Dynamics of in-phase and anti-phase bursting in the coupled pre-Bötzinger complex cells

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Received: 23 June 2016/Revised: 31 August 2016/Accepted: 7 September 2016/Published online: 12 September 2016
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Abstract Activity of neurons in the pre-Bötzinger complex within the mammalian brain stem has an important role in the generation of respiratory rhythms. Previous experimental results have shown that the dynamics of sodium and calcium within each cell may be responsible for various bursting mechanisms. In this paper, we study the bursting dynamics of the two-coupled pre-Bötzinger complex neurons. Using a combination of fast-slow decomposition and two-parameter bifurcation analysis, we explore the possible forms of dynamics that the model network can produce as well the transitions of in-phase and anti-phase bursting respectively.

Keywords Bursting · Bifurcation analysis · Fast-slow decomposition · Pre-Bötzinger complex

Introduction

Respiratory movement is a physiological activity for organism to maintain the basic individual life. Experiments have shown that the pre-Bötzinger complex (pre-BötC) of mammalian brain-stem has a closely relationship with the generation of respiratory rhythm (Smith et al. 1991). Within the pre-BötC, there are some neurons which can

capable of regular oscillatory bursting independently. They can be issued impulses independently by a certain frequency, that is called neuronal firing activity (Smith et al. 1991; Rubin et al. 2009; Gray et al. 1999). Quiescence, bursting and tonic spiking may generate as particular parameters are varied in the pre-BötC. Among of them, bursting is a relatively complex activity pattern that arises in mathematical models for a variety of biological systems. Experiments have shown that neurons with excitatory synaptic coupling can present bursting patterns (Butera et al. 1999a, b).

Bursting rhythms are an important firing patterns of neuronal system in the pre-BötC. Rubin has studied the dynamics of a two-cell network, an excitatory neuron coupled with a tonically active neuron (Rubin 2006). Smith et al. investigated the factors that affect the firing pattern of neurons. They found that the change of ionic concentration and ionic conductivity of the membrane have affected neuronal firing patterns (Smith et al. 1991; Butera et al. 1997, 1999a, b). Smith et al. further investigated the frequency control and synchronization of these model neurons when coupled by excitatory synapses, simulations of pairs of identical cells revealed that increasing tonic excitation increases the frequency of synchronous bursting (Butera et al. 1999b). Bursting and complex synchronous behaviors are important aspects in the study of rhythm dynamics of complex neuronal system (Wang et al. 2011; Guo et al. 2012; Sun et al. 2011; Perc and Marhl 2004a, b).

By geometric dynamical systems techniques, predominantly a fast/slow decomposition and bifurcation analysis approach (Rinzel 1985). Bifurcation structures of bursting oscillations in cells has been studied in detail (Perc and Marhl 2003, 2007; Perc et al. 2007), for example. Best et al. studied a two-cell model network with synaptic coupling and they found that the square-wave bursting is

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replaced by the top hat bursting (also known as fold/fold cycle bursting) over a wide parameter range (Best et al. 2005). The transition from bursting to spiking has been studied in a variety of neuronal models (Bi et al. 2014; Duan et al. 2012; Rinzel 1985; Izhikevich 2000; Jia et al. 2012; Gu and Xiao 2014). The fast-slow decomposition (Rinzel 1985) is an analytic method in the study of bursting activities. The bifurcation of the fast subsystem with respect to the slow variable explain the bursting generation mechanisms. Izhikevich provided a classification of fast-slow bursters (Izhikevich 2000) that are examples among many bursting patterns in neuronal systems. Synchronization transition induced by synaptic delay in coupled fast-spiking neurons has been investigated by Wang et al. (2008). As mentioned in Reference (Best et al. 2005), there are antiphase and in-phase periodic oscillates in the two-coupled pre-BötC neuron model. However, to the authors' knowledge, there are much few studies on the transition mechanisms between different antiphase and in-phase bursting patterns in the coupled pre-BötC neuron model.

Based on previous studies, we will explore transition mechanism of different firing patterns in the coupled neurons. This paper is organized as follows. In Sect. 2, we introduce the Butera model of the two-coupled neurons with excitatory synaptic coupling. In Sect. 3, we briefly state the method of fast-slow decomposition. By the two-parameter bifurcation analysis of two-coupled neurons, we explore the bursting transitions from one bursting pattern to another numerically. The conclusion is in the last section.

