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# Singular Hopf bifurcations and mixed-mode oscillations in a two-cell inhibitory neural network

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ABSTRACT

Recent studies of a firing rate model for neural competition as observed in binocular rivalry and central pattern generators [R. Curtu, A. Shpiro, N. Rubin, J. Rinzel, Mechanisms for frequency control in neuronal competition models, SIAM J. Appl. Dyn. Syst. 7 (2) (2008) 609–649] showed that the variation of the stimulus strength parameter can lead to rich and interesting dynamics. Several types of behavior were identified such as: fusion, equivalent to a steady state of identical activity levels for both neural units; oscillations due to either an *escape* or a *release* mechanism; and a winner-take-all state of bistability. The model consists of two neural populations interacting through reciprocal inhibition, each endowed with a slow negative-feedback process in the form of spike frequency adaptation. In this paper we report the occurrence of another complex oscillatory pattern, the mixed-mode oscillations (MMOs). They exist in the model at the transition between the relaxation oscillator dynamical regime and the winner-take-all regime. The system distinguishes itself from other neuronal models where MMOs were found by the following interesting feature: there is no autocatalysis involved (as in the examples of voltage-gated persistent inward currents and/or intrapopulation recurrent excitation) and therefore the two cells in the network are *not* intrinsic oscillators; the oscillations are instead a combined result of the mutual inhibition and the adaptation. We prove that the MMOs are due to a *singular* Hopf bifurcation point situated in close distance to the transition point to the winner-take-all case. We also show that in the vicinity of the singular Hopf other types of bifurcations exist and we construct numerically the corresponding diagrams.

## 1. Introduction

Mixed-mode oscillations (MMOs) were observed in both experiments and models of systems from chemistry [1–7], physics [8,9] and neuroscience [10–16], and they are defined as complex oscillatory patterns consisting of small amplitude oscillations followed by large excursions of relaxation type, in each periodic cycle. For example, localized structures of large amplitude oscillations on a background of small amplitude oscillations were identified in experiments on the photosensitive $Ru(bpy)_3$-catalyzed Belousov–Zhabotinsky reaction in a thin layer of silica gel with photochemical global negative feedback imposed through illumination [5]; in the neural system, MMOs were found in central pattern generators such as the lower brain stem network (the pre-Bötzinger complex) that generates respiratory rhythm in mammals [11], or in electrophysiological (in vitro) studies of spiny stellate cells in layer II medial entorhinal cortex [10]; more recently, MMOs were also discovered in dusty plasmas [9].

What are the functional consequences of the MMOs in these chemical, physical and biological systems is still an open question, as well as is the understanding of the underlying mechanisms that produce them.

The number, amplitude and shape of small and large excursions in MMOs may vary depending on the specific structure of the system (and so, on the mechanism leading to MMOs) and on the values of certain parameters. Using techniques from dynamical systems and bifurcations theory, several distinct mechanisms have been proposed to explain the occurrence of MMOs such as break-up (loss) of stability of a Shilnikov homoclinic orbit [17,18], break-up of an invariant torus [19], subcritical Hopf-homoclinic bifurcation [20], a (generalized, folded node type) canard phenomenon [21–24], and, more recently, a *singular Hopf* bifurcation [25].

In particular, the last two mechanisms are associated with multiple-timescale dynamical systems. A common feature is that the slow stable and unstable manifolds of the system (situated exponentially close to the critical manifold) play an important role in the generation of MMOs as they are involved in both the definition of the global return map that corresponds to the large relaxation-like excursion, and in the generation of small amplitude oscillations. The intersection between the slow stable and slow unstable manifolds (named the *curve of folds* or, simply, *the fold*) is especially of interest.

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The distinction between a (folded node type) canard generated MMO and a singular Hopf generated MMO comes mainly from the following fact: in the former case there is no equilibrium point of the original system in the neighborhood where the small (subthreshold) oscillations occur, while in the latter there is. The theory has been developed for systems with at least one fast and at least two slow variables since that guarantees that the solutions are generic [25,26].

In the first case, the folded node is an equilibrium of the desingularized flow on the critical manifold but *not* an equilibrium of the original fast–slow system. The folded node belongs to the fold. A whole family of solutions crosses via the folded node singularity from the attracting to the repelling branch of the slow manifold. The folded node possesses a unique (strong) canard and non-unique (weak/secondary) canards which delineate a trapping region (a funnel). Then any solution that ends up in the funnel passes near the folded node singularity and, consequently, experiences a delay; the delay is due to the rotational properties of canards with the primary weak canard having the role of the rotational axis [26].

In the singular Hopf case, an equilibrium of the original fast–slow system exists in the neighborhood of the curve of folds. In fact, a Hopf bifurcation point is on the critical manifold but displaced from the fold by $\mathcal{O}(\varepsilon)$-distance. Then the intersections of the stable and unstable manifolds of this equilibrium point together with those of the slow (stable and unstable) manifolds contribute to the generation of MMOs [25,27].

In a recent paper, Guckenheimer [25] opens an interesting discussion and direction for future research about the differences in the characteristics of MMOs due to singular Hopf points and those created through canards at folded nodes: for example, it seems that in the case of singular Hopf the small oscillations of MMOs start with very low amplitude, then grow slowly before entering the relaxation oscillator phase. In the case of folded nodes, the small oscillations of MMOs decrease and then increase in amplitude, usually with the same number of cycles.

