
Chaotic Dynamics in Neural Systems



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Introduction

Several basic mechanisms of chaotic dynamics in phenomenological and biologically plausible models of individual neurons are discussed. We show that chaos occurs at the transition boundaries between generic activity types in neurons such as tonic spiking, bursting, and quiescence, where the system can also become bi-stable. The bifurcations underlying these transitions give rise to period-doubling cascades, various homoclinic and saddle phenomena, torus breakdown, and chaotic mixed-mode oscillations in such neuronal systems.

Neurons exhibit various activity regimes and state transitions that reflect their intrinsic ionic channel behaviors and modulatory states. The fundamental types of neuronal activity can be broadly defined as quiescence, subthreshold, and tonic spiking oscillations, as well as bursting composed of alternating periods of spiking activity and quiescence. A single neuron can endogenously demonstrate various bursting patterns, varying in response to the external influence of

synapses, or to the intrinsic factors such as channel noise. The co-existence of bursting and tonic spiking, as well as several different bursting modes, have been observed in modeling (Cymbalyuk et al. 2002; Bertram 1993; Canavier et al. 1993; Butera 1998; Frohlich and Bazhenov 2006) and experimental (Hounsgaard and Kiehn 1989; Lechner et al. 1996; Turrigiano et al. 1996) studies. This complexity enhances the flexibility of the nervous and locomotive systems (Rabinovich et al. 2006).

The functional role of chaotic behaviors, and the dynamical and bifurcational mechanisms underlying their onset at transitions between neural activity types like spiking, bursting, and quiescence, has been the focus of various theoretical and experimental studies. Bursting is a manifestation of multiple timescale dynamics, composed of repetitive fast tonic spiking and a slow quiescent phase. It has been observed in various fields of science as diverse as food chain ecosystems (Rinaldi and Muratori 1992), nonlinear optics (DeShazer et al. 2003), medical studies of the human immune system (Shochat and Rom-Kedar 2008), and neuroscience (Steriade et al. 1990). Various bursting patterns, whether regular or chaotic, endogenous, or as emergent network phenomena, are the natural rhythms generated by central pattern generators (CPG) (Briggman and Kristan 2008; Kopell 1988; Marder and Calabrese 1996; Katz 2008; Shilnikov et al. 2008). CPGs are neural networks made up of a small number of constituent neurons that often control various vital repetitive locomotive functions (Marder and Calabrese 1996) such as walking and respiration of humans, or the swimming and crawling of leeches (Kristan et al. 2005; Kristan and Katz 2006; Briggman and Kristan 2006). Polyhythmic bursting dynamics have also been observed in multifunctional CPG circuits that produce several coexisting stable oscillatory patterns or bursting rhythms, each of which is associated with a particular type of locomotor activity of the animal (Jalil et al. 2013; Alacam and Shilnikov 2015; Wojcik et al. 2014). Bursting has also been

frequently observed in pathological brain states (Steriade et al. 1993; Rubin and Terman 2004), in particular, during epileptic seizures (Bazhenov et al. 2000; Timofeev et al. 2002). Neurons in bursting modes differ in their ability to transmit information and respond to stimulation from those in tonic spiking mode and therefore play an important role in information transfer and processing in normal states of the nervous system.

Understanding and modeling the generic mechanisms regulating the neuronal connectivity and the transitions between different patterns of neural activity, including global bifurcations occurring in neuron models and networks, pose fundamental challenges for mathematical neuroscience, with a number of open problems (Guckenheimer 1996). The range of bifurcation and dynamical phenomena underlying bursting *transcends* the existing state of the theory (Belykh et al. 2000; Shilnikov and Cymbalyuk 2004; Doiron et al. 2002; Laing et al. 2003; Rowat and Elson 2004; Shilnikov and Cymbalyuk 2005; Shilnikov et al. 2005a; Channell et al. 2007a; Cymbalyuk and Shilnikov 2005; Shilnikov and Kolomiets 2008; Kramer et al. 2008): This includes the blue sky catastrophe (Shilnikov et al. 2005b, 2014), torus-canard formation and breakdown, and homoclinic inclination/orbit-flip bifurcations, all of which can occur on the transition route to bursting in most square-wave and elliptic bursters. Studies of bursting require nonlocal homoclinic bifurcation analysis, which is often based on the Poincaré return mappings (Shilnikov et al. 1998/2001). Return mappings have been employed for computational neuroscience in Shilnikov and Rulkov (2003, 2004), Chay (1985), and Medvedev (2005). A drawback of mappings constructed from time series is sparseness, as they reflect only the dominating attractors of a system. In some cases, feasible reductions to one or two dimensional mappings can be achieved through slow-fast scale decomposition of the phase variables for the system (Griffiths and Pernarowski 1917–1948). A new, computer assisted method for constructing a complete family of *onto* mappings for membrane potentials, for a better understanding of simple and complex dynamics in

