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## PARABOLIC BURSTING, SPIKE-ADDING, DIPS AND SLICES IN A MINIMAL MODEL \*

MATHIEU DESROCHES<sup>1,2</sup>, JEAN-PIERRE FRANCOISE<sup>3</sup> AND MARTIN KRUPA<sup>1,2,4</sup>

**Abstract.** A minimal system for parabolic bursting, whose associated slow flow is integrable, is presented and studied both from the viewpoint of bifurcation theory of slow-fast systems, of the qualitative analysis of its phase portrait and of numerical simulations. We focus the analysis on the spike-adding phenomenon. After a reduction to a periodically forced 1-dimensional system, we uncover the link with the dips and slices first discussed by J. E. Littlewood in his famous articles on the periodically forced van der Pol system.

**Mathematics Subject Classification.** 37C10, 37C27, 34C23, 37G15, 34C15, 34E17.

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### 1. INTRODUCTION

Bursting is an essential rhythm of neural activity, whether it be intrinsic or extrinsic (upon the application of an external stimulus); ubiquitous in biological data, in particular from the brain, it can be modelled with mathematical equations within different frameworks, in particular parametrised Ordinary Differential Equations (ODEs) with multiple timescale. Slow-fast models of bursting activity have been developed, both biophysically and phenomenologically, and analysed since the 1970s. The seminal work of Rinzel in the mid-1980s [39,40] has led to a first classification of bursting patterns using mathematical criteria, in particular bifurcation theory. Later on, this first classification was completed by Izhikevich [26] generalising the idea of using bifurcations of an auxiliary so-called *fast subsystem* to initiate and terminate the burst of a bursting system. Further bursting classification work were obtained in [2,19]. The third class of Rinzel is denoted *parabolic bursting* and it corresponds to a SNIC-SNIC bursting in the taxonomy introduced by Izhikevich, SNIC standing for Saddle-Node (bifurcation) on an Invariant Circle. This is because the underlying slow-fast bursting system has a two-dimensional fast subsystem displaying a two-parameter family of SNIC bifurcations, which organises the transition from quiescence to burst and back in the full system. The main results of the present paper is the introduction of a new parabolic burster, whose associated *slow subsystem* is integrable and hence in which the spike-adding is more easily analysed. A new light is shed onto this spike-adding structure that organises the burst size in this class of bursting system. Our system has a cylindrical critical manifold with two fold lines along each of which one can find conditions for so-called *folded-saddle singularities* and associated *canard solutions* to exist; recall that canards are solutions staying close to repelling manifolds of slow motion for a long time

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*Keywords and phrases.* parabolic bursting, spike-adding, Littlewood's dips and slices

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interval [1, 17, 30]. Depending on the slow periodic forcing, we obtain spike-adding canard explosions [12, 47] organising the transition from slow oscillation to bursting by passing near one or both folded saddles. In every case, the scenario is the same: the first spike is added via a slow passage near the folded saddle and its associated canard, whereas subsequent ones are added via passages near a *jump-on point* [11] (a point on the fold line where the slow flow points away from the fold in both directions) and a repulsive segment of the folded-saddle canard solution. This provides one step further in understanding better the salient features of parabolic bursting in order to improve current models.

The first important reference on the observation of parabolic bursting in biological data is the famous Plant model on the R15 neuron of the *Aplysia*, which is a mollusk. [35–38] This model is constructed within the conductance framework introduced by Nobel prize winners Alan Hodgkin and Andrew Huxley in their seminal 1952 paper [25]. This five-dimensional model is not singularly perturbed as it does not have an explicit small parameter, however it clearly displays slow-fast dynamics, in the form of parabolic bursting limit cycles, and one can identify 3 fast variables and 2 slow variables. The main state variable is the membrane potential  $V$  and it is fast; the two slow variables,  $x$  and  $Ca$ , are both related to calcium. A typical parabolic bursting cycle  $\Gamma$  produced by this model is shown in Figure 1. Panel (a) shows a phase-space projection onto the  $(x, Ca, V)$ -space, where the green surface is the fast nullsurface obtained by solving for  $V$  the (implicit) equilibrium equation for the fast variables over a range of values of the slow variables  $x$  and  $Ca$ ; such a fast nullsurface is referred to as the *critical manifold*  $S^0$  of the system. The slow dynamics occurs very close to the lower attracting sheets of  $S^0$  and the transition to the fast dynamics occurs as the trajectory reaches the fold curve  $F$  of  $S^0$ . In the particular case of parabolic bursting, the transition from the quiescent (slow) phase to the burst and back both correspond to a passage near  $F$ , which is a curve of SNIC bifurcation points of the fast subsystems; this justifies that the burst starts and terminates with very low frequency. This is better observed when further projecting the orbit together with the SNIC curve  $F$  onto the plane of slow variables; this is done in panel (b) where one can clearly observe the two phases of such a parabolic bursting cycle, separated by  $F$ , the slow phase to the right of  $F$  and the fast phase or burst to the left. Panel (c) shows the membrane potential time profile for the bursting cycle  $\Gamma$ . This highlights the typical features of parabolic bursting. Namely, first the fact that this bursting scenario can be seen as recurrent groups of spikes (bursts) on top of a slow oscillation that is possible due to the presence of two slow variables, here  $x$  and  $Ca$ ; second, the fact that the interspike interval during each burst is small at the beginning and at the end of the burst, hence giving a parabolic-shaped curve if plotted against time. The number of spikes per burst depends very nonlinearly on key parameters of the model (e.g. the sodium maximal conductance) and, from slow spikeless cycles in some parameter regime, the solutions can gain more and more spike as a parameter is varied. These spike-adding transitions were recently analysed in the framework of geometric singular perturbation theory in [13] and it was shown that they are organised by canards of folded-saddle type; see also [14].

