Topological changes in slow-fast systems: chaotic neuron models

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Summary. Spike-adding bifurcations are special bifurcations that are common in slow-fast systems, like neuron models. Two key open questions are how this chaotic behavior is organized and how spike-adding bifurcations influence chaotic behavior. In this talk we show how the orbit-flip (OF) codimension-2 bifurcation points, placed in homoclinic bifurcation curves and related with the spike-adding bifurcations, originate countable pencils of period-doubling and saddle-node (of limit cycles) bifurcation lines, but also of symbolic-flip bifurcations. These bifurcations appear interlaced and generate the different symbolic sequences of periodic orbits, constituting the skeleton of the different chaotic attractors and determining their topological structure.

Neuron models

The wide-range assessment of brain dynamics is one of the pivotal challenges of this century. To understand how an incredibly sophisticated system such as the brain *per se* functions dynamically, it is imperative to study the dynamics of its constitutive elements – neurons. Therefore, the design of mathematical models for neurons has arisen as a trending topic in science for a few decades, since Hodgkin and Huxley developed the first model of action potentials in the neuron membrane [6]. In order to help in the analysis of neuron models simulated realistically within the Hodgkin-Huxley framework [6], a common approach is to use some simplified models. In particular, the 3D Hindmarsh-Rose (HR) model [7] reproduces fairly well the basic oscillatory activities routinely observed in isolated biological cells and in neural networks. Therefore, in our detailed analysis we will consider the HR model, but a similar analysis can be applied to other neuron and fast-slow models. The HR model is described by three nonlinear ODEs:

$$\left\{\begin{array}{l} \dot{x} = y - ax^3 + bx^2 - z + I, \\ \dot{y} = c - dx^2 - y, \\ \dot{z} = \epsilon[s(x - x_0) - z], \end{array}\right. \tag{1}$$

where x is the membrane potential, y the fast and z the slow gating variables for ionic current. The parameters are typically set as follows: $a = 1$, $c = 1$, $d = 5$, $s = 4$, $x_0 = -1.6$, $\epsilon = 0.01$. We will study the system for several values of the remaining parameters: I, the 'external applied current', and b. Note that decreasing the value of the small parameter ϵ increases the number of spikes but it does not change the global behavior. This model fulfills the two basic conditions of being computationally simple but still able to reproduce the main behaviors (the rich firing patterns) exhibited by the real biological neurons.

Spike-adding process and topological structure

Spike-adding bifurcations are special bifurcations that are common in fast-slow systems. They lead to the appearance of extra spikes (turns) in the fast manifold region and are quite important in that they progressively modify the spectrum of periodic orbits of the system and the structure of chaotic attractors. Important examples of such fast-slow dynamics are found in chemical reactions, laser dynamics and in mathematical neuron models. Understanding how to generate and control a burst of spikes in neuron cells, and how chaotic behavior can appear in such systems are some of the most fundamental questions in neuroscience. The key questions that we want to address are: how is this chaotic behavior organized? How do spike-adding bifurcations influence chaotic behavior?

In Fig. 1 we depict schematically on plot (a) the global organization of the chaotic region as being "onion-like" [2], with different lobes that are concentric and going deeper moving from right to left but in a exponentially small scale from left to right beginning on the other side. This structure governs directly the systematic evolution in the spectrum of UPOs and the topological structure of the chaotic attractors in square-wave bursters (or fold/hom bursters) when control parameters change.

On plot (b) we show the (b, I)-parametric sweep using the Spike-Counting (SC) method. This technique permits to detect automatically the spike-adding bifurcations as the loci of parameter space where the number of spikes is incremented [1]. We also observe a main chaotic region with different stripes, where each lobe is clearly connected with the spike-adding process. Bifurcation analysis provides several insights into the spike-adding process and the creation of chaotic lobes. Plot (b) presents several codimension-one bifurcation lines: homoclinic, period-doubling, and fold bifurcations (or saddle-node of limit cycles) as well as spike-adding and some codimension two orbit-flip homoclinic bifurcation points. These bifurcation lines have been obtained using the continuation software `AUTO` and the SC technique. In [1, 2, 8, 4], the role of these bifurcations in the spike-adding process and their influence in the creation of the chaotic structures has been shown.

