

**Weierstraß-Institut**  
**für Angewandte Analysis und Stochastik**  
**Leibniz-Institut im Forschungsverbund Berlin e. V.**

Preprint

ISSN 2198-5855

**Leap-frog patterns in systems of two coupled  
FitzHugh–Nagumo units**

Sebastian Eydam<sup>1</sup>, Igor Franović<sup>2</sup>, Matthias Wolfrum<sup>1</sup>

submitted: June 19, 2018

<sup>1</sup> Weierstrass Institute  
Mohrenstr. 39  
10117 Berlin  
Germany  
E-Mail: [sebastian.eydam@wias-berlin.de](mailto:sebastian.eydam@wias-berlin.de)  
[matthias.wolfrum@wias-berlin.de](mailto:matthias.wolfrum@wias-berlin.de)

<sup>2</sup> Institute of Physics Belgrade  
Pregrevica 118  
11080 Belgrade  
Serbia  
E-Mail: [franovic@ipb.ac.rs](mailto:franovic@ipb.ac.rs)

No. 2514  
Berlin 2018



---

2010 *Mathematics Subject Classification.* 34C15, 34C60.

2010 *Physics and Astronomy Classification Scheme.* 05.45.Xt, 87.19.lj.

*Key words and phrases.* Coupled oscillator systems, multiple timescale dynamics, FitzHugh–Nagumo model.

The authors acknowledge the support by the Ministry of Education, Science and Technological Development of Republic of Serbia under project No. 171017, the DAAD Serbia-Germany Bilateral Project “Emergent Dynamics in Systems of Coupled Excitable Units”, as well as the DFG within the framework of Collaborative Research Center SFB 910.

Edited by  
Weierstraß-Institut für Angewandte Analysis und Stochastik (WIAS)  
Leibniz-Institut im Forschungsverbund Berlin e. V.  
Mohrenstraße 39  
10117 Berlin  
Germany

Fax: +49 30 20372-303  
E-Mail: [preprint@wias-berlin.de](mailto:preprint@wias-berlin.de)  
World Wide Web: <http://www.wias-berlin.de/>

# Leap-frog patterns in systems of two coupled FitzHugh–Nagumo units

Sebastian Eydam, Igor Franović, Matthias Wolfrum

## Abstract

We study a system of two identical FitzHugh-Nagumo units with a mutual linear coupling in the fast variables. While an attractive coupling always leads to synchronous behavior, a repulsive coupling can give rise to dynamical regimes with alternating spiking order, called leap-frogging. We analyze various types of periodic and chaotic leap-frogging regimes, using numerical path-following methods to investigate their emergence and stability, as well as to obtain the complex bifurcation scenario which organizes their appearance in parameter space. In particular, we show that the stability region of the simplest periodic leap-frog pattern has the shape of a locking cone pointing to the canard transition of the uncoupled system. We also discuss the role of the timescale separation in the coupled FitzHugh-Nagumo system and the relation of the leap-frog solutions to the theory of mixed-mode oscillations in multiple timescale systems.

## 1 Introduction

The FitzHugh-Nagumo system is a classical model of neuronal dynamics. As the simplest, yet paradigmatic example of a coupled neuronal system, we investigate here a pair of two identical FitzHugh-Nagumo units with a weak mutual coupling. Such a network motif of two coupled neurons has been considered as a basic building block of central pattern generators [1] and the complex neural networks of the cortex [2, 3, 4, 5]. The dynamics of such systems has typically been investigated in the framework of the synchronization paradigm [6, 7], focusing on the stability of states with phase-locked firing and their potential role in rhythmogenesis [8]. A further remarkable property of these simple circuits is that they are able to generate complex activity patterns where the inter-spike intervals show complex dynamics. A typical example of such patterns is the so-called leap-frog dynamics [9], sometimes also called leader-switching dynamics [10], where the units exchange their order of firing within each oscillation cycle. Such a regime has so far been associated exclusively to class I neural oscillators coupled via strong synapses with complex nonlinear dynamics. In the present paper, we investigate the emergence of leap-frogging dynamics in a system of two classical FitzHugh-Nagumo units interacting only via a small linear coupling. The emerging complex dynamical patterns can be explained as a result of the timescale separation between the activator and the recovery variable. For a single unit, the timescale separation is crucial for the mechanism inducing the rapid change in the amplitude from small subthreshold oscillations to large relaxation oscillations. Introducing a repulsive coupling in the fast variables, the leap-frog patterns emerge in locking cones generated by a complex bifurcation scenario immediately at this transition. The alternation in the spiking order of the units arises from trajectories containing both the small-amplitude subthreshold oscillations and the large-amplitude relaxation oscillations. Such a behavior involving interspersed small- and large-amplitude oscillations is a typical phenomenon in certain classes of slow-fast systems, referred to as mixed-mode oscillations [11, 12, 13]. However, due to the symmetry of our system, a vanishing coupling causes an additional

degeneracy, such that the standard theory for mixed-mode oscillation does not apply. For this reason, our study is rather based on numerical bifurcation analysis using path-following methods.

The dynamics of the considered system of two identical Fitzhugh-Nagumo units is given by

$$\begin{aligned}\frac{dv_{1,2}}{dt} &= v_{1,2} - v_{1,2}^3/3 - w_{1,2} + c(v_{2,1} - v_{1,2}) \\ \frac{dw_{1,2}}{dt} &= \varepsilon(v_{1,2} + b),\end{aligned}\tag{1}$$

where the symmetric linear coupling acts in the fast variables  $v_{1,2}$ . The small parameter  $\varepsilon$  facilitates the timescale separation between the fast variables  $v_i$  and the slow variables  $w_i$ . In the context of neuroscience, the former represent the neuronal membrane potentials, whereas the latter correspond to the coarse-grained activities of the membrane ion-gating channels. For a single unit, the parameter  $b$  mediates the transition from the quiescent regime for  $b > 1$  to the oscillatory regime for  $-1 < b < 1$ . Due to the timescale separation, this is accompanied by a *canard transition* from small-amplitude subthreshold oscillations to the large-amplitude relaxation oscillations. We invoke some basic results derived from singular perturbation theory about the slow-fast structure of the uncoupled FitzHugh-Nagumo unit in Section 2.