There are many other examples of parabolic bursting in biophysical models; see e.g. [3, 10, 29, 44]. We like to mention recent contributions to the electrical activity of GnRH neurones. In [34], Moenter et al. model the fact that GnRH secreting neurons may exhibit parabolic bursting patterns of activity, where the burst is superimposed onto a slow wave representing a rhythm linked to secretory activity; for other type of secretory activity in GnRH neuron models, see [9]. Minimal phase models of parabolic bursters were first introduced by Ermentrout and Kopell with the so-called *theta model* [18], sometimes also referred to as *Atoll model* [28]; see also [46]. Spike-adding via canards in the Atoll model was related to jump-on points in [13]. More generally, canards in slow-fast planar systems defined on the two-torus were studied by Guckenheimer and Ilyashenko in [24] and then by Schurov and collaborators in [41–43] however without any link made to parabolic bursting or spike-adding.

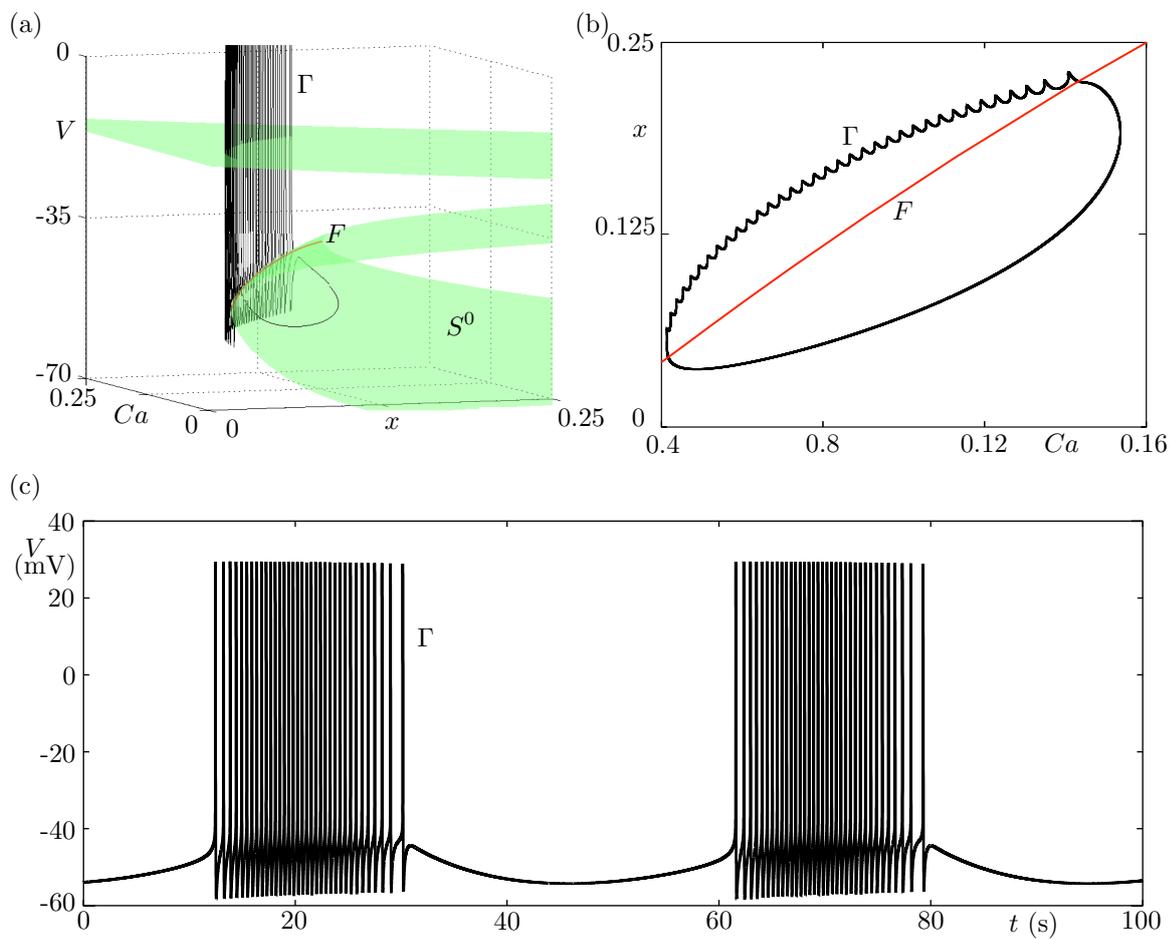


FIGURE 1. Parabolic bursting in Plant model for the R15 neuron of the Aplysia.

