FOLDED SADDLE-NODES AND THEIR NORMAL FORM REDUCTION IN A NEURONAL RATE MODEL∗

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Abstract

The paper investigates the existence of folded singularities in a dynamical system of two fast and two slow equations. The normal form of the system near its fold curve is constructed. Then it is used to determine the analytical conditions satisfied by a folded singularity. In particular, we find that there is a parameter region where folded saddle-nodes of type II exist. In the neighborhood of those points the system possesses a stable folded node and an unstable true equilibrium, and the local dynamics is complex.

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Foreword

This work is a tribute to my mentor, Professor Dr. Adelina Georgescu. I met Dr. Georgescu at the beginning of the year 1997, in Bucharest, Romania. At that time she was the Director of the Institute of Applied Mathematics of the Romanian Academy, and she was very busy reorganizing

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its activity. Nevertheless, she still found time to talk with me and agreed to supervise my doctoral thesis in mathematics.

Our encounter was of incalculable value to my professional development: she enlarged my horizon by pointing out that mathematics can be successfully used to study biological systems; she introduced me to the exciting field of applied dynamical systems and bifurcation theory; she even taught me with patience and critical view how to write a scientific paper. Moreover, when I continued my studies in the United States, she has been supportive; that allowed me to write and finish in parallel two doctoral theses.

I have always admired and respected Professor Adelina Georgescu: she was extremely energetic; passionate about mathematics; dedicated to her work, her family, and her country; a wonderful mentor and collaborator. But most of all, she was an excellent researcher and an example of human and scientific integrity. She passed away at the beginning of May 2010 after a long battle with cancer that she fought with courage and dignity. It was a sad day! Romania lost an important scientist, but we, her disciples, lost much more; we lost a very good friend.

I thank the editors of this special issue for giving me the opportunity to express my deep respect and admiration to my mentor. This paper is written In The Memory of Adelina Georgescu!

1 Introduction

This article is the second in a series of three papers investigating the formation of mixed mode oscillations in a neuronal competition model of two reciprocally inhibitory populations.

Previous studies [4], [8], [9] showed that the system can exhibit a large range of dynamics such as approaching a steady state (equal level of activity) for both populations (the fusion), anti-phase oscillations with the period of oscillations decreasing with strength of the external stimulus (escape), anti-phase oscillations with their period increasing with stimulus strength (release), or a bistability regime of two distinct equilibria assimilated to a winner-take-all situation.

In a more recent paper [2] we reported another possible behavior. This is a more complex pattern of activity called the mixed mode oscillations (MMOs). MMOs consist of two distinct amplitudes in a cycle; some are small amplitude oscillations but they are followed by large exchanges of relaxation-
type. While the formation of small amplitude oscillations can be partially explained through the presence of a singular Hopf bifurcation point [2], the complete mechanism of MMOs is still unclear.

We continue our work from [2] by showing here that there exists a parameter regime where the neuronal rate model possesses folded saddle-node singularities of type II. Note that the model is a slow-fast dynamical system, and its layer problem (or fast sub-system) has a fold curve (see Section 2). A folded singularity is a point on the fold curve which is an equilibrium of an associated desingularized flow [10] (see also Section 4). Obviously, it is not an equilibrium of the full (original) system and therefore it is not easily detected. However its presence is important because it may lead to the formation of canards, and consequently to the formation of MMOs. The canards are solutions with the peculiarity that they cross the fold curve from the attractive slow manifold of the slow-fast system into the repelling branch of the slow manifold, and they stay there for finite time before following a relaxation oscillator trajectory. In the case of folded nodes the canards have rotational properties due to the folded node funnel [10]. Therefore the rotations of the trajectories in the funnel together with the fast relaxation-type part of the trajectory form an MMO solution.

As already mentioned, we find in this paper that folded saddle-nodes singularities of type II exist. These are even more interesting points than the commonly seen folded nodes: in their neighborhood the system has a stable folded node and an unstable true equilibrium. Therefore the local dynamics becomes much more complex; the canard trajectories passing through the folded node funnel into the repelling side of the slow manifold are then influenced by the local stable and unstable manifolds of the true equilibrium. A geometrical approach explaining this interaction and thus completing the proof of how MMOs form in the model is the topic of a next paper [3]. In the present manuscript we focus on preparing the ground necessary to the geometrical approach. We construct the normal form of the system near the fold curve and show that indeed, folded saddle-nodes of type II exist.

2 Slow-fast dynamics and its characteristics in a neuronal rate model

The system we investigate in this paper results from an inhibitory network of two populations of neurons. The activity (spike frequency rate) level of
each population is monitored by variables $u_j$, $j = 1, 2$ which, if taken in isolated environment, would reach a steady state with exponential decay. However since the populations are coupled through inhibitory connections and are subject to an intrinsic slow negative feedback process (the neuronal adaptation), their dynamics is much complex. Moreover, a constant external input is applied, and it modulates the behavior as well. In summary, the system is defined by two pairs of fast-slow equations of the form

$$
\frac{du_j}{dt} = -u_j + S(I - \beta u_k - g a_j),
\tau \frac{d a_j}{dt} = -a_j + u_j
$$

with $j, k = 1, 2$, $k \neq j$. Inhibition has a negative impact on the population-target and is assumed to have strength $\beta$; the input is quantified by parameter $I$; The adaptation variables are $a_j$ and they evolve slowly in time, as opposed to $u_j$, according to a timescale $\tau \gg 1$; the adaptation strength is $g$; the system’s nonlinearities are defined by function $S$ of typical sigmoid shape such as $S(x) = 1/(1 + e^{-r(x-\theta)})$ (the parameters $r$ and $\theta$ are said to control the slope of the gain and the activation threshold ). All parameters $I$, $\beta$, $g$, $\tau$, and $r$ are considered to be positive.

