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CLASSIFICATION OF BURSTING MAPPINGS

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When a system's activity alternates between a resting state (e.g. a stable equilibrium) and an active state (e.g. a stable periodic orbit), the system is said to exhibit bursting behavior. We use bifurcation theory to identify three distinct topological types of bursting in one-dimensional mappings and 20 topological types in two-dimensional mappings having one fast and one slow variable. We show that different bursters can interact, synchronize, and process information differently. Our study suggests that bursting mappings do not occur only in a few isolated examples, rather they are robust nonlinear phenomena.

Keywords: Spiking; bursting; synchronization resonance; maps; 1D; 2D; classification.

1. Introduction

Bursting is ubiquitous in physical and biological systems, especially in neural systems where it plays an important role in information processing [Lisman, 1997; Izhikevich, 2000, 2002; Izhikevich *et al.*, 2003]. Synchronization of bursters is a multiscale phenomenon that may involve synchronization between individual bursts (slow time), of spikes within each burst (fast time), or both [Izhikevich, 2001]. Studying networks of bursters poses challenging mathematical problems. Even simulating such networks is a computational challenge, since thousands of stiff nonlinear ordinary differential equations (ODEs) may be involved.

Bursting dynamics of mappings has recently been investigated by physicists [Rulkov, 2001, 2002; de Vries, 2001; Cazelles *et al.*, 2001; Shilnikov & Rulkov, 2003, 2004; Rulkov *et al.*, 2004; Copelli *et al.*, 2004]. Using a discrete-time system, say $x_{n+1} = f(x_n)$, instead of a system of ODEs, provides one with a number of theoretical and computational advantages. For example, it is possible to explore collective behavior of millions of coupled discrete-time bursters with only modest computational effort.

Many ODE bursters can be reduced to return mappings for Poincaré cross-sections. For example, bursting in a model human pancreatic β-cell has been described in this way, resulting in a mapping [Terman, 1991] that has in it a horse-shoe structure, which implies the possibility of chaotic dynamics. The resulting mapping is implicitly defined and quite complicated. To the best of our knowledge, there have been proposed only six explicit mappings capable of generating bursting activity [Chialvo, 1995; Kinouchi & Tragtenberg, 1996; Rulkov, 2001, 2002; Cazelles *et al.*, 2001; Laing & Longtin, 2002]. Some simulate recently proposed simple model of spiking neurons [Izhikevich, 2003] using Eulier method with 1 ms time step, that is, the mapping

