Interaction of Canard and Singular Hopf Mechanisms in a Neural Model

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Abstract. We consider an ordinary differential equation model for neural competition, presented previously in the study of binocular rivalry, which features two adapting populations of neurons interacting through mutual inhibition. This model is known to exhibit a variety of dynamic regimes, including mixed-mode oscillations (MMOs) featuring alternating small- and large amplitude oscillations, depending on the value of an input parameter. In this work, we use geometric dynamical systems techniques to study the structure of the model in the singular limit as well as the emergence of MMOs in the perturbed system. In particular, exploiting a normal form calculation allows us to numerically compute a way-in/way-out function, which we use to elucidate the interaction of canard and singular Hopf mechanisms for small amplitude oscillations that occur as the input parameter approaches a critical value.

Key words. neural competition, inhibition, mixed-mode oscillations, canards, singular Hopf bifurcation

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1. Introduction. Mixed-mode oscillations (MMOs) are intricate temporal activity patterns that arise in a variety of physical systems. They are periodic in time but show notable changes in amplitude, with each cycle featuring an alternation between small amplitude oscillations and large, fast excursions of relaxation type. Our motivation for studying MMOs comes from the realm of neuroscience. In vitro neural experiments reveal MMOs at both individual neuron and neuronal population levels. For example, intracellular recordings in the rat layer II medial entorhinal cortex identify a class of neurons, called stellate cells, that generate clusters of spikes interspersed with rhythmic subthreshold oscillations [1]. Likewise, population recordings from the pre-Bötzinger complex of neonatal rat brainstem show periodic modulation of the inspiratory component of the respiratory rhythm caused by an increase in neuronal excitability; several types of oscillatory patterns can occur, including MMOs [9]. More recently, MMOs have been found in several computational neuroscience models that use the Hodgkin–Huxley formalism and feature multiple time scales, and the underlying dynamic mechanisms have been studied [13], [26], [27], [25], [16], [30].

In this paper we study the existence of MMOs in a reduced neuronal competition model posed in a firing rate formulation [24], [28]. Compared to Hodgkin–Huxley-type models, this model is significantly simpler, while still very rich in behavior. The system consists of four
ordinary differential equations, involves slow negative feedback and gain function nonlinearities, and depends on a control parameter associated with an external constant stimulus. The relatively simple form of the system is highly advantageous in that it allows for a thorough analytical and numerical investigation, which uncovers an interesting property: the MMO solutions of this system are periodic canards, featuring significant excursions along unstable slow manifolds [3], [14], but their small amplitude oscillations result from the combined effects of canard-induced rotations and proximity to a spiraling unstable manifold of a nearby equilibrium point (Hopf-induced rotations).

As the study of MMOs has developed, the dynamics associated with canard-induced MMOs [29], [32], [5] and Hopf-induced MMOs [18], [19] were separately investigated, although example systems in which an equilibrium point with complex unstable eigenvalues exists near and interacts with a folded node singularity did come to light [21], [26], [25], [33], [23]. Together, one other very recent paper [10] and this work are the first to provide a detailed study of the interaction of canard and singular Hopf mechanisms for the generation of small amplitude oscillations. These two independent works are quite different in scope. The lengthy review paper by Desroches et al. [10] surveys identified types of MMOs, classified by the dynamic mechanisms that generate them, and presents results on several examples, illustrating some of the phenomena associated with particular MMO types. The present paper focuses on a specific system and provides a coherent, relatively detailed case study, progressing from the identification of the ingredients that can conspire to produce MMOs in this system through a variety of calculations that are used to characterize the properties of the system’s MMO patterns. It is our hope that by pulling together tools for the study of MMOs that were originally spread across several papers and by presenting sufficient details of the associated calculations for a particular system, we will provide a useful example for others aiming to apply similar methods. Moreover, one of the ideas that we use to explore the interaction of canard-induced and Hopf-induced rotations is the way-in/way-out function [23], and our work provides what is to our knowledge the first numerical illustration of how this function can be used to gain information about MMOs arising in a particular model problem.

The paper is organized as follows. In section 2, we describe the mathematical model that we consider and the dynamics that emerges under variation of the strength of an external stimulus applied to the modeled neuronal populations. MMOs are among the temporal patterns that are observed, and we subsequently focus on the parameter range where they appear. Section 3 provides a geometrical analysis of the system in this range in the singular limit, showing the existence of special points known as folded saddle-node singularities of type II and the existence of singular canards. In sections 4 and 5, we study the full (perturbed) system by several methods: normal form reduction techniques, a geometrical construction of the slow manifold of the system in the neighborhood of a folded node, and construction of a way-in/way-out function. In particular, these tools allow us to test directly whether both canard-induced and Hopf-induced small amplitude oscillations are present in MMOs occurring for specific parameter values and to demonstrate the existence of MMOs that do display oscillations of both types. Subsequently, in section 6, we interpret the existence of MMOs with respect to the bifurcation diagram of the full system. Finally, in the last section of the paper, we discuss our results and summarize our conclusions.
2. MMOs in an inhibitory network with adaptation. We investigate the mechanism underlying the formation of MMOs in a model for two interacting populations of neurons to which a constant external stimulus is applied. In the model, each population is characterized by an activity measure consisting of a time-dependent firing rate \( u \) and by an adaptation variable \( a \), such that \( a \) is driven by, and acts as a negative feedback on, \( u \). In addition to these interactions, the firing of each population acts to inhibit the activity of the other population. The model takes the form

\[
\begin{align*}
du_1/dt &= -u_1 + S(I - \beta u_2 - ga_1), \\
du_2/dt &= -u_2 + S(I - \beta u_1 - ga_2), \\
\tau da_1/dt &= -a_1 + u_1, \\
\tau da_2/dt &= -a_2 + u_2.
\end{align*}
\]

(2.1)

The parameters \( \beta, g, \) and \( \tau \) are positive and correspond to the intensity with which each population inhibits the other’s firing (\( \beta \)), the strength of adaptation (\( g \)), and the time scale on which adaptation evolves (\( \tau \)). Note that we have assumed that the adaptation process depends linearly on firing rate, but our analytical approach can easily be extended to the case of nonlinear adaptation. Based on the behavior observed in certain neuronal networks, we assume that adaptation is slow, which yields the condition \( \tau \gg 1 \). The external stimulation applied to both neural populations is modeled by the positive parameter \( I \). The function \( S \) represents the nonlinear gain through which inputs to a population affect its firing rate. This function has a sigmoidal shape, often modeled by \( S(x) = 1/(1 + e^{-r(x-\theta)}) \), with parameters \( r > 0 \) and \( \theta \in \mathbb{R} \) used to control its slope and activation threshold. In this paper, although we will use this form of \( S(x) \) for numerical illustrations, we will allow a more general definition for \( S \) as a typical sigmoid. Specifically, we assume that \( S \) is smooth, increases monotonically from \( \lim_{x \to -\infty} S(x) = 0 \) to \( \lim_{x \to \infty} S(x) = 1 \), and changes its convexity (from concave up to concave down) at the threshold value \( x = \theta \). Consequently, \( S \) is invertible, and its inverse \( F := S^{-1} \) satisfies \( \lim_{u \to 0} F(u) = -\infty, \lim_{u \to 1} F(u) = \infty, \lim_{u \to 0} F'(u) = \lim_{u \to 1} F'(u) = \infty, F''(u) < 0 \) for \( u \in (0, u_0) \), \( F''(u) > 0 \) for \( u \in (u_0, 1) \), \( F''(u_0) = 0 \), and \( F'(u_0) = \min(F') \) > 0, where \( u_0 \) is defined as \( u_0 = S(\theta) \).

Recent analytical and numerical studies \[8\], \[28\] show that, under appropriate parameter tuning, the dynamics of system (2.1) changes with \( I \) from (i) a trivial steady state regime in which \( u_1 = u_2 \) (and so, according to the adaptation equations in (2.1), \( a_1 = a_2 = 0 \)), to (ii) an antiphase oscillatory regime, and then to (iii) a bistable regime of nontrivial steady states \( (u_1 \neq u_2) \), say \( e_{st} = (u_{1f}, u_{2f}, u_{1i}, u_{2i}) \) and \( e_{II} = (u_{1f}, u_{1i}, u_{2f}, u_{2i}) \) (Figure 1). The latter is called a winner-take-all regime because it corresponds to the case when, possibly after some transients, one neural population stays active/dominant indefinitely while the other is suppressed. We note that the bifurcation diagram is symmetric with respect to the parameter \( I \), in the sense that regimes of attraction to the trivial equilibrium, say \( e_I = (u_I, u_I, u_I) \), and to oscillations exist for symmetric intervals of \( I \) values above and below the winner-take-all interval. In Figure 1, stable (unstable) equilibria at a given value of \( I \) are represented by points on the thick (dashed) lines; oscillatory solutions are drawn as branched curves of circles with filled circles (open circles) for stable (unstable) orbits. The upper and lower points on these branched curves correspond to the maximum and minimum amplitudes of the oscillation.
Figure 1. Bifurcation diagram of firing rate $u_1$ versus input parameter $I$ for $\beta = 1.1$, $g = 0.5$, $\tau = 100$, and gain function $S(x) = 1/(1 + e^{-(x-\theta)})$ with $r = 10$, $\theta = 0.2$. As $I$ is decreased (increased), the trivial equilibrium $e_I$ loses stability through a supercritical Hopf bifurcation at $I_{HB1} = 1.854$ ($I_{HB2} = 0.1464$). Additional nontrivial equilibria $e_{sI}$ and $e_{iI}$ emerge at a subcritical pitchfork bifurcation at $I_{P1} = 1.594$ (or $I_{P2} = 0.4064$); they become stable simultaneously at a subcritical Hopf point $I_{sH1} = 1.309$ (or $I_{sH2} = 0.6909$). Thick (dashed) lines correspond to stable (unstable) equilibria; filled (open) circle branched curves correspond to stable (unstable) periodic orbits.

The types of dynamics described above occur if network (2.1) satisfies an adaptation (negative feedback)-dominated system condition and a relatively strong inhibition condition [8]. In terms of parameters, these conditions are equivalent to $\beta < g(\tau + 1)$ and $\beta > (1+1/\tau)/S'(\theta)$, which can easily be achieved for large enough $\tau$.

The trivial steady state $e_I$ exists for all values of $I$, but it becomes unstable through a supercritical Hopf bifurcation (HB). The additional equilibria $e_{sI}$ and $e_{iI}$ emerge at a subcritical pitchfork bifurcation (P), and they inherit unstable modes from their "parent" fixed point $e_I$. Therefore, both $e_{sI}$ and $e_{iI}$ have two eigenvalues with positive real part and two eigenvalues with negative real part. Due to the multidimensionality of the eigenspace, the trivial equilibrium $e_I$ does not change its stability properties at P, although one of its eigenvalues takes a zero value there and becomes stable beyond the bifurcation. The system enters the winner-take-all regime through a subcritical Hopf bifurcation (sH), where $e_{sI}$ and $e_{iI}$ become simultaneously stable.

More complex dynamics, in the form of MMOs, occurs at the transition between oscillatory and winner-take-all regimes [7]. A magnified view of the bifurcation diagram from Figure 1 to the right of $I_{sH1}$ has identified a cascade of period-doubling and Neimark–Sacker points through which the periodic orbits lose stability [7]. From $I_{sH1}$ up to this cascade, neither the periodic orbits nor the equilibria $e_I$, $e_{sI}$, $e_{iI}$ are stable. However, for these values of $I$, numerical simulations of (2.1) reveal stable oscillatory patterns that combine small amplitude cycles with large excursions of relaxation type, which are the MMOs (Figure 2). The number of small amplitude oscillations in the MMOs increases significantly as $I$ decreases toward $I_{sH1}$, and each population spends more time in both dominant (up) and suppressed (down) states present for each value of $I$. 

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of the relaxation cycles. A similar sequence of dynamics is seen just to the left of $I_{sH_2}$.

To study MMOs, we now focus on the interval of $I$ close to $I_{sH_1} = 1.309$; for simplicity, we will just call this value $I_{sH}$. The occurrence of small amplitude oscillations can be explained, at least partially, through the presence of a singular Hopf point $I_{singH}$ \cite{7} defined by

$$
\begin{align*}
I_{singH} &= F(\tilde{u}_1) + g\tilde{u}_1 + \beta \tilde{u}_2, \\
F(\tilde{u}_1) - F(\tilde{u}_2) + (g - \beta)(\tilde{u}_1 - \tilde{u}_2) &= 0, \\
F'(\tilde{u}_1)F'(\tilde{u}_2) &= \beta^2.
\end{align*}
$$

For example, for parameter values $\beta = 1.1, g = 0.5$, and function $S(x) = 1/(1 + e^{-r(x-\theta)})$ with $r = 10$ and $\theta = 0.2$, system (2.1) has a singular Hopf point at $I_{singH} = 1.303$.

A normal form construction about $I_{singH}$ shows that the subcritical Hopf value $I_{sH}$ exists in an $O(1/\tau)$ neighborhood of $I_{singH}$ ($I_{sH} > I_{singH}$) and $I_{sH} \rightarrow I_{singH}$ as $1/\tau \rightarrow 0$. Moreover, for $I$ close to $I_{sH}$ with $I > I_{sH}$, the orbit of a point situated near the unstable equilibrium $e_{sI}$ (or $e_{dI}$) rotates several times around the equilibrium, with very slowly increasing amplitude, before leaving its vicinity. The rotational properties result from the fact that the equilibrium $e_{sI}$ (or $e_{dI}$) has two complex conjugate eigenvalues $\lambda_{1,2}(I)$ with positive real part; the slow increase in amplitude is a consequence of having real and imaginary parts of different order of magnitude \cite{7}. In brief, the name singular Hopf for $I_{singH}$ comes from the fact that the ratio $\text{Re}(\lambda_{1,2}(I))/\text{Im}(\lambda_{1,2}(I))$ is of $O(1/\sqrt{\tau})$ order as $1/\tau \rightarrow 0$ \cite{2,4}. How a point on the full MMO trajectory of system (2.1) can repeatedly approach near $e_{sI}$ or $e_{dI}$ remains an open question.

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**Figure 2.** MMOs in the full system obtained at three different values of the stimulation parameter: (A) $I = 1.325$, (B) $I = 1.322$, and (C) $I = 1.315$. As can be seen in the full time courses and the zoomed views shown below them, the number of small amplitude oscillations and the time spent between large excursions increase as $I$ decreases toward the subcritical Hopf bifurcation point $I_{sH_1} = 1.309$. (Other parameter values are $\tau = 100$, $\beta = 1.1$, $g = 0.5$, $r = 10$, and $\theta = 0.2$.)
A primary goal of the present paper is to clarify this issue, along with the mechanisms shaping the behavior of such a trajectory during its approach.

