

Bursting oscillations can be affected by many factors, such as the outward input current, the ionic currents (typically, that of sodium (Na^+), potassium (K^+) and calcium (Ca^{2+})) through the cell membrane and so on. In this paper, we will study the effect of both the maximum of conductance of voltage-gated Ca^{2+} channel g_I^* , and the leak conductance g_L^* on the creation and transition mechanisms of different bursting oscillations. Throughout this study, we only consider the case without external stimulus (which means that $I = 0$).

TABLE 1. Model parameter values [20, 22]

Parameter	Definition	Value
$g_{K,V}^*$	the maximum of conductance of K^+ channel	1700pS
$g_{K,C}^*$	the maximum of conductance of Ca^{2+} -sensitive K^+ channel	10pS
g_L^*	leak conductance	7pS
V_I	Nerst potential for Ca^{2+}	100mV
V_K	Nerst potential for K^+	-75mV
V_L	leak current reversal potential	-40mV
V_C	the reversal potential for Ca^{2+}	215mV
k_C	rate constant for efflux of intracellular Ca^{2+} ions	0.183/ms
ρ	proportionality constant	0.27
λ_n	relaxation time of the voltage-gated K^{2+} channel	350ms

2.2. Method.

2.2.1. *Fast/slow decomposition.* The equations (1)-(3) can be rewritten as following

$$\frac{dV}{dt} = f(V, n, C), \quad (4)$$

$$\frac{dn}{dt} = g(V, n), \quad (5)$$

$$\frac{dC}{dt} = \rho h(V, n, C), \quad (6)$$

where ρ is a small parameter, i.e., $\rho \ll 1$. The intracellular calcium concentration C is therefore a slowly changing variable.

The fast/slow decomposition was introduced by Rinzel [4] to analyze bursting of form (4)-(6). Since ρ is a small parameter, we can analyze the bursting by separately considering the fast behavior of (V, n) subsystem of equations (4)-(5) which is modulated by the slowly changing parameter C . The equation (6) is a slow subsystem and therefore the slow variable C can be considered as the slowly changing parameter of the fast subsystem.

2.2.2. *Bifurcation analysis.* Consider an autonomous system of ordinary differential equations (ODEs):

$$\dot{x} = f(x, \lambda), \quad x \in \mathbb{R}^n, \quad \lambda \in \mathbb{R}^p, \quad (7)$$

where f is a smooth function. A bifurcation occurs at a parameter λ_0 if there are parameter values λ that are arbitrarily close to λ_0 but the corresponding dynamics topologically inequivalent from those of λ_0 . The codimension of bifurcation in system (7) is defined as the difference between the dimension of the parameter space and the dimension of the corresponding bifurcation boundary [23]. Equivalently, the codimension is the number of independent conditions to determine the bifurcation. The codimension of a certain bifurcation is the same in all generic systems depending on a sufficient number of parameters. In this paper, the model system was solved by using a stiff system solver in the numerical package XPPAUT (5.9) [24]. The bifurcation diagrams were computed by AUTO as incorporated in XPPAUT.

3. Bursting with the change of parameter g_I^* .

3.1. Two-parameter bifurcation in the Chay model. Since ρ is small, the intracellular calcium concentration is often considered as a slow variable in the Chay model from equation (3), which controls the dynamics of the fast subsystem (1)-(2).

Fig. 1 shows the Hopf and fold bifurcation curves of the fast subsystem (1)-(2) in two-parameter (C, g_I^*) -plane. The curves in Fig. 1 represent the supercritical Hopf bifurcation (the black curve *suph*) and the fold bifurcation (the blue curves f_1 and f_2) of the equilibrium points of the fast subsystem. The codimension-2 bifurcations include the cusp bifurcation (CP) and the Bogdanov-Takens bifurcation (BT).

3.1.1. Codimension-two cusp bifurcation. Fig. 1 shows that the two fold bifurcation branches f_1 and f_2 terminate at the cusp point CP at $g_I^* = 970.6952$ pS; This implies that when (g_I^*, C) crosses through the cusp point from inside to outside, three equilibrium points of the fast-subsystem (1)-(2) will coalesce into one equilibrium point.

