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# Numerical continuation of canard orbits in slow-fast dynamical systems 

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#### Abstract

. A trajectory of a system with two clearly separated time scales generally consists of fast segments (or jumps) followed by slow segments where the trajectory follows an attracting part of a slow manifold. The switch back to fast dynamics typically occurs when the trajectory passes a fold with respect to a fast direction. A special role is played by trajectories known as canard orbits, which do not jump at a fold but, instead, follow a repelling slow manifold for some time. We concentrate here on the case of a slow-fast system with two slow and one fast variable, where canard orbits arise geometrically as intersection curves of twodimensional attracting and repelling slow manifolds. Canard orbits are intimately related to the dynamics near special points known as folded singularities, which in turn have been shown to explain small-amplitude oscillations that can be found as part of so-called mixed-mode oscillations.

In this paper we present a numerical method to detect and then follow branches of canard orbits in a system parameter. More specifically, we define well-posed two-point boundary value problems that represent orbit segments on the slow manifolds, and we continue their solution families with the package AUTO. In this way, we are able to deal effectively with the numerical challenge of strong attraction to and strong repulsion from the slow manifolds. Canard orbits are detected as the transverse intersection points of the curves along which attracting and repelling slow manifolds intersect a suitable section (near a folded node). These intersection points correspond to a unique pair of orbits segments, one on the attracting and one on the repelling slow manifold. After concatenation of the respective pairs of orbits segements, all detected canard orbits are represented as solutions of a single boundary value problem, which allows us to continue them in system parameters. We demonstrate with two examples - the self-coupled FitzHugh-Nagumo system and a three-dimensional reduced Hodgkin-Huxley model - that branches of canard orbits can be computed reliably. Furthermore, our computations illustrate that the continuation of canard orbits allows one to find and investigate new types of dynamics, such as the interaction between canard orbits and a saddle periodic orbit that is generated in a singular Hopf bifurcation.


[^0]
## 1. Introduction

In many systems of ordinary differential equations one finds that different variables evolve on quite different time scales. Such multiple time-scale systems arise in applications as diverse as chemical reaction dynamics [37, 44, 48, 49], cell modeling [35, 41, 52, 53], electronic circuits [26, 59, 60], and laser systems [11, 20, 22, 23]. A sufficiently large difference between different time scales induces a natural separation of the variables. In the simplest case there are only two time scales and one also speaks of a slow-fast system. The analysis of the planar case of a slow-fast system goes back to the work of Van der Pol in the 1920s [59]. In the famous equation for a radio circuit that bears his name today he discovered a peculiar type of dynamics: periodic orbits that are composed of slow and fast segments of the dynamics, which he named relaxation oscillations [60]. What is more, Benoît et al. [5] discovered so-called canard orbits, which have the counter-intuitive property that they closely follow for some time at least one repelling segment of the fast nullcline, or critical manifold, of the system. In planar slow-fast systems canard orbits exist only in intervals of system parameters that are exponentially small in the time-scale parameter $\varepsilon$. This effect explains the extremely rapid transition from $O(\varepsilon)$-amplitude oscillations to relaxation oscillations with $O(1)$ amplitude in the Van der Pol and related planar slow-fast systems. This phenomenon was later referred to as a canard explosion in the context of two-dimensional models of chemical reactions [12], where it occurs frequently.

More generally, the existence of canard orbits is due to the interaction of the attracting and repelling slow manifolds, which are locally invariant perturbations of the attracting and repelling sheets of the critical manifold. The extreme sensitivity of the canard phenomenon in planar systems stems from the fact that the attracting and repelling slow manifolds are both of dimension one. However, as soon as these manifolds have sufficiently large dimensions, their intersections and, hence, canard orbits, are structurally stable and exist in parameter intervals that are no longer exponentially small.