## 2. A MINIMAL MODEL

We now consider a minimal SNIC oscillator, namely

$$\begin{aligned} \dot{r} &= r(1 - r^2), \\ \dot{\theta} &= a - \sin \theta, \end{aligned} \tag{1}$$

or written in cartesian coordinates

$$\begin{aligned} \dot{x} &= x(1 - x^2 - y^2) - y \left( a - \frac{y}{\sqrt{x^2 + y^2}} \right), \\ \dot{y} &= y(1 - x^2 - y^2) + x \left( a - \frac{y}{\sqrt{x^2 + y^2}} \right). \end{aligned} \tag{2}$$

We then force this minimal SNIC oscillator periodically in  $a$  through the following slow harmonic oscillator

$$\begin{aligned} a' &= \varepsilon(\mu - \mu_c), \\ \mu' &= \varepsilon(a_c - a), \end{aligned} \tag{3}$$

where  $\mu_c$  and  $a_c$  are two real parameters that determine the centre of all periodic orbits solutions to system (3).

Gathering systems (1) and (3) and reparametrising time gives the following two slow / two fast system expressed in the slow time

$$\begin{aligned} \varepsilon \dot{r} &= r(1 - r^2), \\ \varepsilon \dot{\theta} &= a - \sin \theta, \\ \dot{a} &= \mu - \mu_c, \\ \dot{\mu} &= a_c - a. \end{aligned} \tag{4}$$

System (4) is a parabolic burster. Its cartesian critical manifold is the cylinder of equation

$$S^0 := \{(x, y, a, \mu) \in \mathbb{R}^4 \mid x^2 + y^2 = 1, a = y\}. \tag{5}$$

In polar coordinates, the critical manifold  $S^0$  takes the form

$$S^0 = \{r = 1, a = \sin \theta\}. \tag{6}$$

The two fold lines are given by the condition  $\cos \theta = 0$ , that is,  $\theta = \frac{\pi}{2} \bmod \pi$ .

### 2.1. Slow flow and desingularisation

Taking the  $\varepsilon = 0$  limit of system (4) yields the so-called slow subsystem, also referred to as the *reduced system* ( $RS$ ), which captures an approximation of the slow dynamics of the original system, constrained to evolve on the critical manifold  $S^0$ . In the present case, we get

$$\begin{aligned} 0 &= r(1 - r^2), \\ 0 &= a - \sin \theta, \\ \dot{a} &= \mu - \mu_c, \\ \dot{\mu} &= a_c - a. \end{aligned} \tag{7}$$

System (7) is a differential-algebraic equation (DAE). One can gain information about the dynamics of the fast variables  $r$  and  $\theta$  in this singular limit, by differentiating the two algebraic equations of system (7) with respect to time. For the first one, this brings

$$-2r\dot{r} = 0, \tag{8}$$

given the constraint of being on the critical manifold  $S^0$ . Equation (8) implies  $\dot{r} = 0$ , which is consistent with the fact that  $S^0$  is given by  $\{r = 1\}$ . The second algebraic equation of (7), once differentiated with respect to time, gives

$$\dot{a} - \cos \theta \dot{\theta} = 0, \tag{9}$$

to which we add the two slow equations unaffected by the  $\varepsilon = 0$  limit in (7). As is customary since the critical manifold is two-dimensional, we project the resulting limiting system onto a phase plane which we choose to be the  $(\theta, \mu)$ -plane. We obtain the following reduced system

$$\begin{aligned} \cos \theta \dot{\theta} &= \mu - \mu_c, \\ \dot{\mu} &= a_c - \sin \theta, \end{aligned} \tag{10}$$

since we have  $a = \sin \theta$  on  $S^0$ . System (10) is singular along the fold lines of  $S^0$ , that is, at points where  $\cos \theta = 0$ . A classical tool to overcome this problem is to “extend” the reduced system to the fold lines by rescaling time by a factor  $\cos \theta$ . We obtain the so-called *desingularised reduced system (DRS)*

$$\begin{aligned}\theta' &= \mu - \mu_c, \\ \mu' &= \cos \theta (a_c - \sin \theta).\end{aligned}\tag{11}$$

Equilibria of DRS systems located on the fold lines (which appear precisely through the time rescaling that transform the RS into the DRS) are the so-called *pseudo-equilibria* or *folded singularities* of the original system. Therefore one can conclude that system (4) has folded singularities at

$$(\theta, \mu) = (\pi/2 \bmod \pi, \mu_c).\tag{12}$$

The Jacobian matrix at  $(\pm \frac{\pi}{2}, \mu_c)$  is given by

$$\mathbf{J}^\pm = \begin{pmatrix} 0 & 1 \\ 1 \mp a_c & 0 \end{pmatrix}\tag{13}$$

whose determinant is

$$\det(\mathbf{J}^\pm) = -1 \pm a_c.$$

Hence, for  $|a_c| < 1$ , both folded singularities are of saddle type. The eigenvalues are :

$$\lambda_\pm^\pm = \pm \sqrt{1 \mp a_c},$$

and the eigendirections are defined by the linear relation

$$\mu = \lambda \theta.$$

There is a degenerate case at  $a_c = 0$ , where the spike-adding solutions visit both folded saddles in phase space; they only visit one of them (depending on the sign of  $a_c$ ) as soon as  $a_c \neq 0$ . This is best understood by analysing the integrable structure of the DRS; see below and also Figures 2 and 3.