In the case of relaxation oscillations, the global behavior of trajectories of (2.1) for appropriate values of $I$ can be explained through a slow-fast analysis: the up and down states correspond to the epochs in which a trajectory moves along the attractive branches of a slow manifold of (2.1), and transitions between these states take place along fast fibers once a fold curve (or curve of jump points) is reached (see section 3 for more details). Typically, since $e_{sI}$ and $e_{I}$ lie on the repelling branch of the slow manifold, they cannot be closely approached by a point moving along the attractive branches. Nevertheless, there is a special situation when a trajectory of the full system may approach the repelling region of the slow manifold, and remain there for finite time, before jumping away along fast fibers. A trajectory exhibiting this behavior is termed a canard [5], [29] and may exist when the fold curve includes a certain form of defect. The latter is a singularity on the fold curve that acts like a pore, allowing trajectories that enter a special region (the funnel) to pass through it from the attractive to the repelling side of the slow manifold. For this to happen, the singularity needs to be a special type of point, either a folded node or a folded saddle.

The canard phenomenon offers a reasonable mechanism for bringing a point on an MMO of system (2.1) close to $e_{sI}$ (and $e_{I}$, due to the system’s symmetry), where small amplitude oscillations can ensue. To test this idea, we will analyze the dynamics of system (2.1) on the slow manifold close to the fold curve. We will show that, indeed, in a small interval of $I$ values to the right of $I_{sH}$ ($I > I_{sH}$), there exists a stable folded node on the fold curve. Moreover, this folded node lies in the neighborhood of $e_{sI}$ ($e_{I}$).

Before proceeding, we need to clarify one more thing. The theory of canards [5], [29], [23] proves that trajectories of the full system that enter the funnel of the folded node close to a distinguished primary weak canard solution undergo local rotations prior to the fast jump. Therefore, MMOs can occur simply due to small amplitude oscillations in the canard funnel followed by large excursions of relaxation type. In this case, the regular (true) singularity of the full system ($e_{sI}$ or $e_{I}$ in our example) plays no role. On the other hand, as mentioned above, the influence of the singular Hopf point $I_{singH}$ near $I_{sH}$ indicates that $e_{sI}$, $e_{I}$ may be important in structuring MMO solutions of system (2.1), and the presence of a folded node singularity offers the opportunity for trajectories to approach these points. The question is, can we distinguish between these two mechanisms for the generation of small amplitude oscillations, the ingredients for which are present in system (2.1)?

We will show in this paper that system (2.1) has an interesting feature: at the transition from oscillatory to winner-take-all regimes, as $I$ is decreased toward $I_{sH}$, MMOs emerge through a classical folded node canard-induced mechanism. As $I$ is decreased more, however, the resulting MMOs are influenced by both the canard and singular Hopf oscillation mechanisms. Although previous works identified scenarios in which folded nodes and true saddle points were found in close proximity to each other, their relative contributions to small amplitude oscillations within MMOs have not received analytical treatment until recently. An illustration of how varying a parameter allows the Hopf mechanism to start influencing an MMO solution, including beautiful numerical renderings of relevant manifolds for a pair of parameter values before and after this influence emerges, is given in a recent work done independently of ours [10]. In our work, we demonstrate how new way-in/way-out calcula-
Figure 3. Projection of the critical manifold $\Sigma$ on the three-dimensional space $(u_1, a_1, a_2)$ for parameter values $I = 1.4$, $\beta = 1.1$, $g = 0.5$ and gain function $S(x) = 1/\left(1 + e^{-r(x-\theta)}\right)$ with $r = 10$, $\theta = 0.2$ (and inverse $F(u) = \theta + \frac{1}{2} \ln \left(\frac{1}{1+u}\right)$).

tions can be used to estimate for what parameter values the true equilibrium affects the small amplitude oscillations and which oscillations can be attributed to such effects.

3. Geometric analysis of the system in the singular limit case.

3.1. The critical manifold and desingularized reduced flow. We use singular perturbation methods to study the mechanism underlying the formation of MMOs in system (2.1). First, let us write system (2.1) in the form

$$
\begin{align*}
\varepsilon u_1' &= -u_1 + S(I - \beta u_2 - ga_1), \\
\varepsilon u_2' &= -u_2 + S(I - \beta u_1 - ga_2), \\
a_1' &= -a_1 + u_1, \\
a_2' &= -a_2 + u_2
\end{align*}
$$

with $\varepsilon = 1/\tau \to 0$ and the time derivative taken with respect to $\hat{t} = t/\tau$ (i.e., $' = d/d\hat{t}$).

In the singular limit case the system’s dynamics is determined from the solution of two problems. On one hand, we need to solve the reduced system (or slow subsystem) $a_1' = -a_1 + u_1$, $a_2' = -a_2 + u_2$ obtained by setting $\varepsilon = 0$ in (3.1). In this case $u_1$ and $u_2$ are implicit functions of $a_1, a_2$, and the dynamics takes place along the critical manifold $\Sigma$ defined by $-u_1 + S(I - \beta u_2 - ga_1) = 0$ and $-u_2 + S(I - \beta u_1 - ga_2) = 0$. As typically seen in the theory of relaxation oscillators, the projection of $\Sigma$ on the space of one fast and two slow variables (Figure 3) is a cubic-shaped surface:

$$
\Sigma : \left\{ \begin{array}{l}
\mathcal{F}(u_1, a_1, a_2) = I - F(u_1) - \beta S(I - \beta u_1 - ga_2) - ga_1 = 0, \\
u_2 = S(I - \beta u_1 - ga_2)
\end{array} \right.
$$

We can express $\Sigma = \Sigma_a^- \cup \Sigma_a^+ \cup \Sigma_r \cup \mathcal{L}^\pm$ with attracting lower and upper branches $\Sigma_a^\pm$, $\Sigma_a^- \cup \Sigma_a^+$ := $\{(u_1, a_1, a_2) \in \Sigma : \mathcal{F}_{u_1}(u_1, a_1, a_2) < 0\}$, repelling middle branch $\Sigma_r := \{(u_1, a_1, a_2) \in \Sigma :$
Nevertheless, if one wants to characterize the trajectories of (3.1) in the neighborhood of points $P$ in the fast subsystem; specifically, $\Sigma$ can have either three, two, or one equilibrium point (as indicated by the cubic shape of $\Sigma$).

The layer problem describes its dynamics along the fast fibers connecting branches $\Sigma$ characterized by the condition

$$L^\pm : \quad F'(u_1)F'(u_2) = \beta^2$$

together with (3.2). In addition, $L^-$ is defined by $F_{u_1} u_1 > 0$ (local minima of $F$ with respect to $u_1$), and $L^+$ is defined by $F_{u_1} u_1 < 0$ (local maxima). On the fold curve, the condition $F_{u_1} u_1 \neq 0$ is equivalent to $F'(u_1)^{3/2}F''(u_2) - F'(u_2)^{3/2}F''(u_1) \neq 0$, which implies $u_1 < u_2$ along $L^-$ and $u_1 > u_2$ along $L^+$. (This is true for function $S$ shown in Figure 3. Moreover, for such $S$, it can be proven that $F_{u_1} u_1 = 0$ exactly at two points, with coordinates $u_1 = u_2 > 0.5$ with $F'(u_1) = F'(u_2) = \beta$, and $u_1 = u_2 < 0.5$ with $F'(u_1) = F'(u_2) = \beta$, respectively.)

The other problem that needs to be solved is the so-called layer problem (or fast subsystem),

$$
\begin{align*}
\frac{du_1}{dt} &= -u_1 + S(I - \beta u_2 - ga_1), \\
\frac{du_2}{dt} &= -u_2 + S(I - \beta u_1 - ga_2),
\end{align*}
$$

which results from (2.1) with $\varepsilon = 1/\tau = 0$. In this case the slow variables $a_1$ and $a_2$ are constant, say $a_1 = a_0^0$, $a_2 = a_0^2$, while $u_1$ and $u_2$ change rapidly. The critical manifold $\Sigma$ is the set of equilibria of the layer problem. Depending on the values of $a_1$ and $a_2$, the layer problem can have either three, two, or one equilibrium point (as indicated by the cubic shape of $\Sigma$ itself). The transition from three to one equilibrium is due to fold (saddle-node) bifurcations in the fast subsystem; specifically, $\Sigma^-_t$ and $\Sigma^r$ meet at $L^-$, and $\Sigma^+_t$ and $\Sigma^r$ meet at $L^+$. The points of $L^\pm$ are projected along fast fibers of the layer problem onto the opposite attracting branch of $\Sigma$; i.e., if $P$ is the projection map, then $P(L^-) \subset \Sigma^+_a$ and $P(L^+) \subset \Sigma^-_a$.

A singular periodic orbit $\Gamma$ of system (3.1) is a piecewise smooth closed curve that consists of solutions $\Gamma^\pm_a$ of the reduced system which are then concatenated with solutions $\Gamma^-_{-+}$, $\Gamma^+_{+-}$ of the layer problem. $\Gamma^\pm_a$ connect points along $\Sigma^\pm_a$ from the projection curves $P(L^\pm)$ to the fold curves $L^\pm$, while $\Gamma^-_{-+}$ and $\Gamma^+_{+-}$ connect points on $L^- \subset \Sigma^-_a$ to its projection $P(L^-) \subset \Sigma^+_a$ and points on $L^+ \subset \Sigma^+_a$ to its projection $P(L^+) \subset \Sigma^-_a$, respectively. That is, $\Gamma = \Gamma^-_a \cup \Gamma^-_{-+} \cup \Gamma^+_{+} \cup \Gamma^+_{+-}$ (see Figure 5(A)–(B) below, for example).

Let $p^\pm_a$ be the points of intersection between $\Gamma^\pm_a$ and the curves $L^\pm$. As explained above, the reduced system describes the dynamics of system (3.1) on the critical manifold $\Sigma$, while the layer problem describes its dynamics along the fast fibers connecting branches $\Sigma^\pm_a$. Nevertheless, if one wants to characterize the trajectories of (3.1) in the neighborhood of points $p^\pm_a$ and to understand how jumps occur, an alternative approach is necessary. In this context, along $\Gamma^-_a$ in the vicinity of $p^-$ (and similarly for $\Gamma^+_a$ and $p^+$), it becomes important to monitor simultaneously the (slow) time evolution of both groups of variables $a_1$, $a_2$ and $u_1$, $u_2$. This can be done by interpreting solution $\Gamma^-_a$ as an implicit function of slow time $\tilde{t}$ defined on $\Sigma$ according to (3.2). It should satisfy the differential equation $F_{u_1} u'_1 + F_{a_1} a'_1 + F_{a_2} a'_2 = 0$ and therefore the two-dimensional system

$$
\begin{align*}
-F_{u_1} u'_1 &= F_{a_1} (-a_1 + u_1) + F_{a_2} (-a_2 + u_2), \\
a'_1 &= -a_1 + u_1
\end{align*}
$$

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with
\[ u_2 = u_2(u_1, a_1) = (I - F(u_1) - ga_1)/\beta, \]
\[ a_2 = a_2(u_1, a_1) = (I - \beta u_1 - F(u_2))/g, \]
(3.6)

System (3.5) has the advantage of coupling together slow \((a_1)\) and fast \((u_1)\) variables of the original system (3.1). Although the equation for \(u'_1\) in (3.5) is singular along the fold curve \(L^\pm\), this singularity can be addressed by rescaling time \(t \to \tilde{t} = t/(-\mathcal{F}_{u_1})\) (see [5], [29]) such that system (3.5) becomes \(du_1/d\tilde{t} = \mathcal{F}_{a_1}(-a_1 + u_1) + \mathcal{F}_{a_2}(-a_2 + u_2), \) \(da_1/d\tilde{t} = (-a_1 + u_1)(-\mathcal{F}_{u_1})\). A straightforward calculation of \(\mathcal{F}_{u_1}, \mathcal{F}_{a_1}, \) and \(\mathcal{F}_{a_2}\) on the critical manifold leads to the desingularized reduced flow
\[ \frac{du_1}{d\tilde{t}} = -g(-a_1 + u_1) + (-a_2 + u_2) \frac{\beta g}{F'(u_2)}, \]
\[ \frac{da_1}{d\tilde{t}} = \frac{1}{F'(u_2)} (F'(u_1)F'(u_2) - \beta^2) (-a_1 + u_1), \]
(3.7)
with \(u_2\) and \(a_2\) as in (3.6).

**Remark 1.** It is worth noting that the desingularization process changes the direction of flow along orbits situated on the repelling side \(\Sigma_r\) of the critical manifold (since \((-\mathcal{F}_{u_1}) < 0\) on \(\Sigma_r\) while maintaining the original flow direction for orbits belonging to \(\Sigma^\pm_d\). The phase diagram of the desingularized reduced flow (3.7) needs to be interpreted in this context.

Equilibria of the desingularized system (3.7) can either satisfy (i) \(-a_1 + u_1 = 0\) and \(-a_2 + u_2 = 0\), in which case they identify with equilibria of the original system (2.1) and are called regular (or ordinary) singularities, or (ii) \(F'(u_1)F'(u_2) = \beta^2\) and \((-a_1 + u_1) = \frac{\beta}{F'(u_2)}(-a_2 + u_2)\) with \(-a_1 + u_1 \neq 0\), in which case they are not equilibria of the original system but particular points on the fold curve \(L^\pm\), say \(p^\pm_s\), which are called folded singularities [29]. Each folded singularity of (3.7) is classified based on its eigenvalues as a folded focus, folded node, folded saddle, or folded saddle-node point.

As it results from (ii) above, the folded singularity condition for system (2.1) is
\[ \frac{u_1 - a_1}{\sqrt{F'(u_1)}} = \frac{u_2 - a_2}{\sqrt{F'(u_2)}} \]
(3.8)
together with (3.3) and (3.2).