This paper is concerned with the detection and continuation in parameters of isolated structurally stable canard orbits. More specifically, we consider a slow-fast dynamical system in $\mathbb{R}^{3}$ with two slow and one fast variables, of the general form

$$
\begin{align*}
\dot{x} & =g_{1}(x, y, z, \varepsilon)  \tag{1}\\
\dot{y} & =g_{2}(x, y, z, \varepsilon)  \tag{2}\\
\varepsilon \dot{z} & =f(x, y, z, \varepsilon) \tag{3}
\end{align*}
$$

Here $g_{1}, g_{2}$, and $f$ are sufficiently smooth functions, and $\varepsilon>0$ is a small parameter that separates the time scales. There is now a well-established theory about slow-fast dynamical systems of this form (see, for example, $[6,7,8,28,29,56,61]$ ) and, here, we summarise the main results as needed here. As long as $\varepsilon$ is nonzero, system (1)-(3) is equivalent to

$$
\begin{align*}
x^{\prime} & =\varepsilon g_{1}(x, y, z, \varepsilon),  \tag{4}\\
y^{\prime} & =\varepsilon g_{2}(x, y, z, \varepsilon),  \tag{5}\\
z^{\prime} & =f(x, y, z, \varepsilon), \tag{6}
\end{align*}
$$

by means of the time rescaling $\tau=t / \varepsilon$.
Since one is interested in the dynamics for small $0<\varepsilon \ll 1$, it is natural to consider what can be learned from the limits for $\varepsilon=0$ of both systems. A central
object in this context is the critical manifold $S$, which is given by the nullcline of the fast variable $z$, that is, by

$$
\begin{equation*}
S:=\left\{(x, y, z) \in \mathbb{R}^{3} ; f(x, y, z, 0)=0\right\} . \tag{7}
\end{equation*}
$$

Setting $\varepsilon=0$ in system (1)-(3) yields two differential equations for the slow variables $x$ and $y$, which are constrained by equation (3) to lie on the critical manifold $S$; this limit is referred to as the slow subsystem (or the reduced system). The limit $\varepsilon=0$ in (4)-(6), on the other hand, yields a differential equation for the fast variable $z$. This system is referred to as the fast subsystem (or layer system), and the two slow variables $x$ and $y$ enter it as parameters (since their derivatives are zero for $\varepsilon=0$ ). Note that $S$ is a surface of equilibria of the fast subsystem.

The critical manifold $S$ associated with (1)-(3) is a two-dimensional surface in $\mathbb{R}^{3}$ that consists of attracting and repelling sheets $S^{a}$ and $S^{r}$, which generically meet at folds with respect to the fast flow direction $z$. The locus of fold points $F$ on $S$ is given by

$$
\begin{equation*}
F:=\left\{(x, y, z) \in S ; f_{z}(x, y, z, 0)=\frac{\partial f}{\partial z}(x, y, z, 0)=0\right\} . \tag{8}
\end{equation*}
$$

Note that, generically, $F$ is a smooth curve that may have isolated cusp points with respect to the $z$-direction. From now on we consider the dynamics locally near a curve of regular fold points, that is, away from any cusp points that may be present. A point on $S$ may either be attracted to $F$ or repelled from $F$ under the slow flow on the critical manifold $S$. Where $F$ is attracting on $S$, the resulting behaviour is a jump on a fast time scale away from the fold; this is the three-dimensional analogue of the jumps associated with fast segments of relaxation oscillations in planar slow-fast system. On the other hand, where $F$ is repelling on $S$, no jump occurs. The transition between these two cases takes place at special points on $F$ that are called folded singularities. The behaviour near a folded singularity is best understood by considering the slow subsystem near $F$, which can be expressed by

$$
\begin{align*}
\dot{y} & =g_{2}  \tag{9}\\
f_{z} \dot{z} & =-\left(f_{x} g_{1}+f_{y} g_{2}\right) \tag{10}
\end{align*}
$$

where $x$ is uniquely determined by the algebraic condition (7). (If $S$ happens to be a graph over the $(x, z)$-plane only then the roles of $x$ and $y$ need to be exchanged.) The slow flow (9)-(10) is singular along the fold curve $F$. It can be desingularized by applying the time rescaling given by multiplication of the right-hand side with $-f_{z}$ to yield

$$
\begin{align*}
& \dot{y}=-f_{z} g_{2}  \tag{11}\\
& \dot{z}=f_{x} g_{1}+f_{y} g_{2} \tag{12}
\end{align*}
$$

