

# Burst firing transitions in two-compartment pyramidal neuron induced by the perturbation of membrane capacitance

Lei Wang · Shenquan Liu · Jing Zhang · Yanjun Zeng

Received: 27 June 2011 / Accepted: 6 October 2011  
© Springer-Verlag 2011

**Abstract** Neuronal membrane capacitance  $C_m$  is one of the prominent factors in action potential initiation and propagation and then influences the firing patterns of neurons. Exploring the roles that  $C_m$  plays in different firing patterns can facilitate the understanding of how different factors might influence neuronal firing behaviors. However, the impacts of variations in  $C_m$  on neuronal firing patterns have been only partly explored until now. In this study, the influence of  $C_m$  on burst firing behaviors of a two-compartment pyramidal neuron (including somatic compartment and dendritic compartment) was investigated by means of computer simulation, the value of  $C_m$  in each compartment was denoted as  $C_{m,s}$  and  $C_{m,d}$ , respectively. Two cases were considered, in the first case, we let  $C_{m,s} = C_{m,d}$ , and then changed them simultaneously. While in the second case, we assumed  $C_{m,s} \neq C_{m,d}$ , and then changed them, respectively. From the simulation results obtained from these two cases, it was found that the variation of  $C_m$  in the somatic compartment and the dendritic compartment show much difference, simulated results obtained from the variation of  $C_{m,d}$  have much more similarities than that of  $C_{m,s}$  when comparing with the results obtained in the first case under which  $C_{m,s} = C_{m,d}$ . These different effects of  $C_{m,s}$  and  $C_{m,d}$  on neuronal firing behaviors may result from the different topology and functional roles of soma and dendrites. Numerical results demonstrated in this paper may give us some inspiration in

understanding the possible roles of  $C_m$  in burst firing patterns, especially their transitions in compartmental neurons.

**Keywords** Membrane capacitance · Two-compartment pyramidal neuron · Burst firing · ISI · Periodic bifurcation

## Introduction

The activities of neurons are reflected in their electrical behaviors, while these kinds of behaviors are commonly represented as the potential difference between the inside and outside of the neuronal membrane, which are also termed as the membrane potential, with action potential being its most important form. A large number of factors can take part in the generation and propagation of action potential, such as: external stimulus [1], noise (internal or external) [2, 3], specific ion channels [4], membrane capacitance [5], and temperatures [6], etc. Membrane capacitance ( $C_m$ ) as one of the factors may be defined as: (1) the ability to separate and store charge difference between the inside and outside of the neuronal membrane; (2) the quantity of charge required to create a given potential difference; (3) the membrane is a leaky capacitor due to the presence of ion channels. Thus, doing research on  $C_m$  has much significance in qualitative and quantitative understanding of neuronal excitation and activation.

For a long time, the value of  $C_m$  is regarded as a biological constant, for that membrane constituents are broadly similar across different regions of the nervous system [7]. In many neuron models, especially the HH-type models, the parameter  $C_m$  is always treated as a fixed constant [8–17]. However, recent researches showed that the value of  $C_m$  is changeable rather than invariable. Trevelyan et al. [18] and Major et al. [19] have studied the

L. Wang · S. Liu  
Department of Mathematics, South China University  
of Technology, Guangzhou 510640, China

J. Zhang · Y. Zeng (✉)  
Biomedical Engineering Center, Beijing University  
of Technology, Beijing 100022, China  
e-mail: yjzeng@bjut.edu.cn

detailed passive properties of pyramidal cells, finding that the estimated  $C_m$  varies in a small range. Fernández et al. [20] found that membrane capacity is voltage as well as frequency dependent, as the voltage in neurons is always changing due to the internal or external perturbation, so the membrane capacity is bound to alter. There is still some documents mentioned that membrane capacitance may increase during intracellular perfusion with calcium buffered in a certain range [21]. For the values of  $C_m$  in different neurons, or different compartments within neurons are different, several studies have shown that the values of  $C_m$  can be as little as  $0.75 \mu\text{F}/\text{cm}^2$  in hippocampal CA3 pyramidal neurons [19] and as large as  $2.9 \mu\text{F}/\text{cm}^2$  in ventral horn neurons [22].

Many literatures related to  $C_m$  have been subject to intensive research due to their physiological significance. For instance, some researchers studied the measurement of specific membrane capacitance in neurons [7, 23–26]. Amzica et al. [27] investigated the role of membrane capacitance in sleep oscillations and spike-wave seizures. Szlavik [5] gave a detailed analysis of the impact of variations in membrane capacitance on the detected neural-electronic signal, and concluded that larger values of membrane capacitance results in smaller initial changes in potential across the cell membrane, while smaller values of membrane capacitance yield larger initial changes in transmembrane potential that can be sufficient to generate an action potential. These studies are helpful and instructive, but seldom discussed the exact role of  $C_m$  in burst firing patterns, especially the transitions among these patterns. As we have known, burst firing is one of the most important firing behaviors in many neuron systems and neural networks, and it is a prominent feature of pyramidal cells which is also thought to have significant functional roles in reliable signaling and synaptic plasticity [10]. Model studies about neuronal burst firing patterns are many; Duan et al. [12] discussed the influence of the variation in ion conductance and calcium concentration on bursting patterns and their bifurcation modes in Chay neuronal model. Yang et al. [16] investigated integer multiple spiking and its dynamical generation mechanism in the stochastic Chay model; the parameter they studied was ion conductance. Laing et al. [28] studied a novel bursting, named ghostbursting, in a sensory neuron model using periodic external stimulus. So, in this study, we mainly concentrate on the role of  $C_m$  in neuronal burst firing patterns and their transitions. As to the complex structure of neuronal morphology, the value of  $C_m$  in each part of the neuron is likely to be different; for this reason, a minimal two-compartment neuron was introduced in this paper. Based on this neuron model, we discussed the

neuronal firing behaviors when varying  $C_m$  in different compartment, two cases were considered and comparisons between these cases were made. Simulation results presented here not only illustrate the important role of  $C_m$  in the generation, conduction and switching of various neuronal bursting patterns, but also give the transition modes from which we can see how these firing patterns change from one to another.

