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NETWORK TORUS CANARDS AND THEIR MEAN-FIELD LIMITS*

EMRE BASPINAR[†], DANIELE AVITABILE[‡], AND MATHIEU DESROCHES[§]

Abstract. We show that during the transition from and to elliptic burstings both classical and *mixed-type* torus canards appear in a Wilson-Cowan type neuronal network model, as well as in its corresponding mean-field framework. We show numerically the overlap between the network and mean-field dynamics. We comment on that mixed-type torus canards result from the nonsymmetric fast subsystem. This nonsymmetry provides the dynamics linked to an associated canonical form presented in [7], and it occurs mainly due to the three-timescale nature of the Wilson-Cowan type models.

1. Introduction. Many biological systems express complex oscillatory dynamics such as periodic, quasi-periodic, chaotic spiking and bursting oscillations [44], as well as mixed-mode oscillations [19]. Our interest in this work is on elliptic bursting oscillations and slow-fast structures, in particular on *torus canards* [38] appearing at the transition from elliptic bursting regimes to other stable regimes such as tonic firing. We observe such bursting patterns in many experimental recordings, for example in the behavior of dorsal root ganglion neurons [34], in reticular thalamic neurons [43] or in the sepia’s giant axon [5].

The simplest observable biological rhythm is *tonic firing*: cells operating in this regime respond to an input by firing periodic action potentials, as seen in the top row of Figure 1. Another fundamental neuronal regime is *bursting*, which refers to an alternation between phases of low activity (called *silent* or *quiescent*) and phases of high activity (called *active* or *burst*) consisting of a succession of fast oscillations or action potentials; see the bottom row of Figure 1.

Mapping the transition between bursting and tonic spiking regimes, which may carry different information content [39, 48, 53], is a key question in neuroscience, which has partially been addressed in single-cell recordings [2, 41, 58]. In models of single cells the transition may be sharp, and organised by special solutions termed *torus canards*, which we now review briefly.

The theoretical setup for studying complex temporal waveforms of bursting type is based on *slow-fast* dynamical systems of the following type:

$$(1.1) \quad \begin{aligned} u' &= f(u, z, p, \varepsilon), \\ z' &= \varepsilon g(u, z, p, \varepsilon), \end{aligned}$$

where prime denotes a differentiation with respect to time, and where $u \in \mathbb{R}^n$, $v \in \mathbb{R}^m$ are the fast and slow variables, respectively. The time-scale separation is marked by the presence of the small parameter $0 < \varepsilon \ll 1$, and allows to study the system in terms of slow and fast subsystems, approximating the silent and active phases of a neuronal regime, respectively. Finally, the vector p represents other control parameters.

Within this setup, bursting types have been classified by several authors. A first classification of bursting behaviour was proposed by Rinzel [44] and later extended

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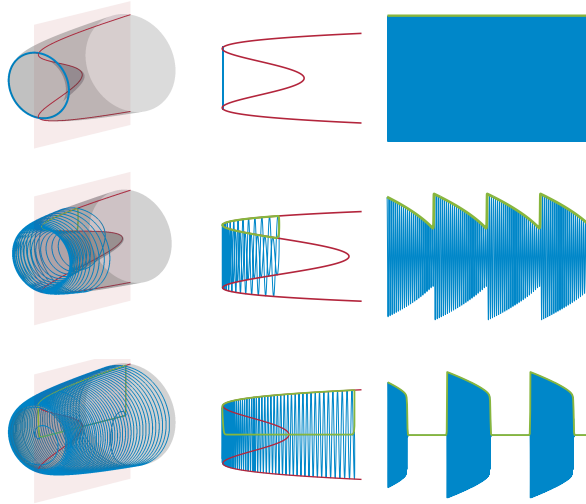


FIG. 1. Transition from tonic spiking (top row) to elliptic bursting (bottom row) via torus canards (central row). In each row: (left) 3D phase space view; (middle) 2D projection onto; (right) time profile of a fast variable.

by Izhikevich [31]. The classification is based on bifurcations of the *fast subsystem*, that is the $\varepsilon = 0$ limit of (1.1): different bursting types are defined depending on the bifurcation causing the onset of the burst, and on the bifurcation causing the termination of the burst. Generically, bursting occurs when $n \geq 2$ and $m \geq 1$.