When (g_I^*, C) takes value from either f_1 or f_2 , the fast subsystem possesses an equilibrium state of which the coefficient matrix of the linearized system has one simple zero eigenvalue $\lambda_1 = 0$ and the other eigenvalue λ_2 with nonzero real part. Therefore, the restriction of equations (1)-(2) to the center manifold has the normal form [23]

$$\dot{\xi} = a\xi^2 + O(|\xi|^3), \quad \xi \in \mathbb{R}^1. \quad (8)$$

At the cusp point CP the eigenvalues are $\lambda_1 = 7.3648 \times 10^{-5} \approx 0$ and $\lambda_2 = -49.7367 < 0$ by CONTENT ([25], a software package for numerical bifurcation analysis of ODEs) in which $\lambda_1 = 0$ is still the only eigenvalue on the imaginary axis, but the normal form coefficient a in equation (8) vanishes: $a = 0$ [23, 25]. Therefore, at the cusp point, the restricted equations of (1)-(2) to the one-dimensional center manifold has the form

$$\dot{\xi} = c\xi^3 + O(|\xi|^4), \quad \xi \in \mathbb{R}^1.$$

In this particular case, we have $c = -0.1162$ (by CONTENT [25]).

From the above discussion, the equations of (1)-(2) near CP is locally topologically equivalent to the normal form [23]:

$$\begin{cases} \dot{\xi} &= \beta_1 + \beta_2 \xi + \sigma \xi^3, \\ \dot{\eta} &= -\eta, \end{cases}$$

where $\sigma = \text{sign}(c) = -1$ and $\eta \in \mathbb{R}^1$, $\beta_1, \beta_2 \in \mathbb{R}$. Therefore, three equilibrium points collide into one point at the cusp point CP, and the projection of the transition set in the parameter plane forms a semicubic parabola.

3.1.2. Codimension-two Bogdanov-Takens bifurcation. The Hopf bifurcation curve *suph* connects the right fold bifurcation curve f_1 at the Bogdanov-Takens (BT) bifurcation point, which is a codimension-two bifurcation point. This point is given by $g_I^* = 1812.0579$ pS. At this BT point, we have a pair of eigenvalues with zero real parts $\lambda_{1,2} = -2.2545 \times 10^{-6} \pm 0.0166i$ of the coefficient matrix of the linearized system of the fast subsystem. The equation in system (1)-(2) near BT is locally topologically equivalent to the normal form

$$\begin{cases} \dot{\eta}_1 &= \eta_2, \\ \dot{\eta}_2 &= \beta_1 + \beta_2 \eta_1 + \eta_1^2 + s\eta_1 \eta_2, \end{cases}$$

where $s = \text{sign}(ab) = -1$ (here $a = 322.778$, $b = -2.6363$ by CONTENT [25]).

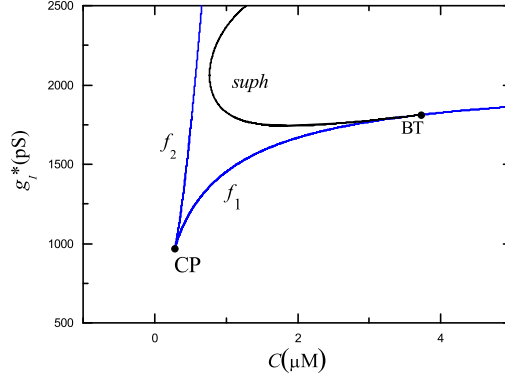


FIGURE 1. Two-parameter bifurcation diagram of equations (1)-(2) with respect to the slow variable C and the parameter g_I^* is plotted in the (C, g_I^*) -plane. All parameter values are taken from Table 1. The curves in the diagram respect the supercritical Hopf bifurcation (the black curve *suph*) and the fold bifurcation (the blue curves f_1 and f_2) of the fast subsystem (1)-(2). The codimension-2 bifurcations of the fast subsystem (1)-(2) are marked by the black points with labels, where CP refers to the cusp bifurcation and BT refers to the Bogdanov-Takens bifurcation.

3.2. Different types of bursting. Fig. 1 implies that when g_I^* increases from 500 pS to 2500 pS, the Chay neuronal model can exhibit different types of bursting as follows.