## Model and method

The model we investigated in this paper is a two-compartment model of pyramidal neuron [10]. The schematic diagram of this neuron is shown in Fig. 1; in the diagram, the ionic currents in each compartment are given. The somatic compartment includes only the channels necessary for spike generation ( $\text{Na}^+$  and  $\text{K}^+$ ) while the dendritic compartment includes a slow potassium and a persistent sodium current.

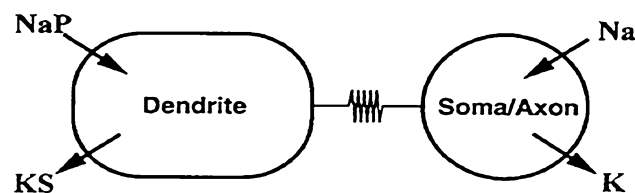
The model descriptions of this pyramidal neuron are as follows:

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

where  $I_{\text{soma}}$  and  $I_{\text{dendrite}}$  are current injections to the compartments. The voltage-dependent conductances are described using standard Hodgkin–Huxley formalism.

$$\frac{dx}{dt} = \phi_x (\alpha_x (1-x) - \beta_x x) \quad \text{or} \quad \frac{dx}{dt} = \phi_x ((x_{\infty} - x)/\tau_x) \quad (2)$$

where  $x$  denotes  $m$ ,  $h$ ,  $n$  and  $q$ , which are gating variables.



**Fig. 1** Schematic diagram of two-compartment pyramidal neuron [10]

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

The basic value of membrane capacitance is  $C_{m,s} = C_{m,d} = 1 \mu\text{F}/\text{cm}^2$ . The asymmetry between the areas of the two compartments is taken into account in the parameter  $P = \text{somatic area}/\text{total area}$  which has a base value of  $p = 0.15$  [10]. Coupling conductance is  $g_c = 1 \text{ mS}/\text{cm}^2$ , temperature scaling factors are  $\phi_m = 10$ ,  $\phi_h = \phi_n = 3.33$ , the ionic conductances are  $g_{\text{Leak}} = 0.18$ ,  $g_{\text{NaP}} = 0.12$ ,  $g_{\text{KS}} = 0.7$ ,  $g_{\text{Na}} = 55$ ,  $g_{\text{K}} = 20$ , and the equilibrium potentials are  $E_{\text{Leak}} = -65$ ,  $E_{\text{Na}} = 55$ ,  $E_{\text{K}} = -90$  (mV).

Simulations were performed using MATLAB software, and the fourth-order Runge–Kutta algorithm was employed to calculate the values of membrane potential with time step being 0.01 ms. We only inject direct current into the dendrite compartment (3.0  $\mu\text{A}$ ), and investigated the somatic action potential in this study.

## Simulation results

In the “Introduction”, we have mentioned that the value of  $C_m$  may not be a fixed constant pervading the complex morphology of neuronal dendrites, or from neuron to neuron, or from compartment to compartment within neurons, and the values of  $C_m$  can be as little as 0.75  $\mu\text{F}/\text{cm}^2$  in hippocampal CA3 pyramidal neurons [19] and as large as 2.9  $\mu\text{F}/\text{cm}^2$  in the ventral horn neurons [22]. For the

important role of  $C_m$  in neuronal action potential generation and propagation, in this section, a simple analysis about the influence of  $C_m$  on neuronal bursting patterns in two cases was conducted; numerical results are presented in sections “The case  $C_{m,s} = C_{m,d}$ ” and “The case  $C_{m,s} \neq C_{m,d}$ ” With computer simulation, a variety of burst firing shapes or patterns are obtained when  $C_m$  varies in a certain region and the transitions between these patterns can show a clear periodic bifurcation phenomenon with the change of  $C_m$ , such as period-adding bifurcation. The index we used to describe the transitions between different firing patterns is the diagram of inter-spike intervals (ISI), and the value of ISI is denoted as the time difference between adjacent peaks in spike trains, which is illustrated in Fig. 2.

