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E. Slepukhina; L. Ryashko

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Stochastic Generation of Bursting Oscillations in the Spiking Region of a 3D Neuron Model with the Lukyanov-Shilnikov Bifurcation

E. Slepukhina[1, a)] and L. Ryashko[2]

[1)]Institute of Applied Mathematics and Statistics, University of Hohenheim, Schloss Hohenheim 1, 70599 Stuttgart, Germany
[2)]Ural Federal University, 51 Lenin str., 620083 Ekaterinburg, Russia

[a)]Corresponding author: Evdokiia.Slepukhina@uni-hohenheim.de

Abstract. A stochastic three-dimensional neuron model with the Lukyanov-Shilnikov bifurcation is studied. We show that in the parameter region where the deterministic system exhibits tonic spiking regime with a single stable limit cycle, noise can induce bursting activity. This stochastic phenomenon is confirmed by changes in spacial and temporal characteristics of oscillations. The probabilistic mechanism of the stochastic generation of bursting is studied by means of the stochastic sensitivity functions and Mahalanobis metrics.

INTRODUCTION

Transitions between various types of oscillations play important role in neural activity. In mathematical models, these transitions are associated with different types of bifurcations of limit cycles. It is known that neuron models can exhibit the period- doubling and adding bifurcations [1, 2, 3] leading to an increase of number of spikes per period of oscillations and followed by a transition to chaotic regime [1, 4]. Specific oscillatory modes can also appear due to canard [5, 6] or torus canard [7, 8, 9, 10] explosions. Multistable regimes with coexisting attractors can be also observed in neuron models [11, 12, 13, 14]. Coexistence of an equilibrium and a limit cycle is associated with a combination of the saddle-node bifurcation of equilibria, Andronov-Hopf and saddle-homoclinic bifurcations [15].

Recently, it has been found [16, 17, 18] that neuron models can exhibit the Lukyanov-Shilnikov bifurcation of saddle-node periodic orbit with noncentral homoclinics [19]. Due to this bifurcation, a bistability regime with two coexisting stable limit cycles can appear. One of the cycles represents tonic spiking oscillations, while another one corresponds to bursting activity, and the type of the system solution depends on initial conditions.

A variety of types of neural activity and transitions between them play a key role in the communicative processes occurring in physiological neural networks. In particular, neural bursting provides great capabilities for coding of information, since bursts can appear with different number of spikes, interspike intervals, frequencies, *etc.*, which can be associated with a unique coding pattern [20]. This and other interesting dynamical properties of neuron models can be used also in artificial neural networks. *E.g.*, recently has been shown [21] that SPOCU transfer function and related artificial neural network can generate random type of Sierpinski carpet, and this feature can be used to improve the performance of neural networks.

Since neurons are subject to various internal and external random disturbances, in modeling of neural activity, it is also important to take into account effects of noise. Moreover, it is well acknowledged that in stochastic nonlinear dynamical systems, specific noise-induced phenomena can appear. In stochastic neuron models, these can be, *e.g.*, noise-induced excitability [22, 23], stochastic [24, 25] and coherence [22, 26, 27, 28] resonances, noise-forced transitions between coexisting attractors [29, 30], chaos–order transformations driven by random disturbances [31].

In this paper, we study the stochastic variant of the Hindmarsh-Rose neuron model [18, 32] with the Lukyanov-Shilnikov bifurcation. Previously, it has been shown that in this model noise can induce transitions between the coexisting limit cycles representing tonic spiking and bursting oscillations [30]. Here, we study possible effects of noise in the other parameter zone of the model, where the spiking limit cycle is the only attractor. For the the parametric analysis we apply the methods of direct numerical simulations and statistics as well as the stochastic sensitivity functions technique and Mahalanobis metrics [33, 34].