We should mention though that even in the case of the singular Hopf, it is possible that a folded node still exists; nevertheless this folded node is there because a parameter of the system varies close to a value where a *folded saddle–node type II singularity* occurs. The folded saddle–node type II singularity corresponds to a transcritical bifurcation where the Hopf point crosses the curve of folds [25,27,28]. That might explain why, in the literature, some models with MMOs that were associated to folded node canards exhibit only the increasing-in-amplitude small oscillations but not the decreasing-in-amplitude ones (see for example [16]).

*Mixed-mode oscillations in a two-cell inhibitory neural network.* We investigate in this paper the existence of MMOs in a neural system with two fast and two slow variables and show that they are associated with a singular Hopf bifurcation. The system models competition between two populations of neurons and has been used to describe perceptual bistability due to ambiguous external stimuli [29–31], or, in a slightly modified form, for central pattern generators [32–34]. For example, binocular rivalry (a classical example of perceptual bistability) is experienced by a person when his/her eyes are exposed simultaneously to two significantly different images. Over a large range of stimulus conditions, the person reports an alternation between the two competing percepts (images) as opposed to a mixture of them. The alternation is therefore called perceptual *rivalry*. In modeling terms, the alternation corresponds on average to an anti-phase periodic solution; competition is implemented via reciprocal inhibition that acts effectively as a fast positive feedback (disinhibition); in addition, a slow negative-feedback process is assumed and it is associated to either the spike frequency adaptation or to the synaptic depression.

A very interesting feature of this model is that its oscillations (simple and/or mixed-mode) are a consequence of *both* coupling and local feedback. In other words, the two cells (populations) in the network are *not* intrinsic oscillators; in fact it can be proved that, once decoupled (see (1) in Section 2 with $\beta = 0$), the only possible state of each cell is the equilibrium [30]. This property distinguishes the system we investigate here from other neuronal models where MMOs were found: coupled-oscillators [12,13,23] or neuron models involving autocatalysis in either an intrinsic process form (like voltage-gated persistent inward currents) or as synaptic process (like intrapopulation recurrent excitation) [14–16,24]. There is no autocatalysis in this two-cell competition network, the alternation being in fact a combined result of mutual inhibition and adaptation. That has direct implications on the return mechanism (large amplitude excursions) involved in the formation of MMOs [27].

Moreover, compared with the models mentioned above, system (1) is relatively simple and so it has the advantage of being tackled much easily with analytical methods. In the following sections we identify and characterize analytically the conditions for a singular Hopf bifurcation to exist at nontrivial equilibria and we construct the associated normal form (Section 3.2). Once the normal form is determined, we use it to explain the existence of MMOs at the transition between rivalry oscillation and winner-take-all dynamical regimes (Section 4). In addition, we numerically investigate the phase space of (1) close to the transition point and identify here several interesting limit point sets (Section 2.1).

## 2. Model description and numerical investigation

The two-cell (two-population) inhibitory neural network with adaptation that we study in this paper is modeled by a four-dimensional system of ordinary differential equations,

$$\begin{aligned}
\frac{\mathrm{d}u_1}{\mathrm{d}t} &= -u_1 + S(I - \beta u_2 - g a_1),\\
\frac{\mathrm{d}u_2}{\mathrm{d}t} &= -u_2 + S(I - \beta u_1 - g a_2),\\
\tau\frac{\mathrm{d}a_1}{\mathrm{d}t} &= -a_1 + u_1,\\
\tau\frac{\mathrm{d}a_2}{\mathrm{d}t} &= -a_2 + u_2,
\end{aligned} \tag{1}$$

where $\tau \gg 1$ and $S$ is a nonlinear gain function of inverse $F = S^{-1}$. The function $S$ satisfies certain conditions such as being differentiable, monotonically increasing from $\lim_{x\to-\infty} S(x) = 0$ to $\lim_{x\to\infty} S(x) = 1$ and with convexity-change (from concave-up to concave-down) at some given value $x = \theta$ (Fig. 1A). Let us define $u_0$ as the value the function $S$ takes at $\theta$, that is $u_0 = S(\theta)$. Then the following conditions are true for the inverse function $F$: $\lim_{u\to 0} F'(u) = \lim_{u\to 1} F'(u) = \infty$, $F''(u) < 0$ for $u \in (0, u_0)$, $F''(u) > 0$ for $u \in (u_0, 1)$, $F''(u_0) = 0$ (see the graph of $F'$ in Fig. 1B). The typical gain function is the sigmoid and it depends on two parameters (positive $r$ and real $\theta$) that control the slope and the activation threshold,

$$S(x) = \frac{1}{1 + \mathrm{e}^{-r(x-\theta)}}. \tag{2}$$

Each fast equation is associated with one population of neurons and describes the time evolution of its spatially averaged firing rate ($u_j$, $j = 1, 2$); each slow equation monitors the (slow) time fatigue accumulation ($a_j$, $j = 1, 2$); competition is achieved through mutual inhibition of strength $\beta$ and negative feedback (such as spike frequency adaptation) of strength $g$; in addition, each population receives external stimulation of equal strength $I$ ($\beta$, $g$ and $I$ are all positive parameters).