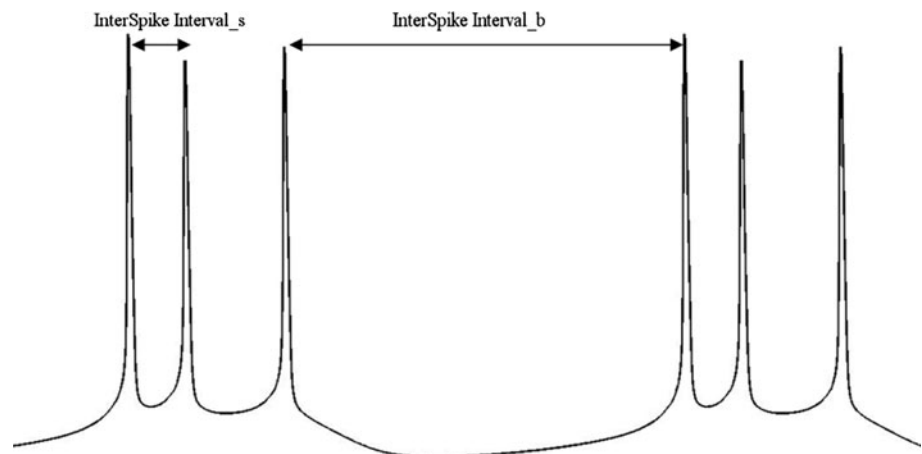
### The case $C_{m,s} = C_{m,d}$

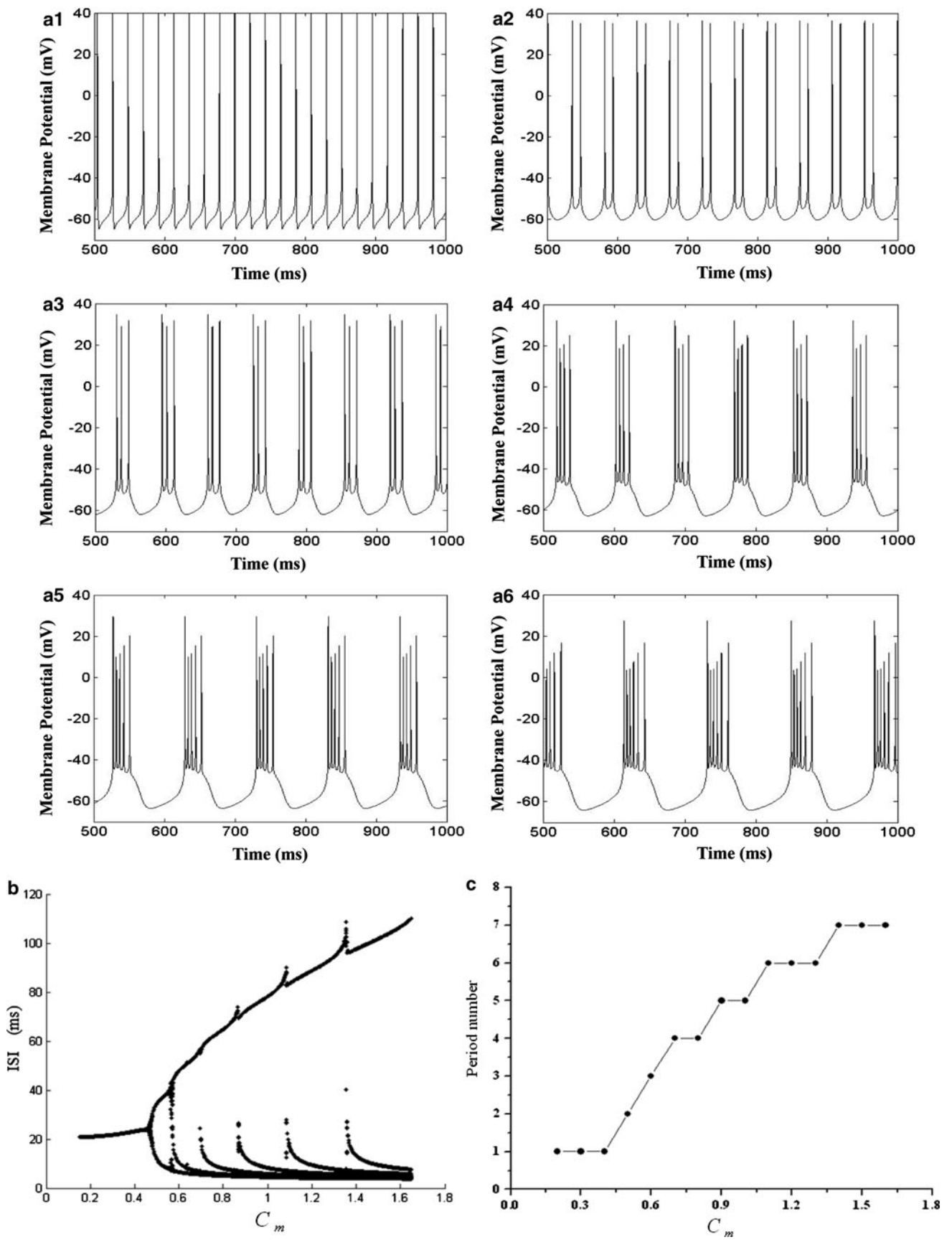
In this section, we assume the values of  $C_m$  in the two compartments are equal, that is  $C_{m,s} = C_{m,d} = C_m$ , the detailed simulation results are demonstrated in Fig. 3.

As we know, membrane capacitance can act as a capacitor, and has the ability to store and separate charge difference between the inside and outside of neuronal membrane so as to create the potential differences. Since the electrical activities of neurons are largely characterized by these potential differences, the role of  $C_m$  participating in neuronal activities cannot be ignored. As one of the neuronal electrical behaviors, bursting is a typical and prominent type, and is thought to have significant functional roles in reliable signaling and synaptic plasticity in some neurons [10]. Thus, discussions about the role of  $C_m$  in burst firing generation were given in this part.

By observing the numerical results shown in Fig. 3a1–a6, it is found that the cell has a clear period-adding firing phenomenon, with the increasing of  $C_m$  from 0.1 to 1.2, the cell period-adding bifurcates from period-1 spiking to period-2 bursting, and then period-adding bifurcates to period-3 bursting. This period-adding bifurcation trend

**Fig. 2** The schematic diagram of inter-spike interval (ISI) in neuronal spike trains. *InterSpike Interval\_s* denotes ISI between adjacent spikes within a burst, *InterSpike Interval\_b* denotes ISI between adjacent bursts





◀ **Fig. 3** Periodic firing patterns and their transition modes with the variation of  $C_m$ . **a1–a6** Periodic firing sequences of pyramidal neuron with the increase of  $C_m$ , the value of  $C_m$  is 0.3, 0.5, 0.6, 0.8, 1.0, 1.2 ( $\mu\text{F}/\text{cm}^2$ ), respectively; **b** ISI versus  $C_m$ ; **c** period number in each burst with respect to  $C_m$

lasts until the period number reaches 7 in this parameter region. These results clearly show that different periodic firing patterns can be generated under different values of  $C_m$ , with the increase of  $C_m$ , the firing patterns change from periodic spiking to periodic bursting, the period number per burst is also showing an uptrend with the increase of  $C_m$ . In order to explore how these different firing patterns change from one to another, we drew the ISI diagram, from which we can see the exact transition mode (see Fig. 3b), and we also drew the diagram of period number in each burst with the variation of  $C_m$  (see Fig. 3c). Simulation results shown in Fig. 3 can give us an apparent variation rule on how  $C_m$  impacts on neuronal burst firing sequences.