As showcased in [13], the presence of a folded saddle on the critical manifold of a parabolic burster organises the transition from the subthreshold (oscillatory) regime to the spiking and then the bursting regime, with the canard associated with the folded saddle organising spike-adding transitions. This type of dynamics also arises in three-time-scale systems as recently shown in [14]. An important object in this spike-adding scenario, unveiled in [13] and justified through qualitative arguments and numerical bifurcation analysis, is a so-called *folded homoclinic bifurcation*; see also [14]. This object refers to a homoclinic bifurcation in the DRS which then, due to the time rescaling, corresponds in the RS to a limiting curve starting at the folded saddle and returning back to it with a finite passage time, hence connecting the faux canard and the (true) canard of the folded saddle. This object terminates the family of small limit cycles in the DRS. The particularity of the current DRS is that it is integrable, therefore one can find explicitly the folded homoclinic connection, as explained below.

## 2.2. Folded homoclinic connection

The DRS (11) is integrable with hamiltonian given by

$$H(\theta, \mu) = -0.5\mu^2 + \mu_c\mu + a_c \sin \theta + 0.25 \cos 2\theta.\tag{14}$$

Therefore, solutions of system (11) correspond to level sets of the function  $H$ , that is, the sets  $\{H = h\}$  for constants  $h$ . Solving the corresponding algebraic equation with respect to  $\mu$  gives the following characterisation

$$\mu = \mu_c \pm \sqrt{\mu_c^2 - \tilde{h}},\tag{15}$$

where  $\tilde{h} = 2(h - a_c \sin \theta - 0.25 \cos 2\theta)$ . Then, the homoclinic connection is the level set of  $H$  that goes through each of the folded saddle  $(\pm \frac{\pi}{2}, \mu_c)$ , which yields  $\tilde{h}_{\text{hom}}^{\pm} = \mu_c^2$ , that is,

$$h_{\text{hom}}^{\pm} = 0.5\mu_c^2 \pm a_c - 0.25. \quad (16)$$

Hence we obtain the equation for the folded homoclinic connections, namely

$$\{(\theta, \mu); -0.5\mu^2 + \mu_c(\mu - 0.5\mu_c) + a_c(\sin \theta \mp 1) + 0.25(\cos 2\theta + 1) = 0\}. \quad (17)$$

When  $a_c = 0$ , there is no homoclinic connection in the DRS (11) but two double heteroclinic connections between the two folded saddles; indeed, equation (17) is clearly satisfied at  $(\pm \frac{\pi}{2}, \mu_c)$  when  $a_c = 0$ . For  $a_c \neq 0$ , each folded saddle has a double homoclinic connection but only one of them interacts with canard solutions; see Figure 2.

### 2.3. Canard-induced spike-adding transitions

The spike-adding process in our minimal system (4) is mediated by canard solutions near each folded-saddle singularity  $\text{fs}^{\pm}$  or both, depending on whether  $a_c$  is zero or nonzero. When  $a_c = 0$ , then solutions are symmetric with respect to  $a$  and spikes are added two by two through transitions during which solutions come close to each folded saddles. Figure 2 presents this adding process for  $a_c = 0$ . All left panels display solutions of system (4) for different initial conditions, together with the folded homoclinic connection and the folded saddles  $\text{fs}^{\pm}$ . Additionally, right panels display the critical manifold  $S^0$  and the fold lines  $F^{\pm}$ . All solutions contain canard segments: (a1)-(b1) spikeless headless canards; (a2)-(b2) two canards with head spikes; (a3)-(b3) two spikes and two headless canards, (a4)-(b4) two spikes and two canards with head spikes.

When  $a_c \neq 0$ , this symmetry is broken and, depending on the sign of  $a_c$ , more and more spikes are added to the solutions near one of the two folded saddles:  $\text{fs}^+$  (resp.  $\text{fs}^-$ ) for  $a_c < 0$  (resp.  $a_c > 0$ ). Figure 3 shows adding transitions near  $\text{fs}^-$  for  $a_c = 0.9$ . Left and central panels show the  $(x, \mu)$ -plane, the latter ones corresponding to zoomed views of the former ones, while the right panels show the  $(x, a, \mu)$ -space, with the same dynamical objects as in Figure 2. The mechanism of spike-adding is similar to the symmetric case  $a_c = 0$  even though it only occurs close to one of the two folded saddles.

