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Bifurcations and multistability in the extended Hindmarsh–Rose neuronal oscillator

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ABSTRACT

We report on the bifurcation analysis of an extended Hindmarsh–Rose (eHR) neuronal oscillator. We prove that Hopf bifurcation occurs in this system, when an appropriate chosen bifurcation parameter varies and reaches its critical value. Applying the normal form theory, we derive a formula to determine the direction of the Hopf bifurcation and the stability of bifurcating periodic flows. To observe this latter bifurcation and to illustrate its theoretical analysis, numerical simulations are performed. Hence, we present an explanation of the discontinuous behavior of the amplitude of the repetitive response as a function of system's parameters based on the presence of the subcritical unstable oscillations. Furthermore, the bifurcation structures of the system are studied, with special care on the effects of parameters associated with the slow current and the slower dynamical process. We find that the system presents diversity of bifurcations such as period-doubling, symmetry breaking, crises and reverse period-doubling, when the afore mentioned parameters are varied in tiny steps. The complexity of the bifurcation structures seems useful to understand how neurons encode information or how they respond to external stimuli. Furthermore, we find that the extended Hindmarsh–Rose model also presents the multistability of oscillatory and silent regimes for precise sets of its parameters. This phenomenon plays a practical role in short-term memory and appears to give an evolutionary advantage for neurons since they constitute part of multifunctional microcircuits such as central pattern generators.

1. Introduction

Chaos can appear in systems of autonomous or non autonomous ordinary differential equations possessing few as three variable and one or two nonlinearities, since the pioneering work of Lorentz [1], Liu et al. [2] and Rössler [3]. Over the years, many other chaotic systems have been discovered [4–8] and there have been many investigations on their dynamical behaviors [9–14]. For example, the building blocks of the central nervous system, neurons, are strongly complex dynamical systems. In order to understand the cell's intrinsic neurocomputational properties, much of present neuroscience research focusses on voltage- and second-messenger-gated currents in individual cells. It is commonly assumed that the knowledge of the currents is enough to find what the cell is doing, and why it is doing it. This is however in contradiction with the

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half-century-old observations, which state that cells having alike currents can yet provide quite different dynamics. In 1948, Hodgkin [15] found that, injecting a DC-current of different amplitude in isolated axons, results in the exhibit of repetitive spiking with different low frequencies and inhibition of responses in a narrow frequency band. Largely ignored by the neuroscience community, these observations were investigated a few decades later by Rinzel and Ermentrout [16]. They show that the observed behaviors are due to different bifurcation mechanisms of excitability. But, the model studied is the one introduced by Hodgkin and Huxley [9] (HH) which is rather complex and time consuming in numerical simulations. The extended Hindmarsh–Rose (eHR) neuronal oscillator is a simpler mathematical model, and it has been shown that it presents most of the HH's characteristics [17]. But from a nonlinear dynamical systems point of view, does the eHR neuronal oscillator behavior bring out how neurons respond to stimulus? Does the model present the multistability mechanism? Our aim is to bring some contribution to the field by studying this model in detail, and by examining these points.

The objective of mathematical models is to find the genuine trade off between accuracy and simplicity. The most important question in computational neuroscience is therefore, which characteristics of the complex dynamics are necessary to observe the specific tasks carried out by a neuron? In 1952, a mathematical model describing neuron activity was provided by Hodgkin and Huxley (HH) [9]. During years, different other models have been developed and studied [18–20]. Here we focus, on the Hindmarsh–Rose (HR), neuronal oscillator [17,21–23], proposed by Hindmarsh and Rose in 1984, after the formulation of their 2-equations model [21]. Their main goal was to model synchronization of firing of two snail neurons in a simple way, without the use of the Hodgkin–Huxley (HH) equations [22,24]. Hence, with the aim to create a neuron model that exhibits triggered firing, some modifications were done on the 2-equations model (by adding an adaptation variable, representing the slowly varying current, that changed the applied current to an effective applied one) to obtain the 3-equations model [21,24]. This model has been very popular in studying biological properties of spiking and bursting neurons. A few years later, Selverston et al. [17], studied a computational and electronic model of stomatogastric ganglion (STG) neurons. They found during their analysis that, biological neurons could be modeled with only three or four degrees of freedom [17]. They focused themselves on the familiar 3-dimensional HR model, and discovered that, in spite of the fact that, this 3-dimensional model can produce several modes of spiking–bursting behaviors seen in biological neurons, its parameter space for chaotic activity is much more limited than observed in real neurons. That is why they proposed a modified version of this model, by adding a fourth term (a slower process) representing the calcium dynamics [17]. The system's complexity increases and it was then able to reproduce the complex dynamical (spiking, bursting and chaotic) behavior of pyloric central pattern generator neurons of the lobster stomatogastric system [17,25].

Over the last decades, some detailed investigations and studies of bifurcations and the dynamics of models such as HH model, Fitzhugh–Nagumo model, Izhikevich model or the third order HR model, have been done [19,26–28]. Particular attention has been devoted to the third order HR model in the cited articles, from which the transitions between quiescent asymptotic behaviors, continuous spiking regimes and global picture of the bifurcation scenario with respect to two parameters, with an outline to the effects of two further parameters have been obtained. Recall that, a better adjustment of the behavior of electronics neurons, when connected to its living counterpart, is represented by the fourth order HR model, compared to the third order model [17,23]. Several details of the shape of spiking–bursting activity, can also be adjusted with the help of this extended model. Furthermore, it presents more complex behavior than the third order model [17,23], and it can describe the calcium exchange between intracellular warehouse and the cytoplasm, to completely produce the chaotic behavior of the stomatogastric ganglion neurons [17,23]. Besides, the region of parameter space where chaos appears is larger than that of the three dimensional equations [29]. Hence, a bifurcation analysis of such model is important to understand transitions between stable bursting solutions and continuous spiking regimes, and the fold of cycles bifurcations cascade, rousing to transitions between quiescent asymptotic behaviors and bursting regimes, as in the third order model; our aim here is to bring some contribution by studying the dynamical behaviors of such model, which may be helpful in understanding how the calcium exchange is operated in the stomatogastric ganglion neurons. Thus, the first goal of our work, is to consider Hopf bifurcations of such a system by applying the normal form theory introduced by Hassard et al. [30]. Afterwards, we use a combination of bifurcation theory and numerical integration to investigate bifurcation points, where stable or unstable bifurcations occur in the system. Even if the HR model dates from 1984, and many dynamical studies are found in the literature [26,27,31–36], no theoretical analysis has been given for its extended model to the best of our knowledge.

Recall that, the most used neuron model for studying behavior of interacting neurons to understand afore problems, are the HH type models [9]. Its complexity needs expensive numerical time for the resolution of the differential equations. That is why, reduced models showing essentially equivalent dynamics such as the HR model presents good properties and are commonly used nowadays for this kind of analysis. In this manuscript, we focused on the latter described with the following system of differential equations [17,23,29,37,38]:

$$\begin{cases} \dot{x} = ay + bx^2 - cx^3 - dz + I_{DC}, \\ \dot{y} = e - fx^2 - y - gw, \\ \dot{z} = \mu[-z + s(x+h)], \\ \dot{w} = v[-kw + r(y+l)]. \end{cases} \tag{1}$$

Here, a, b, c, d, e, f, g, μ, s, h, v, k, r and l, are constants which express the current and conductance based dynamics. I_{DC} represents the injected current. Notice that, this model is relevant since it reproduces the observed