Since the parameters  $b$  and  $\varepsilon$  are taken to be identical for both units, system (1) possesses a  $\mathbb{Z}_2$ -symmetry, being equivariant with respect to exchanging the indices by

$$\sigma : (v_1, w_1, v_2, w_2) \mapsto (v_2, w_2, v_1, w_1).$$

This leads to the appearance of solutions with different symmetry types, reflecting the different states of in-phase and anti-phase synchronization, which will be discussed in Section 2 which concerns the basic types of solutions bifurcating from the stationary regime. Close to the canard transition of the uncoupled system, there appear various types of periodic and chaotic leap-frog patterns in the system with repulsive coupling. Using the software package AUTO [14] for numerical bifurcation analysis by continuation methods, in Section 3 we investigate in detail the complex bifurcation scenarios responsible for the onset of the different types of leap-frogging dynamics. We conclude the paper with an outlook in section 4, discussing the relation of our results to earlier findings on leap-frog dynamics in models of neuronal systems.

## 2 Basic dynamical regimes

We begin our investigation of system (1) by collecting simple stationary and periodic solutions together with their stability and symmetry properties. In the symmetric regime  $v_1 = v_2$  and  $w_1 = w_2$ , the coupling term vanishes and the dynamics (1) is governed by a single FitzHugh-Nagumo system, where the units display simultaneously the well known transition from the quiescent regime with a unique stable equilibrium for  $b > 1$  to the oscillatory regime for  $b < 1$ , mediated by a supercritical Hopf bifurcation at  $b = 1$ . Due to the timescale separation  $0 < \varepsilon \ll 1$ , the bifurcating branch of periodic solutions displays a characteristic transition from small-amplitude harmonic oscillations of period  $\mathcal{O}(\sqrt{\varepsilon})$  to large-amplitude relaxation oscillations of period  $\mathcal{O}(1)$ , called *canard transition*. This scenario has been extensively studied within the framework of singular perturbation theory, viz. in the limit  $\varepsilon \rightarrow 0$ , see e.g. [12] for a recent overview. In Fig. 1 we illustrate the canard transition in the symmetric regime, showing numerical results obtained by path-following methods [14]. In panel (a) we have fixed  $\varepsilon = 0.05$ , displaying the varying period along the branch of periodic orbits emerging from

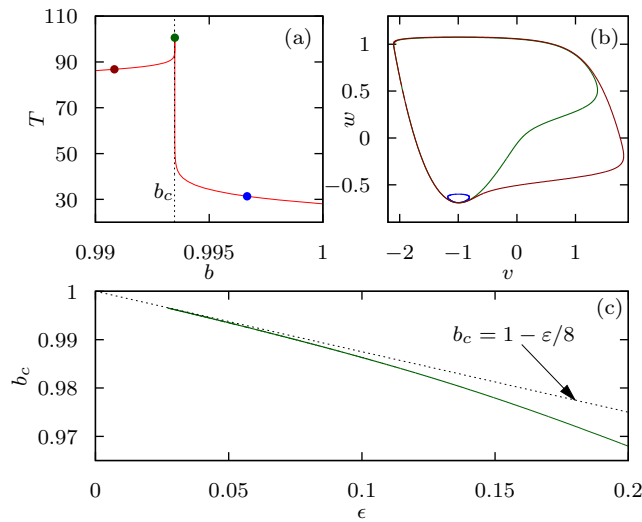


Figure 1: (Color online) (a) Variation of the period  $T$  along the branch of synchronous periodic solutions for varying  $b$  at fixed  $\varepsilon = 0.05$ . (b) Phase portraits of selected periodic solutions: a subthreshold oscillation for  $b_c < b < b_H$  (blue), the canard trajectory  $b_c = b$  (green), and a relaxation oscillations with  $b_c > b$  (red). The corresponding values of  $b$  are indicated by the colored dots in (a). (c) Location of the canard transition  $b_c$  for varying  $\varepsilon$ . Numerical path-following of the periodic solution with maximal period (green line) is compared to asymptotic formula (2), shown dashed.

the Hopf-bifurcation at  $b = b_H = 1$ . Note the nearly vertical transition from small to large periods at the canard transition  $b = b_c$ . The phase portraits of the three orbits shown in panel (b), selected before, after, and immediately at the transition, indicate that the change in the period is accompanied by a transition from small to large amplitudes via *canard trajectories* that follow the unstable part of the slow manifold  $w = v - v^3/3$ . From the neuroscience perspective, this corresponds to a transition route from the quiescent state to the spiking regime via subthreshold oscillations. A detailed asymptotic analysis reveals that the leading order approximation for the location  $b_c$  of the canard transition is given by

$$b_c \approx (1 - \varepsilon/8), \quad (2)$$

see [15]. In Fig. 1(c) we show that for small  $\varepsilon > 0$  this expression (dashed line) provides indeed a good approximation for the actual location of the canard transition (solid green line), which we obtained numerically by path-following in  $\varepsilon$  the trajectory of maximal period (green curve in Fig. 1(b)). Recall that both the regimes of stable equilibrium and of subthreshold oscillations are excitable [16, 17] in a sense that a strong enough perturbation may elicit a large excursion in phase space, i.e. a spiking response in the form of a single relaxation oscillation.

It can be easily seen that the only stationary state of (1) is the symmetric equilibrium

$$(v_1, w_1, v_2, w_2) = (-b, -b + b^3/3, -b, -b + b^3/3), \quad (3)$$

obtained from the single FitzHugh–Nagumo unit. While the symmetry-preserving Hopf bifurcation at  $b = 1$  in the coupled system is analogous to the Hopf bifurcation of the single FitzHugh–Nagumo unit and does not depend on the coupling parameter  $c$ , in the coupled system the symmetric equilibrium may also undergo symmetry-breaking bifurcations. In particular, it may become unstable via a Hopf bifurcation to anti-phase synchronized periodic solutions of the form

$$v_1(t) = v_2(t + \frac{T}{2}), \quad w_1(t) = w_2(t + \frac{T}{2}), \quad (4)$$

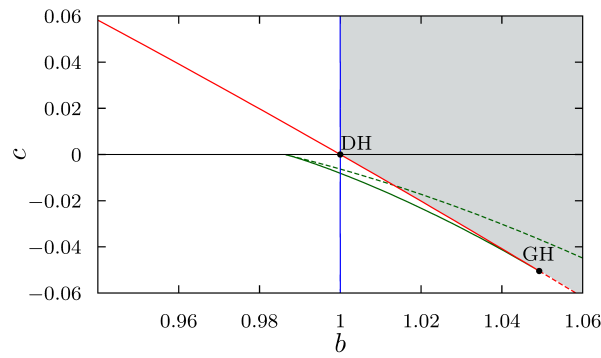


Figure 2: (Color online) Stability region (shaded) of the symmetric equilibrium (3) in the  $(b, c)$ -plane, bounded by in-phase Hopf instability (blue line) and anti-phase Hopf instability (red line). The anti-phase Hopf bifurcation changes from supercritical to subcritical in a generalized Hopf point (GH), where a fold curve of the anti-phase synchronous limit cycles emerges (green line). DH denotes the resonant double Hopf point for decoupled system at  $(b, c) = (1, 0)$ .