From the point of view of the analysis it is important to mention that $\tau$ is assumed to be large enough such that $\varepsilon = 1/\tau$, $0 < \varepsilon \ll 1$ is true. Moreover, we need to summarize some important properties of the function $S$. For consistency let us assume that $S$ is invertible with inverse $F = S^{-1}$, and that $S$ and $F$ are differentiable and monotonically increasing with $S(\theta) = u_0 \in (0, 1)$, $\lim_{x \to -\infty} S(x) = 0$, $\lim_{x \to \infty} S(x) = 1$ and so $\lim_{u \to 0} F(u) = -\infty$, $\lim_{u \to -1} F(u) = \infty$; then $\lim_{u \to 0} F'(u) = \lim_{u \to -1} F'(u) = \infty$. Moreover we assume $F'$ has a local (positive) minimum at $u_0$, so $F''(u) < 0$ for $u \in (0, u_0)$, $F''(u) > 0$ for $u \in (u_0, 1)$ and $F''(u_0) = 0$. Note that, in general, these properties are satisfied by the sigmoid functions used in neuronal applications such as the example above.

The system under analysis is thus

$$
\begin{align*}
\frac{du_1}{dt} &= -u_1 + S(I - \beta u_2 - g a_1), \\
\frac{du_2}{dt} &= -u_2 + S(I - \beta u_1 - g a_2), \\
\frac{d a_1}{dt} &= \varepsilon(-a_1 + u_1), \\
\frac{d a_2}{dt} &= \varepsilon(-a_2 + u_2).
\end{align*}
$$

In the singular limit case $\varepsilon = 0$, variables $a_1$ and $a_2$ are constant, say $a_1 = \bar{a}_1$, $a_2 = \bar{a}_2$ and play the simple role of parameters in the $u_j$-equations. This is called the layer problem or the fast sub-system. The set of equilibrium points for the layer problem is a manifold called the critical manifold; it is
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defined by \(-u_1 + S(I - \beta u_2 - ga_1) = 0, -u_2 + S(I - \beta u_1 - ga_2) = 0\) and, as in most examples of slow-fast dynamical systems, it has a cubic shape [4]. In an equivalent form, the critical manifold, say \(\Sigma\) can be described as follows

\[
\Sigma = \{ (u_1, u_2, a_1, a_2) : u_1, u_2 \in (0, 1), a_1, a_2 \in \mathbb{R} \text{ and } \mathcal{F}(u_1, a_1, a_2) = I - F(u_1) - \beta S(I - \beta u_1 - ga_2) - ga_1 = 0, u_2 = S(I - \beta u_1 - ga_2) \}
\]

(2)

where \(F = S^{-1}\). Importantly, it can be shown that the layer problem can have either three, two or one equilibrium points depending on the values of \(a_1\) and \(a_2\) [4]. The transition from three to one equilibrium occurs at a double-equilibrium point, that is a saddle-node (fold) bifurcation point. A short calculation in (2) shows this happening at \(-F'(u_1) + \beta^2 S'(I - \beta u_1 - ga_2) = 0\) for any constant values \(a_1\), \(a_2\). Due to the invertibility of \(S\) and since at the equilibrium point \(u_2 = S(I - \beta u_1 - ga_2)\) is true, we get \(-F'(u_1) + \beta^2 S'(F(u_2)) = -F'(u_1) + \beta^2 S'(S^{-1}(u_2)) = -F'(u_1) + \beta^2/(S^{-1})'(u_2) = -F'(u_1) + \beta^2/F'(u_2) = 0\). So, the fold curve (or, the curve of saddle-nodes) is defined by

\[
\mathcal{L}^\pm : F'(u_1)F'(u_2) = \beta^2
\]

(3)

together with (2).

Obviously, the fold condition can be also verified by looking into the eigenvalues of the linearized problem. The partial derivatives of the \(u_j\)-equations with respect to \(u_1\) and \(u_2\) are evaluated at a critical point of the layer problem \((u_1^*, u_2^*, a_1^*, a_2^*) \in \Sigma\) and the linearization matrix becomes

\[
\mathcal{A} = \begin{bmatrix}
-1 & -\beta/F'(u_1^*) \\
-\beta/F'(u_2^*) & -1
\end{bmatrix}.
\]

(4)

Clearly, \(\mathcal{A}\) has a zero eigenvalue if and only if condition (3) is true.

The cubic shape of \(\Sigma\) has the following significance: its outer branches \(\Sigma_a^\pm\) consist of stable nodes for the layer problem while the middle branch \(\Sigma_r\) is a set of saddles points. That is obtained by testing the sign of the determinant in (4), or equivalent, the sign of \(\mathcal{F}_{u_1}\). It results indeed that \(\mathcal{F}_{u_1}(u_1, a_1, a_2) < 0\) on \(\Sigma_a^-\) and \(\Sigma_a^+\) as opposed to \(\mathcal{F}_{u_1}(u_1, a_1, a_2) > 0\) on \(\Sigma_r\) [4]. In the perturbed system (1) the dynamics is attracted to either of \(\Sigma_a^\pm\) and repelled away from \(\Sigma_r\). For this reason, \(\Sigma_a^\pm\) are called attractive manifolds and \(\Sigma_r\) is called the repelling (critical) manifold. Thus we can decompose \(\Sigma\) into several significant components like \(\Sigma = \Sigma_a^- \cup \Sigma_a^+ \cup \Sigma_r \cup \mathcal{L}^\pm\).
From the point of view of the fast-slow analysis of (1), the critical manifold has an additional role. Assume in (1) that we change the time according to \( \tilde{t} = \epsilon t \) (\( \tilde{t}' = d/d\tilde{t} \)). System (1) becomes \( \varepsilon u_j' = -u_j + S(I - \beta u_k - ga_j) \), \( a_j' = -a_j + u_j \). Setting now \( \varepsilon = 0 \) we see that \( \Sigma \) is in fact the manifold where the solution of the so-called reduced system (or slow sub-system) lays. The reduced system evolves according to equations \( a_1' = -a_1 + u_1(a_1, a_2) \), \( a_2' = -a_2 + u_2(a_1, a_2) \) where \( u_1 \), \( u_2 \) are implicit functions defined by (2). But note that the formula of \( u_1(a_1, a_2) \) and \( u_2(a_1, a_2) \) on \( \Sigma^+ \) changes when curve \( \mathcal{L}^\pm \) is reached because at \( \mathcal{L}^- (\mathcal{L}^+) \) a node and a saddle of the layer problem collide and annihilate each other. However, another (stable) node exists on the opposite branch \( \Sigma^- (\Sigma^+) \); the trajectory of the full system will be attracted to it and the equations of the reduced system will change accordingly. We say that a 'jump' takes places from \( \Sigma^- (\Sigma^+) \) to \( \Sigma^+ (\Sigma^-) \). The trajectory of the full system is thus a relaxation oscillator [11].