**3.2. Preliminaries on folded singularities and canards.** The importance of folded singularities in slow-fast systems derives from the fact that they provide the opportunity for the reduced flow to cross from \(\Sigma^\pm_d\) to \(\Sigma_r\). From a \(\Sigma_a\)-neighborhood of a folded singularity most trajectories exit, as normally expected, along fast fibers of a slow-fast system such as (3.1). However, some trajectories may cross the fold curve \(L^\pm\) and exit along the slow directions near the repelling part \(\Sigma_r\) of the critical manifold. In the latter case, if trajectories return to the same \(\Sigma_a\)-neighborhood by the global dynamics of the combined slow and fast subsystems, they are called singular canards. The theory of singular canards extends to the \(\varepsilon\)-perturbed slow-fast system through blow-up techniques that allow for the construction of slow manifolds \(O(\sqrt{\varepsilon})\) close to \(L^\pm\) [23], [32].
An interesting case, relevant to the system we analyze in this paper, is that of the folded saddle-node of type II (FSN II). This situation requires the nearby existence of two singularities of the desingularized flow (3.7): a (stable) folded node and a true saddle singularity (see, for example, singularities $N_1$ and $S_1$ in Figure 4(D)). As parameter $I$ changes in (2.1) from the oscillatory regime toward the winner-take-all regime, the folded node and ordinary saddle singularity of (3.7) move closer, merge, and then split again, interchanging their type and stability. Therefore the change in stability occurs at a transcritical bifurcation in system (3.7); the corresponding point $p_s$ on $\mathcal{L}^\pm$ is called an FSN II. (By contrast, a folded saddle-node of type I would correspond to the generic case when both the node and the saddle in system (3.7) are folded singularities, and they merge and then disappear through a classical
saddle-node bifurcation [23].)

Consider values of $I$ in the neighborhood of the point where the FSN II exists, just before the transcritical bifurcation occurs. For these values, system (3.7) has a stable folded node, say $N_1$, and an ordinary saddle singularity $S_1 \in \Sigma_r$. A local analysis near $N_1$ reveals the existence of a singular strong canard (corresponding to the strong stable eigendirection of $N_1$) and of a trapping sector on $\Sigma^+_\alpha$ \textit{(the funnel)}, which is bordered by the strong canard, the folded node, and the curve $\mathcal{L}^\pm$. Trajectories in the funnel that are exponentially close to the strong canard cross $\mathcal{L}^\pm$ and follow along the repelling manifold $\Sigma_r$ but show no oscillations near $N_1$. By contrast, other trajectories within the funnel may be attracted to the weak canard (associated with the weak eigendirection of $N_1$), which imparts rotational properties to them. The FSN II case has an important special feature not present in the usual folded node case [23]: under the flow of (3.7), there exists a one-dimensional \textit{orbital connection} $\gamma_{N_1S_1}$, a trajectory lying in $\Sigma_r$ that connects $S_1$ to $N_1$. Under the regular reduced flow (3.5), the orbital connection $\gamma_{N_1S_1}$ reverses direction, since it lies in $\Sigma_r$, and hence provides a connection from $N_1$ to $S_1$. Trajectories of (3.5) that pass through the funnel and end up in the neighborhood of $\gamma_{N_1S_1}$ are induced to undergo additional rotations as they follow it and, furthermore, can be pushed very close to the ordinary singularity $S_1$. Since $S_1$ is an unstable equilibrium of the original system, its unstable manifold $W^u_{S_1}$ can and in most instances will interfere with the slow dynamics on $\Sigma_r$ before the jump along fast fibers occurs (see next sections for details). To understand the formation of MMOs in the neighborhood of an FSN II, a careful blow-up analysis about $N_1$ will be done in section 4.

\subsection*{3.3. Existence of FSN II singularities for network (2.1).} According to the existing theory, the formation of MMOs in system (2.1) may involve a canard mechanism only if stable folded node singularities exist in some parameter range. Since numerical simulations show MMOs for values of $I$ at the border region between the oscillatory and the winner-take-all regimes (Figures 1 and 2), we will use the simulations as a clue about the parameter range in which to search for such singularities.

We decrease $I$ in the direction of the winner-take-all regime (see the right-hand side of the bifurcation diagram in Figure 1) and monitor the corresponding desingularized phase plane. Equilibria, their type and stability, as well as representative trajectories of (3.7) were numerically identified with XPPAUT [15] and illustrated in Figure 4. (Note that part of the $a_1$-nullcline is a closed curve associated with $\mathcal{L}^\pm$; its interior represents the projection of the repelling part $\Sigma_r$ of the critical manifold, while its exterior corresponds to the attractive surface $\Sigma^-_\alpha \cup \Sigma^+_\alpha$. Note that $\Sigma^-_\alpha \cup \Sigma^+_\alpha$ forms a connected set in this projection because the folds $\mathcal{L}^\pm$ come together and terminate in the full higher-dimensional phase space.)

We find that the desingularized system has nine equilibrium points, out of which four are saddles, one is an unstable node, two are attractive foci, and two are either attractive foci or nodes (Table 1). Due to condition (3.8) and the symmetry of system (2.1), the folded singularities come in pairs of similar types: $(S_3, S_4)$, $(F_3, F_4)$, and either $(F_1, F_2)$ or $(N_1, N_2)$. For example, coordinates $u^*_1$, $a^*_1$ of $N_2$ are equal to coordinates $u^*_2$, $a^*_2$ of $N_1$ and vice versa, and their eigenvalues are scaled by the positive factor of $F'(u^*_1)/F'(u^*_2)$. This relation holds because the eigenvalues $\lambda_1$, $\lambda_2$ of any folded singularity $(u^*_1, a^*_1)$ of (3.7) satisfy the conditions

$$\lambda_1 + \lambda_2 = \frac{g}{F'(u^*_2)}(F'(u^*_1) + F'(u^*_2)),$$

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Types of equilibria of the desingularized system as illustrated in Figure 4.

<table>
<thead>
<tr>
<th>Parameter value</th>
<th>Ordinary singularities</th>
<th>Folded singularities</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I = 1.5$</td>
<td>$S_{1,2}$ Saddle</td>
<td>$F_{1,2}$ Stable foci</td>
</tr>
<tr>
<td></td>
<td>$N$ Unstable node</td>
<td>$F_{3,4}$ Stable foci</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{1,4}$ Saddle</td>
</tr>
<tr>
<td>$I = 1.376$</td>
<td>$S_{1,2}$ Saddle</td>
<td>$N_{1,2}$ Stable nodes</td>
</tr>
<tr>
<td></td>
<td>$N$ Unstable node</td>
<td>$F_{3,4}$ Stable foci</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{1,4}$ Saddle</td>
</tr>
<tr>
<td>$I = 1.315$</td>
<td>$S_{1,2}$ Saddle</td>
<td>$N_{1,2}$ Stable nodes</td>
</tr>
<tr>
<td></td>
<td>$N$ Unstable node</td>
<td>$F_{3,4}$ Stable foci</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_{1,4}$ Saddle</td>
</tr>
</tbody>
</table>

$$\lambda_1 \lambda_2 = \frac{\beta q^2 (u_1^* - a_1^*)}{F'(u_2^*)^2 \sqrt{F''(u_1^*)}} \left( - F''(u_1^*) F'''(u_2^*) \frac{u_1^* - a_1^*}{\sqrt{F'(u_1^*)}} + F'''(u_1^*) \sqrt{F''(u_2^*)} + F''(u_2^*) \sqrt{F'(u_1^*)} \right)$$

with $u_2^*$ defined by (3.6). Consequently, the change from folded focus to folded node occurs simultaneously for points $N_1$ and $N_2$.

The left branch of the strong stable manifold of the folded node $N_1$, together with fold curve $L^-$, forms the border of a trapping region on $\Sigma_a^-$. All trajectories starting in this trapping region remain there and are attracted to $N_1$. This is the funnel of the folded node $N_1$; for example, in Figure 4(D) and (F) the funnel of $N_1$ is the region below the dark green solid curve and to the left of the decreasing brown dotted curve. A similar picture, including the funnel on $\Sigma_a^+$, is obtained in the neighborhood of the other folded node $N_2$.

As we pointed out in Remark 1, the desingularization changes the direction of flow along orbits situated on the repelling manifold $\Sigma_r$ while keeping the correct direction for orbits on $\Sigma_a^\pm$. Thus, for the original reduced system (3.5), all trajectories in the interior of the fold curve flow in the direction opposite to that illustrated in the phase plane of (3.7) in Figure 4(A), (C), (E). In particular, the flow on the heteroclinic connection between $S_1$ and $N_1$ in Figure 4(D) is in fact oriented from $N_1$ to $S_1$ in the original system. This correct interpretation of the phase plane explains why in the perturbed case ($0 < \varepsilon \ll 1$) any trajectory from the funnel of $N_1$, once close enough to $N_1$, will enter the repelling part of the critical manifold (and similarly for $N_2$).

The closer $I$ is to $I_{\text{sing}H}$ (see $I = 1.315$ in Figure 4(F) versus $I = 1.376$ in Figure 4(D)), the closer $S_1$ and $N_1$ become. In fact, it can be easily proven that the desingularized reduced flow (3.7) has an FSN II singularity at the same value of parameter $I$ where the original system (2.1) admits a singular Hopf point, $I_{\text{fsnII}} = I_{\text{singH}}$ with $I_{\text{singH}}$ defined by (2.2).

### 3.4. Existence of singular canards near FSN II singularity.

The existence at $I_{\text{sing}H}$ of the FSN II singularity and, for an entire interval of $I > I_{\text{sing}H}$, the existence of a stable folded node with its associated funnel suggest that canard periodic orbits may exist for system (2.1). For such a solution to exist, initial conditions that start in the funnel of a folded node, say $N_1$, must be brought back to the funnel by the global flow of (2.1), such that a particular trajectory forms a periodic cycle. Therefore, to verify the existence of a singular canard periodic orbit in (2.1), one needs to characterize the global return map. This problem can be solved numerically by computing trajectories of the desingularized flow (3.7) up to the
Figure 5. (A) Global return map and singular canard projected on the \((u_1, a_1)\) plane. (B) Same, but projected on the \((u_1, a_2)\) plane. (C), (D) A zoomed view of (A) along \(\Sigma_a\) and \(\Sigma_{\alpha}^\pm\), respectively. (E), (F) A local zoom around \(P(N_2), N_1\) and \(P(N_1), N_2\), respectively. Numerical results were obtained for parameter values \(\beta = 1.1, g = 0.5\), and \(I = 1.305\), near the FSN II point \(I_{\text{singH}} = 1.303\), using gain function \(S(x) = 1/(1 + e^{-r(x-\theta)})\) with \(r = 10, \theta = 0.2\). Important curves/points are the lower fold curve \(\mathcal{L}^-\) (red solid) and upper fold curve \(\mathcal{L}^+\) (black solid); their projections \(P(\mathcal{L}^-)\) (red dashed) and \(P(\mathcal{L}^+)\) (black dashed); strong canards on both branches \(\Sigma_{\alpha}^\pm\) (green solid), which form boundaries of the corresponding funnels; folded nodes \(N_1, N_2\) on \(\Sigma_{\alpha}^-, \Sigma_{\alpha}^+\); fast fiber projections of \(N_1\) to the opposite branch \(\Sigma_{\alpha}^+\) (blue dashed) and of \(N_2\) to \(\Sigma_{\alpha}^-\) (cyan dashed); their corresponding projection points \(P(N_1), P(N_2)\); and the resulting flow in \(\Sigma_{\alpha}^\pm\) (blue solid) and \(\Sigma_{\alpha}^-\) (cyan solid), attracted to \(N_2\) and \(N_1\), respectively. The singular periodic orbit consists of strong blue, solid blue, dashed cyan, and solid cyan curves.

fold curves \(\mathcal{L}^-, \mathcal{L}^+\) and linking them with appropriate fast fibers described by (3.4), using the procedure detailed in other works (see, for example, \([26, 20, 10]\)). An example computed using XPPAUT \([15]\) is displayed in Figure 5. In performing the calculations for Figure 5, we exploited the fact that system (2.1) is symmetric with respect to the pair of variables \((u_1, a_1)\) and \((u_2, a_2)\). This has important consequences for the desingularized flow, as it implies that
(3.6) and (3.7) remain true under interchanges of indices; that is, for any solution \((u_1, a_1)\) of (3.7), with \((u_2, a_2)\) given by (3.6), its counterpart \((u_2, a_2)\) is a solution of the index-switched form of (3.7), with \((u_1, a_1)\) given by (3.6) with the indices switched as well. This property became apparent in the study of folded singularities (see section 3.3), but it extends to more general trajectories: for any trajectory \((u_1, a_1)\) on \(\Sigma_a^-\) there exists a trajectory on \(\Sigma_a^+\) defined by the corresponding \(u_2, a_2\) and vice versa. Similarly, for any fast fiber given by a solution of (3.4) with initial condition \((u_1, a_2)\) and parameters \((a_1, a_2)\) fixed to pick out a point in \(\Sigma_a^-\) and a terminal point on \(\Sigma_a^+\), there is a corresponding fast fiber with initial condition \((u_2, u_1)\) and parameters \((a_2, a_1)\) connecting \(\Sigma_a^+\) to \(\Sigma_a^-\).

As a result of this symmetry, at \(I = I_{\text{sing}H}\), the desingularized flow (3.7) has not one but two points \(N_1^{fsn}\) and \(N_2^{fsn}\) satisfying the FSN II condition. For an interval of \(I\) close to \(I_{\text{sing}H}\), the desingularized system has two pairs of nearby equilibria consisting of a stable folded node and a saddle ordinary singularity: \(N_1, S_1\) and \(N_2, S_2\), respectively (Figure 4(E)). The two folded nodes belong to opposite branches of the fold curve, specifically \(N_1 \in \mathcal{L}^-\) and \(N_2 \in \mathcal{L}^+\). Within \(\Sigma_a^-\) there exists a sector of solutions of desingularized system (3.7) that are funneled through \(N_1\) to the repelling side \(\Sigma_r\), and symmetrically, \(N_2\) also has such a singular funnel within \(\Sigma_a^+\). Furthermore, the fast fibers from \(N_1\) to \(P(N_1)\) and from \(N_2\) to \(P(N_2)\) are symmetric as well. For the singular canard periodic orbits that we study, each of these fast fibers has its termination point inside the singular funnel on the opposite branch of \(\Sigma\) such that the solution passes through both singular funnels, as illustrated in Figure 5. Correspondingly, we note that the MMOs of the full (perturbed) system (2.1) have small amplitude oscillations on both the suppressed and the dominant phases of each relaxation-like cycle (Figure 2).

Remark 2. The singular canard of (2.1) and generic periodic canards obtained for nonzero \(\varepsilon\) are symmetric, in the sense that they pass through two folded node funnels lying on opposite sides of the attractive slow manifold. While symmetry-related pairs of asymmetric canards were also numerically observed, they exist only in a very limited region of parameter space, far away from our point of interest \(I_{\text{sing}H}\) (\(I_{\text{sing}H}\)); for additional details, please refer to section 6, Figure 12.