An equilibrium of (11)-(12) that lies on the fold $F$ is called a folded equilibrium; one distinguishes between folded nodes, folded saddles, folded foci and folded saddle-nodes $[2,7,8,56,29,61]$. We remark that a folded singularity is generally not an equilibrium of the slow flow. There has been a lot of interest in folded singularities because they are closely associated with canard orbits. Note that the time rescaling reverses the orientation of orbits on $S^{r}$. (This follows the convention that the flow of (11)-(12) and that of the full system (1)-(3) have the same direction near $S^{a}$.) Hence, a folded singularity is a point on the fold $F$ through which trajectories of the slow flow (9)-(10)
may cross form the attracting sheet $S^{a}$ to the repelling sheet $S^{r}$. Any such trajectory is called a singular canard $[7,49,56,61]$.

The main question is what dynamics ensues in a neighbourhood of a folded singularity for nonzero $\varepsilon$. Away from the fold curve $F$ the critical manifold $S$ is normally hyperbolic. Hence, Fenichel theory [24] applies and guarantees the existence of attracting and repelling slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ as smooth perturbations of the attracting and repelling sheets $S^{a}$ and $S^{r}$, respectively. The task is now to determine how $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ intersect and give rise to canard ortbits. More specifically, the question is how canard orbits of system (1)-(3) arise from the slow dynamics on $S$ near a folded singularity. Normal hyperbolicity does not hold at $F$ and, as a consequence, Fenichel theory does not give any information about the interaction between $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$. The theory of folded-node singularities $[7,8,29,56,61]$ addresses this problem and describes how the singular situation near $F$ perturbs for $\varepsilon>0$.

We concentrate here on the case of a folded singularity of node type. It has been shown by the study of a normal form $[2,7,56,57,61]$ that near a folded node the twodimensional slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ intersect transversally along one-dimensional curves, which are the canard orbits of the full system (1)-(3). An important quantity is the eigenvalue ratio $\mu$ (which we define such that $\mu \geq 1$ ) of the desingularized reduced system (11)-(12) evaluated at the folded node. There are two intersection curves that persist for all $\mu>1$, called the strong primary canard $\gamma_{s}$ and the weak primary canard $\gamma_{w}$. They converge as $\varepsilon \rightarrow 0$ to two singular canard orbits, the strong singular canard $\widehat{\gamma}_{s}$ and the weak singular canard $\widehat{\gamma}_{w}$, which correspond to the strongly and weakly attracting directions of the folded node (as an equilibrium of (11)-(12)), respectively. As $\mu$ increases, the number of intersection curves of $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ and, hence, the number of canard orbits, increases; such additional canard orbits are known as secondary canards [61].

Canard orbits near a folded node occur in a robust way as the generic transverse intersection curves of the two-dimensional surfaces $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$. As such, they exist in large regions of parameter space, where they can contribute to the overall observed dynamics in a significant way. In particular, in connection with a return mechanism back to a neighbourhood of the folded node, (secondary) canard orbits have been shown to act as organizing centres for mixed-mode oscillations (MMOs) $[14,28,35,40,41,53,54]$. This type of oscillation is characterized by a pattern of large-amplitude oscillations interspersed with small oscillations. MMOs have been found in numerous fields of applications, most notably in chemical reactions [37, 48, 49, 43, 44, 45] and in the dynamics of cells [35, 41, 46, 52, 53, 54, 58]; see also [13]. In fact, the wish to understand the phenomenon of MMOs has been an important reason for the recent interest in folded singularities.

When one wants to develop the theory of canard orbits further, or apply it to a given system aring in an application, then there is a need to compute and visualize slow manifolds and canard orbits. However, from the numerical point of view there are a number of challenges. First of all, slow-fast systems exhibit strong sensitivity of orbits on initial conditions; this effect becomes more and more pronounced the smaller $\varepsilon$, and it can generally not be avoided when one is interested in phenomena that are due to the slow-fast nature of the system. As a result, the initial value problem is often ill defined, meaning that orbits cannot be computed reliably with numerical integration (simulation of the governing equations). This effect is extreme near canard orbits, that is, where an orbit closely follows a part of a repelling sheet $S_{\varepsilon}^{r}$. In this situation, even the tiniest perturbations (below machine precision) may make the difference between
whether the orbit finally jumps away from $S_{\varepsilon}^{r}$ in one direction of the fast flow or the other. This effect explains the well-known fact that (most of) the canard orbits in the Van der Pol system cannot be found by numerical integration [25, 27, 30].