For the perturbed system (\( \varepsilon > 0 \)), the dynamics have similar properties away from the fold curve. For \( \varepsilon \) sufficiently small Fenichel theory [5] proves the existence of a smooth locally invariant normally hyperbolic manifold \( \Sigma_\varepsilon \); this is an \( \mathcal{O}(\varepsilon) \) perturbation of \( \Sigma \) and the slow dynamics of (1) takes place close to it. Consequently, to fully describe system (1)'s dynamics one only needs to analyze its trajectories close to the fold curve \( \mathcal{L}^\pm \). This is especially important if system (1) has complex trajectories such as mixed-mode oscillations (MMOs). Indeed, MMOs were observed and reported in [2]; they are trajectories that combine small amplitude oscillations with large excursions of relaxation type. While the relaxation oscillator can be explain through classical Fenichel theory and slow-fast analysis (see also [11]), the small amplitude oscillations cannot. MMOs exist in an interval of parameter \( I \) close to a Hopf bifurcation point but the Hopf is subcritical and MMOs exist on the side of it where the equilibrium is unstable. Therefore there is a need to explain how is it possible for the trajectory to stay close to the unstable equilibrium (situated on \( \Sigma_{r,\varepsilon} \)) for a finite time and then jump to the opposite attractive branch of \( \Sigma_{a,\varepsilon} \) instead of directly jumping to it. The answer is found in the theory of canards [10]. The canards are solutions that pass from the attractive manifold \( \Sigma_a \) into the repelling branch \( \Sigma_r \) through a particular type of point on the fold curve. Such a point, say \( p_s \in \mathcal{L}^\pm \), is called a folded singularity. As we will show in Section 4 folded singularities do exist in system (1) suggesting that canards may be possible in (1). We note that the existence of canards per se is not proven here and it is the
where $U$ stands for the transpose. Here $T$ stands for the transpose.

As mentioned in the previous section, $\mathcal{L}^\pm$ is the set of points that correspond to a saddle-node (fold) bifurcation in the layer problem. Since the fold has a one-dimensional normal form we should be able to reduce (1), or its equivalent form (5), to a system of only three variables, two of which being
slow and only one fast. This can be achieved by projection on the center manifold associated with the zero eigenvalue of $A$.

The point $U = (0,0)$ is an equilibrium of the layer problem for $\varepsilon = 0$ and $y_1 = y_2 = 0$. Its associated Jacobian matrix is $A$ which has a zero ($\lambda_1 = 0$) and a negative ($\lambda_2 = -2$) eigenvalue. The corresponding eigenvectors are $q = (-\sqrt{F'(u_2^*)}, \sqrt{F'(u_1^*)})^T$ such that $Aq = 0$, and $\bar{q} = (\sqrt{F'(u_2^*)}, \sqrt{F'(u_1^*)})^T$ with $A\bar{q} = -2\bar{q}$. We will use the adjoint vector $n$ of the matrix $A$ ($A^T n = 0$ with scalar product $n \cdot q = n_1 q_1 + n_2 q_2 = 1$) to construct the projection on the center manifold. (Note that $n$ is defined by $n = (-\sqrt{F'(u_1^*)}, \sqrt{F'(u_2^*)})^T$.)

The solution of the layer problem $U = (U_1, U_2)^T$ is decomposed into its projection on the center manifold ($\sigma q$) and a complementary component $V$ orthogonal to $n$, that is: $U = \sigma q + V$ [7]. Then the coordinate $\sigma$ is the variable on the center manifold that replaces $u_1$ and $u_2$ in system (1) according to the relationship $\sigma = U \cdot n$. This is $\sigma = -\frac{\sqrt{F'(u_1^*)}}{2\beta}(u_1 - u_1^*) + \frac{\sqrt{F'(u_2^*)}}{2\beta}(u_2 - u_2^*)$. The component $V$ depends on $y_1, y_2, \sigma y_1, \sigma y_2,$ and $\varepsilon, \varepsilon \sigma, \varepsilon y_1, \varepsilon y_2$ but includes only $\sigma$-terms starting with quadratic order ($\sigma^2, \sigma^3, \ldots$); it is defines by

$$V = (y_1 q_{10} + y_2 q_{01} + y_1^2 q_{20} + y_1 y_2 q_{11} + y_2^2 q_{02} + \ldots) + (\sigma^2 h_2 + \sigma^3 h_3 + \ldots) + (\sigma y_1 h_{10} + \sigma y_2 h_{01} + \ldots) + (\varepsilon h_{000} + \varepsilon \sigma h_{001} + \varepsilon y_1 h_{100} + \varepsilon y_2 h_{010}) + O(\varepsilon y_1^2, \varepsilon y_2^2, \varepsilon y_1 y_2, \varepsilon \sigma^2, \varepsilon^2 y_1, \varepsilon^2 y_2, \varepsilon^i \sigma^j y_1^k y_2^l), \quad 4 - i = j = k + l. \quad (6)$$

The differential equation that $\sigma$ satisfies on the center manifold is a direct consequence of (5). However its coefficients depend in equal measure on the coefficients of (5) and the admissible values of the vectors $h_j, q_{ij}, h_{ijk} \ldots$ (all orthogonal on $n$) from the definition of $V$.

The projection of system (5) on the center manifold is given below.