Model description

The Butera model (1999a) with excitatory synaptic coupling is described as follows:

$$\dot{v}_i = (-I_{NaP} - I_{Na} - I_K - I_L - I_{tonic-e} - I_{syn-e})/C, \quad (1)$$

$$\dot{h}_i = \epsilon(h_\infty(v_i) - h_i)/\tau_h(v_i), \quad (2)$$

$$\dot{n}_i = (n_\infty(v_i) - n_i)/\tau_n(v_i), \quad (3)$$

$$\dot{s}_i = \alpha_s(1 - s_i)s_\infty(v_i) - s_i/\tau_s, \quad (4)$$

where $i \in \{1, 2\}$, terms on the right-hand side of Eq. (1) denote ionic currents. I_{NaP} , I_{Na} , I_K and I_L represent a persistent sodium current, sodium current, potassium current and leak current respectively. $I_{tonic-e}$ denote the tonic depolarizing current, which is taken to be identical for all neurons. I_{syn-e} represent the synaptic current of an excitatory synaptic input from one neuron to another. Specifically, $I_{NaP} = g_{NaP} m_{P\infty}(v_i)h_i(v_i - E_{Na})$, $I_{Na} = g_{Na}m_\infty^3(v_i)(1 - n_i)(v_i - E_{Na})$, $I_K = g_K n_i^4(v_i - E_K)$, $I_L = g_L(v_i - E_L)$, $I_{tonic-e} = g_{tonic-e}(v_i - E_{syn-e})$, and $I_{syn-e} = g_{syn-e}s_j(v_i - E_{syn-e})$, where $i, j \in \{1, 2\}$ and $i \neq j$. The functions and the

values of parameters in equations are specified in “Appendix”.

Firing patterns in the excitatory synaptic coupled pre-BötC neurons exhibit in-phase and anti-phase bursting (or spiking) under different initial conditions (Sun et al. 2011). When the initial conditions for two-coupled neurons are same, the system will exhibit in-phase bursting. When the initial conditions for two-coupled neurons are different, the system will exhibit anti-phase bursting, as shown in Fig. 1a (in-phase bursting) and Fig. 1c (anti-phase bursting) respectively.

Pattern transition of in-phase and anti-phase bursting

Experiments have shown that when the persistent sodium conductance (g_{NaP}) decreases to a certain range, bursting phenomenon will disappear (Best et al. 2005). That means the persistent sodium conductance(g_{NaP}) of the pre-BötC neurons produce a fundamental role on the generation of bursting rhythm. In this section, we study the effects of sodium conductance on transition mechanism of in-phase and anti-phase bursting.

Fast-slow decomposition

For excitatory coupling neuron model (1)–(4) in the pre-BötC, ϵ is a small quantity, and $\epsilon/\tau_h(v) \ll 1/\tau_n(v)$ for all relevant v . The evolution of h_i is much slower than that of v . Based on the fast-slow decomposition method developed by Rinzel (1985), we can treat h_i as slow variable of the whole system (1)–(4).

The changes of h_1 and h_2 as functions of time t are shown in Fig. 2. The two curves are almost coincident, hence we assume that the slow variables h_1 and h_2 are equal. We can then perform the fast-slow decomposition analysis with a single slow variable h_1 ($h_1 = h_2$). So the fast subsystem includes (1), (3) and (4) while the slow subsystem (2).

Two-parameter bifurcation analysis

Two-parameter bifurcation diagrams of the fast subsystem (1), (3) and (4) with respect to the slow variable h in the (h, g_{Na}) -plane are shown in Fig. 3. Figure 3a, b are two-parameter bifurcation diagrams related to in-phase and anti-phase bursting respectively. Whether the system (1)–(4) exhibits in-phase bursting (Fig. 2a) or anti-phase bursting (Fig. 2b), the fast subsystem equations (1), (3) and (4) undergoes three codimension-2 bifurcation points, that is Bogdanov-Takens bifurcation (BT), cusp bifurcation (CP) and Bautin bifurcation (GH) (Kuznetsov 2005).