neuronal models, both phenomenological and of the Hodgkin–Huxley type (Hodgkin and Huxley 1952), was proposed in Channell et al. (2007b). With this approach, one can study, for example, the spike-adding transitions in the leech heart interneuron model, and how chaotic dynamics in between is associated with homoclinic tangle bifurcations of some threshold saddle periodic orbits (Channell et al. 2009). Qualitative changes in a system’s activity at transitions often reveal the quantitative information about changes of certain biophysical characteristics associated with the transition. This approach has proven to be exemplary in neuroscience for understanding the transitions between silence and tonic-spiking activities (Rinzel and Ermentrout 1989). Moreover, knowledge about the bifurcation (transition) predicts cooperative behavior of interconnected neurons of the identified types (Ermentrout 1993).

In this entry, we discuss nonlocal bifurcations in generic, representative models of neurodynamics, described by high order differential equations derived through the Hodgkin-Huxley formalism. We consider a number of neuroscience-related applications to reveal a multiplicity of causes and their bifurcation mechanisms leading to the onset of complex dynamics and chaos in these models.

Neuronal Activities and Transition Mechanisms

This entry deals with neuronal models, both biologically plausible and phenomenological, that can produce complex and distinct dynamics such as tonic spiking, bursting, quiescence, chaos, and mixed-mode oscillations (MMOs) representing fast spike trains alternating with subthreshold oscillations. MMOs are typical for many excitable systems describing various (electro)chemical reactions, including the famous Belousov-Zhabotinky reaction, and models of elliptic bursters (Wojcik and Shilnikov 2011). Geometrical configurations of slow-fast neuron models for bursting were pioneered in Wang and Rinzel (1995), Rinzel (1985), Rinzel and Ermentrout (1989) and further developed in Bertram et al. (1995), Izhikevich (2000, 2007). Dynamics of such singularly

perturbed systems are determined by and centered around the attracting pieces of the slow motion manifolds. These are composed of equilibria and limit cycles of the fast subsystem (Tikhonov 1948; Pontryagin and Rodygin 1960; Fenichel 1979; Mischenko and Rozov 1980; Andronov et al. 1966; Mischenko et al. 1994; Jones and Kopell 1994; Arnold et al. 1994) that in turn constitute the backbones of bursting patterns in a neuronal model. Using the geometric methods based on the slow-fast dissection, where the slowest variable becomes a control parameter, one can detect and follow the branches of equilibria and limit cycles in the fast subsystem. The slow-fast decomposition allows for drastic simplification, letting one clearly describe the dynamics of a singularly perturbed system. A typical Hodgkin-Huxley model possesses a pair of such manifolds (Rinzel 1985; Jones and Kopell 1994): quiescent and tonic spiking, respectively. The slow-fast dissection has been proven effective in low-order mathematical models of bursting neurons far from the bifurcation points. However, this approach does not account for the reciprocal, often complex interactions between the slow and fast dynamics, leading to the emergence of novel dynamical phenomena and bifurcations that can *only* occur in the whole system. Near such activity transitions, the bursting behavior becomes drastically complex and can exhibit deterministic chaos (Shilnikov and Cymbaluyk 2004; Shilnikov et al. 2005a; Cymbalyuk and Shilnikov 2005; Terman 1992; Holden and Fan 1992; Wang 1993; Feudel et al. 2000; Deng and Hines 2002; Elson et al. 2002).

Slow-Fast Decomposition

Many Hodgkin-Huxley type models can be treated as a generic slow-fast system

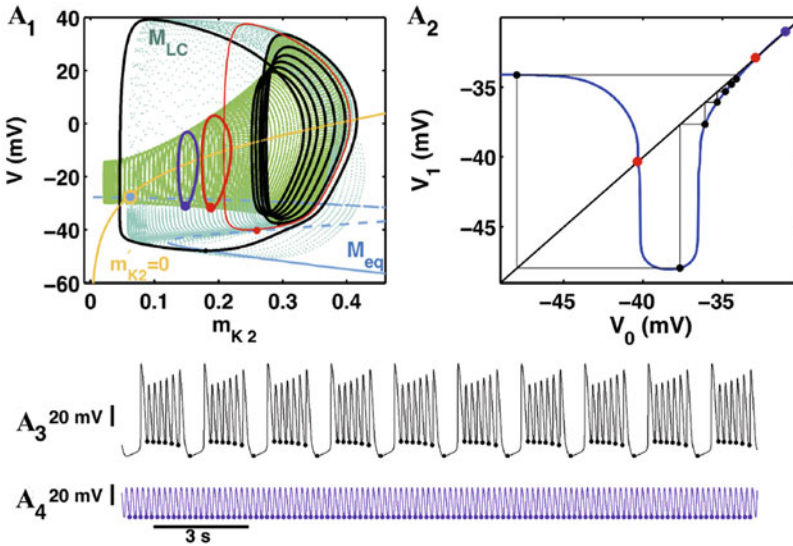
$$\mathbf{x}' = \mathbf{F}(\mathbf{x}, z) \quad z' = \mu G(\mathbf{x}, z, \alpha), \quad (1)$$