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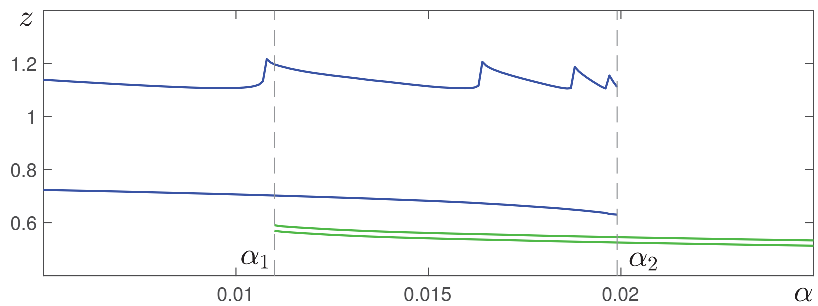


FIGURE 1. Bifurcation diagram of the deterministic system: minimal and maximal values of z-coordinate of limit cycles. Bifurcation points are $\alpha_1 \approx 0.0109$ and $\alpha_2 \approx 0.0199$

DETERMINISTIC MODEL

Consider the following modification [18] of the three-dimensional Hindmarsh-Rose neuron model [32]:

$$\begin{aligned} \dot{x} &= y - ax^3 + bx^2 + I - z \\ \dot{y} &= c - dx^2 - y \\ \dot{z} &= r\left(s(x - x_0) - z - \frac{\alpha}{(z - z_0)^2 + \beta}\right). \end{aligned} \tag{1}$$

Here, the variable x stands for the membrane voltage, and y and z are ion gating variables. In this paper we study the behavior of the system (1) under variation of the parameter α, and other parameters are fixed as in [18]: $a = 1$, $b = 3$, $c = -3$, $d = 5$, $s = 4$, $I = 5$, $r = 0.002$, $x_0 = -1.4$, $\beta = 0.003$, $z_0 = 0.5814335$.

Figure 1 shows minimal and maximal values of z-coordinate along limit cycles of the system (1) for $\alpha \in [0.005, 0.025]$, in dependence on the parameter α. Here, the system exhibits stable limit cycles of two types: one of them represents tonic spiking behavior, another corresponds to bursting oscillations. A feature of this system is a presence of the Lukyanov-Shilnikov bifurcation of a saddle-node periodic orbit with non-central homoclinics [18], due to which a region of bistability with two limit cycles emerges. For $\alpha < \alpha_1 \approx 0.0109$, the only attractor of the system is the stable limit cycle of bursting type. As a result of the Lukyanov-Shilnikov bifurcation at $\alpha = \alpha_1$, a stable limit cycle corresponding to spiking oscillations detaches from the saddle periodic orbit. Thus, in the region $\alpha_1 < \alpha < \alpha_2 \approx 0.0199$, the bursting limit cycle coexists with the spiking one. The bursting limit cycles undergo a sequence of period adding bifurcations resulting in the increase of number of spikes in a train. At the point α_2, the bursting limit cycle disappears due to the saddle-node bifurcation of periodic orbits, and the spiking limit cycle remains the only attractor of the system for $\alpha > \alpha_2$.

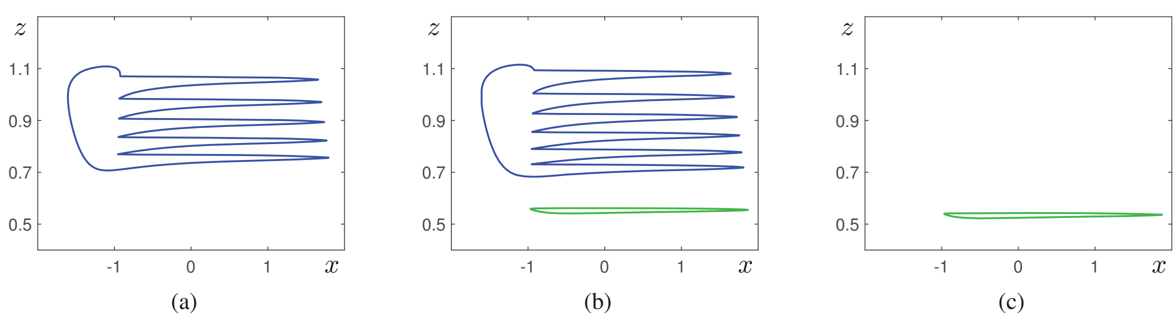


FIGURE 2. Deterministic limit cycles (in projection on $(x,z)-$plane) for a) $\alpha = 0.01$ (bursting) b) $\alpha = 0.015$ (coexistence of bursting and spiking) c) $\alpha = 0.021$ (spiking)

In Figure 2, examples of limit cycles of the system (1) for different values of α are presented. For $\alpha = 0.01$ (Figure 2a), the only attractor of the system is the bursting limit cycle; for $\alpha = 0.015$ (Figure 2b), two limit cycles representing bursting and spiking oscillations coexist, and the type of behavior depends on the initial conditions; for $\alpha = 0.021$ (Figure 2c), the system is monostable with the limit cycle corresponding to the tonic spiking regime.