Fig. 1 Membrane potential v_1 and v_2 with respect to time t with $g_{Na} = 8$ nS. The green line represents v_1 , the red line represents v_2 . **a** In-phase bursting; **b** enlargement part of spikes within bursting of (a);

c anti-phase bursting; **d** enlargement part of spikes within bursting of (c). (Color figure online)

Fig. 2 Plots of h_1 (red) and h_2 (green) as functions of time with $g_{Na} = 8$ nS at the case: **a** in-phase; **b** anti-phase. (Color figure online)

When the coupled neurons exhibit in-phase bursting, the bifurcation curves include subcritical Hopf bifurcation (subh), supercritical Hopf bifurcation (suph), fold bifurcation of equilibrium (f_1 and f_2), fold bifurcation of limit cycles (l) and homoclinic bifurcation of limit cycle (homo), as shown in Fig. 3a. When the coupled neurons exhibit anti-phase bursting, the bifurcation curves are same as that in-phase bursting except that the homoclinic bifurcation of limit cycle (homo) changed to another fold bifurcation of limit cycles (l_1), as shown in Fig. 3b. The change of the

homoclinic bifurcation of limit cycle (homo) (Fig. 3a) to the fold bifurcation of limit cycles (l_1) (Fig. 3b) resulted that the two-coupled neurons exhibit different bursting patterns, that means, in-phase or anti-phase bursting.

Dynamic analysis for in-phase bursting

For g_{Na} increasing in a certain range, the bifurcation structure of the fast subsystem (1), (3) and (4) with respect to the slow variable h ($h_1 = h_2 = h$) is projected onto the (h, V_1) -plane,

Fig. 3 Two-parameter bifurcation diagram of the fast subsystem (1), (3) and (4) with respect to the slow variable h and the parameter g_{Na} . The curves in the diagram display the supercritical Hopf bifurcation (suph), the subcritical Hopf bifurcation (subh), the fold bifurcation (f_1 and f_2) of equilibrium points. The codimension-2 bifurcations of the fast subsystem are marked by points with corresponding labels, where CP refers to the cusp bifurcation, BT to the Bogdanov-Takens

bifurcation and GH to the Bautin bifurcation. The bifurcation curves for limit cycles are different for the case of in-phase and anti-phase. **a** When the coupled neurons exhibit in-phase bursting. The bifurcation curves of the limit cycle are the fold limit cycle bifurcation (l) and the homoclinic bifurcation (homo); **b** when the coupled neurons exhibit anti-phase bursting. The bifurcation curves of the limit cycle are the fold limit cycle bifurcation (l_1 and l_2)

Fig. 4 Fast-slow decomposition of the fast subsystem (1), (3) and (4) with respect to the slow variable h and the parameter g_{Na} changed when the coupled neurons exhibit in-phase bursting. The lower branch (the solid curves) of the Z-shaped curve are nodes, and the middle branches (the dashed curve) are composed of saddles. The

upper branch is made of stable (the solid curve) and unstable (the dashed curve) focuses, with one supercritical Hopf bifurcation point HB. The limit cycles (red curves) bifurcate from HB and then disappear at the homoclinic bifurcation (HC). **a** $g_{Na} = 1.7 \text{ nS}$; **b** $g_{Na} = 1.9 \text{ nS}$; **c** $g_{Na} = 2.2 \text{ nS}$; **d** $g_{Na} = 8 \text{ nS}$. (Color figure online)

as shown in Fig. 4. The equilibrium points form three “S-shaped” curves, in which the stable equilibrium points are described with the black solid line and the unstable equilibrium points, the black dashed line. Note that a family of periodic orbits (red solid line) emanate from the supercritical Hopf (HB) bifurcation on the upper branch of one “S-shaped” curve and terminate at homoclinic bifurcation (HC). The oscillations emerging from these periodic orbits (green) are called the in-phase oscillation, as shown in Fig. 4a–d.

The coupled neurons can exhibit three types of in-phase bursting, which are, the “fold/fold” bursting (Fig. 4a), the “Hopf/homoclinic” bursting via “fold/homoclinic” hysteresis loop (Fig. 4b, c) and the “fold/homoclinic” bursting (Fig. 4d). The fast-slow decomposition of different bursting are shown in Fig. 4a–d respectively for different values of g_{Na} . The trajectory of the whole system (1)–(4) (the green curve) is also superimposed.