4. Selection of MMOs in the perturbed system. The goal of this section is to investigate the behavior of full system (2.1) in the neighborhood of the fold curve \(\mathcal{L}^\pm\) where fast changes between the dominant and suppressed phases of each oscillation take place. In particular, we are interested in the system’s dynamics close to the folded nodes \(N_1\) and \(N_2\). A blow-up analysis about \(N_1\) and \(N_2\) will provide useful information on how certain trajectories from the slow attractive manifold are funneled to the repelling side of the slow manifold; then it will be used to explain and characterize the formation of small amplitude oscillations in the MMOs.

We work with system (2.1) in the form \(du_j/dt = -u_j + S(I - \beta u_k - g a_j),\ da_j/dt = \varepsilon(-a_j + u_j),\ j, k = 1, 2, j \neq k, \varepsilon = 1/\tau,\) and treat it as an \(\varepsilon\)-perturbation of the singular case discussed in section 3. Then we apply the general theory of canards developed for systems with one fast and two slow variables \([5, 23, 29, 32]\).

One apparent impediment to this strategy is that system (2.1) consists of four (not three) variables, two fast and two slow. However, having an additional fast variable does not mean we cannot use the theory of canards; it only adds some complications to the problem. This is true because the critical manifold of (2.1) is still cubic shaped; moreover, the fast transition
between $\Sigma_a^-$ and $\Sigma_a^+$ takes place along curve $\mathcal{L}^\pm$, where $\mathcal{L}^\pm$ is associated with a saddle-node (fold) bifurcation in the fast subsystem. The fold is a codimension one bifurcation, and it can be described by a single-variable equation called the fold normal form. Using this idea, system (2.1) can be transformed into a topologically equivalent three-dimensional system with only one fast variable. Importantly, while the normal form reduction and the (later) blow-up system (2.1) can be transformed into a topologically equivalent three-dimensional system with a way-in/way-out function to geometrically characterize the selection of MMOs.

4.1. The normal form in the vicinity of a folded singularity.

4.1.1. Reduction to the normal form. Consider $0 < \varepsilon \ll 1$ and a value of parameter $I$ for which the critical manifold of (2.1) is cubic-shaped and stable folded nodes $N_{1,2}$ exist. Such properties arise in an entire interval of $I$ values above both the FSN II singularity $I_{sH}$ at $\varepsilon = 0$ and the $\varepsilon$-dependent subcritical Hopf point $I_{sH}$ (e.g., $I_{sH} = 1.309$ at $\varepsilon = 0.01$).

The reduction of system (2.1) is done in three steps: first, it is projected onto the center manifold of its fast subsystem; next, the (now unique) fast equation is brought to its fold normal form can be found in [6]. We only summarize the results below.

For any folded singularity $p = (u_1^*, u_2^*, a_1^*, a_2^*) \in \mathcal{L}^\pm$ of system (2.1), let us define the coefficients

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

$$c_{10} = \frac{g}{2 \beta \sqrt{F'(u_1^*)}}, \quad b_{10} = \frac{g F''(u_1^*)}{4 F'(u_1^*)^2} + \frac{g}{2 \beta \sqrt{F'(u_1^*)}} b_{00},$$

$$c_{01} = -\frac{g}{2 \beta \sqrt{F'(u_2^*)}}, \quad b_{01} = \frac{g F''(u_2^*)}{4 F'(u_2^*)^2} - \frac{g}{2 \beta \sqrt{F'(u_2^*)}} b_{00}$$

and

$$\alpha_1 = \frac{g^2}{8 \beta^4 \sqrt{F'(u_1^*)} |b_{00}|^3} \left( F''(u_1^*) \sqrt{F'(u_2^*)} + F''(u_2^*) \sqrt{F'(u_1^*)} - F''(u_1^*) F''(u_2^*) \frac{u_1^* - a_1^*}{\sqrt{F'(u_1^*)}} \right),$$

$$\alpha_2 = -\frac{g}{2 \beta^2 b_{00}} [F'(u_1^*) + F'(u_2^*)],$$

$$\eta_1 = \frac{1}{|b_{00}|} \left( b_{00} \sqrt{F'(u_2^*)} - \frac{\beta F''(u_2^*)}{4 F'(u_2^*)} \right), \quad \eta_2 = \frac{1}{|b_{00}|} \left( \frac{g F''(u_2^*)}{4 \beta b_{00} \sqrt{F'(u_2^*)}} - 1 \right),$$

$$\eta_0 = \frac{u_1^* - a_1^*}{|b_{00}|}, \quad \eta_3 = -\frac{\sqrt{F'(u_2^*)}}{b_{00}}.$$

The normal form near stable folded nodes $N_{1,2}$ can be specified using these quantities.
Theorem 4.1. Let \( p = (u_1^*, u_2^*, a_1^*, a_2^*) \in \mathcal{L}^* \) be the folded node \( N_1 \) (or \( N_2 \)).

(i) If \( \epsilon > 0 \) is sufficiently small and \( b_{00} \) is nonzero, then, in the neighborhood of \( N_1 \) (\( N_2 \)), system (2.1) is topologically equivalent to

\[
\begin{align*}
\frac{dx}{dt} & = \alpha_1 y + \alpha_2 z + O(\epsilon, x, (y + z)^2), \\
\frac{dy}{dt} & = \eta_0 + \eta_1 x + \eta_2 y + \eta_3 z + O(\epsilon, (y + z)^2), \\
\epsilon \frac{dz}{dt} & = x + z^2 + O(\epsilon, \epsilon(x + y + z), (x + y + z)^3)
\end{align*}
\]

with coefficients \( \alpha_j, \eta_j \) defined by (4.2) and \( \tilde{t} = \epsilon |b_{00}| t \).

(ii) The values \( u_1, u_2, a_1, a_2 \) on a trajectory of (2.1) near \( N_1 \) (\( N_2 \)) are mapped onto \((x, y, z)\) through intermediate variables \( \sigma, y_1, y_2 \). One needs to compute \( \sigma \) according to

\[
\sigma = -\frac{\sqrt{F'(u_1^*)}}{2\beta}(u_1 - u_1^*) + \frac{\sqrt{F'(u_2^*)}}{2\beta}(u_2 - u_2^*)
\]

and \( y_j = a_j - a_j^* \); then, to a first order approximation,

\[
x \approx \frac{c_{10}}{b_{00}} y_1 + \frac{c_{01}}{b_{00}} y_2, \quad y = y_1, \quad z \approx \frac{b_{00}}{b_{00} |b_{00}|} \sigma + \frac{b_{10}}{b_{00}} y_1 + \frac{b_{01}}{b_{00}} y_2.
\]

(iii) The inverse map \((x, y, z) \mapsto (u_1, u_2, a_1, a_2)\) is defined to a first order approximation by

\[
\begin{align*}
u_1 & \approx u_1 - \sigma \sqrt{F'(u_2^*)} - y_1 \frac{g}{4F'(u_1^*)} - y_2 \frac{g}{4\beta} + \epsilon \left( \frac{g(u_1^* - a_1^*)}{8F'(u_1^*)} + \frac{g(u_2^* - a_2^*)}{8\beta} \right), \\
u_2 & \approx u_2 + \sigma \sqrt{F'(u_1^*)} - y_1 \frac{g}{4\beta} - y_2 \frac{g}{4F'(u_2^*)} + \epsilon \left( \frac{g(u_1^* - a_1^*)}{8\beta} + \frac{g(u_2^* - a_2^*)}{8F'(u_2^*)} \right), \\
a_1 & = a_1^* + y_1, \\
a_2 & = a_2^* + y_2,
\end{align*}
\]

\[
(4.6)
\]

together with

\[
y_1 = y, \quad y_2 \approx \frac{b_{00}}{c_{01}} x - \frac{c_{10}}{c_{01}} y, \quad \sigma \approx \frac{b_{00}}{|b_{00}|} z - \frac{b_{01}}{2c_{01}} x + \frac{b_{01}c_{10} - b_{10}c_{01}}{2b_{00}c_{01}} y.
\]

The coefficients \( \alpha_1, \alpha_2, \eta_0 \) play a key role in the analysis of system (4.3) near a folded singularity. The importance of coefficients \( \eta_1, \eta_2, \eta_3 \) becomes apparent in the nonsingular case \( \epsilon > 0 \). The theory that characterizes the dynamics of a system such as (4.3) near an FSN II singularity relies heavily on the terms \( \eta_2 y \) and \( \eta_3 z \) [23]. It also shows that locally, near the folded node, the term \( \eta_1 x \) can be neglected. On the other hand, recent results on singular Hopf bifurcation reveal that the term \( \eta_1 x \) needs to be included if one is interested in the dynamics of system (4.3) near the true singularity \( S_1 \) [18]. This requirement arises because the coefficient \( \eta_1 \) contributes to the leading term of the first Lyapunov coefficient of the equilibrium. Since our goal is to investigate the role of both \( N_1 \) and \( S_1 \) in the formation of small amplitude oscillations in the MMOs, all \( \eta_j \)'s will be taken into account.
4.1.2. Rescaling of the normal form. An $O(\sqrt{\varepsilon})$-perturbation of the reduced flow can be obtained from normal form (4.3) by a choice of certain $O(\sqrt{\varepsilon})$-perturbations of the critical manifold near $N_1$ (similarly for $N_2$). More specifically, Fenichel theory [17] and more recent results of Krupa and Wechselberger [31], [23] prove that for $\varepsilon$ sufficiently small there exist smooth, locally invariant, normally hyperbolic manifolds $\Sigma^{\pm}_{a,\sqrt{\varepsilon}}$ and $\Sigma_{r,\sqrt{\varepsilon}}$ that are $O(\sqrt{\varepsilon})$-perturbations of $\Sigma$ and are located $O(\varepsilon)$ and $O(\sqrt{\varepsilon})$ close, respectively, to the folds of $\Sigma$; the flow on $\Sigma^{\pm}_{a,\sqrt{\varepsilon}}$ and $\Sigma_{r,\sqrt{\varepsilon}}$ is also an $O(\sqrt{\varepsilon})$-perturbation of the flow defined by the slow subsystem. Importantly, this $O(\sqrt{\varepsilon})$ approximation is appropriate for the local study of both $N_1$ and the ordinary singularity $S_1$ (i.e., the equilibrium $e_I$), given that $S_1$ enters an $O(\varepsilon)$-neighborhood of $N_1$ for $\varepsilon \to 0$ [18]. This happens in (4.3) for $I$ sufficiently close to the subcritical Hopf point $I_{sH}$, which itself is an $O(\varepsilon)$-perturbation of $I_{singH}$ [7].

Note that the coefficient $\eta_0$ as defined by (4.2) is zero at $I_{singH}$, so we can assume that the parameter $I$ is chosen such that $\eta_0 = O(\sqrt{\varepsilon})$ for a given, sufficiently small $\varepsilon$. Then, the following redefined parameters,

\[
\mu = \frac{\alpha_1 \eta_0}{\alpha_2^2}, \quad A = \frac{\alpha_1 \eta_{\delta_3}}{\alpha_2 \sqrt{|\alpha_2|} \varepsilon}, \quad B = \frac{\alpha_1 \eta_{\gamma}}{\alpha_2} \varepsilon, \quad C = -\frac{\eta_2}{\sqrt{|\alpha_2|} \varepsilon},
\]

satisfy $\mu, A, C = O(\sqrt{\varepsilon})$ and $B = O(\varepsilon)$, respectively. We should also mention that the coefficients of $\varepsilon$ in all three equations in (4.3) are proportional to $\eta_0$ (see [6]); therefore, under the above assumption, the $\varepsilon$-terms in (4.3) are in fact of size $O(\varepsilon \sqrt{\varepsilon})$.

We next rescale the variables and time in (4.3) according to

\[
X = -\frac{z}{\sqrt{|\alpha_2|} \varepsilon}, \quad Y = \frac{x}{\alpha_2 \varepsilon}, \quad Z = \frac{\alpha_1 y}{\alpha_2 \sqrt{|\alpha_2|} \varepsilon}, \quad t' = i \sqrt{\frac{|\alpha_2|}{\varepsilon}} = t |b_0| \sqrt{|\alpha_2|} \varepsilon
\]

and obtain a topologically equivalent system,

\[
\begin{align*}
\dot{X} &= Y - X^2 + O(\sqrt{\varepsilon}, \varepsilon Y, \sqrt{\varepsilon}(X + Z), \sqrt{\varepsilon}(X + \sqrt{\varepsilon}Y + Z)^3), \\
\dot{Y} &= Z - X + O(\varepsilon, \sqrt{\varepsilon}Y, \sqrt{\varepsilon}(X + Z)^2), \\
\dot{Z} &= -\mu - AX - BY - CZ + O(\varepsilon \sqrt{\varepsilon}, \varepsilon(X + Z)^2),
\end{align*}
\]

or, more concisely, $\dot{X} = Y - X^2 + O(\sqrt{\varepsilon})$, $\dot{Y} = Z - X + O(\sqrt{\varepsilon})$, and $\dot{Z} = -\mu - AX - BY - CZ + O(\varepsilon)$, where the overdot denotes the derivative with respect to $t'$. The normal form

\[
\begin{align*}
\dot{X} &= Y - X^2, \\
\dot{Y} &= Z - X, \\
\dot{Z} &= -\mu - AX - BY - CZ
\end{align*}
\]

is an $O(\sqrt{\varepsilon})$-perturbation of system (2.1) near $N_1$. We use it for the numerical construction of the slow manifold and of other important trajectories near the folded node.

4.2. A geometrical approach to MMOs. The importance of the normal form reduction (4.11) to the investigation of the original (perturbed) system is twofold. It gives a system topologically equivalent to (2.1) that can be studied successfully by numerical integration,
and it provides the basis for the definition of the way-in/way-out function. Indeed, while in the singular case the critical manifold and the singular canard are relatively easily determined, for small nonzero values of \( \varepsilon \) the numerical construction of the slow manifold is problematic. Stiffness-related numerical issues complicate the characterization of trajectories of (2.1) in a neighborhood of either folded node \( N_1 \) or \( N_2 \), where \( S_1, S_2 \) also lie; on the other hand, the small amplitude oscillations of the MMOs occur precisely in that neighborhood. Consequently, to understand MMO formation, one needs to circumvent the numerical integration obstacle. One method is to apply an analytic process of enlargement of the region of interest (the so-called blow-up analysis [14], [22], [29]) and determine the form of an equivalent system (4.11). Alternatively, one can use boundary-value solvers that have been developed for the numerical computation of slow manifolds in other models [11], [12]. Given that we are interested in both the geometrical description of the trajectories and in construction of the way-in/way-out function, we take the former approach.