where $0 < \mu \ll 1$, $\mathbf{x} \in R^n$, $n \geq 2$ and z is a scalar or can be a vector in R^2 (as in the extended Plant model with two slow variables below); α is a control parameter shifting the slow nullcline, given by $G(\mathbf{x}, \alpha) = 0$, in the phase space. In the singular limit $\mu = 0$, the z -variable becomes a parameter of the fast subsystem to detect and

continue the equilibrium state (ES), given by $\mathbf{F}(\mathbf{x}, z) = 0$, and the limit cycles (LC) of the fast subsystem. As long as they (ES/LC) remain exponentially stable, by varying z one can trace down the smooth invariant manifolds in the phase space of (1) such as M_{eq} with the distinct Z-shape typical for many Hodgkin-Huxley type models (see Fig. 1), while the limit cycles form a cylinder-shaped surface M_{lc} . Locally, either is a center manifold for (1) persisting in a closed system, in virtue of (Tikhonov 1948; Pontryagin and Rodygin 1960; Fenichel 1979). The stable upper and lower branches of M_{eq} correspond to the de- and hyperpolarized steady states of the neuron, respectively. Folds on M_{eq} correspond to the saddle-node equilibrium states of the fast subsystem. The unstable de-polarized branch of M_{eq} can be enclosed by the tonic-spiking manifold M_{lc} typically emerging through an Andronov-Hopf bifurcation and terminating through a homoclinic bifurcation, which are the key features of the fast-subsystem of the square-wave bursters (Shilnikov 2012), like the Hindmarsh-Rose model (Barrio et al. 2014) and the Chay model (Chay 1985) (discussed below).

Poincaré Mappings

To elaborate on the nature of complex oscillations like bursting and their evolutions, one needs to examine nonlocal bifurcations that often require the use of Poincaré return maps (Shilnikov and Rulkov 2003, 2004; Chay 1985; Holden and Fan 1992; Deng 1999; Hutt and Beim 2017; Beim Graben et al. 2016; Beim Graben and Hutt 2013, 2015). An obvious drawback of maps constructed from voltage time series is in their sparseness, as they can typically reveal some point-wise attractors of the system that trajectories fast converge to, unless there is a noise or small perturbations are added to get a more complete picture of the underlying structure. In some cases, a feasible reduction to low-dimensional mapping can be achieved through slow-fast scale decomposition of slow phase variables (Shilnikov et al. 1998/2001, 2005b; Griffiths and Pernarowski 1917–1948). We proposed and developed a new computer assisted algorithm for constructing a dense family of *onto* mappings for membrane

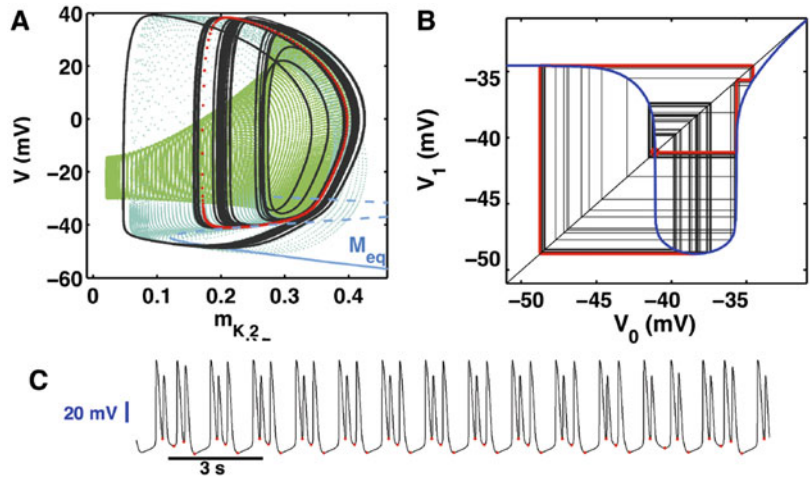


Chaotic Dynamics in Neural Systems, Fig. 1 (A₁) Bistability of the coexisting tonic-spiking and bursting in the 3D phase space of the leech heart interneuron model (3). Inset (A₂) depicts the shape of the corresponding 1D Poincaré map with stable fixed point corresponding to the tonic spiking periodic orbit (purple) with a single voltage

minima, and period-7 bursting orbit, and 2 unstable fixed points (red): the right one separates attraction basins of tonic-spiking (A₄) and bursting (A₃) activities, whereas the left one causes chaotic dynamics at spike adding transitions, see Fig. 2