**Theorem 1.** Let $\varepsilon$ be a sufficiently small positive number ($0 < \varepsilon \ll 1$), and parameters $I, \beta, g$ such that system (1) has a fold curve $L^\pm$. Then, in the neighborhood of any point $p \in L^\pm$, $p = (u_1^*, u_2^*, a_1^*, a_2^*)$, system (1) is topologically equivalent to

$$\frac{d\sigma}{dt} = c_{10} y_1 + c_{01} y_2 + c_{20} y_1^2 + c_{11} y_1 y_2 + c_{02} y_2^2 + b_{000} \sigma^2 + b_{10} \sigma y_1 + b_{01} \sigma y_2 + O(\varepsilon (\sigma + y_1 + y_2), \varepsilon^2, (\sigma + y_1 + y_2)^3),$$

$$\frac{dy_1}{dt} = \varepsilon \left(\frac{u_1^* - a_1^*}{4F'(u_1^*)} + \left(-1 - \frac{g}{4F'(u_1^*)}\right) y_1 + \left(-\frac{g}{4\beta}\right) y_2 - \sqrt{F'(u_2^*)}\sigma\right) y_2.$$
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\[ dy_2/dt = \varepsilon \left[ (u_2^* - a_2^*) + \left( -\frac{g}{4\beta} \right) y_1 + \left( -1 - \frac{g}{4F'(u_2^*)} \right) y_2 + \sqrt{F''(u_1^*)} \right] \]

\[ + O(\varepsilon (\sigma + y_1 + y_2), \varepsilon, (\sigma + y_1 + y_2)^2) \]

with coefficients \( c_{ij}, b_{ij} \) defined by

\[ b_{00} = \frac{1}{4\beta^2} \left( F'(u_2^*)^{3/2} F''(u_1^*) - F'(u_1^*)^{3/2} F''(u_2^*) \right) \]

and

\[ c_{10} = \frac{g}{2\beta \sqrt{F'(u_1^*)}}, \quad c_{01} = -\frac{g}{2\beta \sqrt{F'(u_2^*)}}, \quad c_{11} = -\frac{3g^2}{8\beta^3} b_{00}, \]

\[ c_{20} = \frac{g^2 F''(u_1^*)}{8\beta^2 F'(u_1^*)^{5/2}} + \frac{g^2}{16\beta^2 F'(u_1^*)} b_{00}, \quad c_{02} = -\frac{g^2 F''(u_2^*)}{8\beta^2 F'(u_2^*)^{5/2}} + \frac{g^2}{16\beta^2 F'(u_2^*)} b_{00}, \]

\[ b_{10} = \frac{g F''(u_1^*)}{4F'(u_1^*)^{5/2}} + \frac{g}{2\beta \sqrt{F'(u_1^*)}} b_{00}, \quad b_{01} = \frac{g F''(u_2^*)}{4F'(u_2^*)^{5/2}} - \frac{g}{2\beta \sqrt{F'(u_2^*)}} b_{00}. \]

Proof. Since (5) is a translation of the original system (1), it is obviously topological equivalent to it. Therefore we will focus here only on the proof of the topological equivalence between (5) and (7).

In order to simplify our calculation we will work with vector equations; for this we consider beneficial to introduce the following notation: \( e_1 = (1, 0)^T \), \( e_2 = (0, 1)^T \) and

\[ A_{10} = \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix}, \quad A_{01} = \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix}. \]

Then we express the \( y_j \)-equations from (5) in terms of \( U = \sigma q + V \) with \( V \) defined by (6). It results

\[ dy_1/dt = \varepsilon(u_1^* - a_1^*) + \varepsilon y_1(e_1 \cdot q_{10} - 1) + \varepsilon y_2(e_1 \cdot q_{01}) - \varepsilon \sigma \sqrt{F'(u_2^*)} \]

\[ + O(\varepsilon (\sigma + y_1 + y_2), \varepsilon, (\sigma + y_1 + y_2)^2), \]

\[ dy_2/dt = \varepsilon(u_2^* - a_2^*) + \varepsilon y_1(e_2 \cdot q_{10}) + \varepsilon y_2(e_2 \cdot q_{01} - 1) + \varepsilon \sigma \sqrt{F'(u_1^*)} \]

\[ + O(\varepsilon (\sigma + y_1 + y_2), \varepsilon, (\sigma + y_1 + y_2)^2). \]
A similar calculation apply to the first equation in (5) and implies

\[
dU/dt = y_1[\mathcal{A} q_{10} - \frac{g}{F'(u_1^*)}e_1] + y_2[\mathcal{A} q_{01} - \frac{g}{F''(u_2^*)}e_2]
+ y_1^2[\mathcal{A} q_{20} - \frac{\beta g F''(u_1^*)}{F'(u_1^*)^3} A_{10} q_{10} - \frac{g^2 F''(u_1^*)}{2F'(u_1^*)^3} e_1 + \frac{1}{2} \mathcal{B}(q_{10}, q_{10})]
\]
\[
+ y_2^2[\mathcal{A} q_{02} - \frac{\beta g F''(u_2^*)}{F'(u_2^*)^3} A_{01} q_{01} - \frac{g^2 F''(u_2^*)}{2F'(u_2^*)^3} e_2 + \frac{1}{2} \mathcal{B}(q_{01}, q_{01})]
\]
\[
+ y_1 y_2[\mathcal{A} q_{11} - \frac{\beta g F''(u_1^*)}{F'(u_1^*)^3} A_{10} q_{10} - \frac{\beta g F''(u_2^*)}{F'(u_2^*)^3} A_{01} q_{10} + \mathcal{B}(q_{10}, q_{01})]
\]
\[
+ \sigma^2[\mathcal{A} h_2 - \frac{\beta^2 F''(u_1^*)}{2F'(u_2^*)^2} e_1 - \frac{\beta^2 F''(u_2^*)}{2F'(u_2^*)^2} e_2]
\]
\[
+ \sigma y_1[\mathcal{A} h_{10} - \frac{\beta g F''(u_1^*)}{F'(u_1^*)^{5/2}} e_1 + \mathcal{B}(q, q_{10})] + \varepsilon(\mathcal{A} h_{00})
\]
\[
+ \sigma y_2[\mathcal{A} h_{01} + \frac{\beta g F''(u_2^*)}{F'(u_2^*)^{5/2}} e_2 + \mathcal{B}(q, q_{01})] + \varepsilon\sigma[\mathcal{A} h_{001} + \mathcal{B}(q, h_{000})]
\]
\[
+ \varepsilon y_1[\mathcal{A} h_{100} - \frac{\beta g F''(u_1^*)}{F'(u_1^*)^3} A_{10} h_{00} + \frac{1}{2} \mathcal{B}(q_{10}, h_{000})]
\]
\[
+ \varepsilon y_2[\mathcal{A} h_{010} - \frac{\beta g F''(u_2^*)}{F'(u_2^*)^3} A_{01} h_{00} + \frac{1}{2} \mathcal{B}(q_{01}, h_{000})]
\ldots (12)
\]

The equation of \sigma on the center manifold due to a fold should be at least quadratic in order (with respect to \sigma) so it should take the form

\[
d\sigma/dt = (c_{10} y_1 + c_{01} y_2 + c_{20} y_2^2 + c_{11} y_1 y_2 + c_{02} y_2^2) + b_{00} \sigma^2 + b_{10} \sigma y_1 + b_{01} \sigma y_2 + \varepsilon(d_0 \sigma + d_1 y_1 + d_2 y_2) + \mathcal{C}(y_1^i y_2^j \sigma^k, \varepsilon y_1^i y_2^j, \varepsilon \sigma^i y_2^j, \varepsilon^2) . (13)
\]

Of course its coefficients \( c_{ij}, b_{ij}, \ldots \) are unknown but they are specific to the system that is projected on the center manifold. We will compute them from equation (12).