The case  $C_{m,s} \neq C_{m,d}$

In the preceding section, we investigated the role of  $C_m$  in burst firing generation and transitions with the assumption that the values of  $C_m$  in the two compartments are equal. Thus, from electrophysiology knowledge we understand that neuronal soma and dendrites have many differences, not only in the morphology, but also in the functional roles, especially the impacts they have on neuronal firing properties. Some documents have studied the different roles of soma and dendrite in neuronal firing patterns. Such as, Kamondi et al. [29] studied the theta frequency field oscillations in soma and dendrite of hippocampal pyramidal cells by intracellular recordings, and gave the difference between soma and dendrite in theta oscillation. Magee [30] discussed the exact mechanisms of neuronal dendrites on phase precession in hippocampal CA1 pyramidal neurons. Wong et al. [31] investigated different firing patterns generated in dendrites and soma of CA1 pyramidal neurons in guinea pig hippocampus, intracellular recordings in this research showed that burst firing is more likely elicited in dendrites than soma. All the above researches presented the different functional roles of soma and dendrite in neuronal firing behaviors. In this section, we consider the values of  $C_m$  in somatic compartment and dendritic compartment are different, that is  $C_{m,s} \neq C_{m,d}$ ; see Figs. 4, and 5 for the simulated results.

*Variation of  $C_{m,d}$  when  $C_{m,s}$  is fixed as  $1 \mu\text{F}/\text{cm}^2$*

We can see from Fig. 4a1–a8 that the cell can also show a clear period-adding firing phenomenon, with  $C_{m,d}$  increase from 0.1 to 1.6, the cell period-adding bifurcates from

period-1 spiking to period-2 bursting, and then period-adding bifurcates to period-3 bursting; this period-adding bifurcation trend lasts until the period number reaches 8 in this parameter region, this transition rule is very similar with the one demonstrated in Fig. 3.

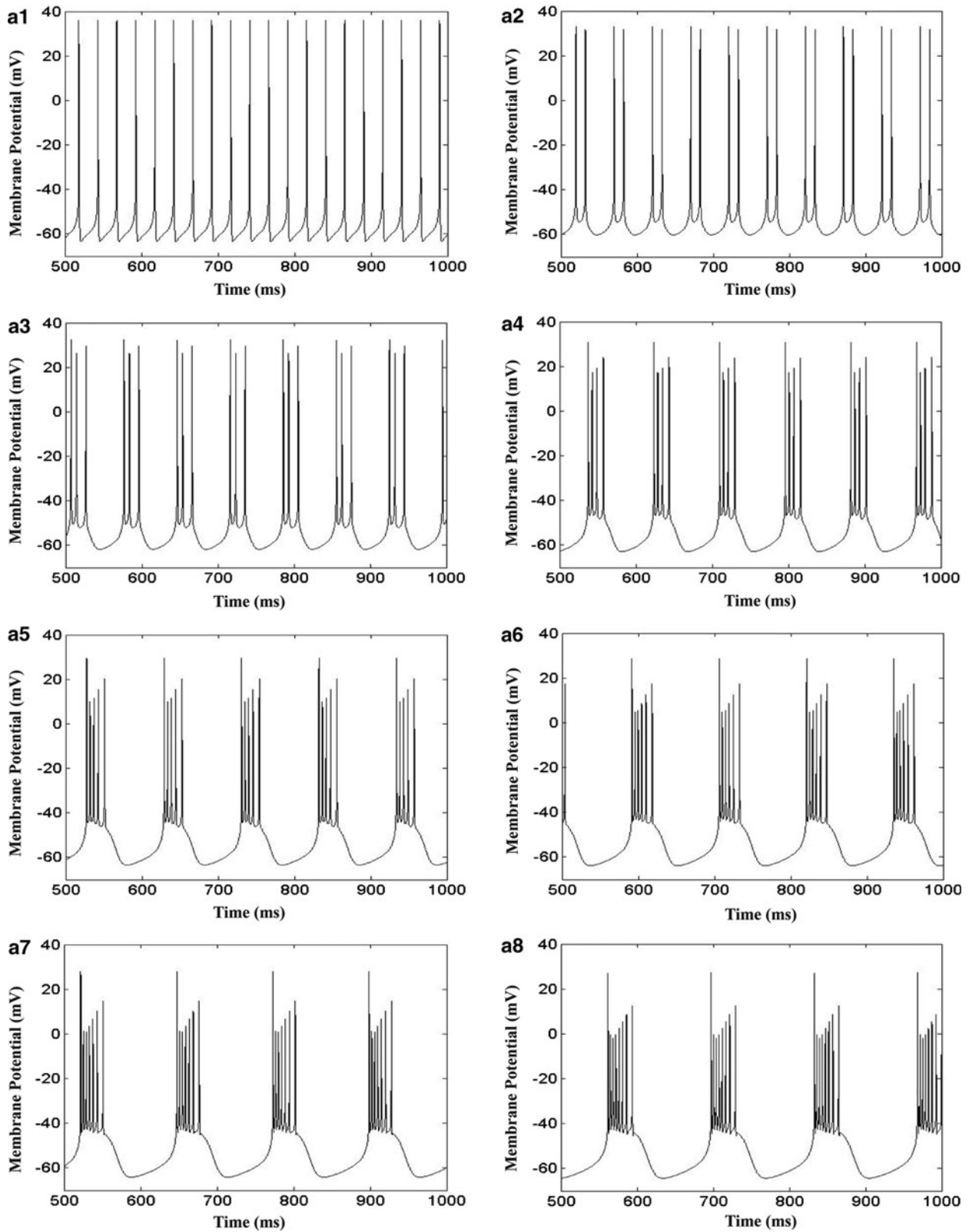
*Variation of  $C_{m,s}$  when  $C_{m,d}$  is fixed as  $1 \mu\text{F}/\text{cm}^2$*

In Fig. 5a, b, we give two firing patterns for different values of  $C_{m,s}$ , and by observing the ISI diagram in Fig. 5c we find that the bifurcation diagram is very different with the diagrams shown in Figs. 3b and 4b, and the change of burst firing patterns is rather little in the similar parameter region. The question then arises as to why the change of  $C_{m,d}$  can produce a bifurcation pattern similar to Fig. 3b, while the variation of  $C_{m,s}$  is so much different from Fig. 3b. The reason may be that burst firing is more easily induced in neuronal dendrites; intracellular recordings on hippocampus CA1 pyramidal cells have shown that burst firing is more likely elicited in dendrites than soma [31]. In the simulation of two-compartment pyramidal neuron in this paper, the variation of  $C_{m,d}$  and  $C_{m,s}$  can both influence the transitions between neuronal bursting behaviors, but the degree of transitions induced by the perturbation of  $C_{m,d}$  and  $C_{m,s}$  is strikingly different.  $C_{m,d}$  is the membrane capacitance in dendritic compartment, so its change can have great impacts on burst firing patterns and the influence on their transitions is vital, while  $C_{m,s}$  is the membrane capacitance in somatic compartment, thus its variation cannot change the bursting shapes or firing patterns greatly. This conclusion may be applicable to some compartmental neurons, but not all compartmental neurons show similar phenomenon like this model.