Once we have located the chaotic structures and established their relation with the spike-adding process, we want to characterize their influence on the structure of the different chaotic attractors. To this aim, the appropriate tool is the study

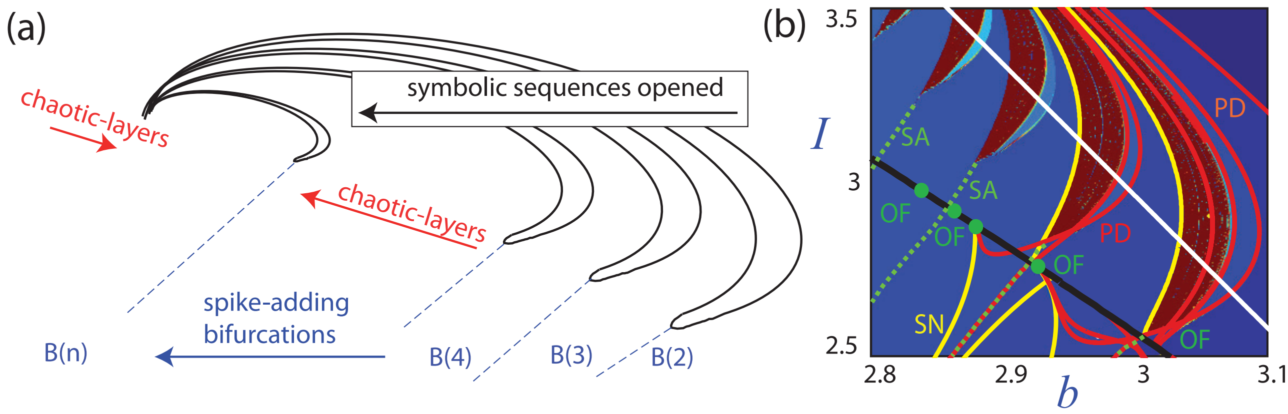

Figure 1: (a) Scheme of the "onion-like" structure of the main chaotic region of the Hindmarsh-Rose model on the (b, I)-parametric plane. The chaotic layers are accumulated in the left side. The spike-adding process changes the stable periodic orbits outside the chaotic region. (b) (b, I)-parametric sweep of the Hindmarsh-Rose model using the Spike-Counting approach. The spike number is color-coded and the number of spikes per burst grows from blue (spiking) to red (chaotic bursting). Several bifurcation lines of limit cycles, that have a relevant role in the spike-adding process, appear superimposed (Black: homoclinic bifurcation, Red: period-doubling (PD), Yellow: fold bifurcation (SN) and Green: spike-adding (SA)) and some codimension two bifurcation points (Green dots: orbit-flip (OF)).

of the topological templates obtained by characterizing the intertwining of the UPOs (unstable periodic orbits) embedded in the chaotic attractors. In [3, 5] it has been stated that in the case of mathematical neuron models, all the attractors analyzed has a topological template embedded in the Smale horseshoe template. These periodic orbits, with different symbolic sequences, constitute the skeleton of the different chaotic attractors and determine their topological structure

Conclusions

In conclusion, we have shown that the topological templates of the chaotic attractors of the Hindmarsh-Rose model, and probably of other neuron models, are subtemplates of the Smale topological template. The spike-adding processes and the bifurcations associated to them are accompanied by a gradual change in the spectrum of periodic orbits embedded in the attractor, and the onion-like structure in parameter space can be understood directly in terms of symbolic dynamics.

The use of several numerical techniques, as continuation techniques, Lyapunov exponents, detection of unstable periodic orbits foliated to the chaotic attractors, template analysis and so on, has played a relevant role in the complete analysis of the problem.

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