where  $T > 0$  is the period. Straightforward calculations provide the bifurcation condition

$$c = \frac{1 - b^2}{2} \quad (5)$$

for this anti-phase Hopf instability of the synchronous equilibrium (3). In Fig. 2, the associated bifurcation curve is shown in the  $(b, c)$ -plane together with the in-phase Hopf instability at  $b = 1$ . For attractive coupling  $c > 0$ , the shaded stability region of the symmetric equilibrium (3) is bounded by the in-phase Hopf instability, shown by the blue line, while for repulsive coupling  $c < 0$ , the stability boundary is given by the anti-phase Hopf (5). For larger negative values of  $c$ , this bifurcation is subcritical, such that no stable branch of anti-phase synchronized oscillations emerges. The criticality changes in a generalized Hopf (Bautin) point, labeled as GH in Fig. 2. From this point emanates a curve of folds of limit cycles, shown by the green line in Fig. 2. The two Hopf bifurcation curves intersect in the resonant double Hopf point (DH) located at  $(b, c) = (1, 0)$ . Note that this point belongs to the line  $c = 0$  where the system decouples, thus behaving neutral with respect to all symmetry-breaking perturbations.

In Fig. 3 are shown the stability regions of the bifurcating periodic solutions. For attractive coupling  $c > 0$ , all synchronous oscillations are stable (blue shaded region), undergoing at  $b = b_c$  the canard transition from small- to large-amplitude oscillations as in the case of a single unit, cf. Fig. 1. For repulsive coupling  $c < 0$ , the situation is more complicated. There is a small region (red shaded in Fig. 3) above the generalized Hopf point and the emanating fold of limit cycles (green curve) where one finds stable anti-phase synchronized oscillations. Surprisingly, there are also stable in-phase synchronized solutions for repulsive coupling  $c < 0$ . They are confined to a narrow region immediately below the canard transition, which is bounded by a curve of period doubling (purple line) and a curve of symmetry-breaking pitchfork bifurcations (light blue line). In particular, for small negative coupling, one encounters a region of bistability, where both the in-phase and anti-phase synchronized oscillations are stable (purple shaded region in Fig. 3). In Fig. 4 are illustrated coexisting stable in-phase and anti-phase synchronous solutions computed for the parameters  $(\varepsilon, b, c) = (0.1, 0.9885, -0.0005)$  from this region. Note that the coexistence region is confined to subthreshold oscillations prior to the canard transition at  $b = b_c$ .

Apart from the in-phase and anti-phase synchronous regimes, there may also appear periodic solutions without any symmetry. For repulsive coupling  $c < 0$  and beyond the canard transition, i.e.  $b < b_c$ , there is a large parameter region admitting a stable regime of *successive spiking*, with both units per-

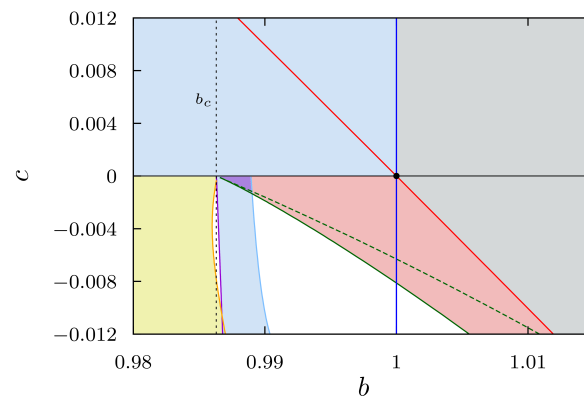


Figure 3: (Color online) Stability regions of basic periodic solutions in the  $(b, c)$  plane for  $\varepsilon = 0.1$ : in-phase synchronous oscillations (blue); anti-phase synchronous subthreshold oscillations (red); coexistence of in-phase and anti-phase subthreshold oscillations (purple); asynchronous oscillations – successive spiking (yellow). Bifurcation curves: in-phase Hopf instability (blue); anti-phase Hopf instability (red); fold of anti-phase synchronous limit cycles (green); subcritical period doubling of in-phase subthreshold oscillations (purple); subcritical symmetry breaking pitchfork of in-phase subthreshold oscillations (light blue); supercritical period doubling of asynchronous oscillations (orange).

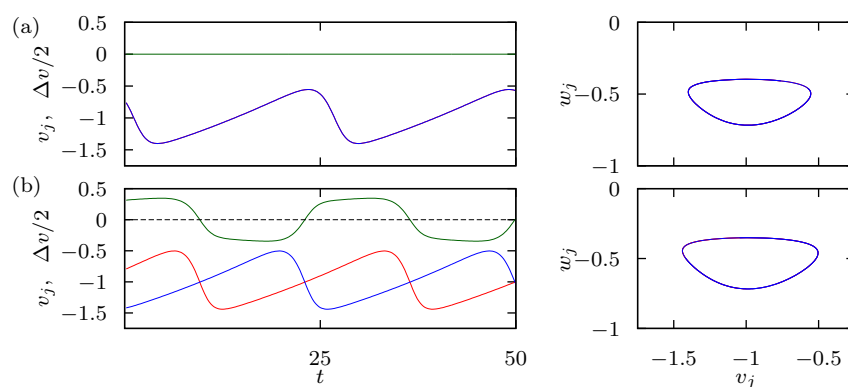


Figure 4: (Color online) Time traces and phase portraits of stable coexisting in-phase synchronous (a) and anti-phase synchronous (b) subthreshold oscillations. Parameters  $(\varepsilon, b, c) = (0.1, 0.9885, -0.0005)$  belong to the coexistence region (purple in Fig. 3). Variables  $v_{1,2}(t)$  are shown in red and blue, whereas the coupling term  $\Delta v = c(v_2 - v_1)$  is indicated in green color.

forming relaxation oscillations shifted in phase. The stability region of this successive spiking, shown in yellow in Fig. 3, is bounded by a curve of supercritical period doubling (orange line). In Fig. 5(a) and Fig. 5(b) are provided the time traces and phase portraits for the regime of successive spiking before period doubling and after several period doubling bifurcations, respectively.

Note that in Fig. 3 several bifurcation curves point towards the canard transition, thus creating a complex scenario where the different dynamical regimes with different symmetry properties bifurcate and interchange their stability. Moreover, there is a region, indicated in white in Fig. 3, where none of the periodic solutions described above is stable. We demonstrate below that in this region the system exhibits several periodic or chaotic regimes characterized by the fact that the trajectory of each unit comprises large relaxation oscillation loops as well as smaller loops of a size comparable to that of subthreshold oscillations. Such type of behavior conforms to *mixed-mode oscillations*, which have been extensively studied for slow-fast systems with a folded node singularity, using geometric singular perturbation methods for the limit  $\varepsilon \rightarrow 0$ . However, due to the phase shift degeneracy at  $c = 0$ , the system (1) does not satisfy the necessary genericity assumptions for these general theoretical results. Hence, we will investigate these mixed-mode type dynamics without invoking the singular limit and instead use simulations and numerical path-following techniques to describe the bifurcation scenario for finite values of  $\varepsilon$ .