## Discussion

The outer membrane of the nerve cells is composed of a lipid bilayer  $\sim 8\text{--}10$  nm thick, which acts as a leaky capacitor. The capacitance per unit area of the membrane is referred to as the specific capacitance  $C_m$ , and is a fundamental parameter in models of the electrical properties of neurons [7]. Neuronal membranes form an essential component of all biological cells. They provide compartment boundaries, maintain mechanical strength, contain many functional proteins, and maintain transmembrane ionic gradients, such ionic gradients are essential for signaling and energy transduction [33]. The variation of specific capacitance  $C_m$  may influence the electrical behavior of neurons in some extent.

Bursting is ubiquitous in physical and biological systems, especially in neural systems where it plays an important role in information processing [34], and it is also



**Fig. 4** Periodic firing patterns and their transition modes with the variation of  $C_{m,d}$ . **a1–a8** Periodic firing sequences of pyramidal neuron with the increase of  $C_{m,d}$ , the value of  $C_{m,d}$  is 0.3, 0.5, 0.6, 0.8,

1.0, 1.2, 1.4, 1.6 ( $\mu\text{F}/\text{cm}^2$ ), respectively; **b** ISI versus  $C_{m,d}$ ; **c** period number in each burst with respect to  $C_{m,d}$

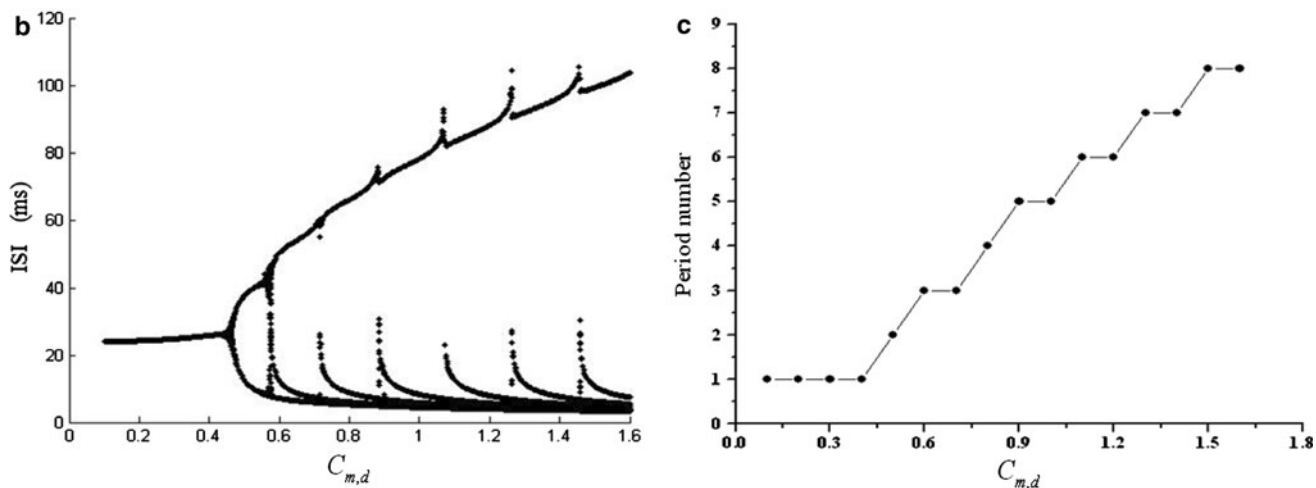


Fig. 4 continued

thought to have significant functional roles in reliable signaling and synaptic plasticity [10]. Many models generating bursting have been subject to intensive research due

to their physiological significance and dynamical complexity [14, 16, 28, 34–36]; the transition between different bursting patterns also attracted the interests of many

