## MULTISTABILITY AND INFINITE CYCLES IN A MODEL OF THE LEECH HEART INTERNEURON

Andrey Shilnikov

Department of Mathematics and Statistics, Georgia State University, Atlanta, GA 30303, USA e-mail: ashilnikov@mathtat.gsu.edu WWW: http://www.mathstat.gsu.edu/matals

Gennady Cymbalyuk and Ronald Calabrese

Biology Department, Emory University, Atlanta, GA 30322, USA e-mail: gcym@biology.emory.edu WWW: http://calabreselx.biology.emory.edu

**Abstract**—We argue that the Lukyanov-Shilnikov bifurcation of a saddle-node periodic orbit with noncentral homoclinics explains the effect of bi-stability observed in a neuron model based on a Hodgkin-Huxley formalism. In this model the dominating regime, depending on the initial state, can be either spiking oscillations or weakly irregular bursting ones. It is also shown how the bifurcation of the blue-sky catastrophe may underlie a continuous transition between the above regimes. We exploit the features of this bifurcation (a) to explain transition from tonic spiking activity to periodic bursting regime; (b) to identify the principal bifurcational parameters in the system; (c) to control the temporal characteristics of bursting behavior via these parameters.

## I. INTRODUCTION

Living neurons are reported to exhibit a plethora of dynamical regimes, either regular or irregular, such as tonic spiking behavior, various bursting and subthreshold oscillations . These regimes reflect complexity of dynamics of membrane ionic currents, operating on different time scales. These ionic currents are commonly quantified through voltage-clamp experiments according to a formalism introduced by Hodgkin and Huxley. Blockade of some groups of the currents simplify the neuron dynamics, and can elicit characteristic behaviors of neurons. Under such conditions we have better chance to thoroughly understand dynamics, these characteristic behaviors can present an interesting phenomena to study from a perspective of the theory of non-linear dynamical systems. One of commonly observed characteristic behaviors is that observed under blockade of  $Ca^{2+}$  currents. In leech neurons, application of divalent ions like  $Co^{2+}$ , which block  $Ca^{2+}$  currents, along with partial block of outward currents, elicit slow plateau-like oscillations with up to 60s period and up to 20 second plateau duration (Fig. 1) [1], [3]. These exper-



Fig. 1. Slow plateau-like oscillations in heart interneurons after bath application of  $\mathrm{Co}^{2+}$ -containing saline and intracellular of  $\mathrm{TEA}^+$ .

iments can be used to understand general biophysical principals of how bursting behavior is generated and how major temporal characteristics like period and burst duration are controlled. A particular subject for theoretical analysis is how these slow temporal characteristics are supported in a system with dynamics based on much faster time scales (time constants of the ionic currents involved supposedly do not exceed one second). In our previous model study [5] we used the model developed in [4] with omitted  $Ca^{2+}$  currents and two K<sup>+</sup> currents to bring the model in accordance with the pharmacological conditions described above. We showed that the classical model presentation of the transient Na<sup>+</sup> current is sufficient for the generation of long plateau behavior due to properties of the window current (transient Na<sup>+</sup> current can be observed in a certain range of membrane potential values as a persistent current, a window current). The simplified model (I) can provide slow plateau-like oscillations with a sufficiently long plateau phase. A noninactivating  $Na^+$  current may be used in a model to explain long inter-plateau intervals.

Here we employ the model described in [5] which is a system of three stiff ordinary differential equations:

$$\frac{dV}{dt} = -2(\bar{g}_{K2} m_{K2}^2 (V - E_K) + g_l (V - E_l) + \bar{g}_{Na} f(-150, 0.0305, V)^3 h_{Na} (V - E_{Na}))$$

$$\frac{d\mathbf{m}_{K2}}{dt} = \frac{f(-83, -0.008, V) - m_{K2}}{\tau_{h_{K2}}},$$

$$\frac{d\mathbf{h}_{Na}}{dt} = \frac{f(500, 0.034, V) - \mathbf{h}_{Na}}{\tau_{h_{Na}}},$$
(1)

where the variables V,  $m_{K2}$ , and  $h_{Na}$  are the membrane potential, activation of the persistent  $K^+$  current ( $I_{K2}$ ) and inactivation of the transient  $Na^+$  current, respectively. The parameters are:  $\bar{g}_{K2}$  is the maximum conductance of  $I_{K2}$ ;  $E_{K^+}$  and  $E_{Na}$  are the reversal potentials of  $K^+$  and  $Na^+$ , respectively;  $\bar{g}_{Na}$  is the maximum conductance of  $I_{Na}$ ;  $g_1$  is the conductance of the leak current;  $E_1$  is the reversal potential of the leak current;  $\tau_{h_{K2}} = 0.8$  and  $\tau_{h_{Na}}$  are the time constants of activation of  $I_{K2}$  and inactivation of  $I_{Na}$ ; the function f is given by  $f(A, V, B) = 1/(1 + e^{A(V+B)})$ .