$$v_{n+1} = 0.04v_n^2 + 6v_n + 140 - u_n + I$$
$$u_{n+1} = 0.004v_n + 0.98u_n$$

if $v_n < 30$, and

$$v_{n+1} = c$$
$$u_{n+1} = u_n + d$$

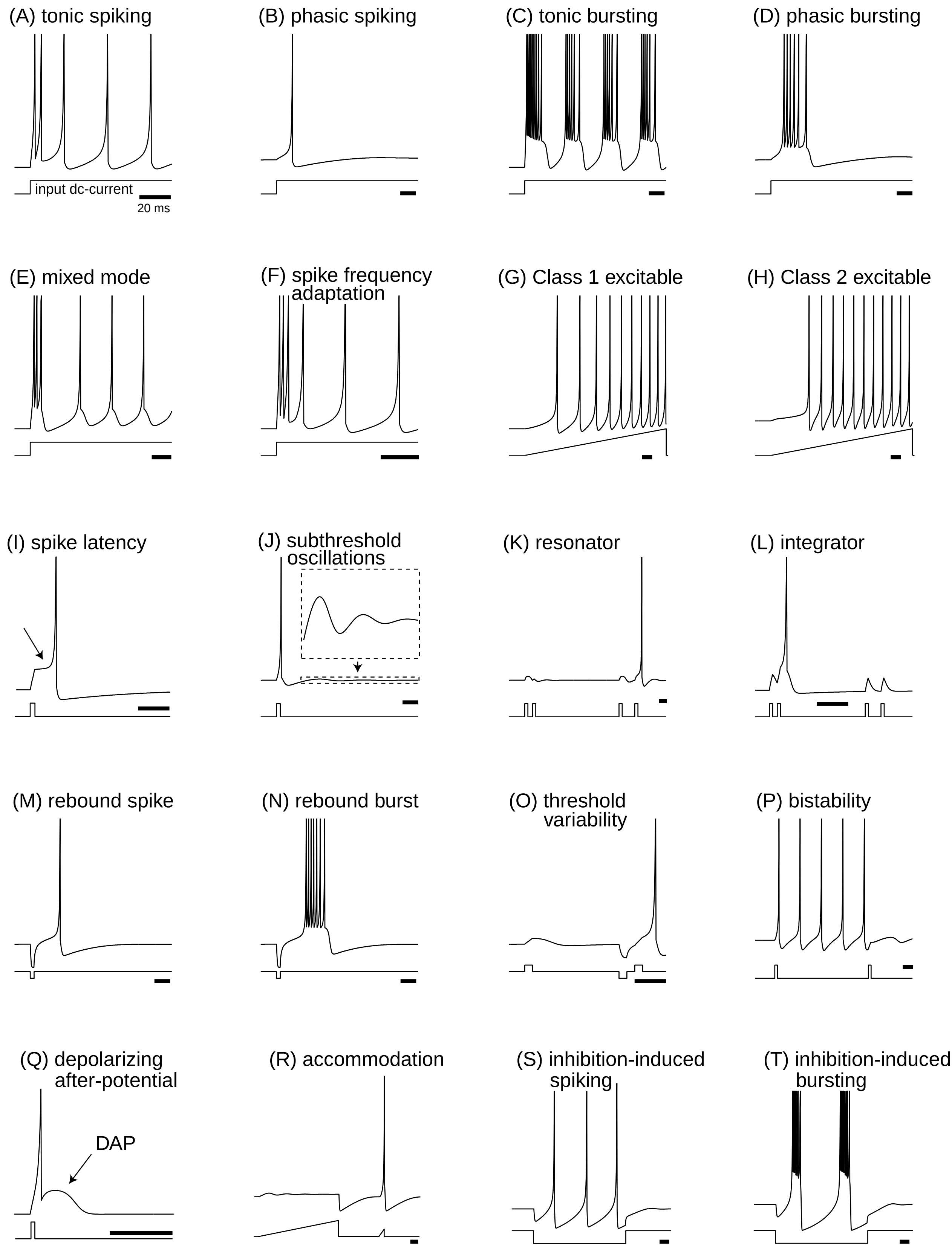

Fig. 1. Summary of the neuro-computational properties of biological spiking neurons [Izhikevich, 2004]. This figure is reproduced with permission from www.izhikevich.com. (Electronic version of the figure and reproduction permissions are freely available at www.izhikevich.com).

otherwise. Depending on the values of the parameters, this mapping can produce a variety of bursting patterns, including those corresponding to IB (intrinsically bursting) and CH (chattering) neocortical neurons. In addition, the simple model can reproduce 20 most fundamental neuro-computational properties of biological spiking neurons summarized in Fig. 1 [Izhikevich, 2004].

Our goal here is to introduce a method for classifying all bursting mappings and patterns using bifurcation theory, and although it is not our primary goal, we also present examples of several interesting bursters. We show that it is important to distinguish between different types of bursters, since different bursters can have different collective computational properties [Hoppensteadt & Izhikevich, 1997].

2. One-Dimensional Mappings

Bursting can occur in planar ODEs and in one-dimensional mappings, and it involves a fast-time scale for spiking and slow-time scale for gaps between spiking events. For example, a hedgehog limit cycle attractor in Fig. 2 (top) corresponds to bursting dynamics in a planar ODE. Similarly, the periodic attractor for a simple unimodal one-dimensional map shown in the middle figure in Fig. 2 also corresponds to bursting behavior. In each case, the behavior has two time scales — fast spiking and slow modulation. During the slow interval, the system remains near an equilibrium, but slowly diverges from it. It eventually jumps into the spiking mode. From the spiking mode the system eventually hits a window of return to near the equilibrium. Repetitive transitions from rest to spiking and back occurs here because the one-dimensional bursting mapping is near a homoclinic bifurcation [Belykh *et al.*, 2000]. That is, we define an orbit $\{x_n\}$ to be *homoclinic* to an equilibrium x^*, if it originates and terminates at x, i.e. $x_n \to x^*$ as $n \to \pm\infty$. A mapping having a homoclinic orbit to an equilibrium x^* (in fact, there is often an infinite family of such orbits) can be perturbed so that a periodic orbit appears [Kuznetsov, 1995]. Such an orbit corresponds to bursting dynamics, since the solution stays long near the equilibrium x^*, yet it makes occasional excursions away from it, as in Fig. 2.