When $g_I^* = 1500$ pS, the system shows the “fold/fold” point-point hysteresis loop bursting, as illustrated in Fig. 2(a). Fig. 2(b) shows the fast/slow decomposition and bifurcation analysis for the “fold/fold” bursting via point-point hysteresis loop in the (C, V) -plane. In this case, the equilibrium points of the fast subsystem with respect to the parameter C form a Z-shaped bifurcation curves with two fold bifurcation points (LP1 and LP2). The fast subsystem exhibits bistability as shown in Fig. 2(b) between the stable node states on the lower branch and the stable focus states on the upper branch of the Z-shaped curve. The quiescent state disappears via a fold bifurcation at LP1 and the firing state disappears via another fold bifurcation at LP2 in the fast subsystem. Thus, the model is capable of “fold/fold” point-point hysteresis loop bursting. From Fig. 1, two fold bifurcations f_1 and f_2 coexist in the region above the point CP where two fold bifurcations coalesce and disappear. Hence, the codimension-2 cusp bifurcation of the fast subsystem is essential to this “fold/fold” type bursting.

Fig. 1 shows that two supercritical Hopf bifurcations occur as g_I^* increases. When $g_I^* = 1770$ pS, the model exhibits the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop, as shown in Fig. 3(a). Fig. 3(b) is the fast/slow decomposition and bifurcation analysis for the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop in the (C, V) -plane of the fast subsystem. Similar to Fig. 2(b), the equilibrium points of the fast subsystem with respect to the parameter C form a Z-shaped bifurcation curves with two fold bifurcation points (LP1 and LP2) and there are two Hopf bifurcation points (H1 and H2). The lower rest states transit to the upper rest

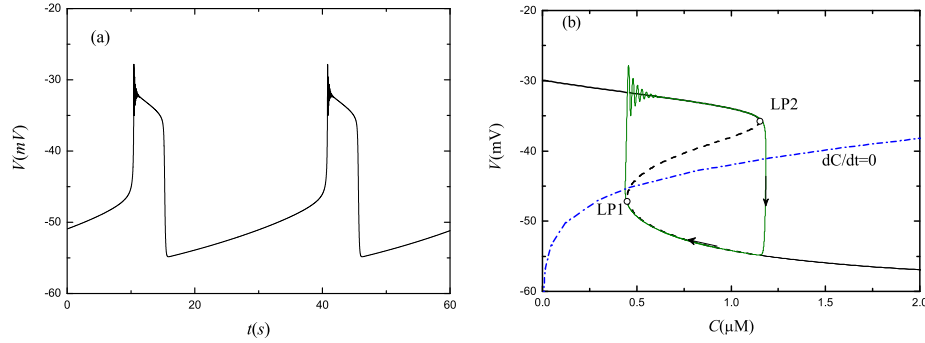


FIGURE 2. “Fold/fold” bursting via point-point hysteresis loop in the Chay model (1)-(3) when $g_I^* = 1500$ pS. Other parameter values are the same as in Fig. 1: (a) time course of the membrane potential; (b) fast/slow decomposition and bifurcation analysis. Bursting solution is superimposed on the bifurcation diagram of the (C, V) -plane of the fast subsystem when C acts as the bifurcation parameter. Thick solid (dashed) lines indicate stable (unstable) states. LP1 and LP2 refer to the saddle-node bifurcation. Direction of the bursting solution is determined by its position related to the C-nullcline ($dC/dt = 0$ shown by the dashed-dot line) which is shown by arrows.

states via the fold bifurcation at LP1. The dynamics as the upper rest state branch shows small decaying oscillation in bursting, which results to the convergence of the trajectory to the stable focus. The up-state disappears and repetitive spiking corresponding to the stable limit cycle appears via the Hopf bifurcation at H1. The spiking state experiences several increasing spikes, and then decreases via another Hopf bifurcation at H2. Thus, we obtain a transition between periodic spiking and quiescence via the supercritical Hopf bifurcation. The bifurcations are observed