According to Izhikevich’s classification, the fast subsystem bifurcations involved in elliptic bursting are as follows: a subcritical Hopf bifurcation, which triggers the onset of burst, and a saddle-node of limit cycles (SLC), which terminates the burst. This scenario is sketched in the bottom row of Figure 1. Owing to the presence of the SLC in the fast subsystem, elliptic bursting supports torus canards. One geometrical property of these torus canard solutions is that their fast oscillations do not stop near the SLC of the fast subsystem, but instead continue along the associated branch of unstable limit cycles. This feature justifies the term “canard” [9, 23] because the fast oscillations follow a repelling object of the fast subsystem; see the middle row in Figure 1. Small variations in parameter space lead from near bursting solutions of this type to amplitude-modulated tonic spiking solutions which: (i) follow the branch of unstable limit cycles of the fast subsystem ($\varepsilon = 0$), and (ii) wind around an invariant torus of the full system ($\varepsilon \neq 0$). The torus originates at a Neimark-Sacker bifurcation of the full system, located in the phase space at a small distance from the SLC bifurcation.

These two salient features justify the name “torus canard”, which were first predicted without a dedicated analysis in a normal form of an elliptic burster by Izhikevich [33]. They were later investigated as a canard phenomenon in computational studies of biophysical models [10, 38], as well as analysed theoretically in idealised models [8, 46, 57, 61]. A recent work sheds new light onto the role of the underlying torus bifurcation [35].

The role and structure of torus canards has become clearer in recent years, albeit several outstanding theoretical questions remain. This is in stark contrast with their

existence at network level, which is by and large unexplored. A nontrivial question is the effect of noise on these canard structures, which are evanescent already at a single-cell level, and which could be destroyed by stochastic fluctuations. The effect of noise on canard-type dynamics has been analysed mostly at single-cell level, and in cases where the canard occurs on the slow part of the dynamics (for instance Van der Pol and FitzHugh-Nagumo models). Torus canard segments, however, occur during the fast phase of the dynamics, which make them more sensitive to perturbation, and they have not been studied in noisy single-cell models, let alone in neuronal network and mean-field models.

In the present article we introduce torus canards in a network of stochastic slow-fast oscillators. A new family of torus canards, *mixed-type torus canards* were found and described in [7] via a canonical framework of elliptic bursting mean-field neuronal models. We provide here both classical and mixed-type torus canards at network level for the first time in the literature. We show the overlap between the network and mean-field torus canards by using bifurcation diagrams, phase space and the patterns in the time domain.

We will first see the microscopic model description based on the single-cell equations. Then we will explain the macroscopic model description, which is the mean-field layout obtained from the single-cell equations at population level. Finally, we will see our results showing the new types of torus canards as well as the comparison between network and mean-field patterns.