STOCHASTIC MODEL

Consider a stochastic variant of the model (1):

$$\begin{aligned} \dot{x} &= y - ax^3 + bx^2 + I - z \\ \dot{y} &= c - dx^2 - y \\ \dot{z} &= r\left(s(x - x_0) - z - \frac{\alpha}{(z - z_0)^2 + \beta}\right) + \varepsilon\xi(t), \end{aligned} \tag{2}$$

where random disturbances are described by the standard white Gaussian noise $\xi(t)$ with the properties $\langle\xi(t)\rangle = 0$, $\langle\xi(t)\xi(t+\tau)\rangle = \delta(\tau)$ and the intensity parameter ε.

In this paper, we consider stochastic effects on the system in the parameter region $\alpha > \alpha_2 \approx 0.0199$ where the original deterministic model is in the monostable regime with a limit cycle representing tonic spiking behavior.

Let us fix $\alpha = 0.021$ and examine possible changes in the system dynamics under variation of the noise intensity ε. Figure 3 shows stochastic trajectories starting from the deterministic limit cycle for $\alpha = 0.021$ and the corresponding time series for two values of ε. For a relatively small noise level $\varepsilon = 0.01$ (see Figure 3a), the stochastic trajectory localizes near the deterministic cycle, and oscillations remain spiking. With an increase of the noise intensity to the value $\varepsilon = 0.03$ (see Figure 3b), one can see that the random trajectory deviates far from the deterministic cycle and the oscillatory regime changes to the bursting one.

This stochastic phenomenon observed for sample trajectories in Figure 3 is also confirmed statistically. Figure 4 represents the plots of power spectrum density (PSD) for $\alpha = 0.021$. For $\varepsilon = 0.01$, the power spectrum density has one peak corresponding to the frequency of spiking oscillations $\nu \approx 0.115$, while for the greater noise intensity $\varepsilon = 0.015$ a new peak over smaller frequencies emerges. This smaller frequency $\nu \approx 0.002$ corresponds to the larger period of the noise-induced bursting oscillations.

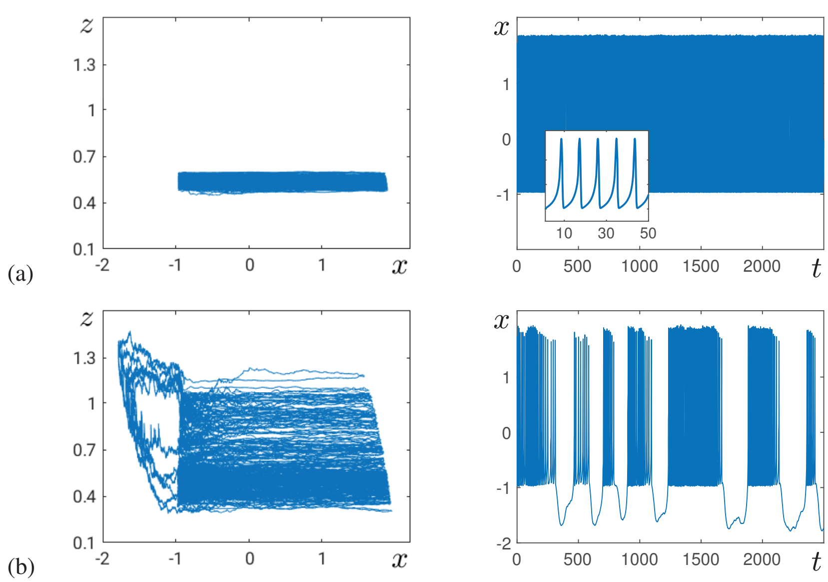


FIGURE 3. Stochastic trajectories (in projections on the $(x,z)-$plane) with the corresponding time series for $\alpha = 0.021$, a) $\varepsilon = 0.01$, b) $\varepsilon = 0.03$

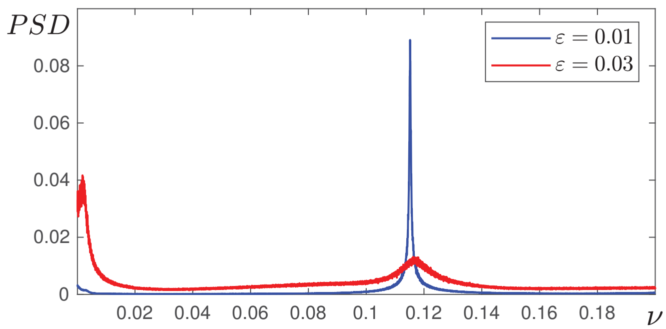


FIGURE 4. Power spectrum density for $\alpha = 0.021$ and $\varepsilon = 0.01$ (blue), $\varepsilon = 0.03$ (red)