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Fig. 2 (A) Chaotic bursting in the phase space of the leech heart interneuron model (3) and the corresponding map (B) at a transition between two and three spikes per burst in the voltage trace (C) due to proximity of the primary homoclinic orbit of the repelling fixed point (red) corresponding to a single minimum of the saddle periodic orbit (red) in (A)



potentials in a Hodgkin–Huxley type neuronal model (Channell et al. 2007a). Such maps let us find and examine both the stable and unstable solutions in detail; moreover, unstable points are often the primary organizing centers globally governing the dynamics of the model in question. The construction of such a map begins with the localization of the tonic spiking manifold M_{lc} in the model, using the parameter continuation

technique or the slow-fast dissection, see Fig. 1. Then, a curve on M_{lc} is defined, which corresponds to minimal (maximal) voltage values, denoted, say, by V_0 . By construction, the 1D map M takes all V_0 (outgoing solutions integrated numerically) on this curve back onto itself, after a single turn around M_{lc} , i.e., $M: V_0 \rightarrow V_1$ for a selected value of the parameter. Two such maps are depicted in Figs. 1 and 2. One can see that

these are noninvertible (Mira 1987; Mira and Shilnikov 2005), unimodal maps with a single critical point (Devaney 1992; Sharkovsky et al. 1997), which happens to be a universal feature of many other square-wave bursters in neuroscience applications. With such maps, one can fully study the attractors, the repellers, and their bifurcations, including saddle-nodes, homoclinic orbits, spike-adding, and period-doubling. We note that detection of homoclinics of a saddle periodic orbit in the phase space of a model is in general *state-of-the-art* and the Poincaré map technique allows us to locate them with ease.

Classifications of Bursting

The existing classifications (Wang and Rinzel 1995; Rinzel 1985; Rinzel and Ermentrout 1989; Bertram et al. 1995; Izhikevich 2000, 2007) of bursting are based on the bifurcation mechanisms of dynamical systems in a plane, which initiate or terminate fast trajectory transitions between the slow motion manifolds in the phase space of the slow-fast neuronal model. These classifications allow us to single out the classes of bursting by subdividing mathematical and realistic models into the following subclasses: elliptic or Hopf-fold subclass (FitzHugh-Rinzel (Wojcik and Shilnikov 2011) and Morris-Lecar models), square-wave bursters or fold-homoclinic subclass (Hindmarsh-Rose model (Shilnikov and Kolomiets 2008; Barrio and Shilnikov 2011), models of pancreatic β -cells, cells in the pre-Botzinger complex, as well as intrinsically bursting and chattering neurons in neocortex); parabolic or circle-circle subclass (model of R15 cells in the abdominal ganglion of the mollusk *Aplysia* (Butera 1998; Alacam and Shilnikov 2015), the reduced leech interneuron model at certain parameter values); and fold-fold subclass, or top hat models (Best et al. 2005), including the reduced heart interneuron model (3) discussed below.

Transition Routes

The current description of the transition routes between tonic spiking and bursting activities is incomplete and remains a fundamental problem for both neuroscience and the theory of dynamical systems. The first theoretical mechanism revealed

in Terman (1992) explained chaos in the so-called square wave bursters (Rinzel 1985) emerging between tonic-spiking and bursting. Later, two global bifurcations that occur at the loss of stability of a tonic spiking periodic orbit through quite novel homoclinic saddle-node bifurcations were discovered and explained. The first transition, reversible and continuous, found in the reduced model of the leech heart interneuron (Shilnikov and Cymbaluyk 2004, 2005) and in a modified Hindmarsh-Rose model of a square-wave burster (Shilnikov and Kolomiets 2008; Shilnikov et al. 1998/2001), is based on the blue sky catastrophe (Shilnikov et al. 1998/2001; Turaev and Shilnikov 1995; Shilnikov and Turaev 1997, 2000; Gavrillov and Shilnikov 2000). This was proven in Shilnikov et al. (2005b) to be a typical bifurcation for slow-fast systems. This striking term (Abraham 1985), the *blue sky catastrophe*, stands for a novel bifurcation of a saddle-node periodic orbit with a 2D unstable manifold returning to the orbit making infinitely many revolutions. After the bifurcation, this homoclinic connection transforms into a long bursting periodic orbit with infinitely many spikes. The burst duration of the orbit near the transition is evaluated by $1/\sqrt{\alpha}$, where $0 < \alpha \ll 1$ is a bifurcation parameter. The second transition mechanism is due to a saddle-node periodic orbit with noncentral homoclinics (Lukyanov and Shilnikov 1978). An important feature of this transition is the bi-stability of co-existing tonic spiking and bursting activities in the neuron model, see Fig. 1. In this case, the burst duration towards the transition increases as fast as $|\ln(\alpha)|$. Another feature of this bifurcation is the transient chaos where the neuron generates an unpredictable number of burst trains before it starts spiking tonically. This phenomenon is a direct consequence of the Smale horseshoe finite shift dynamics in the system (Gavrillov and Shilnikov 1972), which is a rather atypical phenomenon for such slow-fast systems.