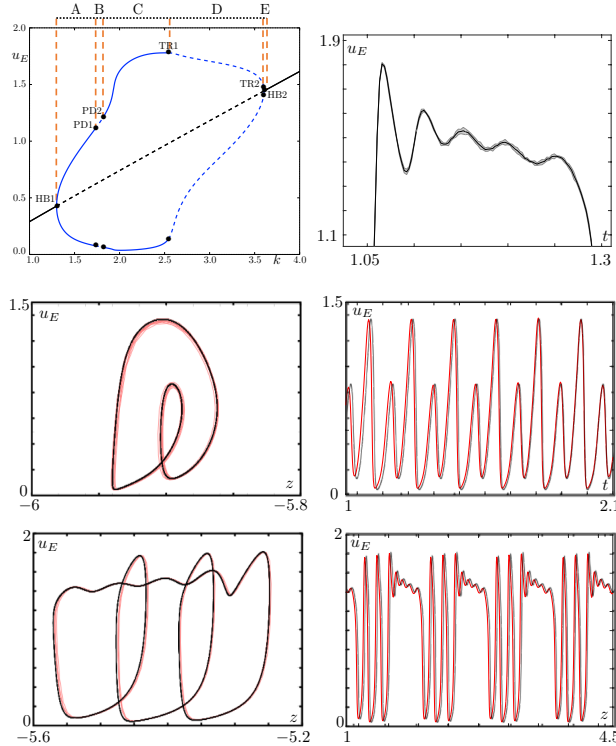


FIG. 2. Top left: Fast subsystem bifurcation diagram of (3.1). Here HB, PD and TR refer to Hopf bifurcation, periodic doubling and torus bifurcation, respectively. Top right: Mean field pattern from region D, and the corresponding variance tube of the network oscillators. Middle and bottom: Representative patterns of regions B, $k = 1.7$ and D, $k = 2.9$.

2. Microscopic framework and network equations. We consider a network of n_e excitatory and n_i inhibitory coupled Wilson-Cowan cells with instantaneous firing rates u_e^i , $i = 1, \dots, n_e$, u_i^j , $j = 1, \dots, n_i$. Henceforth, we will adopt the compact notation $\mathbb{N}_\alpha = \{1, \dots, n_\alpha\}$, $\alpha \in \{e, i\}$, and collect rates into the vectors u_α , $\alpha \in \{e, i\}$ with components

$$(u_\alpha)_i = u_\alpha^i, \quad i \in \mathbb{N}_\alpha, \quad \alpha \in \{e, i\}.$$

The microscopic model, adapted from a previous study [56], is specified by the following set of $2(n_e + n_i) + 1$ stochastic differential equations (SDEs)

$$(2.1) \quad \begin{aligned} \tau_e du_e &= [-u_e + f_e(J_{ee}\langle u_e \rangle + J_{ei}\langle u_i \rangle + z_e + \xi_e)] dt, \\ \tau_i du_i &= [-u_i + f_i(J_{ie}\langle u_e \rangle + J_{ii}\langle u_i \rangle + z_i + \xi_i)] dt, \\ \tau_r dz_e &= [k - \langle u_e \rangle - \langle u_i \rangle] dt, \\ d\xi_e &= -\theta_e \xi_e dt + \sigma_e dW_e, \\ d\xi_i &= -\theta_i \xi_i dt + \sigma_i dW_i, \end{aligned}$$

where $u_\alpha(0), \xi_\alpha(0)$ i.i.d. $N(0, \frac{\sigma_\alpha^2}{2\theta_\alpha})$ for each cell and α . Here $z_e, z_i \in \mathbb{R}$ are scalar adaptation currents [16, 31], common to all neurons within the excitatory and inhibitory populations, respectively. The inhibitory adaptation current z_i is constant, for simplicity, while z_e , is time dependent and its evolution is coupled to the excitatory and inhibitory mean firing rates, defined by the multivariate real-valued function

$$(2.2) \quad \langle \cdot \rangle: \mathbb{R}^n \rightarrow \mathbb{R}, \quad \langle u_\alpha \rangle = \frac{1}{n_\alpha} \sum_{i \in \mathbb{N}_\alpha} u_i.$$

Neurons are coupled through the coefficients $J_{\alpha\beta}$, $\alpha, \beta \in \{e, i\}$. In addition to the adaption current, each neuron receives an impinging stochastic current, which is modeled via an Ornstein-Uhlenbeck process with prescribed covariance σ_α and drift coefficient θ_α . The stochastic currents and corresponding independent Brownian motions are also collected in vectors with components $(\xi_\alpha)_i, (W_\alpha)_i$, with $(i, \alpha) \in \mathbb{N}_\alpha \times \{e, i\}$, respectively. The microscopic model is completed with a choice of current-to-rate transforms, which are expressed in terms of the sigmoidal function $S: \mathbb{R} \rightarrow \mathbb{R}$,