Let us study the stochastic generation of bursting oscillations in this model in more details. Figure 5 displays the mean durations m of active phases of oscillations in dependence on the noise intensity ε for different values of the parameter α. For sufficiently low levels of noise, transitions to bursting oscillations emerge extremely rare and the type of oscillations remains spiking. This means that the duration of the active (spiking) phase of stochastic oscillations is close to infinity. As the noise intensity increases and exceeds some threshold value, noise-induced bursting oscillations start to appear, and the mean durations m sharply decrease. Using the plots of $m(\varepsilon)$ one can estimate the critical values of the noise intensity corresponding to the appearance of bursting oscillations. Figure 5 shows that these threshold values are smaller for α that are closer the to bifurcation point $\alpha_2 \approx 0.0199$.

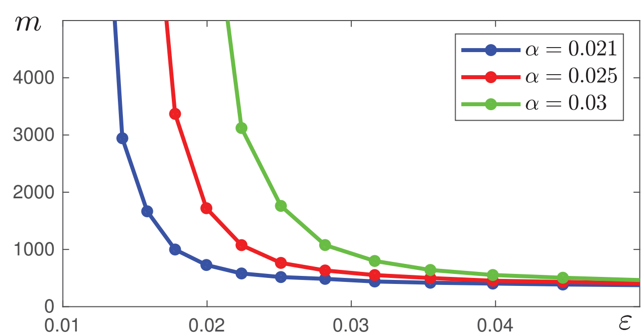


FIGURE 5. Mean durations of active phases of oscillations versus the noise intensity ε, for different values of the parameter α

The noise-induced generation of bursting from the tonic spiking regime may be related to the peculiarities of deterministic phase portrait of the system in this zone. Figure 6 shows two deterministic trajectories starting from different initial points close to the deterministic limit cycle for $\alpha = 0.021$ with the corresponding time series. Indeed, the type of a transition process depends significantly on the initial deviations from the limit cycle. If the deviation from the cycle is sufficiently small, the trajectory approaches the limit cycle monotonously and the oscillations are spiking (see blue trajectory in Figure 6). If the deviation is greater than some threshold, the trajectory first goes far from the limit cycle to the region of greater z and then returns to the cycle through the region with $x < -1$ (see red trajectory in Figure 6). Thus, there exist sub- and suprathreshold zones in the phase space that correspond to different types of the transition process, and one can define a border (pseudoseparatrix) between them. The stochastic generation of bursting oscillations may be caused by noise-induced jumps over the pseudoseparatrix to the suprathreshold zone corresponding to the large-amplitude bursting-type transition process.

An appearance of noise-induced bursting oscillations depends on the distance from the limit cycle to the pseudoseparatrix: the smaller this distance, the more likely the occurrence of bursting oscillations is. For this purpose, Mahalanobis metrics can be used, as it takes into account both geometrical arrangement of a cycle and a separatrix and probabilistic characteristics of a stochastic system. One can calculate the Mahalanobis metrics using the stochastic sensitivity functions (SSF).

Figure 7a shows nonzero eigenvalues $\lambda_{1,2}(t)$ of the SSF matrix for the limit cycle for $\alpha = 0.021$. One can see that