In this paper we present a method that allows one to identify canard orbits and then follow or continue them in parameters. Our method is based on the numerical continuation of solution families of suitably defined and well-posed two-point boundary value problems (BVPs). This general approach has proved very fruitful for the computation of invariant manifolds in general, and for numerical computations in slow-fast systems in particular; see [38] for a recent overview. Note that the solution of a two-point BVP corresponds to an orbit segment of the underlying flow. Importantly, it can be found entirely without numerical integration, for example, with the method of collocation [9].

More specifically, we compute in a first step pieces of interest of attracting and repelling slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$, typically near a folded-node singularity where they are known to interact. The basic idea is to allow one end point to vary along a line on the critical manifold $S$ that is far away from the fold curve $F$, while the other end point is restricted to lie in a plane $\Sigma_{\mathrm{fn}}$ through the folded node and transverse to the flow. The computations are performed with the collocation boundary solver and the pseudo-arclength continuation routines of the package AUTO [18]; details and the necessary boundary conditions are presented in section 2 . We have used this general approach to visualize and study the interaction of $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ in the normal form of a folded node [15], near a folded node in the self-coupled FitzHugh-Nagumo system [16], and near a slow passage through a Hopf bifurcation [17]. The emphasis here is on the detection and continuation of canard orbits. Canard orbits can be identified as transverse intersection points of the one-dimensional curves $S_{\varepsilon}^{a} \cap \Sigma_{\mathrm{fn}}$ and $S_{\varepsilon}^{r} \cap \Sigma_{\mathrm{fn}}$ in the section $\Sigma_{\mathrm{fn}}$. As a result, each canard orbit is represented by two orbit segments, one on $S_{\varepsilon}^{a}$ and one on $S_{\varepsilon}^{r}$ and both ending in $\Sigma_{\mathrm{fn}}$. We concatenate these two orbits segments and represent the canard orbit as the solution of a single two-point BVP; see section 2. This procedure allows us to continue any detected canard orbit in parameters, without the need to recompute the slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$.

Overall, we obtain a numerically reliable and efficient method that produces numerical one-parameter bifurcation diagrams consisting of branches of canard orbits in dependence on chosen system parameters. Its performance is demonstrated with two examples of neuronal systems with folded nodes. In section 3 we consider the selfcoupled FitzHugh-Nagumo system [16], where we continue secondary canard orbits in the time-scale parameter $\varepsilon$ towards the limit of $\varepsilon=0$. We find that all detected secondary canards of the full system converge in the limit $\varepsilon=0$ to the strong singular canard $\widehat{\gamma}_{s}$. This agrees with the theory and demonstrates the accuracy of our method. In section 4 we consider a three-dimensional reduced Hodgkin-Huxley model [33], which is a more realistic model of a neuronal system that is known to exhibit MMOs. We first perform a numerical bifurcation study, which reveals a complicated structure of isolas of MMO periodic orbits with different numbers of small oscillations. Canard orbits are then detected near a folded node of the system. We compute branches of canard orbits as a function of the time-scale parameter $\varepsilon$, as well as an applied current $I$ of the model. In both cases we find interactions between canard orbits and other objects that have not been observed before, and this highlights the potential benefits of canard continuation as an numerical tool. The paper finishes with a discussion of possible research directions where the continuation of canard solutions may be of benefit.

## 2. BVP setup for detection and continuation of canard orbits

Our approach is to find canard orbits as structurally stable intersection curves of relevant parts of an attracting and a repelling slow manifold. The first step is to compute the slow manifolds of system (1)-(3) as a family of two-point boundary value problems; see also [15]. Once a canard orbit has been detected in this way, it can be represented and continued as the solution of a BVP in its own right. Although we present our method here for three-dimensional systems, the BVPs used are well posed in general, meaning that one-dimensional canard orbits can be found in this way also in slow-fast systems with higher-dimensional phase spaces.