### 4.2.1. Periodic canards in the perturbed system.

We discuss in detail the case of \( N_1 \); however, due to the symmetry properties of system (2.1), similar results are true for \( N_2 \) as well. By numerical simulations of system (4.11) we were able to derive approximations to the local perturbed slow manifolds \( \Sigma_{-\sqrt{\varepsilon}}, \Sigma_{\sqrt{\varepsilon}} \), which we denote by \( W_{\text{slow}}^- \) (Figure 6, in yellow) and \( W_{\text{slow}}^+ \) (green), respectively. We also identified the strong stable manifold of the folded node (the strong canard, dark green curve) and the orbital connection between \( N_1 \) and \( S_1 \) (the primary weak canard, red curve).

The trajectories approaching and flowing along \( W_{\text{slow}}^- \) were constructed from initial conditions outside the paraboloid \( Y = X^2 \) and far away from it, starting on the line \( X = 5, Y = 10 \) with \( Z \) varying between \(-2.5 \) and \( 2.5 \) (yellow solid). Additional trajectories (yellow dashed) were drawn from initial conditions obtained as perturbations of points along the fold curve. Likewise, the trajectories approaching and flowing along \( W_{\text{slow}}^+ \) were determined by backward integration of the system (4.11) with initial conditions on the line \( X = -5, Y = 10 \) (\( Z \) taken between \(-1.5 \) and \( 0 \), green solid), and through perturbations of points along the fold curve (dashed green curves). The strong canard (dark green solid) was generated by first using XPPAUT [15] to compute the strong stable manifold of the folded node \( N_1 \) of the desingularized two-dimensional system

\[
\begin{align*}
X' &= Z - X, \\
Z' &= 2X(-\mu - AX - BX^2 - CZ)
\end{align*}
\]

and then taking a point \((X, Z)\) on this curve, together with a \( Y \) coordinate chosen from a small perturbation off of the paraboloid \( Y = X^2 \) (equivalent to \( x + z^2 = 0 \) in (4.3)), as initial conditions for integration of (4.11). The orbital connection (red solid) is the set of points \( \gamma_{N_1S_1} = \{(Z, Z^2, Z) \mid Z \in \mathbb{R}\} \), and it is interpreted as the orbital limit of the primary weak canard in the regular folded node case [23]. Note that the variable \( Z \) in (4.11) evolves relatively slower than \( X \) and \( Y \) since its equation is of order \( O(\sqrt{\varepsilon}) \); therefore, \( \gamma_{N_1S_1} \) is the one-dimensional critical manifold of (4.11). Clearly, both \( N_1 \) and \( S_1 \) belong to \( \gamma_{N_1S_1} \); \( N_1 \) is the origin of the new coordinate system \((X, Y, Z)\), while \( S_1 \) is the equilibrium of the system (4.11), near \( N_1 \), defined by \( BZ^2 + (A + C)Z + \mu = 0 \) and \( Y = X^2, X = Z \). For example, if
Figure 6. Canard solutions and occurrence of small amplitude oscillations for $\tau = 100$ ($\varepsilon = 0.01$), $\beta = 1.1$, $g = 0.5$ and (A) $I = 1.376$, (B) $I = 1.325$, and (C)–(D) $I = 1.315$. The part of the canard corresponding to passage through the funnel to $W_u^{\text{slow}}$ is displayed in magenta; the subset along the fast fibers is in cyan. Other curves are as follows: the stable (yellow) and unstable (green) slow manifolds; the fold curve (brown dashed); the folded node (blue dot) and ordinary equilibrium (red dot); the strong canard (dark-green solid); the orbital connection (red solid); a segment of the periodic orbit of the full system (black solid); and in (C)–(D) the unstable manifold of the equilibrium (blue). A zoom near the equilibrium is shown in (D).

When $\mu, B > 0$ and $A + C > 0$ (see Table 2), then

(4.13) \[ Z_{eq} = -\frac{\mu}{A + C} \cdot \frac{2}{1 + \sqrt{1 - \frac{4B\mu}{(A+C)^2}}} \approx -\frac{\mu}{A + C}. \]

All curves determined by simulations of (4.11) were transformed into the original coordinates $u_1, u_2, a_1, a_2$ according to (4.9), (4.7), and (4.6), then projected on the space $(u_1, a_1, a_2)$ (Figure 6). The folded node (blue dot) and the true equilibrium $e_{II}$ (red dot) are determined directly from (3.2), (3.3), (3.8), and (2.1). Alternatively, they could be defined approximately...
by \( N_1 \) and \( S_1 \) as above. The fold curve (brown dashed) was drawn according to (3.2), (3.3). A trajectory of the full system (2.1) starting from initial condition \( u_1 = 0, u_2 = 1, a_1 = a_2 = 0 \) was included for comparison (black solid).

For \( \tau = 100 (\varepsilon = 0.01), \beta = 1.1, g = 0.5, \) and \( r = 10, \theta = 0.2 \) in the gain function \( S(x) = 1/(1 + e^{-r(x-\theta)}) \), the full system (2.1) has a subcritical Hopf bifurcation at \( I_{sH} = 1.309 \) (Figure 1) and shows MMOs in an interval \( I > I_{sH} \) (Figure 2). Let us consider three different values of the parameter \( I \) to the right of \( I_{sH}: I = 1.376 \) (Figure 6(A)), \( I = 1.325 \) (Figure 6(B)), and \( I = 1.315 \) (Figure 6(C)–(D)). The coordinates of the folded node, the equilibrium, as well as the corresponding values of the coefficients \( \mu, A, B, C \) for those \( I \) values are listed in Table 2. The local dynamics of system (2.1) is complex near the folded node, and it is described below.

<table>
<thead>
<tr>
<th>( I )</th>
<th>Folded node ( u_1 )</th>
<th>Equilibrium ( u_1 )</th>
<th>( \mu )</th>
<th>( A )</th>
<th>( B )</th>
<th>( C )</th>
<th>( \zeta )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.376</td>
<td>( u_1 = 0.36988 )</td>
<td>( u_1 = 0.36873 )</td>
<td>0.1184728</td>
<td>-0.1131719</td>
<td>0.0176295</td>
<td>0.2502331</td>
<td>0.628</td>
</tr>
<tr>
<td>1.325</td>
<td>( u_1 = 0.30964 )</td>
<td>( u_1 = 0.3084 )</td>
<td>0.03815842</td>
<td>-0.0956319</td>
<td>0.01405642</td>
<td>0.2402816</td>
<td>0.091</td>
</tr>
<tr>
<td>1.322</td>
<td>( u_1 = 0.30615 )</td>
<td>( u_1 = 0.30503 )</td>
<td>0.03306483</td>
<td>-0.09438645</td>
<td>0.01381911</td>
<td>0.2396551</td>
<td>0.077</td>
</tr>
<tr>
<td>1.315</td>
<td>( u_1 = 0.298025 )</td>
<td>( u_1 = 0.29724 )</td>
<td>0.02103431</td>
<td>-0.0913761</td>
<td>0.0132535</td>
<td>0.2381732</td>
<td>0.046</td>
</tr>
</tbody>
</table>

On the slow manifold \( W^s_{slow} \), any trajectory that starts above (relative to the fold) the strong canard is attracted to the fold curve and then follows the fast fibers of (2.1), moving away from \( W^s_{slow} \). On the other hand, any trajectory on \( W^u_{slow} \) that starts below the strong canard is funneled through the folded node into a small neighborhood of the unstable manifold \( W^u_{slow} \). Its jump along the fast fibers is therefore delayed. For each such trajectory, we distinguish a segment along \( W^s_{slow} \) (yellow), followed by a segment along \( W^u_{slow} \) (magenta), followed by a segment along the fast fibers (cyan); see Figure 6.

As the general theory of canards predicts [23], the trajectories in the trapping region either start close to the strong canard (e.g., most of the trajectories on \( W^s_{slow} \) that are below the strong canard in Figure 6(A) at \( I = 1.376 \) or are attracted to the orbital connection formed by the primary weak canard (Figure 6(B) and (C)–(D)). The former follow the strong canard into a small neighborhood of \( W^u_{slow} \) and do not display rotational properties. In contrast, the primary weak canard imparts rotational properties to nearby trajectories leading to canard-induced small amplitude oscillations, evidenced in the yellow and magenta segments.
of trajectories on $W^s_{\text{slow}}$ below the strong canard in Figure 6(B) at $I = 1.325$ and Figure 6(C) at $I = 1.315$. Once in the funnel of the folded node, a point is under its strong influence; the dynamics is dictated by the local vector field whose principal component is tangent to the primary weak canard and points away from the folded node, yielding a drift along the fold. However, when the point exits the funnel, it comes under the influence of the vector field between $W^u_{\text{slow}}$ and $W^s_{\text{slow}}$; its trajectory is thus repelled by $W^u_{\text{slow}}$ and attracted to $W^s_{\text{slow}}$. Due to the drift along the fold, the trajectory now approaches the fold curve in a region above the strong canard and is forced to jump away, following the fast fibers of the original system. (A special case occurs in Figure 6(C)–(D) and will be discussed later.)

Once a trajectory jumps away from the fold, its fate is determined by the global return map. If the global return map brings a trajectory back to a neighborhood of $W^s_{\text{slow}}$ near the folded node but above the strong canard, then the trajectory subsequently produces a regular jump. This happens at $I = 1.376$: the trajectory of the full system, while starting in the trapping sector of the folded node, returns above the strong canard. (Dynamics in the neighborhood of the folded node is illustrated in Figure 6(A), but the global return is not shown.) Thus, the periodic orbit of (2.1) is a regular relaxation oscillation. MMOs are periodic canards that develop close to the primary weak canard. Moreover, due to the symmetry of the system, the MMOs in (2.1) that we study are canards for which both jump-up and jump-down fibers originate in the vicinity of a folded node. For example, at both $I = 1.325$ and $I = 1.315$, we show full system trajectories that are canards (Figure 6(B)–(D), black solid curves, and Figure 2(A), (C)).

4.2.2. Changes in the number of small amplitude oscillations. Numerical investigation of system (2.1) shows that the number of small amplitude oscillations in its MMOs increases as the value of parameter $I$ decreases toward $I_{sH}$ (Figure 2). This dynamics is confirmed by the geometrical description of the $O(\sqrt{\varepsilon})$ neighborhood of the folded node; indeed, as $I$ approaches $I_{sH}$, the trapping region on $W^s_{\text{slow}}$ between the strong canard and the primary weak canard expands (Figure 7). An immediate consequence is the occurrence of secondary canards that divide the funnel into subsectors leading to different numbers of small oscillations; the farther from the strong canard a subsector lies, the larger is the number of small oscillations that trajectories passing through it are expected to exhibit [32]. To test how this plays out for system (2.1) for positive $\varepsilon$, we computed the ratio $\zeta(I) = \lambda_1/\lambda_2$ of the eigenvalues of the folded node resulting from the perturbed desingularized system (4.12). For the parameter values considered in Figures 6 and 7, this ratio takes the approximate values given in Table 2. Since the first is greater than $1/3$, no small amplitude oscillations near the folded node are expected at $I = 1.376$. The trapping region is narrow, and initial conditions in the funnel yield trajectories that stay close to the strong canard while entering $W^u_{\text{slow}}$. Indeed, no oscillations are found in the passage along the strong canard; the rotations observed in Figure 6(A) occur farther away from the folded node and are due to the influence of the local vector field between $W^u_{\text{slow}}$ and $W^s_{\text{slow}}$. In the other three cases, $\zeta(I)$ is less than $1/3$, and $\zeta(I)$ decreases with $I$, introducing more subsectors (for example, the analysis done for folded nodes predicts the presence of five subsectors for $I = 1.325$, then six for $I = 1.322$ and 10 for $I = 1.315$ [32]). An empirical observation (see Figure 7(B)–(D)) shows that the distance $\delta(I, \varepsilon)$ between the periodic solution of the full system (black solid) and the strong canard (dark green solid)
Figure 7. Relative position of a periodic solution of the full system (black solid) to the strong canard (dark green solid) in an \( O(\sqrt{\varepsilon}) \) neighborhood of the folded node (blue dot). The trajectory is generated in system (2.1) from initial conditions \( u_1 = a_1 = a_2 = 0 \) and \( u_2 = 1 \). The fold curve (brown dashed), the orbital connection (red solid), and the ordinary equilibrium (red dot) are also included. Parameter values are \( \tau = 100 (\varepsilon = 0.01), \beta = 1.1, g = 0.5, r = 10, \theta = 0.2 \) and (A) \( I = 1.376 \), (B) \( I = 1.325 \), (C) \( I = 1.322 \), (D) \( I = 1.315 \).

increases as \( I \) approaches \( I_{sH} \). Thus, the increase in the number of small oscillations can be explained by the fact that the periodic trajectory of the full system intersects \( W_{\text{slow}}^s \) in a more remote subsector of the funnel (relative to the strong canard) as \( I \) goes to \( I_{sH} \).

An interesting and more complex phenomenon is observed at \( I = 1.315 \). For such \( I \), small amplitude oscillations in MMOs are only partly due to the primary weak canard (Figure 6(C)); others are due to the influence of the ordinary equilibrium (Figure 6(D)). To contrast them with the former canard-induced small amplitude oscillations, we call the latter Hopf-induced small amplitude oscillations. The geometric representation of the \( O(\sqrt{\varepsilon}) \) neighborhood of the folded node shows that most trajectories (including the periodic canard of the full system) are pushed along the orbital connection toward the equilibrium and leave the funnel near it. Inside the funnel, the trajectories undergo a number of rotations (as the general theory of canards predicts [23]); however, because the exit point from the funnel is near the equilibrium, in that vicinity the trajectories are subject to the local vector field and undergo additional rotations.
In the three-dimensional \((X,Y,Z)\) system, the ordinary equilibrium is unstable with one real (negative) and two complex (with positive real part) eigenvalues. Its unstable manifold \(W_{eq}^u\) (Figure 6(C)–(D), blue curve) spirals out until it comes near the intersection of \(W_{slow}^s\) and \(W_{slow}^u\) (in a region above the strong canard of the folded node); then \(W_{eq}^u\) follows the fast fibers of the system moving away from the slow manifold. All canards that leave the funnel of the folded node sufficiently close to the equilibrium point (for example, at \(I = 1.315\), at a distance of order \(O(\varepsilon \sqrt{\varepsilon})\)) follow the dynamics of \(W_{eq}^u\) before jumping away along the fast directions; several new small cycles occur due to the rotational influence of \(W_{eq}^u\). Therefore, when a system has an FSN II singularity (equivalent to a singular Hopf point), it may display oscillations due to both the rotational effect of the folded node funnel and the unstable manifold of the (near Hopf) equilibrium, leading to a more highly oscillatory type of MMOs than predicted by canard theory alone.