In the case $g_{Na} = 1.7 \text{ nS}$, the rest state disappears via fold bifurcation F_1 , and the active state disappears via another fold bifurcation F_2 , so the bursting is called the “fold/fold” type according to the classifications introduced by Izhikevich (2000), as shown in Fig. 4a. When g_{Na} continuously increases, the attracting of periodic orbits gradually appears. So the the rest state transits to upper state via fold bifurcation F_1 , then the trajectory damps and tends to stable focus. When the trajectory goes through the Hopf bifurcation (HB), it begins to oscillate around the stable limit cycle. Finally, the active state disappears via the homoclinic (HC) bifurcation. So the bursting is called the “Hopf/homoclinic” type via “fold/homoclinic” hysteresis loop (Fig. 4b, c).

When $g_{Na} = 2.2 \text{ nS}$, the rest state disappears via fold bifurcation F_1 , and the active state disappears via the homoclinic (HC) bifurcation. So the bursting is called the “fold/homoclinic” type. With the value of g_{Na} increasing further, the supercritical Hopf (HB) bifurcation of the fast subsystem changes to subcritical Hopf (HB) bifurcation, while the type of bursting is the same, as shown in Fig. 4 d.

Note that variation in activity patterns with changes in g_{Na} correspond strongly to changes in the dynamics of the subsystem (1), (3) and (4). According to the fast-slow decomposition and two-parameter bifurcation analysis, we divide parameter region into three subregions, that is region I, region II and region III, as shown in Fig. 3a. The bursting patterns in three subregion are different. We detail the boundaries of subregions of different bursting patterns that arises as parameter g_{Na} is varied. When $1.46 \text{ nS} < g_{Na} < 1.76 \text{ nS}$, between point BT (Bogdanov-Takens) and A, we name it as subregion I in which we have in-phase “fold/fold” bursting. Subregion II is between point A and B ($1.76 \text{ nS} < g_{Na} < 2.55 \text{ nS}$) in which we have in-phase

“Hopf/homoclinic” bursting via “fold/homoclinic” hysteresis loop. When $g_{Na} > 2.55 \text{ nS}$, we name it as subregion III in which we have in-phase “fold/homoclinic” bursting.

Dynamic analysis for anti-phase bursting

For the same parameter sets, the two-coupled neurons with different initial values exhibit anti-phase bursting when g_{Na} increases in a certain range. The bifurcation structure of the fast subsystem (1), (3) and (4) with respect to the slow variable h ($h_1 = h_2 = h$) is projected onto the (h, V_1) -plane, as shown in Fig. 5. Similarly, the equilibrium points form three “S-shaped” curves. Note that a family of periodic orbits (red solid line) emanate from the supercritical Hopf (HB) bifurcation on the upper branch of one “S-shaped” curve. Differently, the stable periodic orbits coincide with unstable limit cycles and then disappear at fold limit cycle bifurcation (LP). The oscillations emerging from these periodic orbits (green) are called the anti-phase oscillation, as shown in Fig. 5a–d.

The coupled neurons can exhibit three types of anti-bursting, which are, the “fold/fold” bursting (Fig. 5a), the “Hopf/fold limit cycle” bursting via “fold/fold limit cycle” hysteresis loop (Fig. 5b, c) and the “fold/fold limit cycle” bursting (Fig. 5d). The fast-slow decomposition of different bursting are shown in Fig. 5a–d respectively for different values of g_{Na} . The trajectory of the whole system (1)–(4) (the green curve) is also superimposed.

In the case $g_{Na} = 1.7 \text{ nS}$, the fast-slow decomposition is same as that “fold/fold” bursting shown in Fig. 4a. As g_{Na} continuously increases, the attracting of periodic orbits gradually appears and the active state disappears via the bifurcation of fold limit cycle (LP). So the bursting is called the “Hopf/fold limit cycle” type via “fold/fold limit cycle” hysteresis loop (Fig. 5b, c).

When $g_{Na} = 8 \text{ nS}$, the rest state disappears via fold bifurcation F_1 , and the active state disappears via the bifurcation of fold limit cycle (LP). So the bursting is called the “fold/fold limit cycle” type, as shown in Fig. 5d.