As is common in the field of numerical continuation of BVPs, we write the vector field under consideration in the rescaled form

$$
\begin{equation*}
\dot{\mathbf{u}}=T \mathbf{g}(\mathbf{u}) \tag{13}
\end{equation*}
$$

A solution of (13) is an orbit segment $\mathbf{u}$ that connects $\mathbf{u}(0)$ to $\mathbf{u}(1)$. Hence, $\mathbf{u}$ on $[0,1]$ corresponds to an orbit segment with integration time $T$ in the original system $\dot{\mathbf{u}}=\mathbf{g}(\mathbf{u})$. The actual integration time $T$ is a free parameter in (13) that is solved for as part of the BVP. In the case we are considering here, $\mathbf{u}=(x, y, z)$ and $\mathbf{g}$ is the right-hand side of system (1)-(3).

The goal is now to specify appropriate boundary conditions to obtain a well-posed two-point BVP, whose (one-parameter family of) solutions are orbit segments that lie (in good approximation) on a relevant part of the required invariant manifold; see [38] for an general overview of this type of numerical methods. The boundary conditions that we use for the computations of slow manifolds and canard orbits are inspired by Fenichel theory. Namely, we require that one end point of each orbit segment lies on a line far away from the fold on the attracting or the repelling sheets of the critical manifold, respectively. Hence, the error at this end point is of size $O(\varepsilon)$ and it initially decays quickly along the orbit segment due to the very strong contraction to the slow manifold (in forward or backward time). The other end point is taken in a suitably chosen section (that is, a two-dimensional plane) transverse to the fold near the folded node, where the interesting dynamics of system (1)-(3) takes place.

For the computation of the attracting slow manifold $S_{\varepsilon}^{a}$ we are looking for orbit segments $\mathbf{u}^{a}$ of (13) subject to the boundary conditions

$$
\begin{align*}
& \mathbf{u}^{a}(0) \in L^{a} \subset S^{a},  \tag{14}\\
& \mathbf{u}^{a}(1) \in \Sigma^{a}, \tag{15}
\end{align*}
$$

where $\Sigma^{a}$ is a suitably chosen section. Similarly, we compute the repelling slow manifold $S_{\varepsilon}^{r}$ as the family of orbit segments $\mathbf{u}^{r}$ that satisfy

$$
\begin{align*}
& \mathbf{u}^{r}(0) \in \Sigma^{r},  \tag{16}\\
& \mathbf{u}^{r}(1) \in L^{r} \subset S^{r}, \tag{17}
\end{align*}
$$

where $\Sigma^{r}$ is a suitably chosen section. For our purposes of locating canard orbits we choose $\Sigma^{a}=\Sigma^{r}$; see below. The BVPs defined by (14)-(15) and (16)-(17), respectively, have a one-parameter family of solutions, which can be computed by numerical continuation, for example with the package AUTO [18]. As with all boundary value problems, an important issue is to find a first solution. In some situations, explicit solutions may be known from which such a first solution may be constructed; see [15] for an example. However, in general no explicit solution is known and a first solution must be found in a different way. We use a homotopy method
introduced in [16] to generate an initial orbit segment; the main idea is to continue intermediate orbit segments via two auxiliary BVPs - the first to obtain an orbit segment from a point on the fold curve $F$ to the section, and the second to move the end point on $F$ along the critical manifold to a suitable distance from $F$; see [16] for details.