5. Canard-induced versus Hopf-induced small oscillations in the MMOs. As seen in previous sections, system (2.1) has an (unstable) ordinary equilibrium \(S_1\) in the \(O(\sqrt{\varepsilon})\) (or even \(O(\varepsilon)\)) neighborhood of the folded node \(N_1\), and there exists an orbital connection from \(N_1\) to \(S_1\). This structure makes it possible for a trajectory passing through the funnel of the folded node, and thus undergoing local oscillations, to reach a neighborhood of the unstable manifold \(W_{eq}^u\) that spirals out from the equilibrium and to be induced to exhibit additional rotations. Unfortunately, this distinction between oscillation types is based on only empirical observations of the local geometrical structures contributing to the system’s dynamics (Figure 6(C)–(D)). A more rigorous approach is needed to distinguish between the canard-induced and the Hopf-induced small cycles in a given MMO.

We investigate this question by computing the delay of a generic solution near the orbital connection (primary weak canard) \(\gamma_{N_1,S_1}\). We use system (4.11) to define a way-in/way-out function, which determines how long a canard trajectory stays within a neighborhood of \(\gamma_{N_1,S_1}\) and provides an estimation of the trajectory’s exit point from this neighborhood. Knowing the (approximate) exit point then helps us identify which of the trajectory’s rotations occur outside of the funnel, being induced by \(W_{eq}^u\).

We follow the construction of the way-in/way-out function for a canonical form of an FSN II singularity given by Krupa and Wechselberger [23]. The main idea is that, since \(\mu,A,C = O(\sqrt{\varepsilon})\) and \(B = O(\varepsilon)\) in (4.11), \(Z\) can be interpreted as a slow variable. The dynamics of (4.11) in an \(O(\sqrt{\varepsilon})\)-neighborhood of the folded node (the origin, \(Z_{FN} = 0\)) is rapidly attracted to the orbital connection \(\gamma_{N_1,S_1}\), which we recall was defined by \(\gamma_{N_1,S_1} = \{(Z,Z^2,Z) \mid Z \in \mathbb{R}\}\) and is in fact the critical manifold of (4.11). The equilibrium of the layer problem for (4.11) has the coordinates \((Z,Z^2)\) with eigenvalues \(-Z \pm \sqrt{Z^2 - 1}\). Therefore it is either an attracting node \((1 \leq Z)\) or focus \((0 < Z < 1)\) or a repelling focus \((-1 < Z < 0)\) or node \((Z \leq -1)\).

For the MMOs that we consider, a positive value of \(Z\) corresponds to the branch of the orbital connection situated in the trapping region of the folded node; therefore, such points in the \((X,Y,Z)\) space are attracted to \(\gamma_{N_1,S_1}\) directly (if \(Z > 1\)) or undergo rotations about it (if \(0 < Z < 1\)). The latter are canard-induced rotations. On the other hand, the ordinary equilibrium stays on the branch of the orbital connection associated with negative \(Z\) (since \(Z_{eq} < 0\) as defined by (4.13)). Close to the folded node \((-1 < Z < 0)\), trajectories still rotate...
In fact, since both the input to and the output from \( \Phi \) belong to \( \gamma_{N_1S_1} \), this time with increasing amplitude (these are also canard-induced oscillations). Eventually the trajectories will leave the funnel at some \( Z \) such that \( Z_{eq} < Z < 0 \), since the equilibrium is unstable. If \(-1 < Z_{eq} \), then only focus-related local dynamics exists near the orbital connection on the unstable manifold \( W^u_{\text{slow}} \). If \( Z_{eq} < -1 \), then a more complicated structure can emerge since the exit point can have \( Z < -1 \), and thus trajectories can be influenced by node-related dynamics while still in the funnel; this case is not discussed here.

As proved in [23], a limit point (the so-called buffer point) exists on the orbital connection, defined as the farthest point from the folded node, measured along \( \gamma_{N_1S_1} \), that any canard passing through the funnel can reach. Its \( Z \) coordinate is denoted by \( Z_b (Z_{eq} < Z_b < 0) \), and it is determined in the following.

### 5.1. The definition of the way-in/way-out function.

In this section we assume that \( \mu, A, B, C \) defined by (4.8) satisfy \( \mu, A, C = O(\sqrt{\varepsilon}) \), \( B = O(\varepsilon) \) and that \( \mu, B > 0, A + C > 0 \) (see Table 2); we define

\[
(p = \dfrac{\mu}{\sqrt{\varepsilon}}, \quad Q = -(A + C)/\sqrt{\varepsilon}).
\]

For a better understanding of the construction of the way-in/way-out function, let us recall the strategy employed by [23]. The goals are (i) to show that a primary weak canard (orbital connection between the folded node and the true equilibrium) continues to exist near \( \gamma_{N_1S_1} \) for \( \varepsilon \neq 0 \), and (ii) to determine how long solutions of (4.11) (or, more generally, of (4.10)) starting in an \( O(\sqrt{\varepsilon}) \)-neighborhood of \( \gamma_{N_1S_1} \) remain in that neighborhood of it. These aims are achieved by first addressing the question, given an initial condition \((X_{in}, Y_{in}, Z_{in}) \) with \( Z_{in} > 0 \) on \( \gamma_{N_1S_1} \), can we find a unique point \((X_{out}, Y_{out}, Z_{out}) \) \( \in \gamma_{N_1S_1} \) with \( Z_{out} < 0 \), and a path between them along which a solution of (4.10) can be analytically defined? A positive answer will allow for the definition of the way-in/way-out function: \((X_{out}, Y_{out}, Z_{out}) = \Phi(X_{in}, Y_{in}, Z_{in}) \).

In fact, since both the input to and the output from \( \Phi \) belong to \( \gamma_{N_1S_1} \), their coordinates satisfy \( X_{in} = Z_{in}, Y_{in} = Z_{in}^2, X_{out} = Z_{out}, Y_{out} = Z_{out}^2 \), and the map is one-dimensional \((Z_{in} \rightarrow Z_{out}) \). Note that the condition \( Z_{in} \in (0, \infty) \) corresponds to the selection of an initial point on \( W^s_{\text{slow}} \) in the funnel of the folded node, while \( Z_{out} < 0 \) is on \( W^u_{\text{slow}} \) past the folded node. In addition, the end point of the path should lie between the folded node and the equilibrium, so its coordinate must satisfy \( Z_{out} \in (Z_{eq}, 0) \). Since for \( \varepsilon \) sufficiently small the value \( Z_{eq} \) is approximately \(-\mu/(A + C) \), we will look for solutions \( Z_{out} \) in the interval where \( \mu + (A + C)Z > 0 \). Once such solutions are found, points in an \( O(\sqrt{\varepsilon}) \)-neighborhood of \( \gamma_{N_1S_1} \) with positive \( Z \)-coordinates can also be mapped to exit points with negative \( Z \)-coordinates, to within \( O(\varepsilon) \), with corresponding estimates of residence times within the neighborhood obtained.

These steps are tackled in [23] by analyzing the system in the complex domain and finding elliptic paths that connect the negative and positive real \( Z \)-axis. To construct such paths, \( \gamma_{N_1S_1} \) which is the critical manifold of (4.10), is first straightened through a change of coordinates \((x_2 := Z^2 - Y, \ z_2 := Z - X) \). Next, the slow variable \( Z \) is mapped into the effective slow time through a reflection \((y_2 := -Z) \) and a positive-time rescaling. Finally, a near-linear transformation is used to bring the system to a form that ensures better control over the leading \( O(\sqrt{\varepsilon}) \) perturbation terms \((\tilde{z}_2 = z_2 - \sqrt{\varepsilon}\varphi_1(y_2), \ \tilde{x}_2 = x_2 + \sqrt{\varepsilon}\varphi_2(y_2, y_2z_2)) \). The following
The system is thus obtained:

\[
\begin{align*}
\dot{x}_2' &= \Psi(y_2, P, Q; \tilde{x}_2, \tilde{z}_2, \sqrt{\varepsilon})(-\tilde{z}_2 + O(\varepsilon, \sqrt{\varepsilon}x_2, \sqrt{\varepsilon}z_2)), \\
\dot{y}_2' &= \sqrt{\varepsilon}, \\
\ddot{z}_2' &= \Psi(y_2, P, Q; \tilde{x}_2, \tilde{z}_2, \sqrt{\varepsilon})(\tilde{x}_2 + 2y_2\tilde{z}_2 + \tilde{z}_2^2 + O(\varepsilon, \sqrt{\varepsilon}x_2, \sqrt{\varepsilon}z_2)),
\end{align*}
\]

where \( \Psi(y_2, P, Q; \tilde{x}_2, \tilde{z}_2, \sqrt{\varepsilon}) = 1/[\mathcal{P} + Qy_2 + a_2\tilde{z}_2 + O(\sqrt{\varepsilon})] \) and prime denotes the differentiation with respect to the new time. In the new coordinates, \( \gamma_{N_1S_1} \) is exactly the \( y_2 \)-axis and is invariant up to order \( O(\sqrt{\varepsilon}) \). This is important because now, along \( \gamma_{N_1S_1} \), the eigenvalues of the layer problem depend only on \( y_2 \); their zero order terms take the form \( \lambda(y_2) = (y_2 - i\sqrt{1 - y_2^2})/(\mathcal{P} + Qy_2) \) and \( \nu(y_2) = (y_2 + i\sqrt{1 - y_2^2})/(\mathcal{P} + Qy_2) \), and these are used in the definition of the way-in/way-out function. It is shown in [23] that \( Z_{\text{out}} \) is the solution of the equation

\[
\int_{-Z_{\text{in}}}^Z \text{Re}(\lambda(s))ds = 0 \quad \text{(if } -1 < Z < 0)\]

or

\[
\int_{-Z_{\text{in}}}^1 \text{Re}(\lambda(s))ds + \int_1^{-Z_{\text{in}}} \text{Re}(\nu(s))ds = 0 \quad \text{(if } Z < -1)\]

We extend here the calculations from [23] to obtain a concise, practical formula for \( (X_{\text{out}}, Y_{\text{out}}, Z_{\text{out}}) = \Phi(X_{\text{in}}, Y_{\text{in}}, Z_{\text{in}}) \). For any given \( Z_{\text{in}} > 0 \), let us define the function \( Z \mapsto \phi(Z; Z_{\text{in}}) \) as follows:

(i) If \( \mu < A + C \), then for any \( -\frac{\mu}{A+C} < Z < 0 \) the function is

\[
(5.2) \quad \phi(Z; Z_{\text{in}}) = \begin{cases} 
\frac{1}{Q}(Z_{\text{in}} - Z) - \frac{Z_{\text{in}}}{Q^2} \ln \left( \frac{\mathcal{P} + Q - Z}{\mathcal{P} + Q - Z_{\text{in}}} \right) & \text{if } Z_{\text{in}} \in (0, 1], \\
\frac{1}{Q}(Z_{\text{in}} - Z) - \frac{Z_{\text{in}}}{Q^2} \ln \left( \frac{\mathcal{P} + Q - Z}{\mathcal{P} + Q - Z_{\text{in}}} \right) + \chi_1(Z_{\text{in}}) & \text{if } Z_{\text{in}} > 1,
\end{cases}
\]

where

\[
\chi_1(Z_{\text{in}}) = -\frac{1}{Q} \sqrt{Z_{\text{in}}^2 - 1} - \frac{Z_{\text{in}}}{Q^2} \ln \left( Z_{\text{in}} + \sqrt{Z_{\text{in}}^2 - 1} \right) + \frac{2\sqrt{Z_{\text{in}}^2 - Q^2}}{Q^2} \arctan \left( \frac{\mathcal{P} + Q}{\sqrt{Q^2 - \mathcal{P}^2}} \sqrt{Z_{\text{in}}^2 - 1} \right) 
\]

(ii) If \( \mu > A + C \), then the function is

\[
(5.3) \quad \phi(Z; Z_{\text{in}}) = \begin{cases} 
\frac{1}{Q}(Z_{\text{in}} - Z) - \frac{Z_{\text{in}}}{Q^2} \ln \left( \frac{\mathcal{P} + Q - Z}{\mathcal{P} + Q - Z_{\text{in}}} \right) & \text{if } Z_{\text{in}} \in (0, 1], \\
\frac{1}{Q}(Z_{\text{in}} - Z) - \frac{Z_{\text{in}}}{Q^2} \ln \left( \frac{\mathcal{P} + Q - Z}{\mathcal{P} + Q - Z_{\text{in}}} \right) + \chi_2(Z_{\text{in}}) & \text{if } Z_{\text{in}} > 1,
\end{cases}
\]

for \(-1 \leq Z < 0\), where

\[
\chi_2(Z_{\text{in}}) = -\frac{1}{Q} \sqrt{Z_{\text{in}}^2 - 1} - \frac{Z_{\text{in}}}{Q^2} \ln \left( Z_{\text{in}} + \sqrt{Z_{\text{in}}^2 - 1} \right) + \frac{\sqrt{Q^2 - \mathcal{P}^2}}{Q^2} \ln \left( \frac{\mathcal{P}Z_{\text{in}} + \sqrt{(\mathcal{P}^2 - \mathcal{Q}^2)(Z_{\text{in}}^2 - 1)}}{\mathcal{P} - \mathcal{Q}Z_{\text{in}}} \right) 
\]
Otherwise, for $-\frac{\mu}{A+C} < Z < -1$ the function is

$$
\phi(Z; Z_{in}) = \begin{cases} 
\frac{1}{B}(Z_{in} - Z) - \frac{\gamma}{B^2} \ln \left( \frac{\gamma/q - Z}{\gamma/q - Z_{in}} \right) - \frac{\gamma}{B^2} \ln \left( -Z + \sqrt{Z^2 - 1} \right) \\
+ \frac{1}{B} \sqrt{Z^2 - 1} - \frac{\gamma^2 - q^2}{q^2} \ln \left( -\gamma/q + \sqrt{(\gamma^2 - q^2)(Z^2 - 1)} \right) & \text{if } Z_{in} \in (0, 1], \\
\frac{1}{B}(Z_{in} - Z) - \frac{\gamma}{B^2} \ln \left( \frac{\gamma/q - Z}{\gamma/q - Z_{in}} \right) - \frac{\gamma}{B^2} \ln \left( -Z + \sqrt{Z^2 - 1} \right) \\
+ \frac{1}{B} \sqrt{Z^2 - 1} - \frac{\gamma^2 - q^2}{q^2} \ln \left( -\gamma/q + \sqrt{(\gamma^2 - q^2)(Z^2 - 1)} \right) + \chi_2(Z_{in}) & \text{if } Z_{in} > 1.
\end{cases}
$$

Given the above definitions, we obtain the following result.