Our classification begins by identifying three structures involved in bursting for one-dimensional mappings: A node, a focus and a fold, as shown

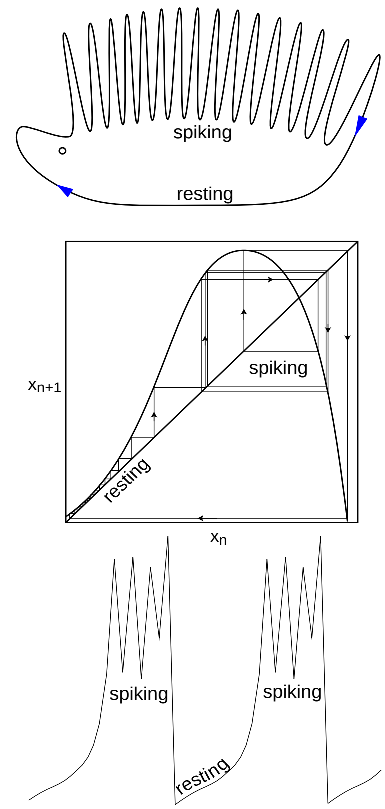

Fig. 2. A hedgehog periodic orbit often corresponds to bursting dynamics in continuous (top) and discrete (bottom) systems [Izhikevich, 2000].

in Fig. 3. Obviously, the equilibrium must be unstable, otherwise the solution never diverges from it. We can classify all such equilibria in one-dimensional mappings in terms of the slope of $F(x)$ at the equilibrium (which we refer to here as being the Floquet multiplier of the equilibrium): Thus, there are three distinct types of homoclinic orbits in one-dimensional mappings, which we summarize in Fig. 3:

- (Node) The homoclinic orbit can be to and from an unstable node, i.e. an equilibrium having Floquet multiplier greater than 1, as in Fig. 3(a) (top). A small perturbation of such a system that shifts the function up makes a returning orbit miss the equilibrium. The resulting slow-time modulation is characterized by a monotone exponential rate of divergence from the rest.
- (Focus) The homoclinic orbit can be to and from an unstable focus, i.e. the equilibrium having Floquet multiplier less than -1, as in Fig. 3(b). A small perturbation of such a system makes the orbit miss the equilibrium. The resulting slow-time