For this, let us note that \( U = \sigma q + V \) implies \( dU/dt = (d\sigma/dt) q + (dV/dt) \), so \( dU/dt = (d\sigma/dt) q + [(dy_1/dt) q_{10} + (dy_2/dt) q_{01} + 2y_1(dy_1/dt) q_{20} + (dy_1/dt) y_2 q_{11} + y_1(dy_2/dt) q_{11} + 2y_2(dy_2/dt) q_{21} + \ldots] + [2\sigma(d\sigma/dt) h_2 + \ldots] + (y_1 h_{10} + y_2 h_{01})(d\sigma/dt) + \sigma[(dy_1/dt) h_{10} + (dy_2/dt) h_{01}] + \varepsilon(d\sigma/dt) h_{001} + \varepsilon(dy_1/dt) h_{100} + \varepsilon(dy_2/dt) h_{010} + \ldots \)
We then replace \(d\sigma/dt\), \(dy_1/dt\), \(dy_2/dt\) according to (13), (10) and (11) and obtain
\[
dU/dt = y_1(c_{10}q) + y_2(c_{01}q) + y_1^2(c_{20}q + c_{10}h_{10}) + y_2^2(c_{02}q + c_{01}h_{01})
+ y_1y_2(c_{11}q + c_{10}h_{10} + c_{01}h_{01}) + \sigma^2(b_{00}q) + \sigma y_1(b_{10}q + 2c_{10}h_{2})
+ \sigma y_2(b_{01}q + 2c_{01}h_{2}) + \varepsilon[(u_1^* - a_1^*)q_{10} + (u_2^* - a_2^*)q_{01}]
+ \varepsilon\sigma[d_0q + (u_1^* - a_1^*)h_{10} + (u_2^* - a_2^*)h_{01} + \sqrt{F'(u_1^*)q_{10}}
- \sqrt{F'(u_2^*)q_{10}}] + \varepsilon y_1[c_{10}h_{001} + d_1q + (e_1 \cdot q_{10} - 1)q_{10} + (e_2 \cdot q_{10})q_{01}
+ 2(u_1^* - a_1^*)q_{20} + (u_2^* - a_2^*)q_{11}] + \varepsilon y_2[c_{01}h_{001} + d_2q + (e_1 \cdot q_{01})q_{10}
+ (e_2 \cdot q_{01} - 1)q_{01} + 2(u_2^* - a_2^*)q_{02} + (u_1^* - a_1^*)q_{11}] + \ldots
\]

The compatibility condition between (12) and (14) allows us to determine the vectors \(q_{ij}, h_j, h_{ij}, \ldots\) in (6) together with coefficients \(c_{ij}, b_{ij}, \ldots\) in (13). This implies
\[
c_{10}q = \mathcal{A}q_{10} - \frac{g}{F'(u_1^*)}e_1 \quad \text{and} \quad c_{01}q = \mathcal{A}q_{01} - \frac{g}{F'(u_2^*)}e_2;
\]
\[
c_{20}q + c_{10}h_{10} = \mathcal{A}q_{20} - \frac{\beta gF''(u_1^*)}{F'(u_1^*)^3}A_{10}q_{10} - \frac{g^2 F''(u_1^*)}{2F'(u_1^*)^3}e_1 + \frac{1}{2} \mathcal{B}(q_{10}, q_{10}),
\]
\[
c_{02}q + c_{01}h_{01} = \mathcal{A}q_{02} - \frac{\beta gF''(u_2^*)}{F'(u_2^*)^3}A_{01}q_{01} - \frac{g^2 F''(u_2^*)}{2F'(u_2^*)^3}e_2 + \frac{1}{2} \mathcal{B}(q_{01}, q_{01}),
\]
\[
c_{11}q + c_{10}h_{10} + c_{01}h_{01} = \mathcal{A}q_{11} - \frac{\beta gF''(u_1^*)}{F'(u_1^*)^3}A_{10}q_{10} - \frac{\beta gF''(u_2^*)}{F'(u_2^*)^3}A_{01}q_{10}
+ \mathcal{B}(q_{10}, q_{10}),
\]
\[
b_{00}q = \mathcal{A}h_2 - \frac{\beta^2 F''(u_1^*)}{2F'(u_1^*)^2}e_1 - \frac{\beta^2 F''(u_2^*)}{2F'(u_2^*)^2}e_2,
\]
\[
b_{10}q + 2c_{10}h_2 = \mathcal{A}h_{10} - \frac{\beta gF''(u_1^*)}{F'(u_1^*)^{5/2}}e_1 + \mathcal{B}(q, q_{10}),
\]
\[
b_{01}q + 2c_{01}h_2 = \mathcal{A}h_{01} + \frac{\beta gF''(u_2^*)}{F'(u_2^*)^{5/2}}e_2 + \mathcal{B}(q, q_{01}), \quad \text{and so forth.}
\]

The orthogonality principle \(n \cdot V = 0\) (equivalent to \(n \cdot q_{ij} = 0, n \cdot h_j = 0, n \cdot h_{ij} = 0, \ldots\)) together with the property \(n \cdot q = 1\) implies \(q_{10} = (-\frac{g}{4F'(u_1^*)}, -\frac{g}{4F'(u_1^*)})^T, q_{01} = (-\frac{g}{4F'(u_2^*)}, -\frac{g}{4F'(u_2^*)})^T\) and \(h_2 = \frac{1}{832} (F'(u_2^*)^{3/2}F''(u_1^*) + F'(u_1^*)^{3/2}F''(u_2^*))\) and determines the coefficients from (8) and (9).
Therefore the projection on the center manifold is successful and it satisfies (7). The topological equivalence between (5) and (7) is then a direct consequence of the center manifold theorem [1], [7].