$$(2.3) \quad S(x, \rho, \nu, \theta, \sigma) = \frac{\rho}{2} \left[1 + \operatorname{erf} \left(\frac{2\theta\nu x}{\sqrt{2(4\theta^2 + \nu^2\sigma^4)}} \right) \right],$$

as the vector-valued functions $f_\alpha: \mathbb{R}^n \rightarrow \mathbb{R}^n$,

$$(2.4) \quad (f_\alpha(y))_i = S(y_i, \rho_\alpha, \nu_\alpha, \theta_\alpha, 0). \quad (i, \alpha) \in \mathbb{N}_\alpha \times \{e, i\}.$$

In (2.1), solution $\xi_\alpha(t)$ with $\alpha \in \{e, i\}$ is a Gaussian process with mean and variance

$$(2.5) \quad \begin{aligned} \mathbb{E}\xi_\alpha(t) &= e^{-t\theta_\alpha} \mathbb{E}\xi_\alpha(0), \\ \operatorname{var} \xi_\alpha(t) &= e^{-2t\theta_\alpha} \operatorname{var} \xi_\alpha(0) + \sigma_\alpha \frac{1 - e^{-2t\theta_\alpha}}{2\theta_\alpha}, \end{aligned}$$

respectively. Moreover, $\xi_\alpha(t+h)$, with h denoting a small time step, can be written as

$$(2.6) \quad \xi_\alpha(t+h) = e^{-h\theta_\alpha} \xi_\alpha(t) + \eta(t),$$

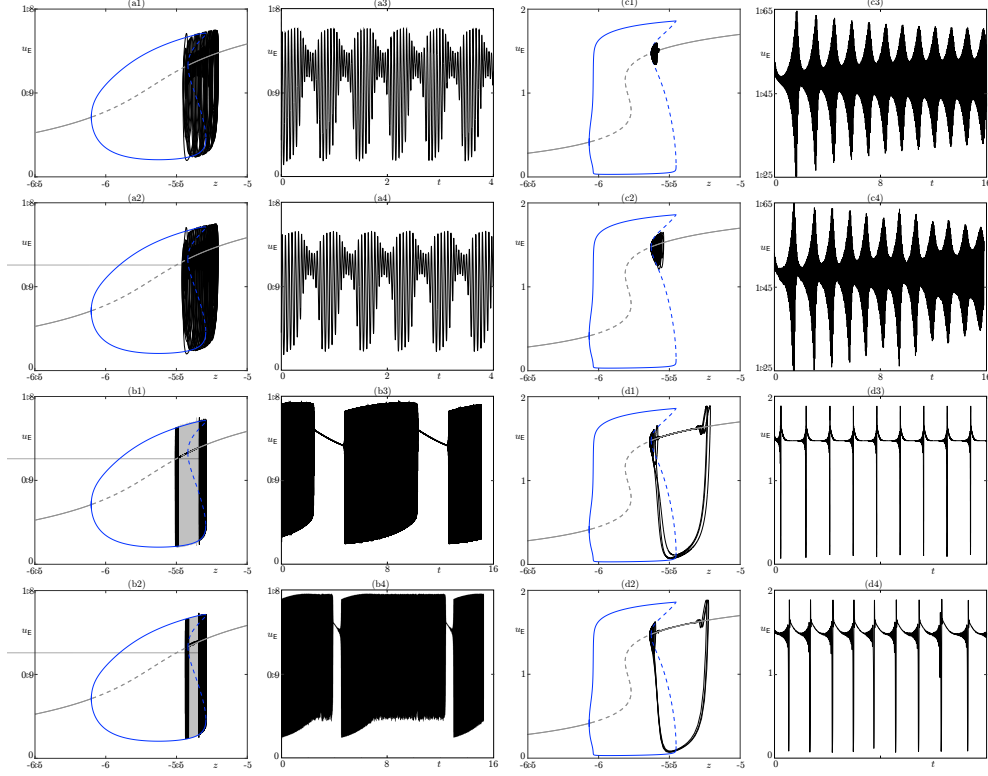


FIG. 3. *Torus canards in network and mean field settings, both in phase plane superimposed onto the fast subsystem bifurcation diagram and in time domain. Top and bottom rows in each panel correspond to mean field and network settings, respectively. a) headless, $k = 2.536083$, b) with head, $k = 2.60988$, c): headless mixed-type, $k = 3.60118$, and d): mixed-type with head, $k = 3.60110$.*