Chaos in Neuron Models

In this section, we present the basic mechanisms and routes to chaos in a variety of biophysically

realistic neuronal models exhibiting rich and complex dynamics including tonic spiking, bursting, and quiescence. A bifurcation describing a transition between neuronal activities typically occurs near saddle (unstable) orbits and results from reciprocal interactions involving the slow and fast dynamics of the model. Such interactions lead to the emergence of new dynamical phenomena and bifurcations that can occur only in the full model, but not in either of the slow or the fast subsystem. Chaotic dynamics can be characterized by unpredictable variations in the number of spikes during the active phases of bursting and/or the subthreshold oscillations. This phenomenon of chaotic dynamics is generally atypical in slow-fast systems as it occurs within narrow parameter windows only near the transition boundaries. Indeed, robust and regular dynamics of slow-fast neuron models contrast those of real bursting neurons exhibiting a phenomenal time dependent variability of oscillatory patterns.

Leech Heart Interneuron Model: Period Doubling Cascades and the Blue Sky Catastrophe

We first illustrate and discuss the onset of chaotic dynamics in the reduced (3D) model of the leech heart interneuron (see Eq. (3) of Appendix). This is a *typical* slow-fast Hodgkin-Huxley type (HH) model describing the dynamical interplay of a single slow variable – persistent potassium current, I_{K2} , and two fast variable – the sodium current, I_{Na} and the membrane voltage V that can be recast in this generic form (Shilnikov and Cymbalyuk 2005; Shilnikov et al. 2005a; Shilnikov 2012; Neiman et al. 2011):

$$CV'_i = -\sum_j I_j - \sum_i I_i^{\text{syn}}, \quad \tau_h h' = f_\infty(V) - h, \quad (2)$$

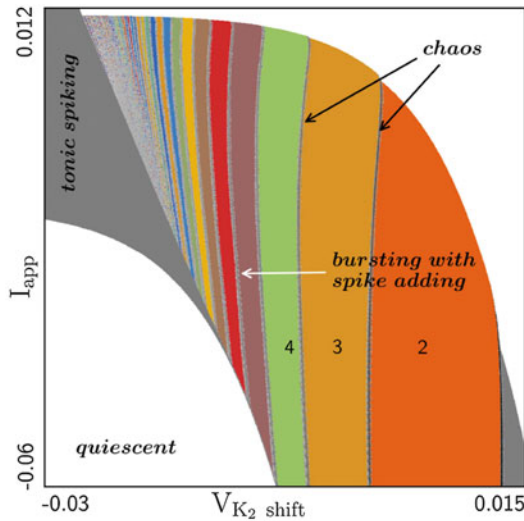
where C is a membrane capacitance, V is a transmembrane voltage, I_j stands for various in/outward currents including synaptic ones, $0 \leq h \leq 1$ stands for a gating (probability) variable, f_∞ is a sigmoidal function, and τ_h is a time-scale, fast or slow, specific for specific currents.

This model shows a rich set of dynamics and can produce various types of complex chaotic and

bistable behaviors, including the period-doubling cascade *en a route* from tonic spiking through bursting (Shilnikov and Cymbalyuk 2004; Cymbalyuk and Shilnikov 2005), as well as various types of homoclinic chaos. Following the period-doubling cascade, the model demonstrates a terminal phase of chaotic tonic spiking that coexists alongside another periodic tonic spiking activity. For a different set of parameter values compared to the period doubling cascade, the model can also exhibit the blue sky catastrophe as a continuous and reversible mechanism of the transition between bursting and tonic spiking. Figure 1 explains the nature of bi-stability in this model as it exhibits the co-existing tonic-spiking and bursting oscillations corresponding to the stable fixed point (FP) (purple) and the period-7 orbit in the 1D map, whose basins are separated by an unstable FP representing a saddle periodic orbit (red) on the 2D manifold M_{1c} in the 3D phase space. The role of the other unstable (red) FP is revealed by Fig. 2. It is shown that the spike-adding in bursting is accompanied with an onset of chaotic dynamics orchestrated by the homoclinic orbits and bifurcations involving the other saddle orbit, see more details in Shilnikov et al. (2014), Channell et al. (2009), Wojcik and Shilnikov (2011), Shilnikov (2012), Barrio et al. (2014), Barrio and Shilnikov (2011), and Neiman et al. (2011). Figure 3 shows the bifurcation diagram of the system constructed as a parametric sweep using our previously developed symbolic toolkit called the *Deterministic Chaos Prospector* (Pusuluri et al. 2017; Pusuluri and Shilnikov 2018, 2019) to process symbolic sequences extracted from wave-form traces and analyze activity types and underlying bifurcations. This bifurcation diagram identifies the regions of quiescence, tonic spiking, as well as bursting with spike adding cascades. The noisy regions near the boundaries of spike addition reveal the occurrence of chaos. In addition, the blue sky catastrophe takes place at the noisy region near the boundary between bursting and tonic spiking.