**Theorem 5.1.** Consider the canonical form (4.11) of the perturbed system (2.1) obtained for $\varepsilon$ sufficiently small. Let us assume that $\mu, A, B, C$ defined by (4.8) satisfy $\mu, A, C = O(\sqrt{\varepsilon})$, $B = O(\varepsilon)$ and $\mu, B > 0$, $A + C > 0$.

(i) Let $p_c = (X_c, Y_c, Z_c)$ be the entry point of a trajectory of (4.11) into the trapping region of the folded node. Then let $(X_{in}, Y_{in}, Z_{in})$ with $Z_{in} > 0$ ($X_{in} = Z_{in}$, $Y_{in} = Z_{in}^2$) be the projection of $p_c$ onto the orbital connection $\gamma_{N_1 S_1}$. There is a unique (negative) solution $Z_{out} \in (-\frac{\mu}{A+C}, 0)$ of the equation $\phi(Z_{out}; Z_{in}) = 0$ defined by (5.2)–(5.4), and the trajectory’s exit point from the funnel is $O(\varepsilon)$ near $(X_{out}, Y_{out}, Z_{out})$ with $X_{out} = Z_{out}$, $Y_{out} = Z_{out}^2$.

(ii) The maximal delay point in the funnel of the folded node (the buffer point) is defined as $X_b = Z_b$, $Y_b = Z_b^2$ with $Z_b$ the limit value of the implicitly defined function $Z_{out}$,

$$
Z_b = \lim_{Z_{in} \to \infty} Z_{out}.
$$

**Proof.** Consider $\lambda(s) = (s - i\sqrt{1 - s^2})/(P + Qs)$, $\nu(s) = (s + i\sqrt{1 - s^2})/(P + Qs)$ with $P, Q$ defined by (5.1). We compute $\text{Re}(\lambda(s))$, $\text{Re}(\nu(s))$ explicitly in the complex plane (e.g., we first compute $\text{Re}(\lambda(s + i\bar{s}))$ and then set $s = 0$) and get

$$
\text{Re}(\lambda(s)) = \begin{cases} 
(s + \sqrt{s^2 - 1})/(P + Qs) & \text{if } s < -1, \\
s/(P + Qs) & \text{if } s \in (-1, 1), \\
(s - \sqrt{s^2 - 1})/(P + Qs) & \text{if } s > 1
\end{cases}
$$

and

$$
\text{Re}(\nu(s)) = \begin{cases} 
(s - \sqrt{s^2 - 1})/(P + Qs) & \text{if } s < -1, \\
s/(P + Qs) & \text{if } s \in (-1, 1), \\
(s + \sqrt{s^2 - 1})/(P + Qs) & \text{if } s > 1
\end{cases}
$$

The function $\phi$ in (5.2)–(5.4) results directly from integration of $\int_{-Z_{in}}^{Z_{in}} \text{Re}(\lambda(s)) \, ds$ (if $-1 < Z < 0$) and $\int_{-Z_{in}}^{1} \text{Re}(\lambda(s)) \, ds + \int_{1}^{-Z_{in}} \text{Re}(\nu(s)) \, ds$ (if $Z > -1$), respectively. ■
5.2. Geometrical interpretation of the way-in/way-out function. We can use the definition of the way-in/way-out function to estimate the exit point of the periodic canard (MMO) solution from the funnel of the folded node for system (2.1). This process allows us to classify the small amplitude oscillations (SAOs) in the MMO as canard-induced or Hopf-induced oscillations, observing in particular that some of the SAOs occur outside the funnel as $I$ approaches the subcritical Hopf ($I \to I_{sH}$). For numerical illustration, we choose two parameter values ($I = I_1 := 1.325$ and $I = I_2 := 1.315$) that appear to yield two qualitatively distinct types of SAOs (see section 4.2.2). We conclude with the numerical identification of the position of the buffer point—the point along the orbital connection that represents the limitation of what can be reached by a trajectory in the funnel—and comment on its theoretical role for the classification of canard-induced and Hopf-induced SAOs.

5.2.1. Numerical estimation of the exit point of a canard from the folded node funnel. Let $\tilde{p}_c = (u_{1c}, u_{2c}, a_{1c}, a_{2c})$ be a point where the MMO solution of (2.1) intersects the trapping region of the folded node (this is what we have called the entry point into the funnel; see Figure 8, black square). This intersection is determined in an approximate, geometric way: we choose $\tilde{p}_c$ to be a point within an $O(\sqrt{\varepsilon})$ neighborhood of the slow manifold $W^s_{\text{slow}}$ from which the emerging trajectory (black solid) stays in that neighborhood and follows $W^s_{\text{slow}}$. We identify a trajectory on $W^s_{\text{slow}}$ that the MMO tracks and observe that this curve is below the strong canard, which we take as a verification that $\tilde{p}_c$ belongs to the trapping region of the folded node. As an additional test for correctness, we also confirm that $\tilde{p}_c$ lies a distance less than $\sqrt{\varepsilon}$ from the folded node and thus that all computations done in system (4.11) remain valid for (2.1) as well. Indeed, the distance between the entry point and the folded node is $d_{\tilde{p}_c, N_1} = 0.03524$ at $I = 1.325$ and $d_{\tilde{p}_c, N_1} = 0.03657$ at $I = 1.315$; since $\varepsilon = 0.01$, these
distances satisfy \(d_{p_{2},N_{1}} < \sqrt{\varepsilon}\) (in fact, they are of order \(O(\varepsilon)\)).

In practice, we first map \(\tilde{p}_e\) into \(p_e = (X_e, Y_e, Z_e)\) according to transformations (4.4), (4.5), and (4.9), and then we define its projection on the orbital connection (primary weak canard) \(\gamma_{N_{1},S_{1}}\). Since \(\gamma_{N_{1},S_{1}}\) is the critical manifold of system (4.11), for \(I\) sufficiently close to \(I_{SH}\), the trajectories that we follow within the trapping region of the folded node will be rapidly attracted to a small neighborhood of \(\gamma_{N_{1},S_{1}}\); therefore, a reasonable projection of \(\tilde{p}_e\) on the orbital connection is \((X_{in}, Y_{in}, Z_{in})\) with \(Z_{in} := Z_e, X_{in} = Z_{in}\), and \(Y_{in} = Z_{in}^{2}\) (Figure 8, red triangle). The way-in/way-out function applied to \(Z_{in}\) yields the exit point \((X_{out}, Y_{out}, Z_{out})\) according to Theorem 5.1, which is then transformed back to \(\tilde{p}_{out}\) in \((u_1, u_2, a_1, a_2)\) space by (4.9), (4.7), and (4.6) (Figure 8, black triangle).

The values of \(\tilde{p}_{out}\) obtained at \(I_1 = 1.325\) and \(I_2 = 1.315\) are in good agreement with the general picture of the local dynamics of \((2.1)\) in the vicinity of the folded node.

We adopted the following convention to split SAOs into canard-induced and Hopf-induced subsets: we use local maxima in \(u_t\) to count oscillations, we label as canard-induced (\#c) all of those up to and including the first cycle with its maximum beyond \(\tilde{p}_{out}\), and we declare the remainder to be Hopf-induced (\#H). At \(I = I_1\), the canard (MMO) trajectory of the full system undergoes two rotations in the funnel and leaves it close to \(\tilde{p}_{out}(I_1)\); the two SAOs are canard-induced, which we denote as \(2c0H\). In contrast, at \(I = I_2\), the periodic canard shows only (about) four SAOs in the funnel before leaving it near \(\tilde{p}_{out}(I_2)\); four additional rotations occur outside of the funnel, and they are a dynamical consequence of the unstable manifold of the equilibrium. Thus, at \(I = I_2\), the SAOs are of type \(4c4H\). In the latter case, \(\tilde{p}_{out}:I_2\) falls closer to the equilibrium (at \(O(\varepsilon\sqrt{\varepsilon})\) distance; \(d_{\tilde{p}_{out}(I_2), Eq} = 0.0026\), as opposed to the former example where it is only at \(O(\varepsilon)\) distance from the equilibrium (\(d_{\tilde{p}_{out}(I_1), Eq} = 0.0121\)).

5.2.2. Numerical classification of SAOs for canard trajectories. To illustrate the definition of the way-in/way-out function for several values of \(Z_{in}\), we consider \(I_2 = 1.315\) at \(\varepsilon = 0.01\) (Figure 9). Since both canard-induced and Hopf-induced SAOs occur at \(I_2\), we would like to investigate the influence of \(Z_{in}\) (and accordingly, of \(Z_{out}\)) on the total number of SAOs of a canard solution and, in particular, on how the SAOs split into canard-induced and Hopf-induced subclasses (\#c \#H).

We use the strategy outlined above to identify numerically the entry points \(\tilde{p}_e\) into the funnel for several distinct trajectories of system (2.1) and to compute \(Z_{in}\) and \(Z_{out}\) for each. The calculation of \(Z_{out}\) leads to the estimation of the exit point \(\tilde{p}_{out}\) and allows for the classification of the SAOs.

In Figure 9(B)–(C) we show two canards of five and eight SAOs, respectively, generated from two distinct initial conditions in (2.1). The larger \(Z_{in}\) is, the larger (in absolute value) \(Z_{out}\) becomes, but the mapping is nonlinear; in fact, the way-in/way-out function saturates at the buffer point value \(Z_b\), which at \(I_2 = 1.315\) is near \(Z_{eq}\) (Figure 9(A)). An increase in \(|Z_{out}|\) translates into an increase in the total number of SAOs, and in both \#c and \#H (Table 3). Notably, if \(Z_b \approx Z_{eq}\), then the number of Hopf-induced oscillations dominates as \(Z_{out} \rightarrow Z_b\).

It is well established that the global return map plays an important role in the selection of SAOs in canards related to folded node singularities. For example, all canards at \(I = 1.325\), after the first, initial condition-dependent iteration of the return map, follow the MMO attractor with two SAOs (2c0H). However, our numerical study points out a more complex
Figure 9. Classification of SAOs using the way-in/way-out function. (A) $Z_{in}$ (red dot) and $Z_{out}$ (black dot) computed according to Theorem 5.1 for several trajectories of the full system (2.1) at $I = 1.315$ and $\tau = 100$ ($\epsilon = 0.01$); the folded node, equilibrium, and buffer points satisfy $Z_{FN} = 0$, $Z_{eq} = -0.14327866$, and $Z_{b} = -0.14519155$. Depending on their entry point in the funnel, the trajectories display $n = 3, 4, \ldots, 13$ SAOs. (B)–(E) Based on the way-in/way-out function, the SAOs from panel (A) are numerically classified into canard-induced (#c; solid black) and Hopf-induced (#H; solid gray) subsets (see Table 3). The trajectories with five SAOs (B) and eight SAOs (D) are shown in the $(u_1, a_1, a_2)$-space and have the form $3c2H$ and $4c4H$, respectively. Their $u_1$-timecourses are also included (C), (E).

phenomenon that occurs in systems with FSN II singularities. In such systems, the distance between $Z_b$ and $Z_{eq}$ influences the maximum possible number of SAOs for a canard. Specifically, the closer $Z_b$ is to $Z_{eq}$, the more likely it is that a canard will have many SAOs (see, e.g., Table 3), whereas if $Z_b$ is far from $Z_{eq}$, the number of Hopf-induced SAOs that can occur will be limited. Therefore, the range of possible numbers of SAOs is a priori constrained by
Types of canards in system (2.1) at $I = 1.315$ and $I = 1.325$ ($\tau = 100$). The classification is based on the way-in/way-out function (see Figure 9(A) for $I = 1.315$). The maximum number of SAOs found numerically for canard trajectories in system (2.1) depends on $I$ ($\text{maxSAO} = 5$ at $I = 1.325$; $\text{maxSAO} = 13$ at $I = 1.315$). All trajectories tend to the system’s periodic canard in one iteration of the global return map. (The periodic canard has two SAOs at $I = 1.325$ and eight SAOs at $I = 1.315$.)

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Figure 10. Distances between the buffer point and the equilibrium (solid line); the buffer point and the folded node (dotted line); and the equilibrium and the folded node (dashed line) for $\tau = 100$ ($\varepsilon = 0.01$) and an interval of $I$ where system (2.1) has folded nodes ($I > I_\alpha = 1.309$). At $I = 1.315$ and $I = 1.325$ the distance between the actual exit point of the MMO and the equilibrium was also computed (dots, left panel; see also Figure 8). As $I$ approaches $I_\alpha$, the buffer point lies at an $O(\varepsilon^2)$ distance from the equilibrium (right panel). Note that the (Euclidean) distance is computed directly in the space $(u_1, u_2, a_1, a_2)$.

The position of the buffer point and is selected by the global return map within this range. To gain more insight into the dependence of the buffer point position on the parameter value $I$, we next determine the relative distances between the equilibrium, the folded node, and the buffer as $I \to I_\alpha$.

5.2.3. Numerical interpretation of the buffer point. We computed $Z_b$ and the buffer point $\tilde{p}_b$ over the entire interval of values $I$ where system (2.1) has a folded node at $\varepsilon = 0.01$, $I \in [1.31, 1.38]$. While in principle the buffer point is never reached ($Z_b = \lim_{Z_{in} \to \infty} Z_{out}$), computing it is still useful because its location provides a good indication of how close to the equilibrium a canard trajectory can possibly go.

The (Euclidean) distances between the buffer point and the equilibrium, $d_{\tilde{p}_b,Eq}$ (Figure 10, solid line); between the buffer point and the folded node, $d_{\tilde{p}_b,N_i}$ (Figure 10, dotted line); and between the equilibrium and the folded node, $d_{Eq,N_i}$ (Figure 10, dashed line), calculated in $(u_1, u_2, a_1, a_2)$ space, indicate that the buffer point approaches the equilibrium as $I \to I_\alpha$. 

Table 3

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More precisely, we can observe numerically that $d_{\tilde{p},E_q} = O(\varepsilon^2)$ while $d_{\tilde{p},N_1} = O(\varepsilon)$ as $I \to I_{sH}$; although $d_{\tilde{p},E_q}$ and $d_{\tilde{p},N_1}$ scale differently with $\varepsilon$, they both tend to zero as $\varepsilon \to 0$. This convergence corresponds to the fact that $I_{sH} = I_{singH}$ at $\varepsilon = 0$, at which point there occurs a transcritical bifurcation for the desingularized system in which the folded node and the equilibrium merge, such that $d_{E_q,N_1} \to 0$. Since the buffer point lies between the folded node and equilibrium, its distance from each of the others is squeezed to zero as $\varepsilon \to 0$ as well.