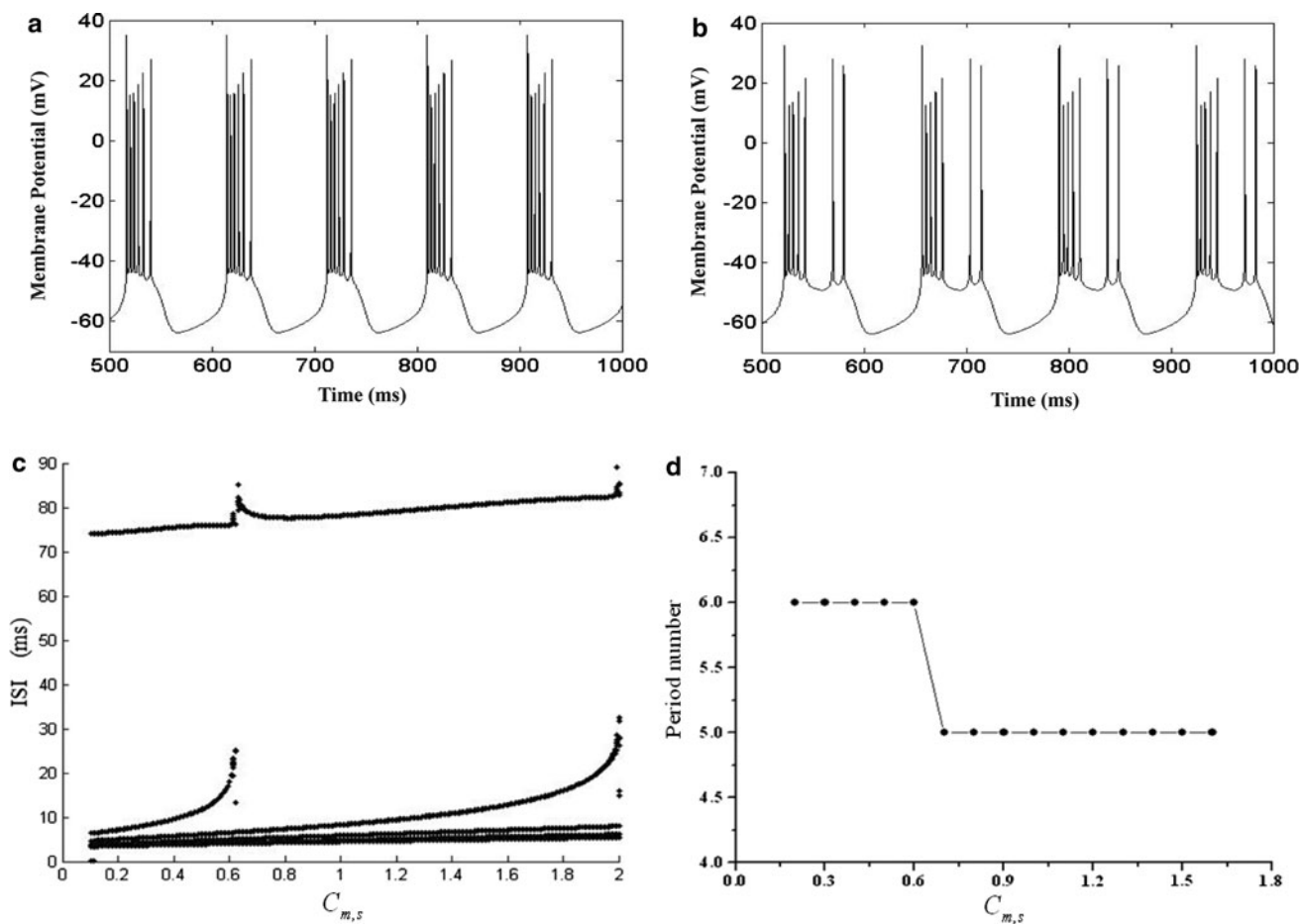
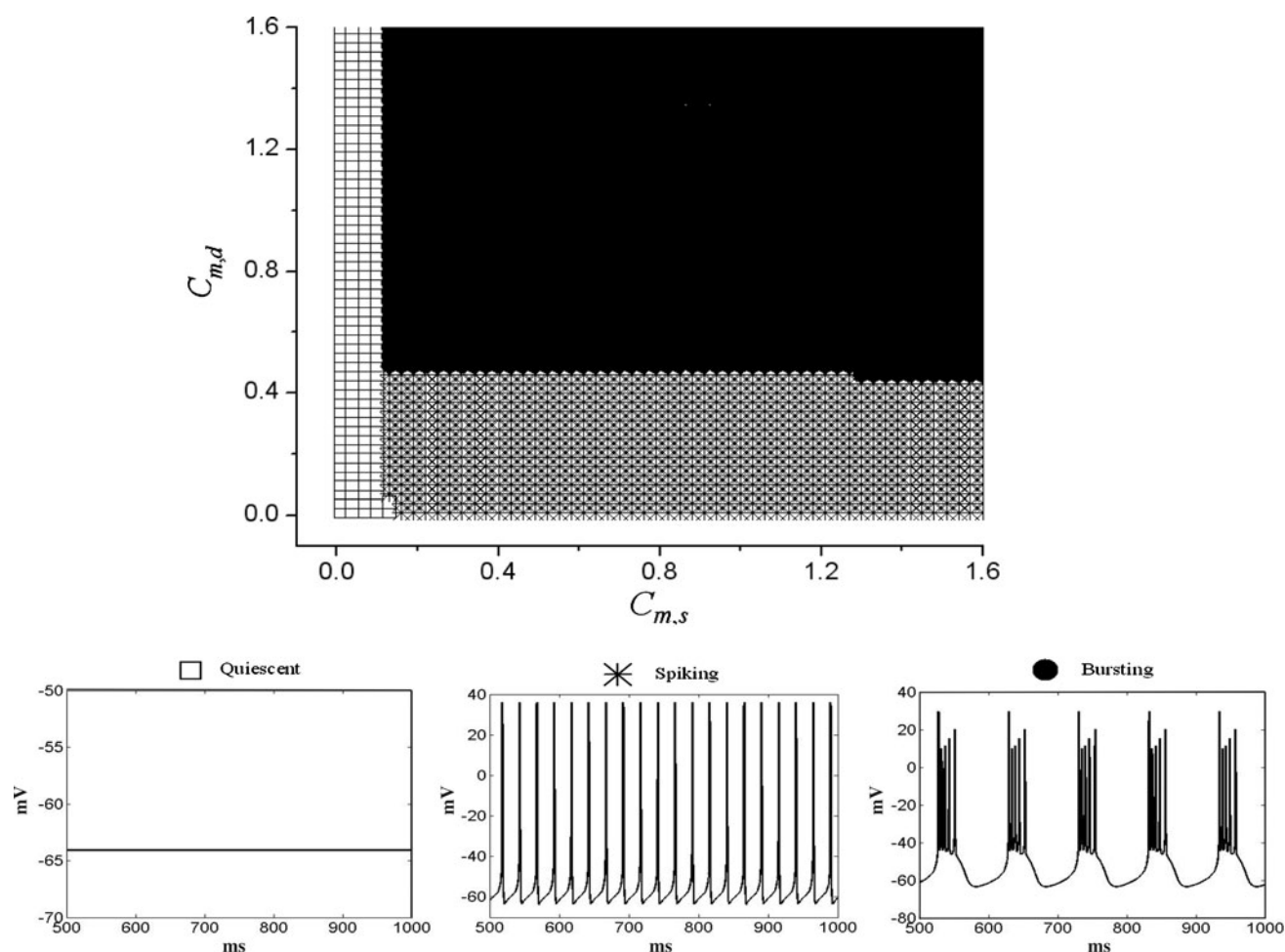