One of the most fascinating nonlinear effects is that the neuron may produce both tonic spiking and bursting oscillations depending on the initial state. In terms of dynamical systems this means that in the phase space of the proper slow-fast system there must be two co-existing attractors with rather complex basins of attraction. Another challenge for the theoretical analysis is to explain the continuous transition from one regime to another as the control parameters vary slightly. Obviously this subtle effect is to be described properly within a framework of the methods qualitative theory of slow-fast systems. Needless to mention that some other crucial qualitative issues like the variability of the number of spikes in a burst, search for the control parameters which can prolong the rest phase of the bursting regime, etc, are to be discussed as well. The analysis below of two distinct bifurcations of a saddle-node periodic orbit with homoclinics provides the answers to the these questions.

## **II. BIFURCATION MENU**

Understanding of intrinsic dynamics of the neuron and the principal mechanisms underlying the transi-



Fig. 2. Co-existence of spiking and bursting modes in model (I) at  $\bar{g}_{K2} = 30$ nS,  $E_K = -0.06995$ V,  $E_{Na} = 0.045$ V,  $\bar{g}_{Na} = 200$ nS,  $g_l = 8$ nS,  $E_l = -0.046$ V,  $\tau_{h_{K2}} = 0.8$  and  $\tau_{h_{Na}} = 0.04$ . The small round periodic orbit corresponds to the tonic-spikes shown in (c); the topology of the bursting cycle (b) is revealed in Figure 3 below.

tions between the regimes can be gained using the methods of the qualitative theory of slow-fast dynamical systems, see recent [5], [?], [6].

Let us consider such a 3D formalized system in the following appropriate form:

$$\dot{\mathbf{x}} = F(\mathbf{x}, \alpha) - z, \qquad \dot{z} = \mu G(\mathbf{x}, z, \alpha),$$
 (2)

where  $\mathbf{x} = (x, y)$  is a fast variable, z is a slow one,  $\alpha$  is a vector of control parameters,  $0 < \mu << 1$  is a small parameter. The function  $G(\mathbf{x}, z, \alpha)$  is assumed linear in  $\mathbf{x}$ . We also suppose that at  $\mu = 0$ , when the

z-variable becomes a parameter in the fast subsystem, the equilibria and limit cycles of the latter evolve as zvaries so that as shown in Fig. 3. The Z-shaped curve here is the surface  $M_{eq}$  of equilibria of the fast subsystem, which is determined by  $z = F(\mathbf{x}, \alpha)$ . When  $z \leq z_{AH}$  the fast subsystem has a single stable equilibrium state  $O_1$  that loses stability through the supercritical Andronov-Hopf bifurcation when  $z > z_{AH}$ . The fold points correspond the saddle-nodes. Within  $z_{SN} < z < z_{SN}^*$  the fast system has three equilibria: a stable one  $O_2$  on the lower branch of  $M_{eq}$ ; the middle segment corresponds to the saddle point O at which the divergence of the vector field (II) is negative; the upper branch corresponds to the unstable focus  $O_1$  surrounded by the stable limit cycle.  $M_{LC}$ denotes the parabolic-shaped surface foliated by the stable limit cycles of the fast subsystem at the corresponding values of z. This surface terminates at  $z = z_H$  when the stable limit cycles adheres to the homoclinic loop of the saddle and disappears.

The middle (orange) curve in Fig. 3 that crosses the surface  $M_{eq}$  is a nucline: the surface determined by the equation  $G(\mathbf{x}, z, \alpha) = 0$ . The intersection point is an equilibrium state of the united system, which is a saddle, typically. It is assumed that G < 0 (G > 0) below (above) the nucline.

When  $0 < \mu << 1$  the dynamics of system (II) under the above assumptions is of two time scales. The fast component is due to the momentary jumps near the fold on  $M_{eq}$  at  $z = z_{SN}$  and at the termination point  $z = z_H$  on  $M_{lc}$ . The slow component reveals on the the so-called surface of slow motions which is  $\mu$ -close to the corresponding segments on  $M_{LC}$  and  $M_{eq}$  of the unperturbed fast subsystem that correspond to the attracting rough limit cycles and equilibria, respectively.