### 3 Complex dynamical regimes at the canard transition

In order to numerically examine the different types of solutions of system (1), we have performed a parameter sweep with respect to  $b$  at fixed  $c = -0.01$  and  $\varepsilon = 0.1$ , see Fig. 6. After each increment in the sweeping parameter  $b$ , we have discarded a transient and then have sampled the return times between consecutive crossings of the Poincaré section  $w_1 = -2/3$ . Sweeping has been carried out in forward (red points) and backward direction (blue points), allowing us to detect potential coexisting stable regimes. Note that the return times  $T_n \approx 50$  correspond to a single round trip of the unit  $j = 1$  along the relaxation oscillation orbit, while the return times  $T_n < 30$  correspond to a round trip following a subthreshold oscillation orbit. In Fig. 6, one can identify the regime of successive spiking in regions I and II, the in-phase subthreshold oscillations in regions II–IV, and the anti-phase subthreshold oscillations in region VII. In addition, we find the periodic regime displayed in Fig. 7(a), which is the only attractor in region V and coexists with the in-phase subthreshold oscillations in region IV. Note that

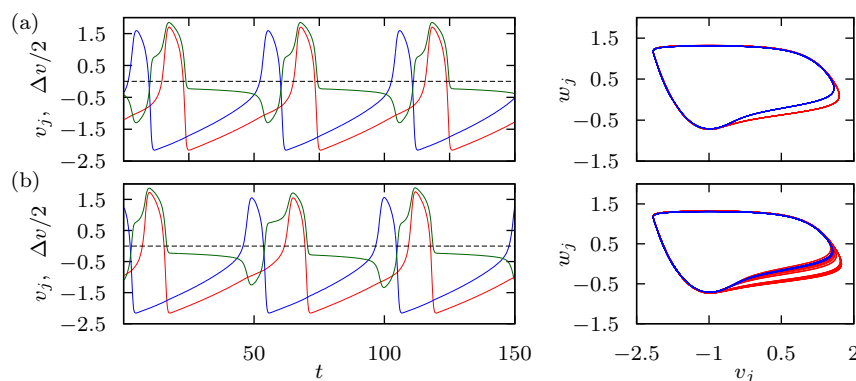


Figure 5: (Color online) Time traces and phase portraits of stable asymmetric successive spiking: (a) – before period doubling ( $b = 0.98625$ ) and (b) – after several period doubling bifurcations ( $b = 0.98692$ ). The remaining parameters are  $(\varepsilon, c) = (0.1, -0.01)$ . Colors as in Fig. 4.



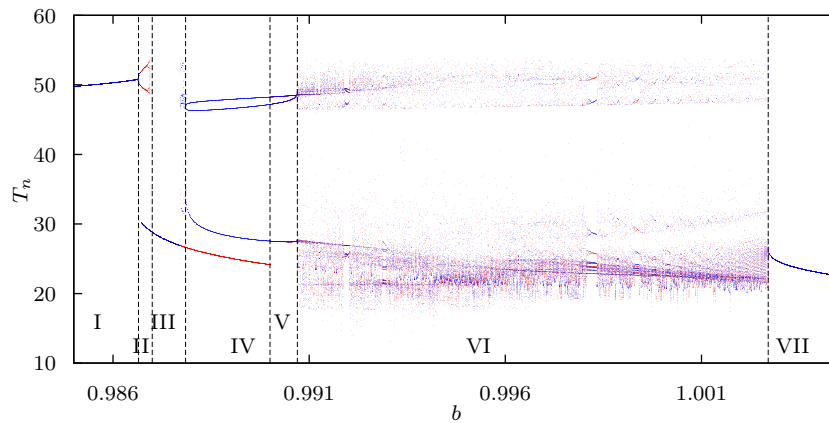


Figure 6: (Color online) Sampled return times between consecutive crossings of the hyperplane  $w_1 = -2/3$  for varying  $b$  and  $(c, \varepsilon) = (-0.01, 0.1)$ . Red and blue points correspond to different sweeping directions in  $b$ .

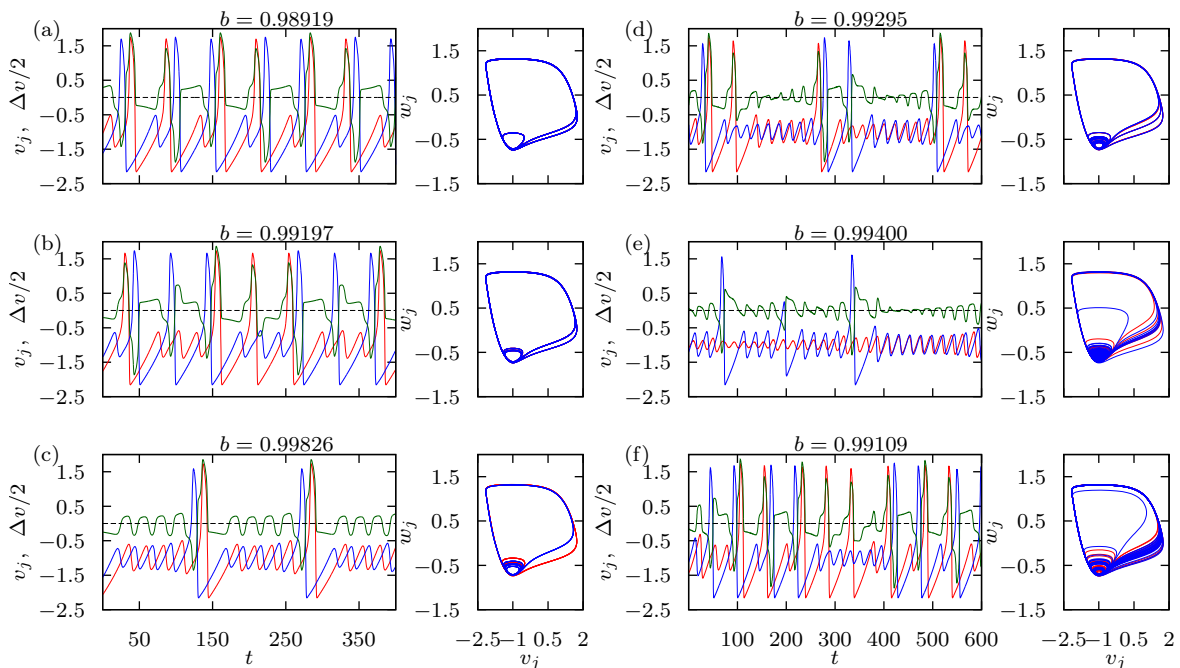


Figure 7: (Color online) Time traces and phase portraits of selected trajectories from regions V and VI in Fig. 6: Simple leap frogging in (a); periodic orbits with space-time symmetry in (b) and (d); asymmetric periodic orbit with several subthreshold oscillations in between successive spikes in (c); chaotic regimes in (e) and (f). Other parameters and colors as in Fig. 4.