As noted above, although the location of the buffer point does not yield a prediction of the exit point of the MMO from the funnel, as the way-in/way-out function $Z_{in} \to Z_{out}$ does, it provides a lower bound on how closely trajectories can approach the equilibrium. As the distances between the buffer point and the equilibrium and folded node both decrease with decreasing $I$, the opportunity arises for canard trajectories leaving the funnel to become close to the equilibrium and thus be influenced by its local vector field. In light of the small distance between the folded node and the equilibrium, together with the proximity of the buffer point and the equilibrium for $I$ sufficiently close to $I_{sH}$, it is expected that a significant portion of the SAOs of the MMO solution for such $I$ result from the influence of the unstable manifold $W_{eq}^u$ and thus are Hopf-induced oscillations.

6. Symmetric canards and their relation to the full system bifurcation diagram. For the analysis of a dynamical system, an interesting question is if and how the existence of MMO canard solutions relates to the bifurcation diagram of the full system. In general, this problem is highly nontrivial, given that existent numerical packages that deal with bifurcation diagrams (e.g., AUTO, MatCont) rely on computation of Jacobians and eigenvalues and are limited to the detection of local bifurcations. On the other hand, canard solutions are associated with the existence of folded singularities (nodes) that are not equilibria of the full system and hence cannot be detected by standard local bifurcation diagram techniques.

We address this question in the context of our case study. In this section, we compare the bifurcation diagram of full system (2.1), in the relevant part of the parameter space, with the information gathered through the investigation of MMOs. A previous study of the bifurcation diagram for the interval of $I$ between supercritical Hopf ($I_{HB}$) and subcritical Hopf ($I_{sH}$) revealed that the limit cycle (regular oscillation) born at $I_{HB}$ becomes unstable at a value $\bar{I}$ with $I_{HB} > \bar{I} > I_{sH}$; this event is followed by a cascade of Neimark–Sacker and period-doubling bifurcations, but the stability of the limit cycle is never recovered [7]. To allow for comparison, we redraw the bifurcation diagram of (2.1) for the same set of parameters used in this paper to investigate MMOs (Figure 11) and find that the regular oscillatory solution (black, filled circles) born at the supercritical Hopf at $I_{HB} = 1.85357$ becomes unstable at approximately $\bar{I} = 1.34381$. (The bifurcation type at $\bar{I}$ is unknown. However, numerical simulations of system (2.1) in a parameter range with $\tau$ much smaller indicate a loss of stability through a Neimark–Sacker bifurcation [7].) At the subcritical Hopf bifurcation at $I_{sH} = 1.30909$, an unstable limit cycle (red, open circles) emerges around each nontrivial equilibrium $e_{1I}, e_{sI}$; it then disappears through a fold of limit cycles at $\bar{I} = 1.30711$, where it merges with one of two additional unstable limit cycles (yellow/green, open circles). The latter are formed in a double homoclinic bifurcation to the trivial equilibrium $e_I$ at $\bar{I} = 1.33079$. The bifurcation diagram indicates that as $I \downarrow \bar{I}$, the large limit cycle (black, open circles)
approaches the homoclinic loops and disappears at $\bar{I}$. The period of the large limit cycle found for $I > \bar{I}$ and the period of the unstable cycles that exist for $I < \bar{I}$ blow up ($T \to \infty$) at $\bar{I}$; see Figure 11(C).

Since stable MMO solutions are detected in (relatively) the same range $I \in (I_{sH}, \bar{I})$, it is tempting to assume that their appearance is directly related to the cascade of instability-type bifurcations seen in the diagram of the full system. While a proof of an exact relationship remains an open problem, our numerical results rather cast doubt on this connection.

Consider system (2.1) with $\varepsilon = 0.01$ (i.e., $\tau = 100$, and other parameters as in Figure 11) and decrease $I$ from $I_{HB}$ down toward $I_{sH}$. At about $I = 1.38$, the system starts to admit folded node singularities with associated funnels on both lower and upper branches of the slow

**Figure 11.** Bifurcation study of system (2.1). (A) Bifurcation diagram of $u_1$ versus $I$. Other parameter values are $\tau = 100$, $\beta = 1.1$, $g = 0.5$, $r = 10$, $\theta = 0.2$. Branches of stable (unstable) equilibria are represented by solid (dashed) black lines; filled (open) circles correspond to stable (unstable) limit cycles. (B) Zoomed view of (A) taken about $I = 1.33079$, where the green and yellow curves emanate from the equilibrium branch $e_1$. (C) Period of limit cycles from panel (A). (D) Legend of notation.
manifold. At this point, the system has the structure in place to form MMOs, but they do not occur due to the properties of the global return map.

Although it is near $\tilde{I} = 1.34381$ where MMOs first are found, we did find MMOs for values of $I$ that are larger than $\tilde{I}$. The MMOs that are observed at largest $I$ are asymmetric; they are periodic canards passing through the funnel of a folded node only on one side of the attractive slow manifold (Figure 12(B), $(a_1)$). Due to the symmetry of the system, these types of MMOs come in symmetry-related pairs. Interestingly, some of the MMOs in this region are exotic, in that the global return map misses the funnel at certain cycles on only one side of the attractive slow manifold (Figure 12(B), $(a_2)$).

A further decrease in $I$ reveals symmetric MMOs with the same number of SAOs on both upper and lower branches of the relaxation cycle. We use the notation $1_n^1$ to denote an MMO with $n$ small oscillations on each branch. Smaller $I$ leads to larger $n$ for MMOs, starting with $1_1^1$ at about $I = 1.3434$ to, for example, $1_{46}^{146}$ near $I_{sH}$ at about $I = 1.31$ (Figure 12(A), (C)). Numerical computation shows that the periods of the MMOs increase as $I$ tends to $I_{sH}$.

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**Figure 12.** (A) Period and signatures of MMOs in system (2.1) for $\varepsilon = 0.01$ ($\tau = 100$). Other parameters are as in Figure 11. A zoom of the diagram for $I \in [1.315, 1.345]$ is given on the right side. (B) Two examples of symmetry-related asymmetric MMOs, $(a_1)$ $1_1^{10}; 1_0^{11}$ and $(a_2)$ $1_0^{11}; 1_1^{10}$. (C) Legend of notation. Each term $1_x$ indicates that $x$ SAOs occur on the lower branch of the relaxation cycle (defined with respect to $u_1$, hence the 1), while each term $1^y$ refers to $y$ SAOs occurring on the upper branch. For example, $1_0^{11}$ MMOs travel along the lower branch without passing through the folded node funnel, pass through the funnel, and exhibit one SAO on the upper branch, and then repeat periodically.
with discontinuities between subclasses of $1_n^{1^n}$-type. We also found that there exist regimes (intervals of $I$) of bistability or abrupt jumps between different types of solutions as $I$ varies, including bistability between regular oscillations and asymmetric MMOs, apparent jumping between $1_0^{1^1}, 1_0^{1^1}1_1^{1^1},$ and $1_1^{1^1}$ MMOs, and bistability between $1_n^{1^n}$ and $1_{n+1}^{1^{n+1}}$ types of MMOs. The transition from one type of MMO to the next, as $I \rightarrow I_{sH}$, may occur through a local hysteresis; alternatively, MMOs of consecutive signatures may simply lie on isolated curves (isolas) that extend over partially overlapping intervals of $I$. Nevertheless, there is no reliable indication that the occurrence of MMOs is in any way related to the instabilities of the limit cycle born at $I_{HB}$. Note that another example in which MMOs were shown to be situated on isolas is the Koper model [21], discussed in [10]. However, that system seems to exhibit multistability between isolas of MMOs with different signatures in certain parameter ranges, and we did not find this property in system (2.1). Since there are several fundamental differences between system (2.1) and the Koper model (e.g., the singular Hopf in [21] is supercritical, while it is subcritical here), one may expect differences in the structure of the parametric curves for MMOs as well. Further investigation of (2.1) is thus needed to sort out the exact mechanisms through which it yields transitions between MMO types, but this is beyond the scope of this paper.

Comparison of the empirical data provided by Figures 10 and 12(A) supports the hypothesis that the distances between the buffer point, the folded node, and the true equilibrium influence the number of SAOs, $n$, in the $1_n^{1^n}$ MMO. As $I$ decreases, and these distances shrink, the likelihood of Hopf-induced SAOs increases, and $n$ increases correspondingly, presumably beyond the bounds predicted by theory of canards [32]. More precise statements about the link between $d_{\tilde{p}_b, E_q}$ and the number of SAOs in the MMOs of system (2.1), as well as their $\#c \#H$ classification, will require additional theoretical investigations.

7. Discussion. We studied the underlying mechanism for the formation of MMOs in an inhibitory reduced neural network with adaptation. We used singular perturbation theory, normal form reduction, methods from the theory of canards, and numerical simulations to establish the existence of MMOs that consist of periodic canards as solutions of system (2.1). They are formed in the funnel of a folded node, which occurs near a folded saddle-node of type II singularity (equivalent here to a singular Hopf point).

Due to the FSN II singularity, an unstable equilibrium of the full system exists in the neighborhood of the fold curve (and the folded node). In addition, there is an orbital connection between the folded node and the ordinary equilibrium with important implications for the local dynamics. The folded node has a double role: first, it behaves like a pore on the fold curve, allowing certain trajectories on the slow stable manifold to cross into the unstable region. This passage introduces a delay in trajectories’ escape from the neighborhood of the fold. At the same time, the folded node creates a funnel around the orbital connection, which induces SAOs in MMOs as they pass through. This description is, however, incomplete: under certain conditions a canard trajectory may be pushed along the orbital connection into a small neighborhood of the unstable equilibrium. As a result, it will follow the spiraling behavior of the unstable manifold of the equilibrium, leading to additional SAOs of the MMO. We distinguish between the former (canard-induced rotations) and the latter (Hopf-induced rotations) forms of MMOs through calculation of a way-in/way-out function.
The network analyzed in this paper consists of two populations of neurons that inhibit each other, and it has been used in the modeling of several neural processes such as perceptual bistability and central pattern generation. The control parameter in the model is the strength of an external stimulus, which strongly influences the network’s dynamics; for example, an increase in the stimulus strength \( I \) generically leads to a change from a unique (low level) steady state, to antiphase oscillations (with period increasing with \( I \)), to MMOs, and then to bistability of winner-take-all type, followed by a return to MMOs, antiphase oscillations (with period decreasing with \( I \)), and a unique (high level) steady state [7], [8], [28]. This richness in behavior is somewhat surprising due to the simplicity of the system, which has only four ordinary differential equations, two of which are linear. Fundamentally, however, the nonlinearity of the gain function, the system’s slow-fast time scale separation, and the network symmetry provide sufficient ingredients to generate dynamical complexity. This combination of complex dynamics and relatively simple structure allows us to perform a thorough analytical and numerical study of the formation and characteristics of MMOs for this system.

In particular, although FSN II points and their associated features arise in a variety of models, to the best of our knowledge, this work and [10] are the first to implement new theoretical developments to examine the interaction of the SAO mechanisms that they induce. In a study completed independently in parallel with this one, Desroches et al. [10] discuss two other examples of canard-induced and Hopf-induced MMOs: the Koper model and a reduced form of the Hodgkin–Huxley model. In the Koper model, MMOs appear near an FSN II point associated with a supercritical singular Hopf bifurcation, and their properties are studied both analytically and numerically. The reduced Hodgkin–Huxley system features an FSN II point at a subcritical Hopf bifurcation, but due to the complexity of the model equations, its MMOs are studied mostly numerically. By contrast, the focus of this paper is on a coherent, detailed analytical and numerical investigation of a single system with an FSN II at a subcritical Hopf bifurcation. The components of this analysis include the geometrical analysis of the singular limit case, a normal form construction, the numerical generation of slow manifolds, and the interpretation of the existence of MMOs in the context of the bifurcation diagram of the full system. In addition, we present a first numerical implementation of a recently introduced way-in/way-out function [23] and use it to propose a classification of the SAOs of MMOs into canard-induced and Hopf-induced types. Indeed, because the singular Hopf bifurcation for system (2.1) is subcritical, the complication of dealing with a branch of stable limit cycles that converges to the singular Hopf point is avoided, making this analysis tractable. Our derivation of formulas and performance of calculations associated with the way-in/way-out function for this subcritical example problem represent important steps for the complete understanding of the interaction between canard-induced and Hopf-induced mechanisms in the formation of MMOs. Because we focused on system (2.1), a systematic comparison of the similarities and differences between subcritical and supercritical singular Hopf scenarios still remains for future work. We can point out, as a preliminary finding, that the relation of the branches of MMOs with different SAO signatures to the full system bifurcation diagram differs between our work and that in the supercritical Koper example in [10], but the details of these relations and the extent to which they arise from the criticality of the singular Hopf bifurcation remain for future investigation.

Another distinctive feature of the dynamics studied here is that the existence of MMOs in
system (2.1) is a network property. Indeed, it can be easily verified that in the absence of the connections between populations, each population in system (2.1) cannot oscillate [8]. The oscillations that arise (regular or mixed-mode) result from the interplay of reciprocal inhibition and slow negative feedback (adaptation); the former allows one population to suppress the other, while the latter leads to an eventual role reversal. This emergent dynamics differs from the canard-induced MMOs seen in other computational neuroscience models, which occur due to intrinsic properties of individual neurons [26], [27], [25], [16].

A final interesting property of the MMOs in system (2.1) is that the transition between the dynamics on the slow manifold and that along the fast fibers occurs near a folded node on both lower and upper branches of the slow manifold, symmetrically. While a similar property was recently observed in the Koper model [10], there it is described as arising in a very small parameter regime. Moreover, for that system, such MMOs show only one SAO on each branch of the slow manifold. By contrast, in system (2.1), symmetric MMOs with signature $1_n1^n$ occur throughout most of the interval of bifurcation parameter values where MMOs arise, including a significant range where $n > 1$. We note that asymmetric MMOs do exist for system (2.1), but they are limited to a narrow parameter range at the transition between regular oscillations and MMOs. While this feature is a consequence of the system’s structure, it still makes (2.1) the unique example in the literature, to our knowledge, predominantly exhibiting MMOs with canard behavior and SAOs in both the active and silent phases of each cycle.

REFERENCES