where $\eta(t) \text{i.i.d. } N(0, \frac{\sigma_\alpha^2}{2\theta_\alpha}(1 - e^{-2h\theta_\alpha}))$ for each time $t \in (0, \infty)$ [4]. Therefore, the choice of $\xi_\alpha(0)$ in (2.1) allows to write $\xi_\alpha(t) \text{i.i.d. } N(0, \frac{\sigma_\alpha^2}{2\theta_\alpha})$ and generate $\xi(t)$ directly from the distribution independently for each time $t \in [0, \infty)$.

Henceforth we will refer to (2.1)–(2.4), with suitable choices of the control parameters, as the *microscopic model*. We mention in passing that τ_α , $\alpha \in \{e, i, r\}$ set the characteristic timescales of the excitatory and inhibitory population, and the one of the inhibitory recovery variable, respectively.

3. Macroscopic description. The microscopic model comprises $n_p = n_e + n_i$ neurons, and admits an exact mean-field limit. In this limit one considers $n_\alpha \rightarrow \infty$, $\alpha \in \{e, i\}$, so that $n_p \rightarrow \infty$ and $n_\alpha/n_p \rightarrow \delta_\alpha \in (0, 1)$, where δ_α are the non-vanishing mean-field population ratios [56].

To make the statement more precise, we start by observing that the stochastic currents $(\xi_\alpha)_i$ are decoupled from other state variables. Henceforth we assume

$$(\xi_\alpha)_i(0) \text{i.i.d. } N(0, \frac{\sigma_\alpha^2}{2\theta_\alpha}), \quad (i, \alpha) \in \mathbb{N}_\alpha \times \{e, i\},$$

which implies

$$(\xi_\alpha)_i(t) \text{i.i.d. } N\left(0, \frac{\sigma_\alpha^2}{2\theta_\alpha}\right), \quad (i, \alpha) \in \mathbb{N}_\alpha \times \{e, i\},$$

for all $t \in [0, \infty)$.

The independence and identical distribution of the microscopic input currents is a direct consequence of the modelling assumptions, as they evolve according to decoupled Ornstein-Uhlenbeck processes. Notably, a similar property holds for the other state variables in the model, as $n_p \rightarrow \infty$: in this limit, if the initial conditions are independent, then the stochastic processes $(u_e)_i, (u_i)_i, i \in \mathbb{N}_\alpha$, and z_e are independent and converge in law towards stochastic processes $u_e^\infty, u_i^\infty, z_e^\infty$, respectively.

The stochastic processes $u_e^\infty, u_i^\infty, z_e^\infty$ satisfy a system of 3 *implicit* SDEs, which we omit here for brevity. These evolution equations are a stepping stone to derive a macroscopic description of the model: using the implicit SDEs, it can be shown [55,56] that the expectations

$$U_e = \mathbb{E}u_e^\infty, \quad U_i = \mathbb{E}u_i^\infty, \quad Z_e = \mathbb{E}z_e^\infty,$$

satisfy the following system of ODEs

$$(3.1) \quad \begin{aligned} \tau_e U_e' &= -U_e + F_e(J_{ee}U_e + J_{ei}U_i + Z_e), \\ \tau_i U_i' &= -U_i + F_i(J_{ie}U_e + J_{ii}U_i + z_i), \\ \tau_r Z_e' &= k - U_e - U_i, \end{aligned}$$

where

$$F_\alpha: \mathbb{R} \rightarrow \mathbb{R}, \quad F_\alpha(x) = S(x, \rho_\alpha, \nu_\alpha, \theta_\alpha, \sigma_\alpha), \quad \alpha \in \{e, i\}.$$

In other words, there exists a macroscopic description of the network model, which closes at the level of the expectations of the mean-field variables, that is, the system given in (3.1) is exact. The *macroscopic model* (3.1) is a set of 3 ODEs, and the noise levels of the underlying, microscopic input currents occur as parameters of the nonlinear functions F_α .