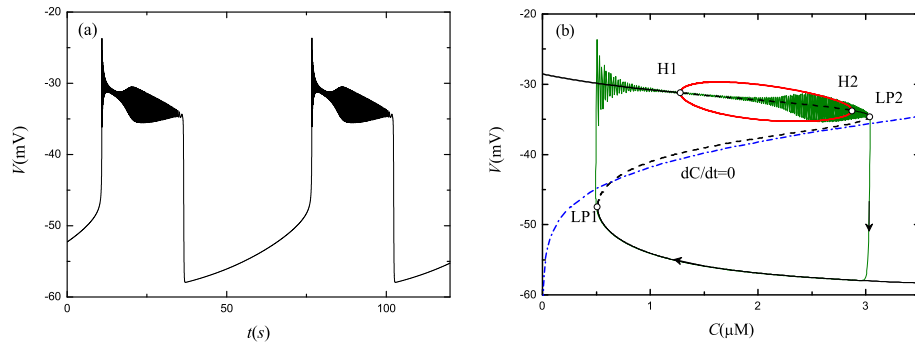


FIGURE 3. Bifurcation diagram of the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop when $g_I^* = 1770$ pS. Notations are the same as in Fig. 2. H1 and H2 refer to the Hopf bifurcation (supercritical). The red lines between H1 and H2 represent the maximum and minimum values of V for the limit cycles.

from down-state to up-state and from up-state to down-state via the fold bifurcations at LP1 and LP2, respectively. Therefore, we conclude that the model exhibits the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop.

As g_I^* increases further, the “Hopf/homoclinic” bursting via “fold/homoclinic” hysteresis loop can be obtained by setting $g_I^* = 1800$ pS, as shown in Fig. 4(a). Fig. 4(b) presents the fast/slow decomposition and the bifurcation analysis for the “Hopf/Homoclinic” bursting via the “fold/homoclinic” hysteresis loop in the (C, V) -plane. The quiescent state disappears via the supercritical Hopf bifurcation, and the periodic spiking disappears via the homoclinic bifurcation (HC).

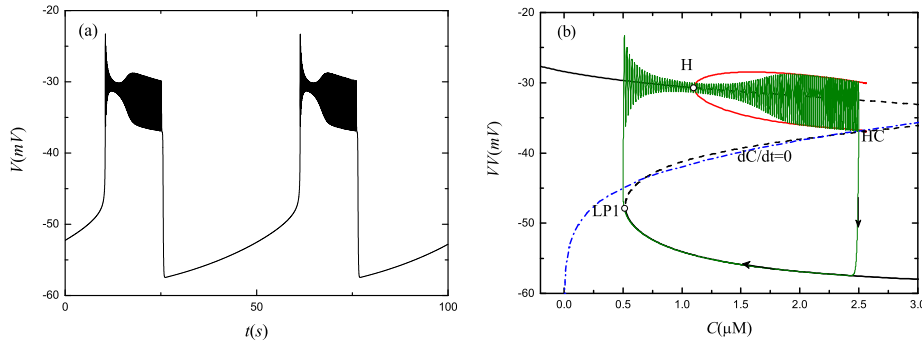


FIGURE 4. Bifurcation diagram of the “Hopf/homoclinic” bursting via the “fold/homoclinic” hysteresis loop when $g_I^* = 1800$ pS. Notations are the same as that in Fig. 2

From the above discussion, for different values of the parameter g_I^* , the Chay model can exhibit different firing patterns, such as the “fold/fold” bursting, the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop and the “Hopf/homoclinic” bursting via the “fold/homoclinic” hysteresis loop. The “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop looks like the “Hopf/homoclinic” type and then can be considered as the intermediate state between the ‘fold/fold’ bursting and the “Hopf/homoclinic” bursting.

4. Bursting with the change of parameter g_L^* . In this section, we choose the leak conductance g_L^* as an inherent bifurcation parameter to investigate the influence of the leak conductance of the current on both the two-parameter bifurcation structure and the firing patterns.

We take $g_I^* = 1800$ pS (and other parameters are the same as those as given in Fig. 1), and apply the two-parameter bifurcation analysis of the fast subsystem (1)-(2) with respect to C and g_L^* . The result is shown in Fig. 5. The curves in Fig. 5 show the supercritical Hopf bifurcation (*suph*) and the fold bifurcation (f_1 and f_2) of the equilibrium points of the fast subsystem, respectively. The cusp bifurcation CP and the Bogdanov-Takens bifurcation are two codimension-2 bifurcations.