Remark 1. In this paper we took the Lyapunov-Schmidt projection approach to construct (7) from (5). However, a similar result is obtained if Carr’s center manifold reduction method is used [1]. If the latter approach is considered, the system under analysis will be system (5) together with an additional equation for \( \varepsilon \) \( (d\varepsilon/dt = 0) \). All \( U_1, U_2, y_1, y_2, \varepsilon \) are treated as variables and the reduction is made around the point \((0, 0, 0, 0; 0)\). It can be verified that at \((0, 0, 0, 0; 0)\) the linearization matrix of the 5-dimensional dynamical system has four zero eigenvalues and one negative eigenvalue \((-2)\), and that the theory developed by Carr applies.

System (1) can now be reduced to its fold normal form in the neighborhood of a point on the fold curve. The goal is to use the 3-dimensional system (7) and apply transformations that change the fast equation of \( \sigma \) into the fold normal form \( dz/dt = x + z^2 \) plus higher order terms.

Before we proceed let us mention that the coefficient \( b_{00} \) of \( \sigma^2 \) in (7) can take either sign. If \( u_1^* < u_0 < u_2^* \) we have \( F''(u_1^*) < 0 < F''(u_2^*) \); so \( b_{00} \) is negative. On the other hand if \( u_1^* > u_0 > u_2^* \) then \( F''(u_1^*) > 0 > F''(u_2^*) \) and \( b_{00} \) is positive. \((u_0)\) is the local minimum point of \( F'\); see page 72.) For example, let us take parameter values \( \beta = 1.1, g = 0.5, I = 1.315 \) and function \( S(x) = 1/(1 + e^{-r(x-\theta)}) \) with \( r = 10, \theta = 0.2 \). Then \( p_- = (0.2980253, 0.9587985, 0.2919871, 0.944903, 0.2919871) \in \mathcal{L}^- \) and by symmetry \( p_+ = (0.9587985, 0.2980253, 0.944903, 0.2919871) \in \mathcal{L}^+ \). Since \( u_0 = S(\theta) = 0.5 \) we have \( b_{00}(p_-) < 0 \) and \( b_{00}(p_+) > 0 \). In fact, in this example almost all points of \( \mathcal{L}^- \) have \( u_1^* < u_2^* \) and \( b_{00} < 0 \) while almost all points of \( \mathcal{L}^+ \) have \( u_1^* > u_2^* \) and \( b_{00} > 0 \). Only at the intersection of \( \mathcal{L}^- \cap \mathcal{L}^+ \) there are two points with \( b_{00} = 0 \); they satisfy \( u_1^* = u_2^* \) such that \( F'(u_1^*) = F'(u_2^*) = \beta \), and they correspond to a cusp bifurcation in the layer problem (not discussed here).

There are three main steps of the reduction to the normal form of the 3-dimensional fast-slow system (7): i) a timescale proportional to \( b_{00} \) followed by ii) a linear transformation depending on all variables \((\sigma, y_1, y_2)\), then iii) a close to linear change of variables depending only on \( y_1 \) and \( y_2 \). They are explained in detail in the proof of the next theorem.
**Theorem 2.** Let $\varepsilon$ be a sufficiently small positive number ($0 < \varepsilon \ll 1$), and parameters $I, \beta, \sigma$ such that system (1) has a fold curve $\mathcal{L}^\pm$.

Let $p \in \mathcal{L}^\pm$, $p = (u_1^*, u_2^*, a_1^*, a_2^*)$ be a point on the fold curve such that $b_{00} \neq 0$ where $b_{00}$ is defined by (8).

Then in the neighborhood of $p$, system (1) is topologically equivalent to

\begin{align*}
x' &= \alpha_0 + \alpha_1 y - \alpha_2 z + \mathcal{O}(\varepsilon, x, (y + z)^2), \\
y' &= \alpha_3 + \eta_2 y + \eta_3 z + \mathcal{O}(\varepsilon, x, (y + z)^2), \\
\varepsilon z' &= x + z^2 + \mathcal{O}(\varepsilon, \varepsilon(x + y + z), (x + y + z)^3) \tag{15}
\end{align*}

with coefficients

\[\alpha_0 = \frac{g}{2\beta b_{00}|b_{00}|} \left( \frac{u_1^* - a_1^*}{\sqrt{F'(u_1^*)}} - \frac{u_2^* - a_2^*}{\sqrt{F'(u_2^*)}} \right), \tag{16}\]

and

\begin{align*}
\alpha_1 &= -\frac{g^2}{8\beta^3 \sqrt{F'(u_1^*)}|b_{00}|^3} \left[ F''(u_1^*) \sqrt{F'(u_2^*)} + F''(u_2^*) \sqrt{F'(u_1^*)} \\
&\quad - F''(u_1^*) F''(u_2^*) \left( \frac{u_1^* - a_1^*}{2\sqrt{F'(u_1^*)}} + \frac{u_2^* - a_2^*}{2\sqrt{F'(u_2^*)}} \right) \right], \\
\alpha_2 &= \frac{g}{2\beta^2 b_{00}^2} [F'(u_1^*) + F'(u_2^*)], \quad \alpha_3 = \frac{u_1^* - a_1^*}{|b_{00}|}, \\
\eta_2 &= \frac{1}{|b_{00}|} \left( \frac{gF''(u_2^*)}{4\beta b_{00} \sqrt{F'(u_2^*)}} - 1 \right), \quad \eta_3 = -\frac{\sqrt{F'(u_2^*)}}{b_{00}}. \tag{17}
\end{align*}

**Proof.** Based on theorem 1 it is sufficient to show that system (7) is topologically equivalent to (15).

Scaling the time with $b_{00}$ allows us to reduce the coefficient of $\sigma^2$ to the unity in the fast equation. In order to maintain the initial orientation along the trajectories, we make the transformation independent of the sign of $b_{00}$. That is achieved with the time change $t \mapsto \tilde{t} = |b_{00}| t$ and the equation for $\sigma$ in (7) becomes $d\sigma/d\tilde{t} = \frac{1}{|b_{00}|} \left( c_{10} y_1 + c_{01} y_2 + c_{20} y_1^2 + c_{11} y_1 y_2 + c_{02} y_2^2 + b_{00} \sigma^2 + b_{10} \sigma y_1 + b_{01} \sigma y_2 + \cdots \right)$.