The slow motion on  $M_{LC}$  is similar to a helix drifting towards the increasing of the z-variable with step of order  $\mu$ . Having averaged the fast motion over the period of the stable limit cycle in the unperturbed fast system, we get the following slow subsystem:

$$\bar{z} = \mu G(z, \alpha),$$

$$\tilde{G}(z) = \frac{1}{T(z,\alpha)} \int_{0}^{T(z,\alpha)} G(\varphi(t; z, \alpha), z) dt,$$
(3)

where  $x = \varphi(t, z, \alpha)$  is a limit cycle of period  $T(z, \alpha)$ in the fast subsystem. This system is defined on the slow manifold corresponding to the equilibria of the corresponding Portryagin averaged fast subsystem. In Fig. 3 the corresponding branch is labelled by  $\bar{x}$ . It originates at the Andronov-Hopf bifurcation and terminates at the homoclinic loop.

A point of transverse intersection of the nucline G = 0 with the the manifold  $\bar{x}$  corresponds to a rough equilibrium state of the united averaged system, and hence to a structurally stable periodic orbit in [II]. However, if such a point is due to the tangency of the nucline with  $\bar{x}$ , then the periodic orbit will be of a saddle-node type.

Next we discuss the ways the bifurcation of such a saddle-node periodic orbit can unfold. This depends on the global behavior of its 2D unstable manifold  $W_{L_{sn}}^u$ .

Figure 3 illustrates the Lukyanov-Shilnikov bifurcation [9] right after a saddle-node periodic orbit  $L_{sn}$ de-couples. A partial unfolding of the bifurcation is

![](_page_2_Figure_10.jpeg)

Fig. 3. The unstable manifold of the saddle periodic orbit separates the attraction domain of the stable periodic orbit corresponding to tonic spikes, and that of a helix-with-a-handle-shaped attractor corresponding to the burst mode of the neuron. At the bifurcation moment the stable manifold  $W^s$  of the saddle periodic orbit becomes the strongly stable (non-leading) manifold  $W^{ss}$  of the saddle-node one.

shown in Fig. 4. One of the greatest features of this bifurcation is that the complex dynamics persists nevertheless even *after* the double periodic orbit has vanished. On the other hand, after the double cycle decouples, the stable manifold of the saddle cycle separates the attraction domain of the stable one from that of an helix-like attractor corresponding to the bursting oscillations, see Figs. 2 and 4.

The scenario [7] of the blue-sky catastrophe in such a slow-fast system is given in Fig. 5 [7]. Here, the unstable manifold of the saddle-node periodic orbit  $L_{sn}$  comes back to  $L_{sn}$  making infinitely many revolutions on the cylinder-like surface of the slow motion

![](_page_3_Figure_0.jpeg)

Fig. 4. Unfolding of the Lukyanov-Shilnikov bifurcation of a saddle-node fixed point with non-central homoclinics. The two bifurcation curves originating from the origin correspond to the very first and last homoclinic tangencies between the stable and unstable manifolds of the saddle fixed point. It is seen that the complex hyperbolic structure due to transverse homoclinic crossings persists after the saddle-node point vanishes.

 $M_{LC}$ . The stability of the infinite cycle is due to the contraction at a saddle-node equilibrium state of the fast subsystem. It is important to stress here that the above mechanism provides a smooth transition from a regime of continuous spiking oscillations to bursting ones. It also explains well the order of alteration of the number of inter-spikes in a single burst. Next to the critical moment a phenomena of elliptic bursts is observed, see Fig. 6 Thus, by manipulating the height and shape of the nucline, one can vary the existing dynamical regimes. In particular, the resting phase of the burst can be prolonged due to the similar effect of the dynamical memory that exists near the phantom of the vanished saddle-node point on the lower branch of the slow motion surface. This may explain the very wide duration range (up to 20 seconds) of the plateau-like oscillations observed in the leech heart interneuron.

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![](_page_3_Figure_8.jpeg)

Fig. 5. The blue sky catastrophe. Here, the middle curve is the nucline; the dashed curve is the surface of slow motion comprised, respectively, of the stable equilibria of the fast subsystem as well as and ones of the averaged fast subsystem over the period of its stable limit cycles.

![](_page_3_Figure_10.jpeg)

Fig. 6. Illustration of a blue sky catastrophe in the Hindmarsh-Rose model [10], [8] in accordance with Fig. 5.

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