Fig. 5 Burst firing patterns and their transition modes with the variation of  $C_{m,s}$ . a, b Two burst firing patterns under different values of  $C_{m,s}$ , from left to right the value of  $C_{m,s}$  is 0.2 and 0.625 ( $\mu\text{F}/\text{cm}^2$ ), respectively. c ISI versus  $C_{m,s}$ ; d period number in each burst with respect to  $C_{m,s}$



**Fig. 6** Top different firing patterns with the variation of  $C_{m,d}$  and  $C_{m,s}$ , hollow block denotes the pattern is quiescent, \* denotes the pattern is spiking, while solid round denotes the pattern is bursting. Bottom the corresponding membrane potential maps of these three cases

researchers [12, 17, 37–39]. Fast/slow bifurcation analysis is the most popular approach to study the bifurcation structure contained in the transition between different firing patterns. For instance, Tsaneva-Atanasova et al. [37, 38] have used this approach to study the burst firing in endocrine cells. Duan et al. conducted two-parameter analysis of firing activities in the Chay neuronal model using this approach [17]. Except for fast/slow analysis approach, the diagram of ISI is also a commonly used approach which can describe the transition among various firing patterns to some extent [16, 39–41]. In this study, the ISI diagram was used to analyze the transition between different bursting patterns induced by the variation of membrane capacitance  $C_m$ .

By determining the exact mechanisms of bursting, one can gain insight into an array of firing behaviors and the nature of transitions between them. This understanding can facilitate the study of how different factors might influence firing patterns [10]. In this paper, the electrophysiology parameter  $C_m$  which is an important factor in action

potential generation and propagation was discussed in a two-compartment pyramidal neuron. From the analysis of numerical results presented in this paper, we can observe that, pyramidal neurons which have functional roles in reliable signaling and synaptic plasticity can exhibit a variety of firing patterns with the variation of  $C_m$ , not only periodic spiking, but also various bursting patterns. Bifurcation diagrams of ISI we drew can show a more intuitive results about how these firing patterns change from one to another; period-adding bifurcation phenomenon contained in the ISI diagram may give us some clues in understanding the possible roles that membrane capacitance  $C_m$  plays in burst firing transitions in pyramidal neurons. Furthermore, the diagram of different firing patterns under different values of  $C_{m,d}$  and  $C_{m,s}$  was also presented, as shown in Fig. 6, different kinds of firing patterns may exist in different combination of  $C_{m,d}$  and  $C_{m,s}$ . For a given  $C_{m,d}$ , the increase of  $C_{m,s}$  may result in the transition of firing patterns from quiescent to spiking or from quiescent to bursting; these kinds of transition mainly exist between the



similar firing patterns, such as spiking or bursting. While for a given  $C_{m,s}$ , the increase of  $C_{m,d}$  may give rise to the transition of firing patterns from spiking to bursting, these kinds of transition largely exist between different firing patterns, i.e., spiking and bursting. Finally, by comparing the diagrams of burst firing transitions under the variation in  $C_m$ ,  $C_{m,d}$ , and  $C_{m,s}$ , we get a further understanding of the different roles membrane capacitance plays in different compartments of neurons.

It is worth noting that we have mainly discussed the role of membrane capacitance  $C_m$  in burst firing patterns and their transitions in a two-compartment neuron in the present study, while  $C_m$  is only one of the factors which can influence neuronal firing properties. Other factors such as: external stimulus [1], noise (internal or external) [2, 3], specific ion channels [4], temperatures [6], the spatial-temporal interactions between soma and dendrite [32] and area parameter  $p$  (=somatic area/total area) [42] et al. which are also very important in neuronal firing activities can be given full attention in a future study of this neuron model. Furthermore, the approach of fast/slow analysis can also be used to study the detailed bifurcation structures contained in the transition modes presented in this study.

## Conclusion

In this paper, we gave a simple analysis about the possible roles of membrane capacitance  $C_m$  in burst firing transitions based on a two-compartment model of pyramidal neuron using computer simulations, and two cases of the variation of  $C_m$  in different compartments were considered. With the aid of ISI diagrams, we demonstrated the transition modes between different burst firing patterns with the increase of  $C_m$ , the numerical results we obtained not only illustrate the important role of  $C_m$  in the generation and switching of various neuronal bursting behaviors or periodic firings, but also give the exact transition modes from which we can learn how these firing patterns transfer from one to another.