Period-Doubling in the Chay Model

The Chay model is a simple, realistic biophysical model for excitable cells, producing endogenous



Chaotic Dynamics in Neural Systems, Fig. 3 Bi-parametric sweep of the leech heart interneuron model (3) using the symbolic toolkit *Deterministic Chaos Prospector* (Pusuluri et al. 2017; Pusuluri and Shilnikov 2018; Pusuluri and Shilnikov 2019) to process wave-form traces and to reveal regions of quiescent behavior, tonic spiking, as well as bursting activity with spike adding cascades: from 2 spikes (orange zone) to 3 spikes (yellowish zone), next to 4 spikes (light green zone) and so forth. The noisy regions near the boundaries of spike addition reveal the occurrence of chaos, while the noisy boundary between tonic spiking and bursting portrays the blue sky catastrophe (Shilnikov and Cymbaluyk 2004) corresponding to infinitely long bursting

chaotic behavior (see its Eq. (5) of Appendix). The model transitions from tonic spiking to bursting via period-doubling bifurcations, whereby chaotic dynamics can also arise. Figure 4 shows the 2D (V, Ca) -phase space projection of the Chay model with a period-4 orbit and a chaotic bursting orbit, along with the corresponding Poincaré return map. The model goes through a period-doubling cascade and then immediate chaotic bursting, before regular bursting as the bifurcation parameter $g_{K,c}$ increases.

Torus Breakdown in the Bull Frog Hair Cell Model

Next, we consider the hair cell model based on experimental studies of basolateral ionic currents in saccular hair cells in bullfrog (Hudspeth and Lewis 1988; Catacuzzeno et al. 2003, 2004; Rutherford and Roberts 2009). This is a further

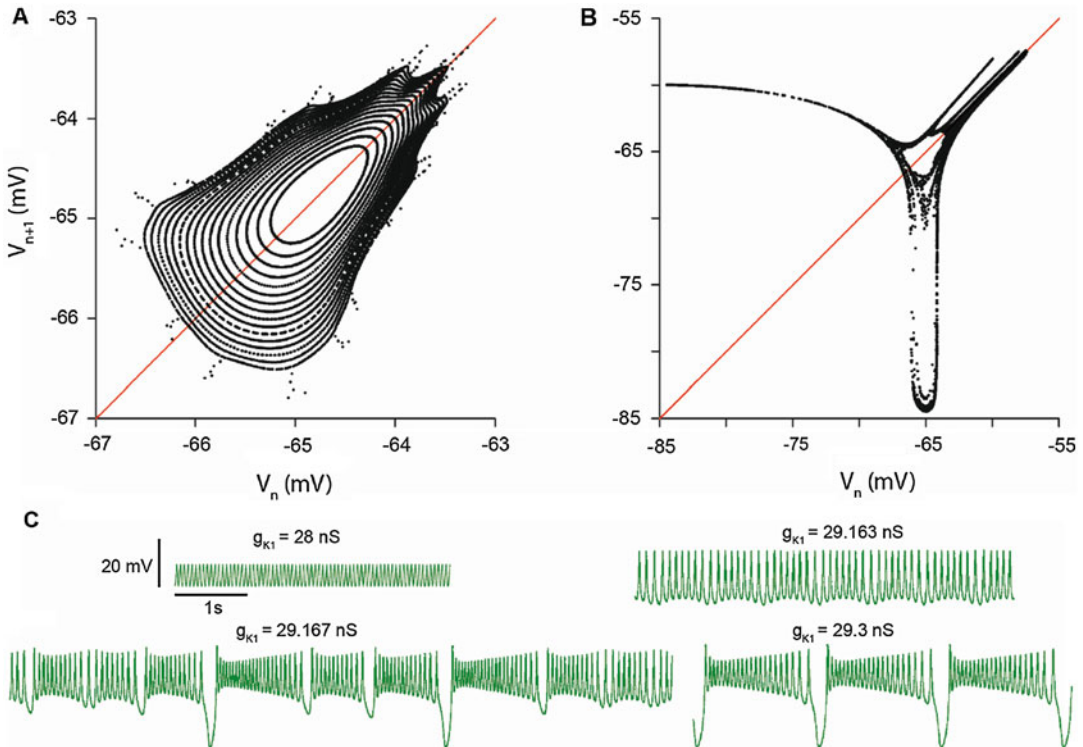
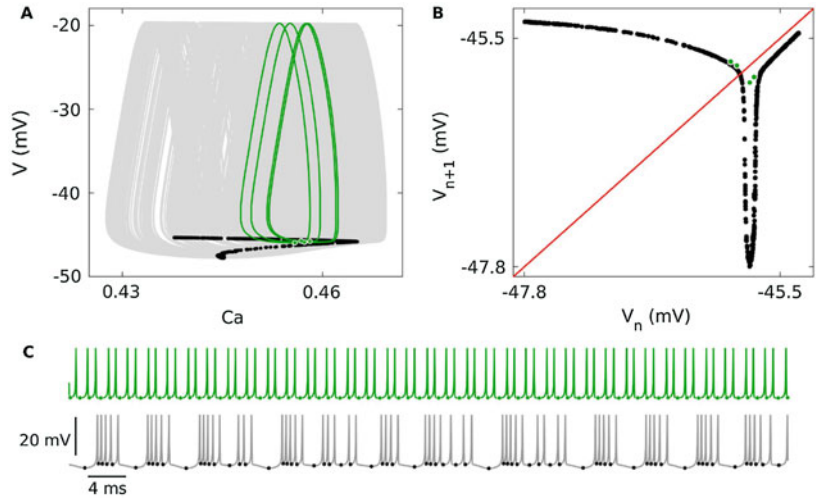
extension of the model of the Hodgkin-Huxley type developed in Catacuzzeno et al. (2004) that includes 12 coupled nonlinear ordinary differential equations, see Neiman et al. (2011) for its detailed description. In this model, the transition from bursting to tonic spiking is due to a torus bifurcation (TB) that leads to onset of quasi-periodic dynamics (Ju et al. 2018). Closer to this bifurcation the torus breaks down causing the onset of chaotic bursting in the system. In case of a supercritical TB, through which a stable torus emerges at the fold of the tonic spiking manifold M_{LC} (like one in Fig. 1), its development, growth and breakdown can be well studied using the Poincaré return maps. For example, Fig. 5a depicts that, right after the supercritical TB in the hair cell model, a stable torus (invariant circle) emerges from a stable tonic-spiking periodic orbit and grows from smooth and ergodic to non-smooth to resonant as the bifurcation parameter g_{K1} increases. Later, when the torus breaks down (starting at $g_{K1} = 29.213$ nS), bursting becomes chaotic as shown in the Poincaré map (Fig. 5b). Figure 5c illustrates the route from tonic spiking to bursting with chaotic dynamics at the torus breakdown.