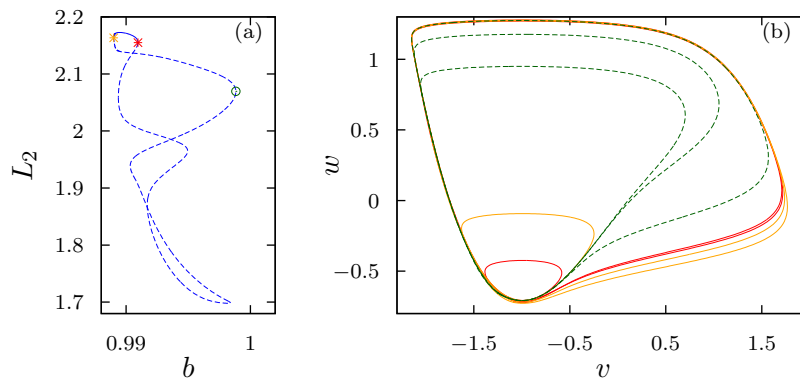


Figure 8: (Color online) (a) Branch of simple leap-frog solutions for varying  $b$  and fixed  $c = -0.01$ ,  $\varepsilon = 0.1$ . The stability region (solid curve) is bounded by two folds of limit cycles (yellow and red crosses). At all other folds (e.g. green circle) both branches are unstable (dashed curves). (b) Phase portraits of limit cycles at the folds are indicated by a symbol of corresponding color from panel (a).

due to the space-time symmetry (4), the phase portraits of the trajectories of both units in the  $(v, w)$ -plane coincide. This periodic regime can be characterized as follows. Within one period, each unit performs two round trips along the relaxation oscillation orbit and one round trip along a subthreshold oscillation orbit. The spikes of the two units again occur with a phase shift as in the successive spiking regime. However, as a result of the inlaid subthreshold oscillations, the spiking order gets reversed for every pair of successive relaxation oscillations. This regime of alternating spiking order with a single subthreshold oscillation performed between each pair of successive spikes is referred to as *simple leap-frogging*. We shall discuss the underlying bifurcation scenario and its dependence on the slow-fast structure of the system in the following section.

In region VI, one observes chaotic behavior, interrupted by some small parameter intervals of more complicated periodic behavior. Examples of chaotic orbits are shown in Fig. 7(e) and Fig. 7(f). More complicated periodic orbits from some of the periodic windows in region VI are provided in Fig. 7(b)–(d). The periodic orbits in panels (b) and (d) carry the space-time symmetry (4), which leads to a similar exchange in the spiking order as the leap-frog orbit in panel (a). The periodic solution in panel (c) is asymmetric, displaying successive spikes with fixed spiking order similar to Fig. 4(a), but interspersed with several almost anti-phase subthreshold oscillations.

### 3.1 Simple leap-frogging

The dynamical regime of leap-frogging illustrated in Fig. 7(a) is a periodic regime where successive spikes occur with an alternating spiking order. The alternation is induced by a subthreshold oscillation of the leading unit, whereby the lagging unit, passing without such a small loop, can overtake the current leader and spike the next time first. During the next spiking event, the units follow an analogous scenario but with interchanged roles, which results in the space-time symmetry (4). In Fig. 8(a) is provided the branch of leap-frogging solutions for varying  $b$  and fixed  $(c, \varepsilon) = (-0.01, 0.1)$ . The branch has the shape of a closed curve and is stable only within a small region bounded by two folds of limit cycles. A continuation of these folds in the two parameters  $(b, c)$ , shown as black curves, provides the purple stability region shown in Fig. 9(a). The latter has the shape of a linear cone and points to the canard transition of the uncoupled periodic regime at  $(b, c) = (b_c, 0)$ . However, for the chosen value of  $\varepsilon = 0.1$ , the exact bifurcation structure in the vicinity of this point could not be reliably resolved numerically. Therefore, in order to gain a better understanding of the bifurcation structure at

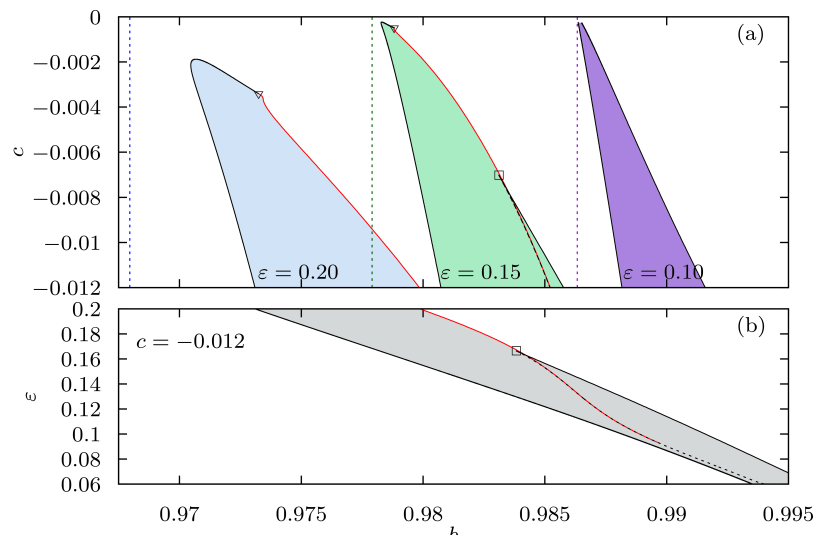


Figure 9: (Color online) (a) Stability regions of the simple leap-frog solutions in the  $(b, c)$ -plane for fixed  $\varepsilon \in \{0.2, 0.15, 0.1\}$  are shown in blue, green and purple, respectively. The vertical dashed lines of corresponding color indicate the location  $b_c(\varepsilon)$  of the canard transition of the synchronous oscillations. (b) Stability regions of the simple leap-frog solutions in the  $(b, \varepsilon)$ -plane for fixed  $c = 0.012$ . In both panels, the stability regions are bounded by curves of fold bifurcations (solid black lines) and curves of pitchfork bifurcations (shown by red color). Triangles and squares indicate pitchfork-fold interaction and cusp points.