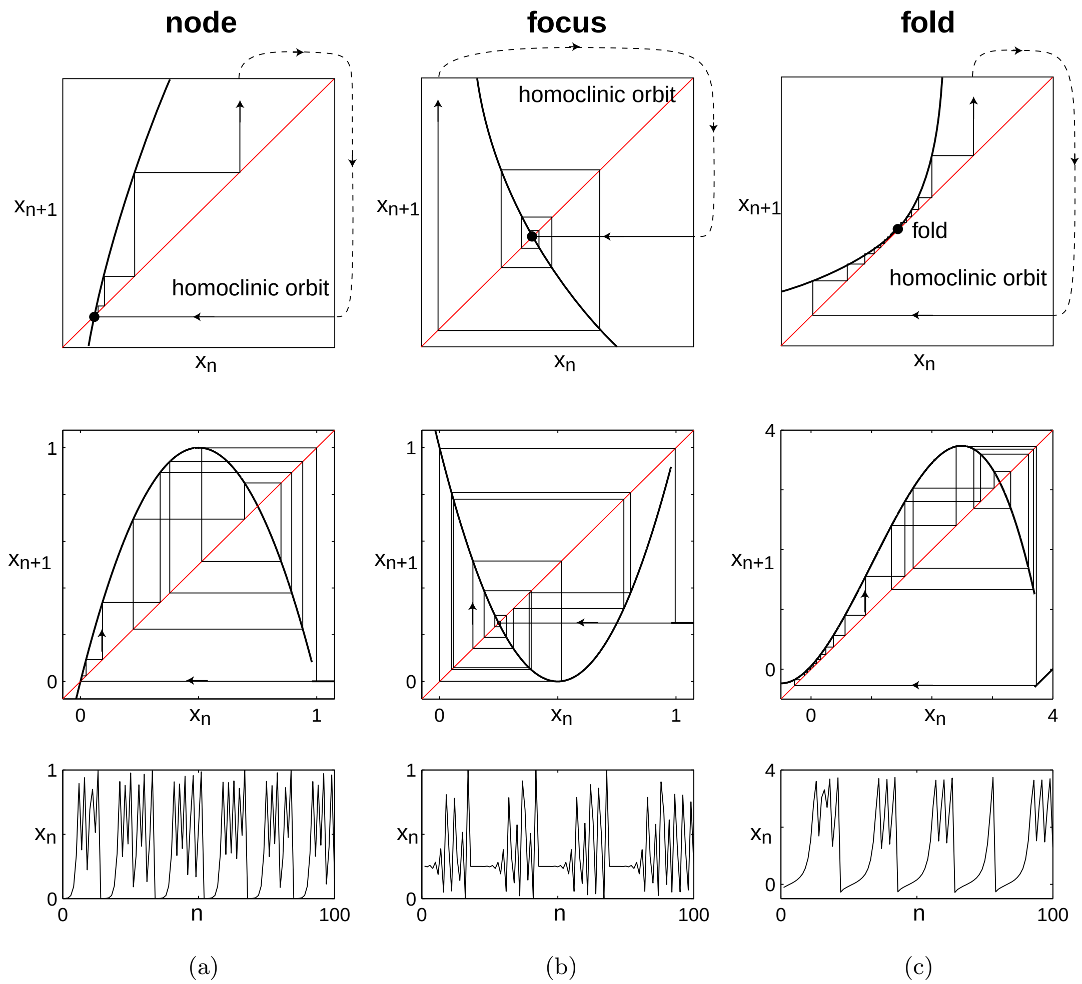

Fig. 3. Classification of bursting in one-dimensional mappings. (a) $F(x) = 4x(1-x)$ when $x < 0.98$, and $0.000098x$ when $x > 0.98$. (b) $F(x) = 1 - 4x(1-x)$ when $x < 0.98$, and $0.25 + 0.00003x$ when $x > 0.98$. (c) $F(x) = -0.25 + 2x - 0.3(x-1)^3$ when $x < 3.7$, and $x - 4$ when $x > 3.7$.

behavior is characterized by growing oscillatory divergence.

- (Fold) The homoclinic orbit can be to and from a fold equilibrium having Floquet multiplier equal to 1, as in Fig. 3(c). (Such a system is said to be near saddle-node on invariant circle bifurcation.) A small perturbation that shifts $F(x)$ up results in the disappearance of the equilibrium. The resulting slow-time behavior is characterized by a linear rate of divergence from a neighborhood of where the node vanished.

This identifies three distinct types of bursting in one-dimensional mappings, which we name "node", "focus", and "fold" burster, respectively. The burster proposed by Cazelles *et al.* [2001] is of the "node" type, since their system can be perturbed to have a homoclinic orbit to a node equilibrium, similar to the one in Fig. 3(a).

Notice that in all three cases above the system is near a bifurcation of co-dimension one, i.e. only one constraint is imposed. Other possible cases, such as a homoclinic orbit to an equilibrium at a flip bifurcation [Kuznetsov, 1995], would result in co-dimension two or higher bifurcations, since two or more constraints are imposed. The classification above is complete for co-dimension-1 bursting in one-dimensional mappings.

3. Fast/Slow Mappings

We give a complete classification of co-dimension-1 bursters in fast/slow systems of the following form, by extending ideas developed for singularly