Fig. 5 shows that when $g_L^* = 5$ pS, there are two fold bifurcations (located in f_1 and f_2) and one Hopf bifurcation (located in *suph*) for the fast subsystem. The fast subsystem exhibits bistability between the stable node state on the lower branch and the stable limit cycle state on the upper branch of the Z-shaped curve as shown in Fig. 6(b). In this case, we have a bursting of the “Hopf/homoclinic” bursting

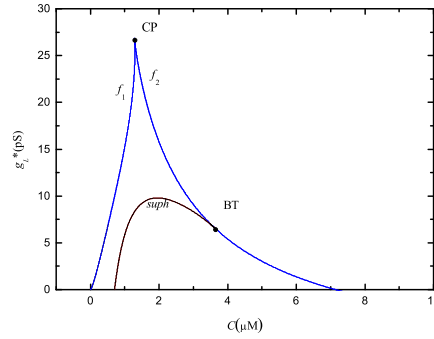


FIGURE 5. The two-parameter bifurcation diagram of equations (1)-(2) with respect to the slow variable C and the parameter g_L^* is plotted in the (C, g_L^*) -plane, where $g_I^* = 1800$ pS.

via the “fold/homoclinic” hysteresis loop, as shown in Fig. 6. This type of bursting is the same as that in Fig. 4.

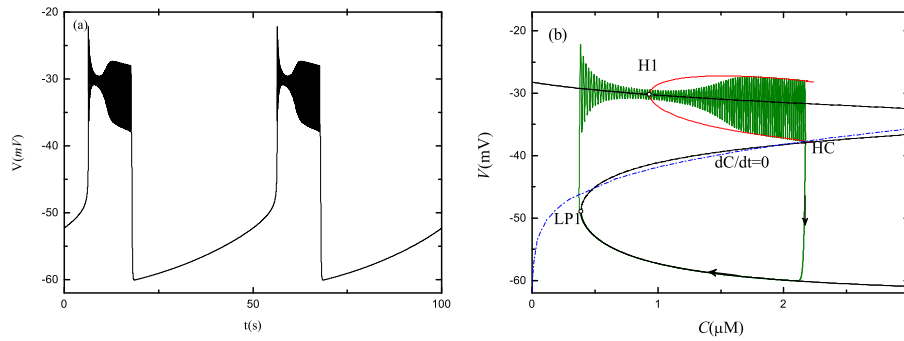


FIGURE 6. Bifurcation diagram when $g_I^* = 1800$ pS and $g_L^* = 5$ pS.

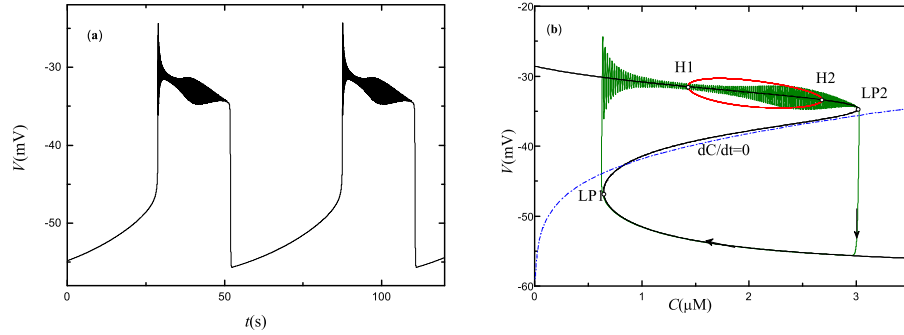
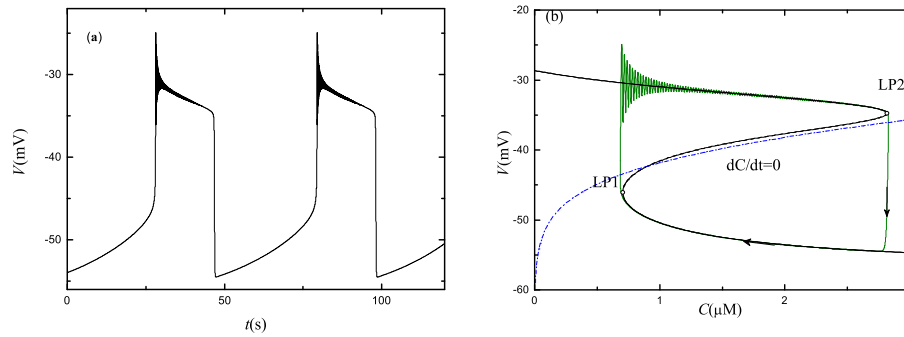
In Fig. 5, a codimension-2 Bogdanov-Takens bifurcation occurs at $g_L^* = 6.4676$ pS. This BT point is the origin of the homoclinic bifurcation curve [23], which brings up a “Hopf/homoclinic” bursting.