Chaotic Mixed-Mode Oscillations in the Extended Plant Model

The conductance-based Plant model of endogenous parabolic bursters was originally developed to model the R15 neuron in the abdominal ganglion of the slug *Aplysia Californica* (Butera 1998). This was later extended and adapted to model the swim CPG of the sea slug *Melibe Leonina*, see Alacam and Shilnikov (2015) for details of the model and the equations. This model can produce chaotic bursting activity, as shown in Fig. 6a near the boundary between tonic spiking and bursting activity. In addition, the model exhibits complex chaotic *mixed mode oscillations* (MMOs) near the transition between bursting and the co-existing hyper-polarized quiescence state. Figure 6b illustrates the model generating spike-varying bursts and small amplitude subthreshold oscillations. Such chaotic MMOs coexist with a hyperpolarized quiescent state resulting in bistability due to a subcritical

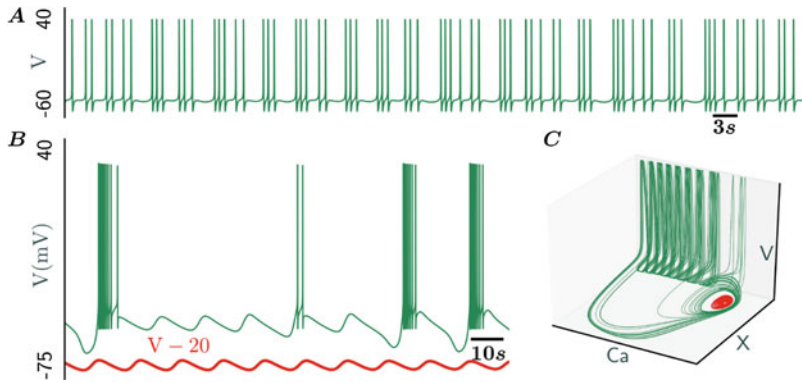
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Fig. 4 (A) The (V, Ca) phase space projection overlaying a period-4 orbit (green, $g_{Kc} = 11.12$) and a chaotic bursting trajectory (grey, $g_{Kc} = 11.5$) generated by the Chay model. Here V_{\min} – minimal values, labeled with green and black dots in the voltage traces (C), are used to generate 1D Poincaré return maps: $V_{\min}^{(n)} \rightarrow V_{\min}^{(n+1)}$ in Inset (B)