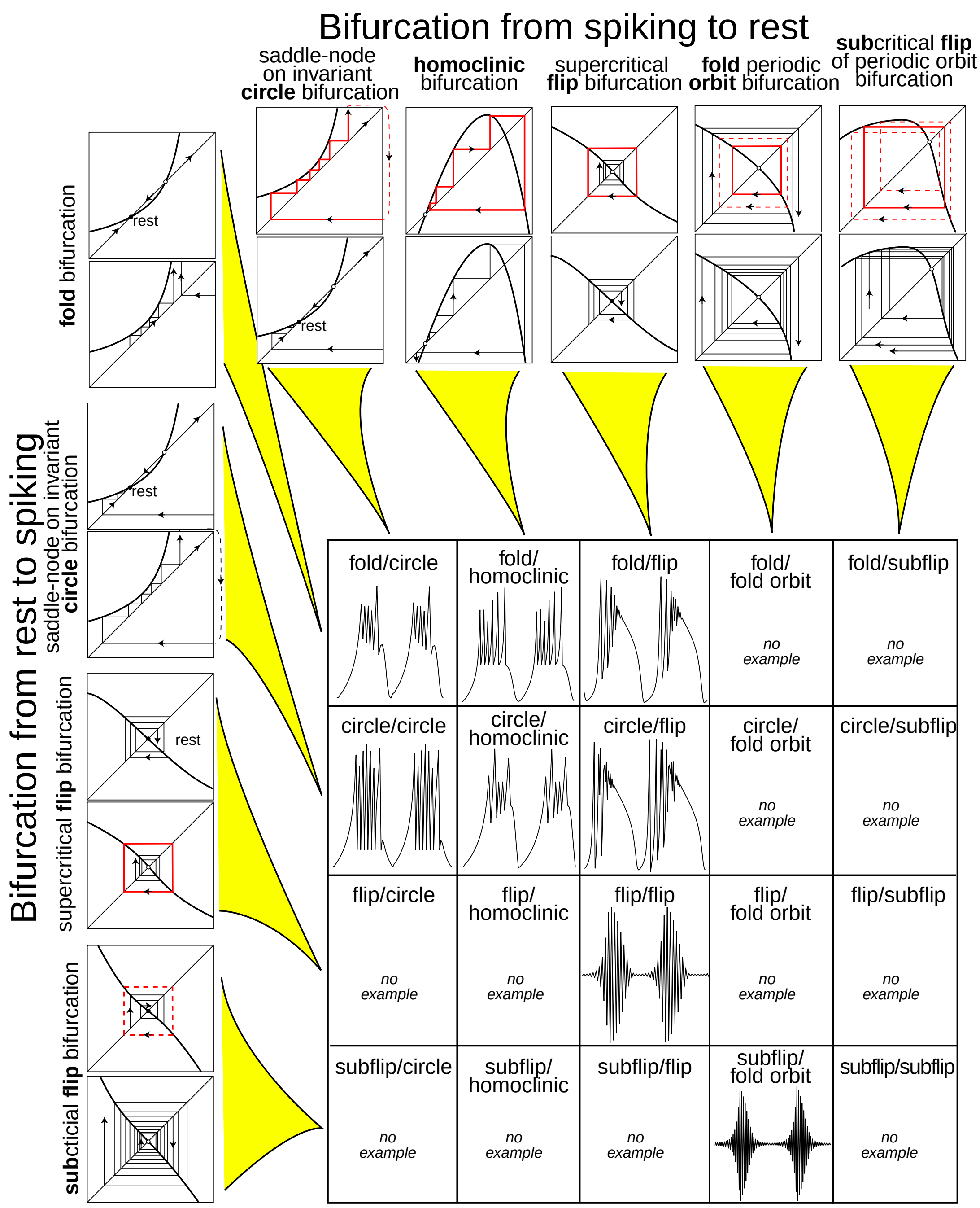

Fig. 4. Classification of bursting in two-dimensional fast–slow mappings. Examples: "fold/circle" $f(x, y) = 1/2 + x + x^2 - y^2$, if $x > 1$, then $x \leftarrow -y/4$, $g(x) = 1 + x$, if $y > 1$, then $y \leftarrow -1$, $\varepsilon = 0.075$; "circle/circle" $f(x, y) = 1/2 + x + x^2 - y^2$, if $x > 1$, then $x \leftarrow -1/2$, $g(x) = 1 + x$, if $y > 1$, then $y \leftarrow -1$, $\varepsilon = 0.05$; "fold/homoclinic" $f(x, y) = x + x^2 + y$, if $x > 1$, then $x \leftarrow 1/5$, $g(x) = 1/5 - x$, $\varepsilon = 0.01$; "circle/homoclinic" $f(x, y) = 1/2 + x + x^2 - y^2$, if $x > 1$, then $x \leftarrow y/4$, $g(x) = 1 + x$, if $y > 1$, then $y \leftarrow -1$, $\varepsilon = 0.075$; "fold/flip" $f(x, y) = (3/2 + y)x - x^3 + y$, $g(x) = 1/4 - x$, $\varepsilon = 0.05$; "flip/flip" $f(x, y) = (-3/2 + y^2)x + x^3$, $g(x) = 1 + x^2$, if $y > 1$, then $y \leftarrow -1$, $\varepsilon = 0.05$; "subflip/fold orbit" $f(x, y) = yx - 1/2x^3 + x^5$, $g(x) = x^2 - 0.1$, $\varepsilon = 0.01$.