The next step is to group all second-order terms involving $\sigma$ into a unique term. We would like to have the coefficient of the quadratic term in the normal form equal to 1. For this reason, if $b_{00} < 0$ we need to consider a
reflection of the variable $\sigma$ according to $\sigma \mapsto (-\sigma)$. However this issue can be easily resolved if the coefficient of $\sigma$ in the new transformation is simply $b_{00}/|b_{00}|$; this will take care of the eventual sign change in the case of $b_{00} < 0$.

We define the linear change of variables $z = \frac{b_{00}}{|b_{00}|}\sigma + \frac{b_{10}}{2|b_{00}|}y_1 + \frac{b_{01}}{2|b_{00}|}y_2$ and use it to modify the fast equation. The new fast variable is $z$ and it satisfies the equation $\frac{dz}{dt} = \frac{c_{10}}{b_{00}}y_1 + \frac{c_{01}}{b_{00}}y_2 + \left(\frac{c_{20}}{b_{00}} - \frac{b_{10}^2}{4b_{00}^2}\right)y_1^2 + \left(\frac{c_{11}}{b_{00}} - \frac{b_{10}b_{01}}{2b_{00}^2}\right)y_1y_2 + \left(\frac{c_{02}}{b_{00}} - \frac{b_{01}^2}{4b_{00}^2}\right)y_2^2 + z^2 + O(\varepsilon, \varepsilon(z + y_1 + y_2), (z + y_1 + y_2)^2)$.

The slow equations of $y_1, y_2$ change as well and they become:

$$
\varepsilon^{-1}dy_1/d\tilde{t} = \frac{1}{|b_{00}|}(u_1^* - a_1^*) + y_1 \frac{1}{|b_{00}|} \left(-1 - \frac{a}{4F'(u_1^*)} + \frac{b_{10} \sqrt{F'(u_1^*)}}{2b_{00}}\right) - z \sqrt{F'(u_1^*)} + 
$$

$$
y_2 \frac{1}{|b_{00}|} \left(-g - \frac{b_{01}\sqrt{F'(u_2^*)}}{2b_{00}}\right) + O(\varepsilon, \varepsilon(z + y_1 + y_2), (z + y_1 + y_2)^2),
$$

$$
\varepsilon^{-1}dy_2/d\tilde{t} = \frac{1}{|b_{00}|}(u_2^* - a_2^*) + y_1 \frac{1}{|b_{00}|} \left(-\frac{b_{10}\sqrt{F'(u_1^*)}}{2b_{00}}\right) + z \sqrt{F'(u_1^*)} + 
$$

$$
y_2 \frac{1}{|b_{00}|} \left(-1 - \frac{g}{4F'(u_2^*)} - \frac{b_{01}\sqrt{F'(u_2^*)}}{2b_{00}}\right) + O(\varepsilon, \varepsilon(z + y_1 + y_2), (z + y_1 + y_2)^2).
$$

At last, we use an almost linear transformation to reduce the fast equation to the normal form of a fold bifurcation.

The change of variables $(y_1, y_2) \mapsto (x, y)$ defined by $x = \frac{c_{10}}{b_{00}}y_1 + \frac{c_{01}}{b_{00}}y_2 + \left(\frac{c_{20}}{b_{00}} - \frac{b_{10}^2}{4b_{00}^2}\right)y_1^2 + \left(\frac{c_{11}}{b_{00}} - \frac{b_{10}b_{01}}{2b_{00}^2}\right)y_1y_2 + \left(\frac{c_{02}}{b_{00}} - \frac{b_{01}^2}{4b_{00}^2}\right)y_2^2 + \ldots$ and $y = y_1$, and the change to slow time $t \mapsto \tilde{t} = \varepsilon \tilde{t}$ ($\tilde{t} = d/d\tilde{t}$) leads directly to system (15). Systems (15) and (1) are indeed topologically equivalent. □

**Remark 2.** The theory of canards associated with folded singularities is developed from the normal form of fast-slow systems with one fast and two slow equations [6]. Therefore this theory can be used as a tool in the study of the system (15); the latter is now in the required normal form. Previous studies on folded singularities and canards [6], [10] show that the first order $x$-terms in the $x$- and $y$- equations play no essential role in the analysis. For this reason we did not specifically include them here. But their coefficients can be calculated in a similar way to those in (16) and (17). For example, the coefficient $\eta_1$ of $x$ in the $y$- equation is: $\eta_1 = \frac{1}{|b_{00}|} \left(b_{00}\sqrt{F'(u_2^*)} - \beta F''(u_2^*)\right)$. Similarly, the coefficients of $\varepsilon$-terms in all equations can be determined and they are: $\hat{\varepsilon}_x = \frac{g^2}{16\beta^2 b_{00}^2 |b_{00}|} \left(\sqrt{F'(u_2^*)} - \sqrt{F'(u_1^*)}\right) \left(\frac{u_1^*-a_1^*}{\sqrt{F'(u_1^*)}} + \frac{u_2^*-a_2^*}{\sqrt{F'(u_2^*)}}\right)$, $\hat{\varepsilon}_y =$
4 An example of folded saddle-node singularity of type II in the neuronal model (1)

Through reduction to the normal form, the critical manifold $\Sigma$ of (1) has been transformed (up to the quadratic terms in (15) into the paraboloid $\tilde{\Sigma}$: $\mathcal{G}(x,y,z) = x + z^2 = 0$. The fold curve has been projected locally into a straight line, the $y$-axis. This is because the condition for fold is $\mathcal{G} = \mathcal{G}_z = 0$ that implies $x = z = 0$; so the projection of the fold curve $\mathcal{L}^\pm$ is $\{(0,y,0) : |y| < \delta\}$. The attractive branch $\tilde{\Sigma}_a^\pm$ is defined by $\mathcal{G}_z < 0$, i.e. $z < 0$ while the repelling branch $\tilde{\Sigma}_r$ is defined by $\mathcal{G}_z > 0$, or $z > 0$. The origin $(0,0,0)$ is the point on the resulting fold that corresponds to $p \in \mathcal{L}^\pm$.