4. Results. Classical torus canards, both headless and with head, were shown previously [32, 35, 61]. Here we find for the first time classical torus canards in a stochastic network of elliptic bursters as well as in their mean-field limit; see Figure 3 a) and b). Moreover, we have recently identified a new torus scenario, namely *headless mixed-type torus canards* and *mixed-type torus canards with head*, as well as given their complete characterization using a generalized normal form [7] corresponding to a canonical elliptic bursting system supporting all types of torus canards. Here we provide all these types of torus canards, including mixed-type ones, at network level; see Figure 3 c) and d).

The bifurcation diagram of the fast subsystem associated with (3.1) is presented in Figure 2, with k as the control parameter. We divide the main branch of limit cycles into 5 regions, each region is highlighted by vertical bands and representative patterns associated with regions B and D are given in the middle and bottom panel, respectively. When increasing k from 1 onward, system (3.1) undergoes a first supercritical Hopf bifurcation (HB1). As k increases through region A, stable limit cycles that correspond to tonic population spikes in the time domain approach a first period-doubling bifurcation (PD1) through which they lose their stability. Increasing k past PD1, the system undergoes further PDs forming a cascade route to chaos with irregular population spikes in the time domain. Beyond this chaotic regime, the system

develops mixed-mode oscillations and then arrives at a stable tonic spiking regime via PD2. The system's behavior is symmetric with respect to k values between PD1 and PD2. We provide two representative patterns on the phase plane and in the time domain in Figure 2, where the mean field and network results are superimposed.

The stable tonic spiking regime loses its stability via the Neimark Sacker bifurcation TR1, around which classical torus canards are found [32, 35, 61]; see Figure 3 a) and b). Mixed-type torus canards disappear for larger k values and periodic elliptic bursting oscillations emerge. The elliptic bursting oscillations persist until a second torus bifurcation (TR2) as k increases. At the vicinity of TR2, the elliptic bursting oscillations become degenerate and mixed-type torus canards appear in region E; see Figure 3 c) and d). In Figure 3, we compare torus canards from both the network and its mean-field limit.

Occurrence of the mixed-type torus canards requires that (slow) Z_e nullcline intersects the critical manifold at a single point for each k value. This condition is fulfilled in *Leidenator* [7], which is the associated canonical form to (3.1), by a perturbative term in the slow variable equation. This requirement in (3.1) is satisfied by the nonsymmetry of the fast variables resulting from: 1) $\tau_e \neq \tau_i$ (albeit close to each other), 2) Z_e is dynamical whereas z_i is constant. Those two properties play the analogous role of the aforementioned perturbative term.

5. Conclusion. In this work, we found for the first time classical torus canards [32, 35, 61] at network level. Furthermore, we also found in the same network, given by (2.1), a new class of torus canards called mixed-type torus canards and analysed them at mean-field level in a companion article [7]. We compared both classical and mixed-type torus canards obtained from the mean-field setting (3.1) with those obtained from the network setting (2.1). Those results show numerically that the torus canard phenomena observed in the relevant canonical form *Leidenator* [7], in both classical sense and mixed-type sense, can be produced by real neural models at both network and mean-field levels.

This work has multiple potential follow-ups, it can for instance be extended in following two directions. First, the above results are somewhat influenced by the fact that the mean-field is not symmetric [7]. If one rescues the symmetry, how it can affect network behaviour is an interesting question for future work. Second, network torus canards might be present in other types of bursting networks. Which network models give rise to classical and mixed-type torus canards, and what role do these structures play at network level, in link e.g. with synchronisation properties of the network, is also an interesting open question.

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