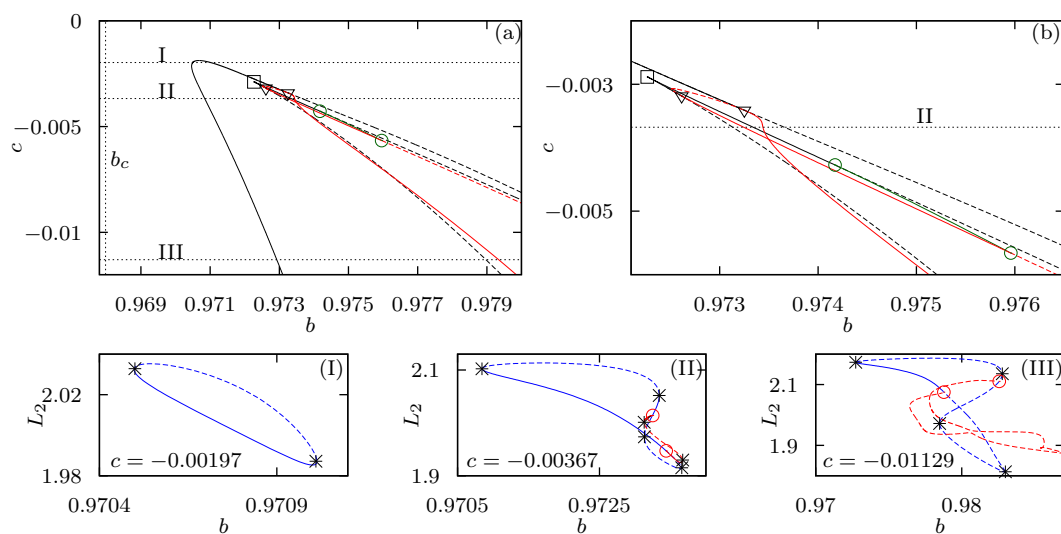


Figure 10: (Color online) (a) Bifurcations of the simple leap-frogging solutions in the  $(b, c)$ -plane for  $\varepsilon = 0.2$ . (b) Enlarged view of the region where the complexity of the bubble increases. Bifurcation curves: folds of limit cycles (black), pitchfork bifurcations (red), torus bifurcations (green). Solid curves indicate bifurcations delimiting the stability region; Dashed bifurcation curves involve only unstable states. Codimension-two bifurcations: cusps of limit cycles (squares), pitchfork-fold (triangles), torus (green circles). (I)–(III) Solid/dashed curves indicate stable/unstable branches of leap-frogging solutions with folds points (stars) and pitchfork bifurcations (circles). Asymmetric branches emerging from pitchfork bifurcations (red circles) are shown in red. The chosen values of  $c$  are indicated in panels (a) and (b).

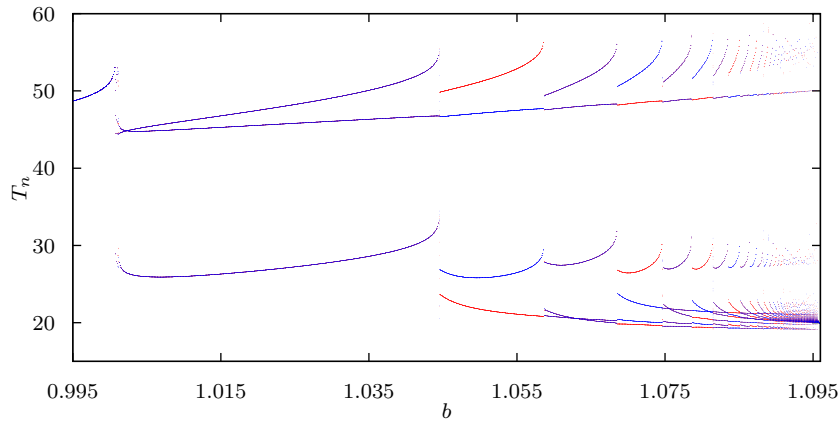


Figure 11: (Color online) Sampled return times between consecutive Poincaré events of  $v_1 = -b$  (red) or  $v_2 = -b$  (blue) for varying  $b$  and fixed  $(c, \varepsilon) = (-0.1, 0.1)$ .

the tip of the stability cone, we increased the value of  $\varepsilon$ . In Fig. 9(b) is shown the associated stability region in the  $(b, \varepsilon)$ -plane. For the fixed values of  $\varepsilon = 0.15$  and  $\varepsilon = 0.2$ , we calculated again the stability cones in the  $(b, c)$ -plane, see the green and blue regions in Fig. 9(a). For these larger values of  $\varepsilon$ , it becomes apparent that the cones are clearly detached from the line  $c = 0$ , and that the sharp tip of the cone is actually formed by a single smooth curve of fold bifurcations. However, there is a codimension-two point close to the tip where a curve of symmetry-breaking pitchfork bifurcations crosses through the fold and becomes the stability boundary of the leap-frogging regime. The pitchfork curves are plotted red in Fig. 9. For larger  $\varepsilon = 0.15$  (see the green stability cone in Fig. 9(a)), we observe another cusp point where the branch of stable leap-frogging folds over, such that its stability region is again delineated by a fold (black curves in Fig. 9).

For  $\varepsilon = 0.2$  we were able to completely resolve the bifurcation scenario in the vicinity of the tip, see Fig. 10. At small coupling  $c = -0.00195$  the branch of leap-frogging solutions emerges as a small bubble (panel (I)). For stronger coupling, this closed branch folds over and a further pair of folds emanates from a cusp point. Moreover, through symmetry-breaking pitchfork bifurcations, there appears a branch of *asymmetric* leap-frogging solutions, which is also folded in an increasingly complex fashion, sometimes even featuring a small region of stability (see panel (II)). Another type of codimension-two bifurcation points are 1:1-resonances, which give rise to branches of torus bifurcations. Figure 9 shows that for smaller  $\varepsilon$ , this complicated bifurcation scenario is contracted to a small vicinity of the canard transition of the uncoupled periodic regime at  $(b, c) = (b_c, 0)$ . The presumably exponential scaling of this contraction would clarify why already for  $\varepsilon = 0.1$  the bifurcations at the tip of the cone could not be reliably resolved by our numerics.