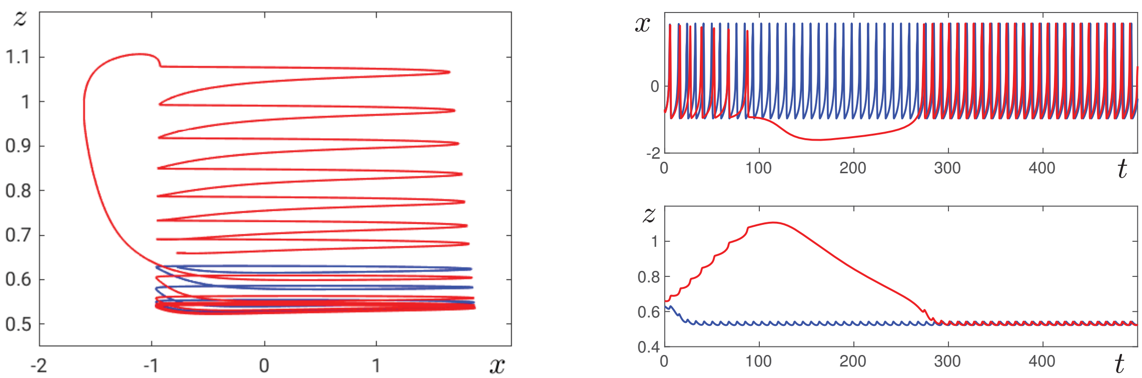
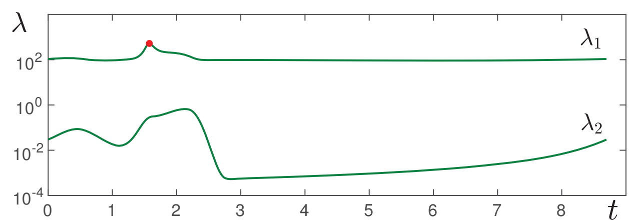


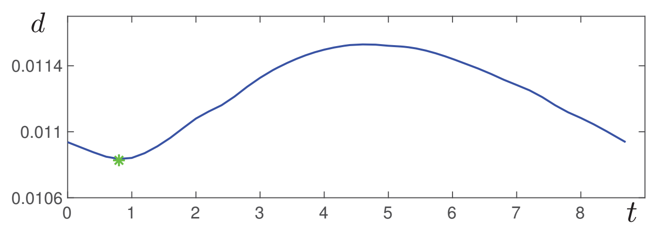
FIGURE 6. Deterministic trajectories for different initial conditions for $\alpha = 0.021$ with corresponding time series

the stochastic sensitivity for different regions of cycle is not uniform. Maximal value of $\lambda_1(t)$ corresponds to the zone of the cycle with the largest dispersion of random trajectories from it.

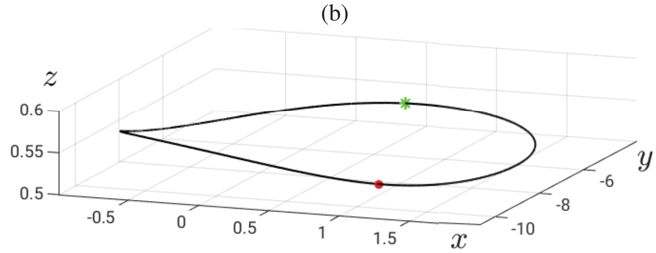
Figure 7b displays the plot of the Mahalanobis distance $d(t)$ from the points of the cycle for $\alpha = 0.021$ to the pseudoseparatrix. The minimum of $d(t)$ corresponds to the region of the cycle, from where jumps to the suprathreshold zone are the most likely. Note that this region differs from the one with the maximal stochastic sensitivity. Figure 7c shows the limit cycle for $\alpha = 0.021$ in the phase space and marks the regions corresponding to the minimum of the Mahalanobis distance and the maximum of the SSF.



(a)



(b)



(c)

FIGURE 7. a) Nonzero eigenvalues of SSF matrix for $\alpha = 0.021$; b) Mahalanobis distance between the limit cycle and the pseudoseparatrix; c) Limit cycle and regions corresponding to the maximum of SSF (red circle) and to the minimum of Mahalanobis distance (green asterisk)

CONCLUSION

We studied effects of random disturbances on the modified Hindmarsh-Rose neuron model which exhibits the Lukyanov-Shilnikov bifurcation. We considered the parameter zone where the system without noise has a single stable limit cycle corresponding to the tonic spiking regime of neural activity. We showed that in this region, noise can generate bursting oscillations. This phenomenon was observed for sample trajectories and corresponding time series, and furthermore was confirmed by statistics, such as mean durations of active phases of oscillations and power spectrum density. We suggested an explanation of the probabilistic mechanism for the stochastic generation of bursting in this model. It can be related to the existence of a pseudo-separarix which detaches in the phase space points corresponding to different types of transition processes, and to stochastic sensitivity of limit cycles. We computed the stochastic sensitivity function for a limit cycle in the considered parameter zone and the Mahalanobis distance between the cycle and the pseudo-separatrix that allowed us to find the zone of transition to the region where bursting activity is generated.

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