The analysis of the trajectories along the paraboloid (critical manifold) $\tilde{\Sigma}$ in the neighborhood of $(0,0,0)$ can be done though a blow-up approach [6], [10]. Thus, starting from $x = -z^2$ we get $x' = -2zz'$ and so (15) implies $-2zz' = \alpha_0 + \alpha_1 y - \alpha_2 z + \mathcal{O}((y+z)^2)$ and $y' = \alpha_3 + \eta_2 y + \eta_3 z + \mathcal{O}((y+z)^2)$.

Last step clarifies why we did not particularly take into account the linear $x$-terms in the first two equations in (15); simply because they turn into higher order (quadratic) terms when computed on the critical manifold. So they do not change the system’s dynamical characteristics in the neighborhood of $(0,0,0)$ (see below).

The two-dimensional system in $z$ and $y$ is however singular at $z = 0$; but the blow-up technique deals with it by time-rescaling $\hat{t} \mapsto s = \hat{t}/(-2z)$ (notation: $\cdot = d/ds$). Therefore we obtain the so-called desingularized flow

$$\begin{align*}
\dot{z} &= \alpha_0 + \alpha_1 y - \alpha_2 z + \mathcal{O}((y+z)^2), \\
\dot{y} &= -2\alpha_3 z + \mathcal{O}((y+z)^2). 
\end{align*}$$

(18)

A point of the fold curve that is an equilibrium of the desingularized system without being an equilibrium of the original (full) system is called a folded singularity [6]. Therefore (assuming we work in the singular case $\varepsilon = 0$) let us check when $(0,0,0)$ satisfies this property for (15) and (18) respectively; we conclude that $(0,0,0)$ is a folded singularity if and only if $\alpha_0 = 0$ and $\alpha_3 \neq 0$. Based on equations (16) and (17) that is equivalent to

$$\frac{u_1^* - a_1^*}{\sqrt{F'}(u_1^*)} = \frac{u_2^* - a_2^*}{\sqrt{F'}(u_2^*)} \quad \text{with} \quad u_1^* \neq a_1^*, \ u_2^* \neq a_2^*.$$
For example, at $\beta = 1.1$, $g = 0.5$, $I = 1.343$ and function $S(x) = 1/(1 + e^{-r(x-\theta)})$ with $r = 10$, $\theta = 0.2$ we found at least one folded singularity: $p_f = (0.3307008, 0.9611521, 0.3124687, 0.9167623)$. Interesting, in the neighborhood of $p_f$ there exist an equilibrium of the full system (1) with coordinates $e = (0.32903, 0.95431, 0.32903, 0.95431)$. Obviously, $e$ satisfies the conditions $u_1 = a_1$ and $u_2 = a_2$ which are not true for $p_f$.

Assume in the following that $\alpha_0 = 0$ (and that $\varepsilon \approx 0$).

In the normal form (15), the equilibrium $e$ corresponds to the following point: $x = -z^2$, $z = \frac{a_1}{a_2}y$ and $\alpha_3 + \eta_2y + \eta_3z = 0$, that is $e$ maps into $\left( -\frac{a_1^2a_2^2}{(\eta_2a_2+\eta_3a_1)^2}, -\frac{\alpha_2a_3}{\eta_2a_2+\eta_3a_1}, -\frac{\alpha_1\alpha_3}{\eta_2a_2+\eta_3a_1} \right)$. However if $\alpha_3 \to 0$ then $e \to p_f$ (the regular singularity collides with the folded singularity $p_f$). This is the general case of the folded saddle-node singularity of type II analyzed in detail by Krupa and Wechselberger [6].

We can identify now what conditions system (1)’s parameters need to satisfy in order to have a folded saddle-node singularity of type II. They are $\alpha_3 = 0$ (and of course $\alpha_0 = 0$) together with the critical manifold and fold curve constraints. In terms of original system, these conditions become $u_1 = a_1$, $u_2 = a_2$ with $F(u_1) = I - \beta u_2 - ga_1$, $F(u_2) = I - \beta u_1 - ga_2$, and $F'(u_1)F'(u_2) = \beta^2$. Consequently, we get $I = F(u_1) + \beta u_2 + gu_1$ with $F'(u_1)F'(u_2) = \beta^2$ and $F(u_1) - F(u_2) = (g - \beta)(u_1 - u_2)$. A more detailed study of the system’s dynamics in the neighborhood of a folded saddle-node singularity of type II can be found in [3]. Here we only show that this particular type of points exists in (1).

**Theorem 3.** There exist values of parameters $\beta$, $g$, $I$ and gain functions $S$ such that system (1) has folded saddle-node singularities of type II.

**Proof.** It is enough to provide an example. As above, we consider $\beta = 1.1$, $g = 0.5$ and function $S(x) = 1/(1 + e^{-r(x-\theta)})$ with $r = 10$, $\theta = 0.2$. The value of $I$ results after solving for appropriate $u_1$ and $u_2$ solutions of the algebraic system $F'(u_1)F'(u_2) = \beta^2$ and $F(u_1) - F(u_2) = (g - \beta)(u_1 - u_2)$. That happens at about $u_1 = 0.2841539$ and $u_2 = 0.9575702$ and implies $I = 1.303009$. Therefore (independent of the value of parameter $\varepsilon$), at $\beta = 1.1$, $g = 0.5$, $I = 1.303009$ and $r = 10$, $\theta = 0.2$ in function $S(x) = 1/(1 + e^{-r(x-\theta)})$, system (1) has a type II folded saddle-node singularity. \qed
5 Discussion

We have investigated the existence of folded singularities in a neuronal rate model of reciprocally inhibitory populations. In particular, we found that folded saddle-nodes of type II exist and we constructed the normal form reduction of the system in their neighborhood. The importance of the folded saddle-node of type II stays in its property to have near it (through perturbation of the system’s parameters) of both a stable folded node and an unstable true equilibrium. The former generates a funnel through which canard solutions can pass while the latter modulates the canard trajectory through its stable/unstable manifolds (not shown). Therefore the presence of folded saddle-nodes of type II in this model offers a hint on where to search (in the parameter space) for more complex behaviors. Indeed, based on the results from this paper, a detailed geometrical description of the system in the neighborhood of a folded saddle-node of type II can be obtained. This will be presented in a future manuscript [3].

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References