### 3.2 Multiple leap-frogging

We have observed that the stable simple leap-frog solutions emerge already at very weak negative coupling and are accompanied with a regime of complicated or chaotic mixed-mode oscillations. However, for stronger negative coupling, one finds a different scenario. In Fig. 11 we show different dynamical regimes for varying parameter  $b$ , now with  $c = -0.1$ , while  $\varepsilon$  is fixed again to 0.1. Similar to Fig. 6, we have for each  $b$  value sampled the return times between consecutive Poincaré events where one of the units crosses  $v_j = -b$  in increasing direction. For this stronger repulsive coupling we find a sequence of periodic patterns with a gradually increasing number of subthreshold oscillations

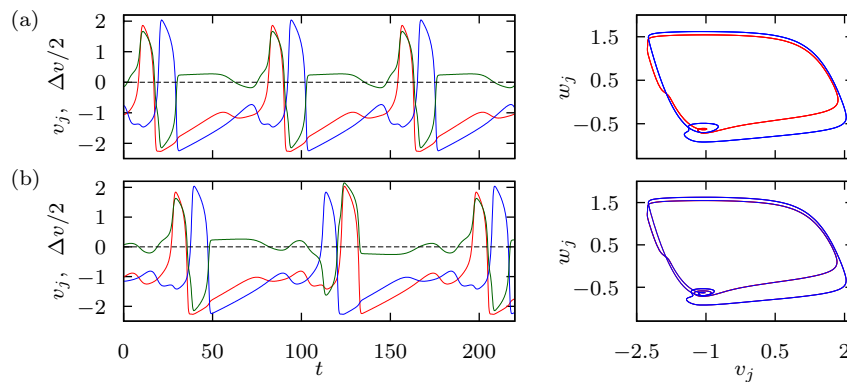


Figure 12: (Color online) Time traces and phase portraits of double leap-frogging at  $b = 1.05$  (a) and triple leap-frogging at  $b = 1.065$  (b). Other parameters are  $(\varepsilon, c) = (0.1, -0.1)$ . Colors as in Fig. 4.

between two subsequent relaxation oscillations. Beginning from the regime of successive spiking at the left edge of the diagram, the system switches to the simple leap-frogging regime, characterized by two slightly different return times  $T_n \approx 50$  corresponding to round trips along the relaxation oscillation orbit and a single return time  $T_n < 30$  corresponding to the subthreshold oscillation following only after every second spike. Due to the symmetry (4) and the alternating spiking order, the units leave an identical trace in the respective return times. The time traces typical for the subsequent dynamical regime at larger  $b$  are shown in Fig. 12(a). Here, the subthreshold oscillations follow after each spike, which results in an asymmetric solution with fixed leader and laggard unit, distinguished by slightly different return times for the small loop and the relaxation oscillation. Note that the subthreshold oscillations, performed almost in anti-phase, allow for the units to interchange the leadership twice. This is why we call this regime *double leap-frogging*. Increasing  $b$  further, we find another regime, again with the space-time symmetry (4) and an alternating spiking order, now caused by a triple interchange of leadership while performing the small loops, see Fig. 12(b). The following periodic regimes for larger  $b$  exhibit a further increasing number of subthreshold oscillations and are successively either of the asymmetric type with fixed spiking order or of the type with the space-time symmetry and an alternating order of spiking, characterized by an even and odd number of leadership exchanges, respectively.

We have examined the stability regions of the double leap-frogging regime for varying  $c$  and different values of  $\varepsilon$ , see Fig. 13. In contrast to the case of simple leap-frogging, these regions do not extend to a close vicinity of the degeneracy at  $c = 0$ . Under varying  $\varepsilon$ , their position with respect to the parameter  $b$  does not adapt to the canard transition  $b_c(\varepsilon)$  of the symmetric oscillations, as in case of the simple leap-frogging. The stability boundaries are outlined by curves of period doubling (orange) and curves of fold bifurcations (black), and do not involve any codimension-two bifurcations. This scenario for larger negative coupling, which is characterized by subsequent periodic patterns with different numbers of large relaxation oscillations and small loops, conforms, except for the different symmetry types, to the results of the asymptotic theory of mixed-mode oscillations at a folded node singularity.

## 4 Discussion and outlook

In the present study, we have demonstrated that a variety of complex leap-frog patterns may emerge in a simple system comprised of two FitzHugh–Nagumo units with linear repulsive coupling in the fast variables. This complex dynamical scenario appears for parameter values in a vicinity of the canard

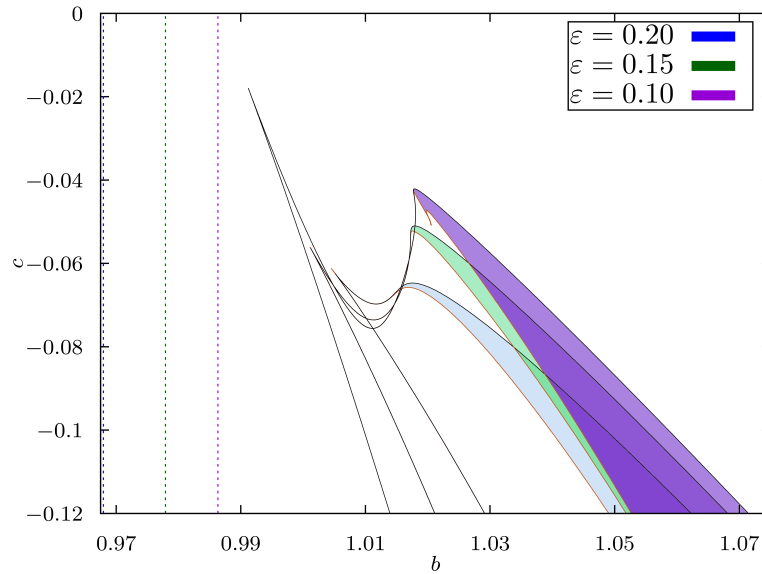


Figure 13: (Color online) Stability regions of the double leap-frog solutions in the  $(b, c)$ -plane for fixed  $\varepsilon \in \{0.2, 0.15, 0.1\}$  are presented in blue, green and purple, respectively. The left boundary of each region is given by a curve of period doubling bifurcations (orange), whereas the right one is provided by a fold curve (black).

transition of the uncoupled system and involves periodic solutions of different symmetry types. For larger repulsive coupling we obtain periodic regimes combining different numbers of small subthreshold and large relaxation oscillations, which resemble the general results for mixed-mode oscillations in slow-fast systems. For almost vanishing coupling, where the system gains an additional degeneracy, the situation is different. The stability region of the regime of simple leap frogging has the shape similar to a locking cone that approaches extremely close to the canard transition at vanishing coupling. Close to the tip of the cone, we have found a complex bifurcation scenario, which for decreasing  $\varepsilon$  is contracted to a close vicinity of the degenerate canard. This contraction happens at a very fast and presumably exponential rate, such that already for moderately small values of  $\varepsilon$  a reliable numerical treatment became unfeasible and it would be a challenging task to perform an analytically study of this scenario in the singular limit  $\varepsilon \rightarrow 0$ .