perturbed ordinary differential equations [Rinzel, 1987; Bertram *et al.*, 1995; Izhikevich, 2000].

$$x_{n+1} = f(x_n, y_n) \tag{1}$$

$$y_{n+1} = y_n + \varepsilon g(x_n) \tag{2}$$

where the fast variable, x_n, describes spiking behavior, the slow variable, y_n, is like a slowly changing parameter that modulates the spiking dynamics, and $\varepsilon \ll 1$ describes the time scale of parameter variation. We assume that f and g are piecewise continuous functions, and g may also depend on y_n, ε, and external noise. The quasi-static approximation to solutions of (1, 2) first sets $\varepsilon = 0$ and treats y_n as being a constant parameter. Bursting occurs when for some values of y Eq. (1) exhibits equilibrium dynamics, while for others it exhibits periodic dynamics. When ε is small, the variable x_n exhibits bursting dynamics because y_n slowly moves between those regimes.

An important observation made regarding neuronal bursting [Rinzel, 1987] is that bursting behavior depends less on specific ionic currents than on the type of bifurcations that the fast subsystem undergoes as the slow variable changes; see review by Izhikevich [2000]. Motivated by this, we base our classification on bifurcation properties of the fast variable. First, we consider all possible co-dimension-1 bifurcations of an *equilibrium* that lead to loss of its stability or its disappearance: There are only four such bifurcations [Kuznetsov, 1995], which are listed in the left column in Fig. 4:

- *Fold* bifurcation: A stable and an unstable equilibrium coalesce and annihilate each other. The solution leaves a neighborhood of the equilibria.
- *Saddle-node on invariant circle* bifurcation is similar to the fold bifurcation, except that the solution returns to a neighborhood of the equilibrium. Such a bifurcation results in an oscillation having very large period.
- *Supercritical flip* bifurcation results in the appearance from the equilibrium of a small amplitude period-2 stable periodic orbit.
- *Subcritical flip* bifurcation results when an unstable periodic orbit shrinks to a point that becomes unstable.

There are only five co-dimension-1 bifurcations of a *stable periodic orbit* in which the fast variable goes from being active to an equilibrium [Kuznetsov, 1995]. These are listed in the top row in Fig. 4 (the other co-dimension-1 bifurcations of periodic orbits, such as supercritical flip bifurcation, do not lead to transitions from spiking to resting, and hence are not listed here).

- *Saddle-node on invariant circle* bifurcation: The period of oscillation becomes infinite as a saddle-node (fold) equilibrium appears on the circle.
- *Homoclinic* bifurcation: The periodic orbit attractor becomes a homoclinic orbit to an unstable node equilibrium. Its period also becomes infinite.
- *Supercritical flip* bifurcation: The periodic orbit shrinks to a point.
- *Fold periodic orbit* bifurcation: The stable periodic orbit is approached by an unstable one, they coalesce and annihilate each other.
- *Subcritical flip of periodic orbits* bifurcation: A stable periodic orbit is surrounded by an unstable periodic orbit of twice the period, which glues to the stable one and make it lose stability.

Any combination of a bifurcation from equilibrium (there are only four of them) and of a bifurcation from a periodic orbit attractor (there are only five of them) results in a distinct type of burster; hence, there are exactly 20 possible bursters, which we name according to the bifurcations involved; see Fig. 4. For example, both of Rulkov's bursters [Rulkov, 2001, 2002] are of the "fold/homoclinic" type, since the transition from rest to spiking in those bursters occurs via a fold bifurcation and the transition from spiking to rest occurs via a homoclinic bifurcation. Since every co-dimension-1 bifurcation of an equilibrium or of a one-dimensional periodic orbit is accounted for in Fig. 4, our classification of co-dimension-1 bursters in fast/slow two-dimensional mappings is complete. The empty boxes in Fig. 4 correspond to bursters that have not yet been discovered.

4. Computational Properties

It is well-known from studies of biophysical models of neurons that the nature of a bifurcation from rest determines important computational abilities of a neuron: For example, it might be an integrator or a resonator [Izhikevich, 2000; Izhikevich *et al.*, 2003].