### 2.4. Comparison with the classical example of biophysical parabolic burster: Plant model

Our minimal system shares a number of similarities with Plant model, which is the main example of biophysical neuron model (i.e. based upon the Hodgkin-Huxley formalism) displaying parabolic bursting. Indeed, in [13] it was shown that Plant model, seen as a slow-fast dynamical system (even though there is no explicit small parameter) possesses a folded-saddle singularity and that spikes are added via transitions involving the canard (true and false) solutions associated with this folded saddle. System (4) possesses two folded saddles and the first added spikes, which corresponds to the transition from slow (spikeless) periodic solutions to solution with one or two (depending on the value of  $a_c$ ) passes close to the folded saddles  $\text{fs}^{\pm}$  and follow their associated true canards. However, whether or not  $a_c = 0$ , from the second spike-adding transition onward, spikes are added in the system via solutions that one can term *jump-on canards* [11] and they do not pass very close to folded saddles anymore. Indeed, as apparent on Figure 2 (a3)-(b3) and (a4)-(b4), after the initial adding transitions, further spike are added from the other side (here, above) of the folded saddle and, hence, do not follow its true canard on the repelling side. Instead, trajectories involve in these spike-adding cross the fold line  $F^{\pm}$  after having complete a fast segment and connect to a repelling slow manifold. This sequence attracting fast segment / repelling slow segment is what defines a jump-on canard. In Figure 2 (a3)-(b3) and (a4)-(b4), the second (and subsequent) pair of spikes is added in this way. Furthermore, in the non-symmetric case corresponding to  $a_c \neq 0$ , a similar event occurs. In Figure 3 (a3)-(c3) and (a4)-(c4), one clearly observes the second spike being added on the side of the folded saddle  $\text{fs}^-$  but not so close to it, as the result of a jump-on canard explosion. Therefore, our minimal model display a spike-adding scenario that can be seen as a mix between the

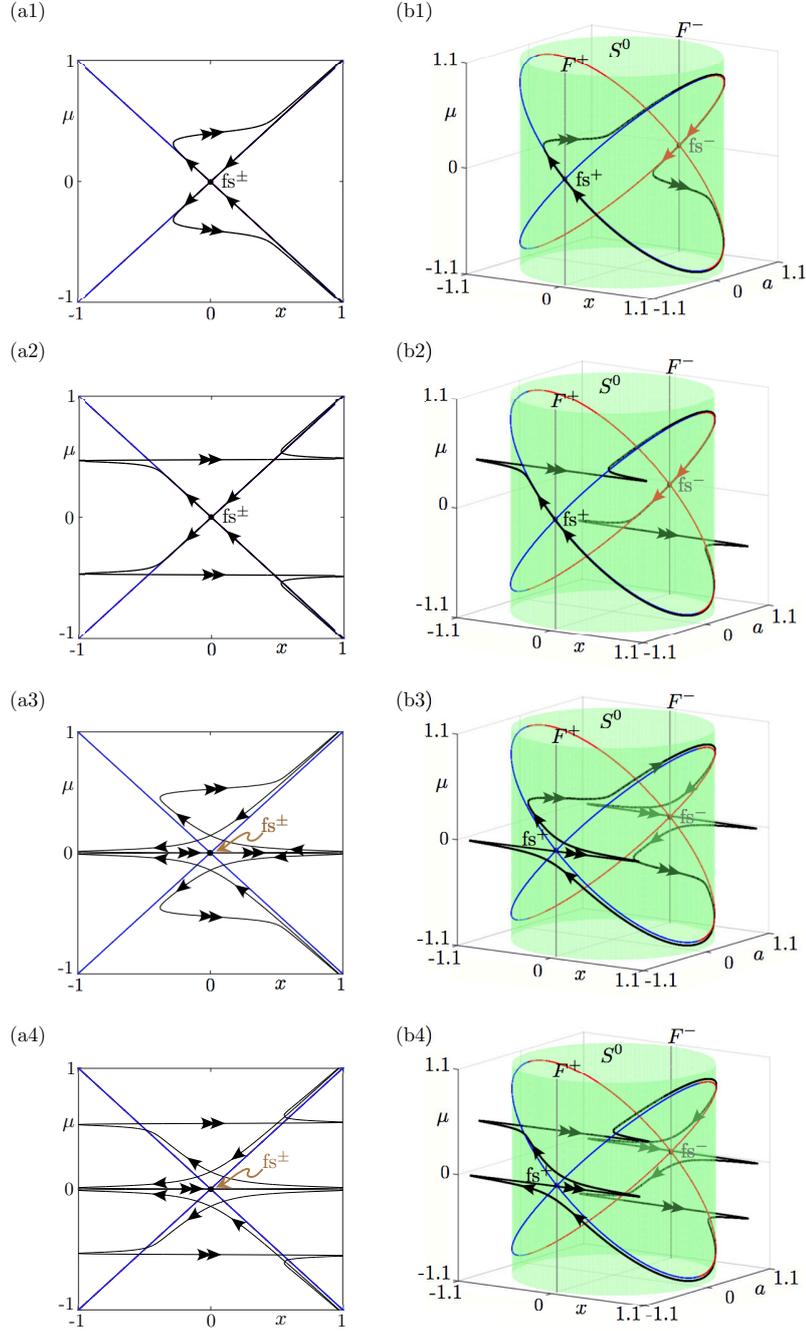


FIGURE 2. Spike-adding in system (4) for  $a_c = \mu_c = 0$ . Panels (ai) display a planar projection of the solutions; panels (bi) show phase-space representations of the solutions together with the critical manifold  $S^0$  and its fold lines  $F^\pm$ . In all panels, blue and red curves are two folded heteroclinic connections obtained as specific level sets of the Hamiltonian (14).

folded-saddle-canard adding scenario from Plant model, and the jump-on-canard scenario from the theta model from Ermentrout and Kopell; see [13] for details.

