Commun Nonlinear Sci Numer Simulat 22 (2015) 574–586

Contents lists available at ScienceDirect

Commun Nonlinear Sci Numer Simulat

journal homepage: www.elsevier.com/locate/cnsns

Spike initiating dynamics of the neuron with different adaptation mechanisms to extracellular electric fields

Guosheng Yi, Jiang Wang, Bin Deng *, Xile Wei

School of Electrical Engineering and Automation, Tianjin University, Tianjin 300072, PR China

ARTICLE INFO

Article history:
Received 14 December 2013
Accepted 24 July 2014
Available online 1 August 2014

Keywords:
Extracellular electric field
Adaptation
Two-compartment neuron
Spike initiating dynamics
Bifurcation
Biophysical basis

ABSTRACT

In this paper, we address how adaptation mediated by different biophysical mechanisms modulates neuronal spike initiating dynamics to extracellular electric fields. We incorporate two adaptation currents, i.e., voltage-sensitive potassium current (I_M) and calcium-sensitive potassium current (I_{AHP}), into a reduced two-compartment neuron model, and extensively investigate the modeling behavior to a range of electric fields. With phase plane analysis, it is shown whether neuron continues to spike depends on whether adaptation currents could be sufficiently activated to stabilize membrane potential at subthreshold voltages. With stability and bifurcation analysis, we find the steady-state spiking in the neuron with I_M occurs through a Hopf bifurcation, whereas it is generated through a saddle-node on invariant circle (SNIC) bifurcation in the cases of I_{AHP} or no adaptation. By identifying the biophysical basis for these dynamics, we observe that I_M could alter the competitive outcomes between kinetically mismatched opposite currents to result in a Hopf bifurcation, while I_{AHP} cannot alter these competitive outcomes. From this, we conclude that different modulations of spike initiating dynamics derive from the biophysical mechanism responsible for distinct adaptation currents. Our study suggests that the adaptation mediated by different mechanisms indeed has different effects on neuronal dynamics to electric field stimulus. It could contribute to uncover the underlying mechanism of how neuron encodes electric field signals.

1. Introduction

Recently, electromagnetic field stimulation has been used to investigate almost all areas of cognitive neuroscience. For instance, it is now a promising approach for studying brain physiology and function, as well as brain-behavior relations [1–3]. As a noninvasive stimulation, it is also widely applied in clinic to study and treat a number of neuropsychiatric and pain disorders [1], such as movement disorders, Alzheimer's disease, schizophrenia, epilepsy, myofascial pain syndrome, depression, stoke and so on. The fundamental of the action mode for this special stimulus modality is that it affects neuronal activity and ultimate behavior through the generation of an extracellular electric field in the interested brain tissue [3]. Despite the rapid growth in interest and applications of this technique, the basic mechanisms of action remain incompletely understood. The key to this problem is how extracellular electric field interacts with and modifies neuronal encoding dynamics [3].

* Corresponding author. Address: School of Electrical Engineering and Automation, Tianjin University, No. 92 Weijin Road, Tianjin 300072, PR China. Tel./fax: +86 022 27402293.

E-mail address: dengbin@tju.edu.cn (B. Deng).

http://dx.doi.org/10.1016/j.cnsns.2014.07.020

Spike-frequency adaptation, which refers to the reduction of firing rate during sustained stimulation, is a ubiquitous neurobiological phenomenon in the nervous system and can be observed in many neurons [4–6]. It plays an important role in neuronal information processing and can improve neuronal encoding [5–10], such as improve spike coding of different frequency signals [9], mediate selective response to looming stimulus [10], or facilitate extraction of transient communication signals from background oscillations [6]. A variety of ionic currents can lead to spike-frequency adaptation. Two primary types of such adaptation currents are slow voltage-sensitive potassium currents (e.g., M-type currents, I_M) [11] and calcium-sensitive potassium currents (e.g., AHP-type currents, I_{AHP}) [12]. One critical distinction between these two adaptation currents is that the activation of I_M does not rely on spike generation, whereas activation of I_{AHP} is spike dependent [9,11–13]. This different activation mechanism for I_M and I_{AHP} could produce disparate effects on neuronal encoding of stimulus information [5,8,9,14,15]. Then, to capture the full encoding strategies of the neuron to extracellular electric fields, it is necessary to involve these two forms of adaptation in neuron models for exploring its modulations of dynamic behaviors.

Different neuronal encoding has been shown to derive from distinct spike initiating dynamics [16,17], that is, how individual spikes are initiated. Mechanistic understanding of spike initiation could help us interpret neurons employ what rules to determine when and why they spike, i.e., the mechanisms of neural encoding [17]. In computational neuroscience, the mechanisms of spike initiation are usually studied with nonlinear dynamic system theory [16]. There are many ways to describe the dynamical properties of spike initiation, such as phase plane, equilibrium stability and bifurcation [16–20]. With these methods, Prescott et al. [5,8] demonstrated that the nonlinear interaction between adaptation and shunting could control a switch between integration and coincidence detection in pyramidal neurons. They also proposed that different adaptation mechanisms have opposite effects on neuronal spike-rate coding and spike-time coding [9]. Further, neuronal encoding schemes are also related to the myriad ion channels expressed in neuron membranes [16,17,21,22]. The outcomes of nonlinear competitions between different ionic currents could represent different spike initiating dynamics [16,17]. Many researches adopted it to interpret the biophysical basis of spike initiating dynamics. It is shown that translating dynamical explanations of spike initiation into biophysically interpretable mechanisms could also clearly provide greater insight into neural encoding [17]. Thus, exploring how two adaptation currents interact with other ionic currents is crucial to explain how different biophysical properties of adaptation impact neuronal encoding of electric field stimulus. However, there are still no studies using these methods to investigate the spike initiating dynamics of the neuron with different adaptation mechanisms to electric field stimulus.

To address this question, we first develop a simple two-compartment neuron model which incorporates two adaptation mechanisms and an extracellular electric field parallel to the somatic-dendritic axis. Then, we use phase plane, stability and bifurcation analysis to investigate the dynamical mechanism of spike initiation in the cases of different adaptation currents. Finally, we identify the biophysical basis for those dynamics by analyzing the nonlinear competitions between adaptation current with other ionic currents. To the best of our knowledge, this is the first study with regard to the dynamical and biophysical mechanism of spike initiation for the neuron with different adaptation mechanisms to electric field stimulus.

2. Model and method

2.1. Two-compartment neuron model in the presence of extracellular electric field

We use a two-compartment model to describe the interactions between extracellular electric field and neuronal activity. It is the minimum individual neuronal unit that can represent the spatial polarization of extracellular electric field in neurons [23–25]. A schematic representation of our model is shown in Fig. 1. The schematic gives the ionic currents that determine

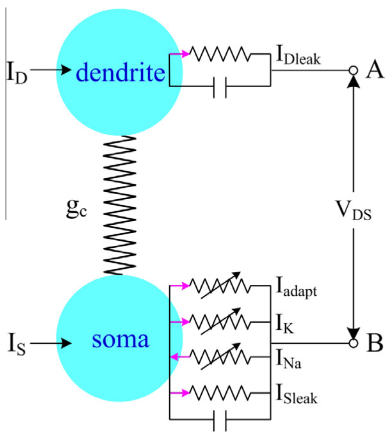

Fig. 1. A schematic of the currents and conductances in our two-compartment neuron. The direction of current flow is represented by a pink arrow. Adaptation current is involved in somatic compartment, and the coupling strength between soma and dendrite is governed by parameter g_c. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)