When the bifurcation is of a fold type (the upper half of the table in Fig. 4), the burster acts as an integrator; that is, the stronger the input, the sooner the burster responds. In contrast, when the bifurcation is of a flip type (the lower half of the table in Fig. 4), the burster exhibits subthreshold oscillations, and it acts as a resonator; that is, it responds only to inputs having appropriate frequency and phase, as shown in Fig. 5. When an oscillatory input to a resonator is in-phase with the intrinsic oscillation, the transition to spiking is facilitated. However, when the input is anti-phase with the oscillation, the transition to spiking can be significantly delayed. Thus, the type of bursting

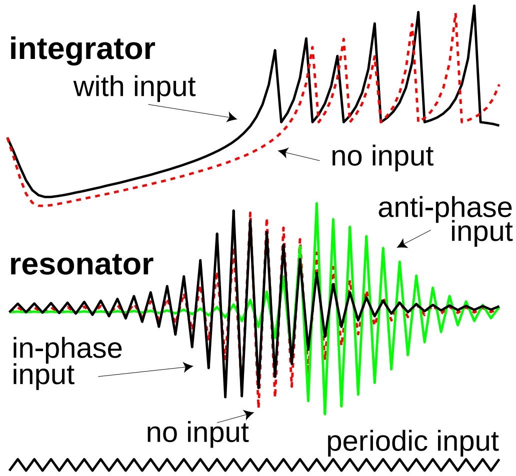

Fig. 5. Integrators and resonators have different neuro-computational properties: They react differently to oscillatory input. Shown are simulations of "fold/homoclinic" and "subflip/fold orbit" bursters from Fig. 4 with fast subsystem of the form $f(x_n, y_n) + 0.035(-1)^n$.

determines how the burster reacts to an input, such as that coming from other bursters, which is an important aspect of neuro-computation, see [Izhikevich, 2000].

5. Discussion

Classification of phenomena is important in all areas of science, especially in mathematics. In this short paper we use bifurcation theory to classify topological types of bursting in mappings. Our study shows that such bursting is a robust nonlinear phenomenon that can occur in many different ways. Our classification scheme provides a useful framework for studying the dynamical mechanisms of all possible bursters, and it is intended to organize the many examples of bursters that will emerge in the near future.

Bursting in one-dimensional mappings occurs because of the system's proximity to a homoclinic bifurcation. Solutions near a homoclinic orbit spend part of their time in a small neighborhood of an equilibrium (resting state) and part far from the equilibrium (spiking state), thereby exhibiting bursting behavior; see Fig. 3. Such bursting does not require a fast/slow system. The apparent multiscale behavior in Fig. 3 appears because of the properties of homoclinic orbits.

We also consider bursting in two-dimensional fast/slow mappings of the form (1, 2). Using classical ideas developed for ODEs (see review by Izhikevich [2000]), we identify four bifurcations of equilibrium that may lead to spiking, and five bifurcations of periodic orbit attractors that may lead to rest; hence, there are $4 \times 5 = 20$ different types of bursters in such mappings. We suggest naming the bursters according to the bifurcations involved, so that the nomenclature is self-explanatory and consistent with that used for ODEs [Izhikevich, 2000]. Since we exhaust all possible combinations of co-dimension-1 bifurcations of equilibria and a periodic orbits in one-dimensional maps (1), our classification is complete. Remarkably, the resulting classification scheme is so general as to explain and predict some neuro-computational properties and to name bursters that have yet to be discovered (empty boxes in Fig. 4).

Even though we consider bifurcations of periodic attractors, many bursters that we have found exhibit chaotic behavior. The nonperiodicity manifests itself in random inter-burst periods and random durations of activity. This may not be surprising, since, e.g. all one-dimensional bursters in Fig. 3 exhibit Pomeau–Manneville intermittency. One can easily get rid of chaos and create a periodic 1D-bursting by setting the slope of the "reset step" (when $x > 0.98$) to zero. To get rid of chaos in 2D-bursting is more difficult, though we do not have an explanation for that.

Considering bursting in mappings in contrast to bursting in ODEs provides a number of advantages, mostly mathematical simplicity and computational efficiency needed for simulations of large networks, due to the minimal numerical problems entailed. Nevertheless, as we see in Sec. 4, considering mappings is not a compromise or a trade off, since bursting in mappings has many important neuro-computational properties seen in ODEs and in biological neurons.

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