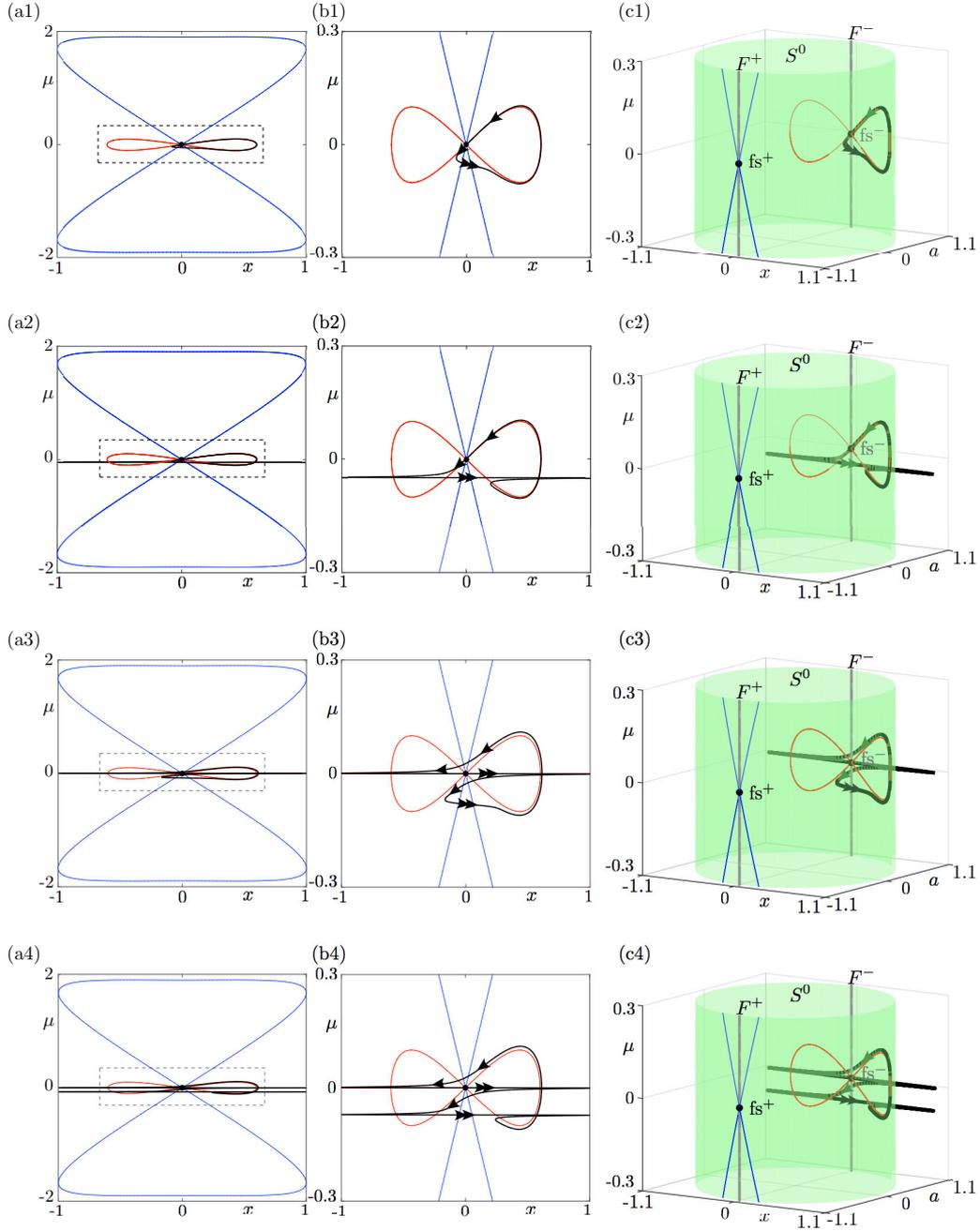


FIGURE 3. Spike-adding in system (4) for  $\mu_c = 0$  and  $a_c = 0.9$ . Panels (bi) display zooms of panels (ai); panels (ci) show phase-space representations of the solutions together with the critical manifold  $S^0$  and its fold lines  $F^\pm$ . In all panels, blue and red curves are folded homoclinic connections obtained as specific level sets of the Hamiltonian (14).