## References

- Hodgkin AL, Huxley AF (1952) A quantitative description of membrane current and its application to conduction and excitation in nerve. *J Physiol* 117(4):500–544
- Plesser HE, Gerstner W (2000) Noise in integrate-and-fire neurons: from stochastic input to escape rates. *Neural Comput* 12(2): 367–384
- White JA, Rubinstein JT, Kay AR (2000) Channel noise in neurons. *Trends Neurosci* 23(3):131–137
- Wu N, Enomoto A, Tanaka S, Hsiao CF, Nykamp DQ, Izhikevich E, Chandler SH (2005) Persistent sodium currents in mesencephalic V neurons participate in burst generation and control of membrane excitability. *J Neurophysiol* 93(5):2710–2722
- Szlavik RB (2003) Strategies for improving neural signal detection using a neural–electronic interface. *IEEE Trans Neural Syst Rehabil Eng* 11(1):1–8
- Yuan CQ, Zhao TJ, Zhan Y, Zhang SH, Liu H, Zhang YH (2009) Environmental impacts on spiking properties in Hodgkin–Huxley neurons with direct current stimulus. *Chin Phys Lett* 26:118701
- Gentet LJ, Stuart GJ, Clements JD (2000) Direct measurement of specific membrane capacitance in neurons. *Biophys J* 79(1):314–320
- Ferguson KA, Campbell SA (2009) A two compartment model of a CA1 pyramidal neuron. *Can Appl Math Q* 17(2):293–307
- Graham BP (2001) Pattern recognition in a compartment model of a CA1 pyramidal neuron. *Netw Comput Neural Syst* 12(4): 473–492
- Kepecs A, Wang XJ (2000) Analysis of complex bursting in cortical pyramidal neuron models. *Neurocomputing* 32–33:181–187
- Yin HB, Cox CL, Mehta PG, Shanbhag UV (2009) Bifurcation analysis of a thalamic relay neuron model. *Proc Am Control Conf*, pp 337–342
- Duan LX, Yang ZQ, Liu SQ, Gong DW (2011) Bursting and two-parameter bifurcation in the Chay neuronal model. *Discrete Contin Dyn B* 16:445–456
- Wang XJ (1998) Calcium coding and adaptive temporal computation in cortical pyramidal neurons. *J Neurophysiol* 79(3): 1549–1566
- Wang XJ (1999) Fast burst firing and short-term synaptic plasticity: a model of neocortical chattering neurones. *Neuroscience* 89(2):347–362
- Han CX, Wang J, Deng B (2009) Fire patterns of modified HH neuron under external sinusoidal ELF stimulus. *Chaos. Solitons Fractals* 41(4):2045–2054
- Yang ZQ, Lu QS, Gu HG, Ren W (2002) Integer multiple spiking in the stochastic Chay model and its dynamical generation mechanism. *Phys Lett A* 299:499–506
- Duan LX, Lu QS, Wang QY (2008) Two-parameter bifurcation analysis of firing activities in the Chay neuronal model. *Neurocomputing* 72(1–3):341–351
- Trevelyan AJ, Jack J (2002) Detailed passive cable models of layer 2/3 pyramidal cells in rat visual cortex at different temperatures. *J Physiol* 539:623–636
- Major G, Larkman AU, Jonas P, Sakmann B, Jack JJ (1994) Detailed passive cable models of whole-cell record CA3 pyramidal neurons in rat hippocampal slice. *J Neurosci* 14(8):4613–4638
- Fernández JM, Bezanilla F, Taylor RE (1982) Distribution and kinetics of membrane dielectric polarization. II. Frequency domain studies of gating currents. *J Gen Physiol* 79(1):41–67
- Cater TD, Zupancic G, Smith SM, Wheeler-Jones C, Ogden D (1998) Membrane capacitance changes induced by thrombin and calcium in single endothelial cells cultured from human umbilical vein. *J Physiol* 513:845–855
- Thurbon D, Lüscher HR, Hofstetter T, Redman SJ (1998) Passive electrical properties of ventral horn neurons in rat spinal cord slices. *J Neurophysiol* 80(1):2485–2502
- Kim MH, von Gersdorff H (2010) Extending the realm of membrane capacitance measurements to nerve terminals with complex morphologies. *J Physiol* 588:2011–2012
- Johnson SL, Thomas MV, Kros CJ (2002) Membrane capacitance measurement using patch clamp with integrated self-balancing lock-in amplifier. *Pflugers Arch* 443(4):653–663
- Golowasch J, Thomas G, Taylor AL, Patel A, Pineda A, Khalil C (2009) Membrane capacitance measurements revisited:

- dependence of capacitance value on measurement method in nonisopotential neurons. *J Neurophysiol* 102(4):2161–2175
26. Chitwood RA, Hubbard A, Jaffe DB (1999) Passive electrotonic properties of rat hippocampal CA3 interneurons. *J Physiol* 515: 743–756
  27. Amzica F, Neckelmann D (1999) Membrane capacitance of cortical neurons and glia during sleep oscillations and spike-wave seizures. *J Neurophysiol* 82(5):2731–2746
  28. Laing CR, Longtin A (2003) Periodic forcing of a model sensory neuron. *Phys Rev E* 67:051928
  29. Kamondi A, Acsády L, Wang XJ, Buzsáki G (1998) Theta oscillations in somata and dendrites of hippocampal pyramidal cells in vivo: activity-dependent phase-precession of action potentials. *Hippocampus* 8(3):244–261
  30. Magee JC (2001) Dendritic mechanisms of phase precession in hippocampal CA1 pyramidal neurons. *J Neurophysiol* 86(1):528–532
  31. Wong RK, Stewart M (1992) Different firing patterns generated in dendrites and somata of CA1 pyramidal neurons in guinea-pig hippocampus. *J Physiol* 457:675–687
  32. Traub RD, Jefferys JG, Miles R, Whittington MA, Tóth K (1994) A branching dendritic model of a rodent CA3 pyramidal neurone. *J Physiol* 481:79–95
  33. Tepper HL, Voth GA (2006) Mechanisms of passive ion permeation through lipid bilayers: insights from simulations. *J Phys Chem B* 110(42):21327–21337
  34. Izhikevich EM, Hippensteadt F (2004) Classification of bursting mappings. *Int J Bifurcat Chaos* 14:3847–3854
  35. van Elburg RA, van Ooyen A (2010) Impact of dendritic size and dendritic topology on burst firing in pyramidal cells. *PLoS Comput Biol* 6(5):e1000781
  36. Osinga HM, Tsaneva-Atanasova KT (2010) Dynamics of plateau bursting depending on the location of its equilibrium. *J Neuroendocrinol* 22(12):1301–1314
  37. Tsaneva-Atanasova K, Osinga HM, Riess T, Sherman A (2010) Full system bifurcation analysis of endocrine bursting models. *J Theor Biol* 264(4):1133–1146
  38. Teka W, Tsaneva-Atanasova K, Bertram R, Tóth J (2011) From plateau to pseudo-plateau bursting: making the transition. *Bull Math Biol* 73(6):1292–1311
  39. Tan N, Xu JX, Yang HJ, Hu SJ (2003) The bifurcation mechanism arousing the phenomenon of “sensitivity of non-periodic activity” in neurons. *Acta Biophys Sin* 19:395–400
  40. Yang ZQ, Lu QS (2004) Characteristics of period-adding bursting bifurcation without chaos in the Chay neuron model. *Chin Phys Lett* 21:2124
  41. Zheng YH, Lu QS, Wang QY (2006) Suppression of chaos and phase locking in two coupled nonidentical neurons under periodic input. *Chin Phys Lett* 23:3176
  42. Feng JF, Li GB (2001) Behaviour of two-compartment models. *Neurocomputing* 38–40:205–211