Chaotic Dynamics in Neural Systems, Fig. 5 Poincaré return map, $V_{\min}^{(n)} \rightarrow V_{\min}^{(n+1)}$, for the consecutive V_{\min} values in voltage traces generated by the hair cell model. (A) Evolution of stable invariant circles (IC) from ergodic to resonant with further nonsmooth torus breakdown as the g_{K1} parameter is increased from 29.185 through 29.2073 nS. (B) Chaotic bursting after the torus breakdown

at $g_{K1} = 29.213$ nS. The flat, stabilizing section of the map corresponds to hyperpolarized quiescence, while multiple sharp folds reveal a ghost of the nonsmooth IC in the depolarized range. (C) En route from tonic spiking to regular bursting, the voltage trace undergoes quasi-periodicity and chaotic bursting. (This figure is adapted from Ju et al. (2018))



Chaotic Dynamics in Neural Systems, Fig. 6 The extended Plant model can exhibit chaotic bursting near the boundaries of tonic spiking and bursting with spike-adding (A) as well as bistability with chaotic mixed mode oscillations (green) and hyperpolarized quiescence (red) near the transitions between bursting with spike-adding

and hyperpolarized quiescence (B). The corresponding phase space projection of the bistable states of (B) is shown in (C). Following a subcritical Andronov-Hopf bifurcation, a saddle periodic orbit (not seen) separates the chaotic mixed mode bursts (green) from the hyperpolarized quiescent state with spiral convergence (red)

Andronov-Hopf bifurcation that gives rise to a saddle periodic orbit whose stable manifold separates the chaotic bursting activity (green) from the stable (spiraling) hyperpolarized quiescent state (red) as shown in Fig. 6c. As the parameters are varied, gradually the system transitions from this bistable state to the monostable hyperpolarized quiescence, or vice versa, to a dominant bursting activity.

Acknowledgments This work was funded in part by the NSF grant IOS-1455527 and the RSF grant 14-41-00044 at Lobachevsky University of Nizhny Novgorod. We thank the Brains and Behavior initiative of Georgia State University for providing pilot grant support and the doctoral fellowships of K. Pusuluri and H. Ju. We acknowledge the support of NVIDIA Corporation with the Tesla K40 GPUs used in this study. Finally, we are grateful to all the current and past members of the Shilnikov NeurDS lab for productive discussions.

Appendix

Leech Heart Interneuron Model

The reduced leech heart model is derived using the Hodgkin-Huxley formalism:

$$\begin{aligned} CV' &= -I_{Na} - I_{K2} - I_{leak} + I_{app}, \\ \tau_{Na} h'_{Na} &= h_{Na}^{\infty}(V) - h, \\ \tau_{K2} m'_{K2} &= m_{K2}^{\infty}(V) - m_{K2}, \end{aligned} \quad (3)$$

with

$$\begin{aligned} I_{leak} &= 8(V + 0.046), \\ I_{K2} &= 30m_{K2}^2(V + 0.07), \\ I_{Na} &= 200[m_{Na}^{\infty}(V)]^3 h_{Na}(V - 0.045), \end{aligned}$$

and where V is the membrane potential, $C = 0.5$; h_{Na} is a fast ($\tau_{Na} = 0.0405$ sec) activation of I_{Na} , and m_{K2} ; I_L describes the slow ($\tau_{K2} = 0.25$ sec) activation of I_{K2} , I_{app} is an applied current. The steady states $h_{Na}^{\infty}(V)$, $m_{Na}^{\infty}(V)$, $m_{K2}^{\infty}(V)$, of the gating variables are given by the Boltzmann equations given by

$$\begin{aligned} h_{Na}^{\infty}(V) &= [1 + \exp(500(0.0333) + V)]^{-1}, \\ m_{Na}^{\infty}(V) &= [1 + \exp(-150(0.0305) + V)]^{-1}, \\ m_{K2}^{\infty}(V) &= [1 + \exp(-83(0.018) + V_{K2}^{shift} + V)]^{-1}. \end{aligned} \quad (4)$$

The bifurcation parameter V_{K2}^{shift} of the model is a deviation from the experimentally determined voltage $V_{1/2} = 0.018$ V corresponding to the half-activated potassium channel, i.e., to

$m_{K2}^\infty(0.018) = 1/2$. In its range, V_{K2}^{shift} is $[-0.025; 0.0018]V$ the upper boundary corresponds to the hyperpolarized quiescent state of the neuron, whereas the model produces spiking oscillations at the lower end V_{K2}^{shift} values and bursts in between.

Chay Model

The 3D Hodgkin-Huxley type Chay model reads as follows:

$$\begin{aligned} V' &= -g_I m_\infty^3 h_\infty (V - V_I) - g_{K,C} n_\infty^4 (V - V_K) \\ &\quad - g_{K,C} \frac{C}{1+C} (V - V_K) - g_L (V - V_L), \\ n' &= (n_\infty[V] - n) / \tau_n[V], \\ C' &= \rho \{ m_\infty^3 h_\infty (V_C - V) - k_C C \}, \end{aligned} \quad (5)$$

where n represents the gating variable of the voltage-sensitive K^+ channel and C represents the intracellular free calcium concentration. See (Chay 1985) for the detailed description.

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