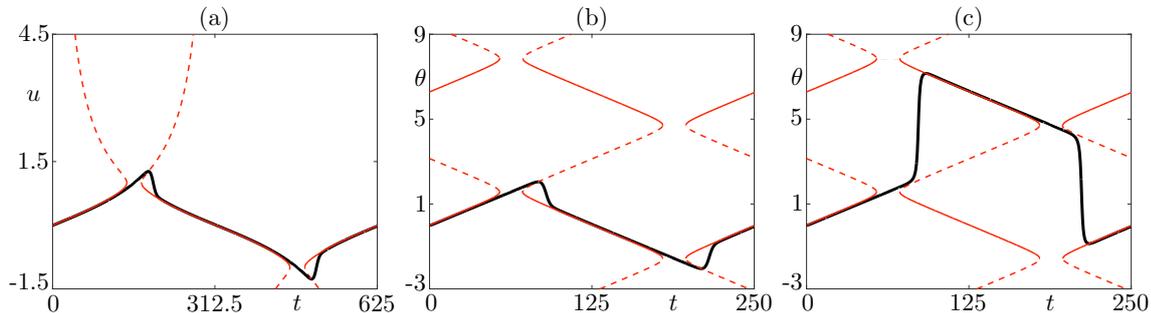


FIGURE 4. Time series of canard cycles of our minimal parabolic burster together with branches of the critical manifold evaluated along each cycle. (a) headless canard for the model in  $u$ ; (b) headless canard for the model in  $\theta$ ; (c) canard with head for the model in  $\theta$ .

### 3. LINK WITH THE DIPS AND SLICES BY J. E. LITTLEWOOD

Our minimal system's equation can be written as a one-dimensional ODE with a periodic forcing, namely

$$\theta' = a(\varepsilon t) - \sin \theta, \quad (18)$$

where  $a$  is a circular function. Posing  $u = \tan \frac{\theta}{2}$ , one can rewrite (after some rearranging) equation (18) as

$$u' = \frac{1}{2} (1 + u^2) a(\varepsilon t) - u. \quad (19)$$

While equation (19) is more amenable to analysis than equation (18), it is the opposite when it comes to numerical treatment; see our explanations below. These equivalent equations both take the form of a nonlinear ODE with a slow periodic forcing, a topic on which a large body of knowledge has been accumulated over the past few decades, that is, since a series of seminal papers by Cartwright and Littlewood on the forced van der Pol equation published over more than a decade from the mid-1940s until the late 1950s. Part III and IV of this series were published by Littlewood alone and in there he introduced the notions of *dips* and *slices* [32, 33]. These notions aimed to describe solutions of the forced van der Pol that follow an attracting motion up to a fold of the (now referred to as) critical manifold up to one of its fold lines and then go past the fold line for a short segment after which either the solution goes back to the attracting region where it came from (this is the “dip”) or it is pushed away towards the other attracting region, near the other fold line (this is the “slice”). Later on, Grasman further analysed these solutions [20, 21] and related dips and slices to canards in a recent entry on relaxation oscillations [22]. Canards in the singular limit  $\varepsilon = 0$  of the forced van der Pol system, in link with folded-saddle singularities, were studied by Szmolyan and Wechselberger in [45], and by Guckenheimer and collaborators in a series of paper [7, 23].

The idea of Littlewood is closely related to our minimal model is its form (19) and it can be summarised as follows. Considering (minimally) a one-dimensional ODE of the form

$$x' = f(x, a(\varepsilon t)), \quad (20)$$

where  $a$  is a periodic function and  $\varepsilon > 0$  a small parameter. Then system (20) can be seen as a slow-fast system where  $x$  is fast and  $a$  is slow. Its critical manifold is (in the formulation of (20)) is time-dependent and periodic, it is given by the implicit equation  $f(x(t), a(\varepsilon t)) = 0$ . Similar to the case where one looks at these objects in phase space, one can identify parts of the time-dependent critical manifold that are attracting or repelling, simply by solving the additional implicit equation  $f_x(x(t), a(\varepsilon t)) = 0$ . Of course, one can rewrite the non-autonomous one-dimensional system with slow time-periodic forcing (20) as an autonomous two-dimensional

slow-fast system of the form

$$\begin{aligned}x' &= f(x, a(s)), \\s' &= \varepsilon,\end{aligned}\tag{21}$$

where the slow time-periodic forcing has been made into a contribution coming from a second state variable  $s$  whose evolution equation is simply a slow drift. Then, in a very similar fashion as in Rinzel's slow-fast dissection for bursting already mentioned in the introduction, one can plot in the same  $(t, x)$ -plane a given solution of (20) superimposed on top of the time-dependent critical manifold that is evaluated along the solution under consideration. Indeed, the classical slow-fast dissection would mean to compute the bifurcation diagram of the fast subsystem associated with system (21), which corresponds to the same equation as (20) but with a bifurcation parameter  $s$  as opposed to the slow time-dependent term  $\varepsilon t$ . Then, computing the bifurcation diagram of this fast subsystem in  $s$  and then plotting it superimposed on top of a periodic solution of the full system (21) would exactly amount to performing a slow-fast dissection. Instead, plotting the time-dependent critical manifold of system (20) in time on top of that periodic solution is effectively plotting a rescaled version of the bifurcation diagram of the fast subsystem of (21), with rescaling factor being  $1/\varepsilon$ . Thus, the two approaches are very similar and provide similar type of information. The latter one is simply adapted to system of the form of (20), which are sometimes referred to as *adiabatic systems* [5]; on this topic, we refer the reader to the work of Berglund [4, 6] in which time-dependent critical manifold are superimposed in the time domain onto periodic solutions of such systems, yet without references to Littlewood's dips and slices and no direct link made with canards.