Fig. 7 (b) shows the fast/slow decomposition and the bifurcation analysis for the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop for $g_L^* = 9$ pS, which is similar to that in Fig. 3. The fast subsystem undergoes two Hopf bifurcations and two fold bifurcations.

When $g_L^* = 10$ pS, the fast subsystem undergoes two fold bifurcations. The neuron exhibits the bursting of the “fold/fold” type as shown in Fig. 8, which is the same as that in Fig. 2.

As g_L^* further increases, the Hopf bifurcation may disappear and then two fold bifurcations f_1 and f_2 come to the same point CP ($g_L^* = 26.8226$ pS), which is a codimension-2 cusp bifurcation, as shown in Fig. 5.

The above discussions show that the Chay neuronal model has three types of bursting near the codim-2 BT bifurcation, including the “Hopf/homoclinic” bursting via the “fold/homoclinic” hysteresis loop, the “Hopf/Hopf” bursting via the

FIGURE 7. Bifurcation diagram when $g_I^* = 1800$ pS and $g_L^* = 9$ pS.FIGURE 8. Bifurcation diagram when $g_I^* = 1800$ pS and $g_L^* = 10$ pS.

“fold/fold” hysteresis loop and the “fold/fold” bursting. These three types of bursting also occur when the parameter g_I^* is changed. The two-parameter bifurcation structure of the fast subsystem are similar when either g_I^* or g_L^* is considered as the control parameter. The two-parameter bifurcation structure of the fast subsystem, especially the relative position of the Hopf bifurcation curves and the fold bifurcation curves, play a key role in determining the types of bursting that are occur in the model.

5. Conclusion. In this paper, bursting oscillations in the Chay neuronal model were studied by the fast/slow decomposition and the two-parameter bifurcation analysis. Different kinds of bursting modes were studied for several chosen set of parameter values. In particular, bursting near the codimension-2 bifurcation points were investigated by the multiple time scale and the two-parameter bifurcation analysis.

Among the cases discussed in Section 3 and Section 4, the fast subsystem undergoes a codimension-2 cusp and a Bogdanov-Takens bifurcations, as shown in Fig. 1 and Fig. 5, respectively. Furthermore, the Hopf bifurcation curve locates in the region which is enclosed by two fold bifurcation curves f_1 and f_2 . The relative position of the Hopf bifurcation curves and the fold bifurcation curves in Fig. 1 are similar to that in Fig. 5. In brief, the bifurcation structures near the codimension-2 cusp bifurcation and Bogdanov-Takens bifurcation as discussed in

Section 3 are very similar to those in Section 4. Therefore, the transition mechanisms between different electrical firing activities in both cases are similar. When either the parameter g_I^* increases or g_L^* decreases, the Chay model is able to exhibit three types of bursting, which include the “fold/fold” bursting, the “Hopf/Hopf” bursting via the “fold/fold” hysteresis loop and the “Hopf/homoclinic” bursting via the “fold/homoclinic” hysteresis loop.

From discussions in this paper, the relative position of the codimension-1 bifurcation curves and the codimension-2 bifurcation points of the fast subsystem can give additional information to determine possible types of bursting in the Chay neuronal model. Therefore, the bifurcation structures of the fast subsystem can provide crucial information for the bursting patterns in neuronal models under given parametric conditions.

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