Qualitatively, the onset of the leap-frog patterns may be explained as a result of a strong sensitivity to perturbations of the relaxation oscillation of a single FitzHugh-Nagumo unit just above the canard transition. There, already very small perturbations applied during the passage near the fold singularity of the slow manifold can deviate the trajectory away from the relaxation oscillation, giving rise to one or several loops conforming to subthreshold oscillations. Such a behavior of phase-sensitive excitability and the resulting response to excitations by noise of a single FitzHugh-Nagumo unit has been studied in [18]. Similar phenomena where the excitations arise from interactions in more complex networks have been studied in [19].

So far, the conditions relevant for the emergence of leap-frog patterns have mostly been considered within the context of neuroscience, especially in terms of relation to synchronized states. It has been known that such patterns cannot be obtained within the framework of weak-coupling theory for a pair of phase oscillators, because alternating order of firing cannot be described by reduction to an autonomous flow on the corresponding torus [21, 22, 23]. Thus, it was first believed that in order to observe the leap-frog solutions, one has to complement the phase oscillator dynamics by a complex

synaptic coupling involving a finite synaptic time constant [24]. The suggested alternative has been to augment the simple phase dynamics by an additional negative phase branch corresponding to strong hyperpolarization after the spiking event, as in case of the quadratic integrate-and-fire neuron model [24]. With regard to relaxation oscillators, the leap-frog patterns have first been observed as near-synchronous states where the complete phase synchronization is perturbed by *strong* inhibitory or excitatory coupling [25, 26]. Later research focused on class I neural oscillators represented by Wang-Buzsáki [27] or Morris-Lecar model [24, 28]. In both instances, it has been found that the appropriate inhibitory non-instantaneous synaptic dynamics is crucial for the onset of leap-frog dynamics. In particular, in case of Morris-Lecar oscillators, such patterns are facilitated by the fact that the strong coupling causes the neurons to become transiently trapped in the subthreshold (excitable) state during a certain interval of the oscillation cycle, which allows for the exchange of the spiking order between the units [24]. Our findings are different from the above studies in two aspects: (i) the onset of leap-frog patterns is reported for the first time in a system of *weakly* coupled *excitable* units, and (ii) the mechanism behind the exchange of leadership involves subthreshold oscillations, typically observed in class II excitable systems [11, 12, 13].

## Acknowledgments

This work was supported by the Ministry of Education, Science and Technological Development of Republic of Serbia under project No. 171017, the DAAD Serbia-Germany Bilateral Project "Emergent Dynamics in Systems of Coupled Excitable Units", as well as the DFG within the framework of Collaborative Research Center SFB 910. The authors thank O. E. Omel'chenko and N. Semenova for fruitful discussions.

## References

- [1] R. C. Elson, A. I. Selverston, R. Huerta, N. F. Rulkov, M. I. Rabinovich, and H. D. I. Abarbanel, *Phys. Rev. Lett.* **81**, 5692 (1998).
- [2] R. Milo, S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon, *Science* **298**, 824 (2002).
- [3] E. Bullmore, and O. Sporns, *Nat. Rev. Neurosci.* **10**, 186 (2009).
- [4] O. Sporns, *Networks of the brain*, (MIT Press, Cambridge, 2011).
- [5] S. Song, P. J. Sjöström, M. Reigl, S. Nelson, and D. B. Chklovskii, *PLoS Biol.* **3**, e68 (2005).
- [6] A. Pikovsky, M. Rosenblum, and J. Kurths, *Synchronization, a Universal Concept in Nonlinear Science*, (Cambridge Univ. Press, Cambridge, 2003).
- [7] E. M. Izhikevich, *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting* (MIT Press, Cambridge, 2007).
- [8] G. Buzsáki, *Rhythms of the Brain*, (Oxford University Press, Oxford, 2009).
- [9] P. Goel, and G. B. Ermentrout, *Physica D* **163**, 191 (2002).
- [10] C. D. Acker, N. Kopell, and J. A. White, *J. Comp. Neurosci.* **15**, 71 (2003).

- [11] M. Desroches, J. Guckenheimer, B. Krauskopf, C. Kuehn, H. M. Osinga, and M. Wechselberger, *SIAM Rev.* **54**, 211 (2012).
- [12] C. Kuehn, *Multiple Time Scale Dynamics*, (Springer International Publishing, Switzerland, 2015).
- [13] M. Desroches, B. Krauskopf, and H. M. Osinga, *Chaos* **18**, 015107 (2008).
- [14] E. J. Doedel, and B. E. Oldeman, *AUTO-07P: Continuation and bifurcation software for ordinary differential equations*, (Concordia University, Montreal, 2012).
- [15] S. M. Baer, T. Erneux, *SIAM J. Appl. Math.* **46**, 721 (1986).
- [16] V. A. Makarov, V. I. Nekorkin, and M. G. Velarde, *Phys. Rev. Lett.* **86**, 3431 (2001).
- [17] B. Lindner, J. Garcia-Ojalvo, A. Neiman, and L. Schimansky-Geier, *Phys. Rep.* **392**, 321 (2004).
- [18] I. Franović, O. E. Omel'chenko, and M. Wolfrum, *WIAS Preprint No. 2465*, doi:10.20347/WIAS.PREPRINT.2465 (2017).
- [19] G. Ansmann, K. Lehnertz, and U. Feudel, *Phys. Rev. X* **6**, 011030 (2016).
- [20] N. Semenova, A. Zakharova, V.S. Anishchenko, and E. Schöll, *Phys. Rev. Lett.* **117**, 014102 (2016).
- [21] M. Golubitsky, K. Josic, and E. Shea-Brown, *J. Nonlin. Sci.* **16**, 201 (2006).
- [22] E. M. Izhikevich, and Y. Kuramoto, *Weakly coupled oscillators*, *Encyclopedia of Mathematical Physics*, Elsevier **5** 448 (2006).
- [23] F. C. Hoppensteadt, and E. M. Izhikevich, *Weakly connected neural networks*, (Springer, New York, 1997).
- [24] M. Oh, and V. Matveev, *J. Comput. Neurosci.* **26**, 303 (2009).
- [25] A. Bose, N. Kopell, and D. Terman, *Physica D* **140**, 69 (2000).
- [26] Y. D. Sato, and M. Shiino, *Phys. Rev. E* **75**, 011909 (2007).
- [27] S. K. Maran, and C. C. Canavier, *J. Comput. Neurosci.* **24**, 37 (2008).
- [28] *Frontiers of Applied and Computational Mathematics*, edited by D. Blackmore, A. Bose and P. Petropoulos, (World Scientific, Singapore, 2008).