On Figure 4, we show the result of this procedure for the  $u$ -version (19) of our minimal model with a headless canard solution in panel (a), and for the theta model (18) with a headless canard in panel (b) and with a canard with head in panel (c). As it clearly appears on this figure, canard solutions follow attracting and repelling branches of the time-dependent critical manifold. Hence, in the time domain, when headless canard solutions leave the vicinity of a repelling branch of the (time-periodic) critical manifold, they jump back to an attracting branch with similar values of the fast variable and this corresponds to what Littlewood calls a *dip*. Likewise, when canards with head leave the vicinity of a repelling branch of the critical manifold, they jump to an attracting branch with different values of the fast variable and this corresponds to what Littlewood calls a *slice*. Note that, in the  $u$ -variable, the time-dependent critical manifold has only one stable segment, which means that only dips (headless canards) are possible; see Fig. 4 (a). This is in contrast with what happens in the  $\theta$ -variable, where the time-dependent critical manifold has multiple stable segments, hence allowing for both dips (headless canards) and slices (canards with head); see Fig. 4 (b)-(c). Without directly referring to the work of Littlewood, Marc Diener has studied similar representation of canards in one-dimensional dynamical systems with slow periodic forcing [15, 16]. Finally, the idea was also present in the doctoral work of Jean-Louis Callot [8].

We remark that this approach to characterise different canard solutions in the time domain also works in planar slow-fast systems with a constant forcing. However, it requires to be able to solve the equation corresponding to the critical manifold for the fast variable. The prototypical autonomous canard system in the plane is the van der Pol oscillator, in which canards were first identified and analysed as such [1]. Since the critical manifold is the graph of a cubic polynomial in the fast variable  $x$ , one can solve it in  $x$  by radicals. Hence, one can play the same game and evaluate the critical manifold in time along a given canard solution. In Figure 5, we show the result of this procedure for a headless canard (a), the maximal canard (b) and a canard with head (c). The same phenomenon as in the forced van der Pol occurs, and it confirms that, in the most classical and historical sense, headless canards correspond to dips while canards with head correspond to slices. At the transition between dips and slices, the boundary between these two sub-families of canards, namely the maximal canard, corresponds to the longest dip possible.

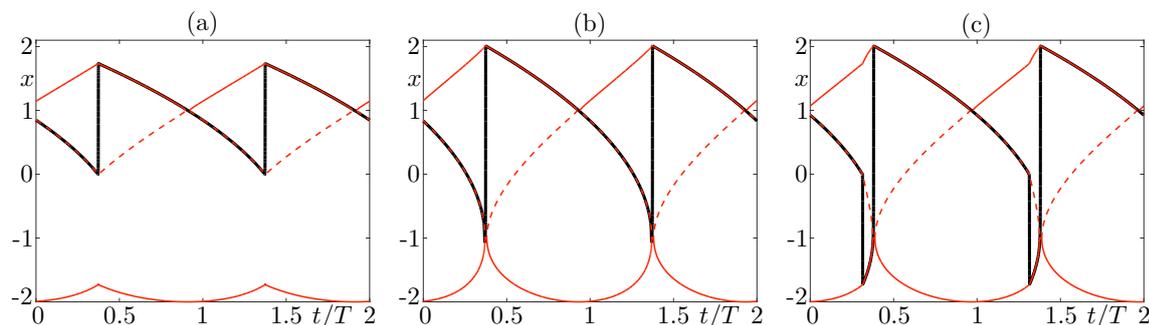


FIGURE 5. Time series of canard cycles of the van der Pol oscillator together with the three branches of the critical manifold ( $x$  as functions of  $y$ ) evaluated along each cycle. (a) headless canard; (b) maximal canard; (c) canard with head.

#### 4. CONCLUSION

This article introduces a minimal model of parabolic bursting with integrable slow flow, obtained by forcing harmonically a minimal model of a SNIC oscillator. We analyse this new parabolic burster, in particular its slow flow and spike-adding structure. We further discuss the links with a classical work of J. E. Littlewood. We believe that this approach can help further understanding the parabolic bursting's main properties in biophysical models, through minimal models. An important question in neuroscience is that of encoding of information (coming from external stimuli) via neuronal activity. There are several paradigms underpinning this question and associated hypothesis regarding how the neural coding is implemented by the Brain. Rate coding considers that the rate of neural activity (ie the firing rate) is the main quantity that encodes information; this is the basic of neural networks. Other approaches consider that spikes and their timing are equally (if not more) important, and this has led to the emergence of spiking neural networks. However, spikes are very rapid events and there is a third approach which considers that groups of spikes or bursts have a stronger chance to possess an encoding power. In the context of burst coding [27, 31], it is therefore important to be able to control the size of bursts in given neuron models. Hence, spike-adding transitions become potential key regulator of neural activity and of neural coding. We believe that minimal models as the one proposed here are important as they offer further amenities to analysis and control while being computationally tractable which, once embedded in a network architecture, could bring new insight into this coding through bursts. This is clearly beyond the scope of the present paper and will be a very interesting topic of future work.

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