Given the different initial conditions for the same parameter sets, the two-coupled neurons exhibit anti-phase bursting. We divide parameter region into three subregions, that is region I, region II and region III, as parameter g_{Na} is varied (shown in Fig. 3b). When $1.62 \text{ nS} < g_{Na} < 1.90 \text{ nS}$, between point BT (Bogdanov-Takens) and C, we name it as subregion I in which we have anti-phase “fold/fold” bursting. Subregion II is between point C and D ($1.90 \text{ nS} < g_{Na} < 2.69 \text{ nS}$) in which we have anti-phase “Hopf/fold limit cycle” bursting via “fold/fold limit cycle” hysteresis loop. When $g_{Na} > 2.69 \text{ nS}$, we name it as subregion III in which we have anti-phase “fold/fold limit cycle” bursting.

Fig. 5 Fast-slow decomposition of the fast subsystem (1), (3) and (4) with respect to the slow variable h and the parameter g_{Na} changed when the coupled neurons exhibit anti-phase bursting. The Z-shaped

curve is the same as that in Fig. 4, but the limit cycles disappear via the fold limit cycle bifurcation (LP). **a** $g_{Na} = 1.7 \text{ nS}$; **b** $g_{Na} = 1.9 \text{ nS}$; **c** $g_{Na} = 2.2 \text{ nS}$; **d** $g_{Na} = 8 \text{ nS}$

Conclusions

In this paper, we have taken the model introduced by Butera for two-coupled neurons in pre-BötC, which yields in-phase and anti-phase bursting as particular parameter are varied, and applied a previously developed fast/slow decomposition method (Rinzel 1985) to obtain the transition mechanism of the in-phase and the anti-phase bursting respectively. With different parameter sets, the single pre-BötC neuron can exhibits different firing patterns. Under different initial conditions, firing patterns in the excitatory synaptic coupled pre-BötC neurons exhibit in-phase and anti-phase bursting (or spiking) for the same parameter sets. Based on the the fast-slow decomposition analysis, we interpret the types of in-phase bursting and anti-phase bursting. The results shown that for the in-phase bursting, two-coupled neurons yield the “fold/fold” bursting, the “Hopf/homoclinic” bursting via “fold/homoclinic” hysteresis loop and the “fold/homoclinic” bursting as the parameter g_{Na} varied; the “fold/fold” bursting, the “Hopf/fold limit cycle” bursting via “fold/homoclinic” hysteresis loop and the “fold/fold limit cycle” bursting for the anti-phase bursting respectively. The boundaries of

different types for in-phase and anti-phase bursting are obtained by two-parameter bifurcation analysis respectively. Our analysis of transitions establishes which switches between dynamic regimes are possible and hence is more comprehensible. The results obtained in this paper is helpful for the further understanding of the dynamics of the Butera model for pre-BötC neuron and the generation of the respiratory rhythm. It is promising to extend this method to investigate the dynamics of three coupled or even more pre-BötC neurons in the future work.

Acknowledgments This work is supported by National Natural Science Foundation of China (11472009), Science and Technology Project of Beijing Municipal Commission of Education (KM201410009012) and Construction Plan for Innovative Research Team of North China University of Technology(XN07005).

Appendix

For $x \in \{s, m_p, m, h, n\}$, the function $x_\infty(v)$ takes the form $x_\infty(v) = \{1 + \exp[(v - \theta_x)/\sigma_x]\}^{-1}$, and for $x \in h, n$, the function $\tau_x(v)$ takes the form $\tau_x(v) = \tau_x / \cosh[(v - \theta_x)/2\sigma_x]$. The parameter values are listed in the Table 1.

Table 1 Parameter values used in the model

Parameter	Value	Parameter	Value	Parameter	Value	Parameter	Value
$g_{\text{ionic}-e}$	0.4 nS	E_L	−65.0 mV	τ_s	5 ms	θ_n	−29 mV
$g_{\text{syn}-e}$	8 nS	$E_{\text{syn}-e}$	0 mV	θ_s	−10.0 mV	σ_{mp}	−6 mV
g_{NaP}	5 nS	C	21 pF	σ_s	−5 mV	σ_h	6 mV
g_L	2.8 nS	τ_h/ϵ	10,000 ms	θ_{mp}	−40 mV	σ_m	−5 mV
E_{Na}	50.0 mV	τ_n	10 ms	θ_h	−48 mV	σ_n	−4 mV
E_K	−85.0 mV	α_s	0.2 ms ^{−1}	θ_m	−34 mV		

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