The choice of the sections $\Sigma^{a}$ and $\Sigma^{r}$ depends on the purpose of the computation. If the end sections $\Sigma^{a}$ and $\Sigma^{r}$ are different and chosen to lie past the folded node one may obtain insight into how $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ intersect as surfaces in a neighbourhood of the folded singularity; see $[15,16,17]$ for examples of such visualizations. In this paper we want to detect and then continue canard orbits. Therefore, we choose $\Sigma^{a}=\Sigma^{r}=\Sigma_{\mathrm{fn}}$, where $\Sigma_{\mathrm{fn}}$ is a plane transverse to the fold curve $F$ and such that it contains the folded node. Canard orbits correspond to intersection points of the two curves $S_{\varepsilon}^{a} \cap \Sigma_{\mathrm{fn}}$ and $S_{\varepsilon}^{r} \cap \Sigma_{\mathrm{fn}}$, which are traced out in good approximation by $\mathbf{u}^{a}(1)$ and $\mathbf{u}^{r}(0)$ satisfying the boundary conditions (14)-(15) and (16)-(17), respectively. A canard orbit can therefore be detected numerically as a pair of orbit segments $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ that satisfy $\mathbf{u}^{a}(1)=\mathbf{u}^{r}(0)$. In reality, it suffices to identify pairs of orbit segments such that $\left|\mathbf{u}^{a}(1)-\mathbf{u}^{r}(0)\right|$ is sufficiently small. This procedure has been used in $[15,16,17]$ to draw canard orbits together with slow manifolds for fixed values of the parameters of the system under consideration.

The focus here is on the continuation of the detected canard orbits themselves without the need to recompute the slow manifolds at each step. In principle, they could be continued as a pair of orbit segments that meet in a specified section. However, this has a number of disadvantages in terms of numerical stability. Namely, it may be nessecary to continue the section (and possibly the folded node). Furthermore, there may be the need for different discretizations of two orbit segments, especially when their lengths or shapes change differently during a calculation. Therefore, we define and continue a canard orbit as the unique solution $\mathbf{u}^{c}$ of a single BVP. To this end, we concatenate $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ at $\Sigma_{\mathrm{fn}}$, which involves rescaling the total integration time back to $[0,1]$ so that $T=T^{c}=T^{a}+T^{r}$ in (13). Then, provided $\left|\mathbf{u}^{a}(1)-\mathbf{u}^{r}(0)\right|$ is small enough, a simple Newton step in AUTO converges to an orbit segment $\mathbf{u}^{c}$ of (13) subject to the boundary conditions

$$
\begin{align*}
& \mathbf{u}^{c}(0) \in L^{a} \subset S^{a},  \tag{18}\\
& \mathbf{u}^{c}(1) \in L^{r} \subset S^{r} ; \tag{19}
\end{align*}
$$

see already figure 1 panel (c). The two boundary conditions (18) and (19) effectively force the orbit segments to follow the attracting sheet $S^{a}$ of the critical manifold to near the fold curve $F$, and then to follow the repelling sheet $S^{r}$ up to a prescribed distance from $F$.

Canard orbits of (1)-(3) correspond to transverse intersections between slow manifolds, which persist for nearby values of any system parameter. Hence, the twopoint boundary value problem given by (13) subject to boundary conditions (18) and (19) is well posed. It has isolated solutions that can be continued with AUTO to compute branches of canard orbits. In the next sections, we demonstrate this method by detecting and continuing canard orbits in two neuronal slow-fast systems - the self-coupled FitzHugh-Nagumo system and a three-dimensional reduction of the Hodgkin-Huxley equations. In these calculations we use for the AUTO collocation BVP solver interpolating polynomials of degree 3 throughout ( $\mathrm{NCOL}=4$ ); the number of mesh intervals NTST was chosen between 200 and 800 , depending on the particular calculation.

## 3. Canard orbits in the self-coupled FitzHugh-Nagumo system

The self-coupled FitzHugh-Nagumo system [19] models a single neuron that is subject to synaptic coupling from itself; it is given by

$$
\begin{align*}
v^{\prime} & =h-\frac{v^{3}-v+1}{2}-\gamma s v  \tag{20}\\
h^{\prime} & =-\varepsilon(2 h+2.6 v)  \tag{21}\\
s^{\prime} & =\beta H(v)(1-s)-\varepsilon \delta s \tag{22}
\end{align*}
$$

see also [16]. The variables $v, h$, and $s$ represent the membrane voltage potential of the neuron, the inactivation of the sodium channels and the synaptic coupling, respectively. The self-coupling term $-\gamma s v$ in (20)-(22) is introduced to mimic the dynamics of a synchronous network of neurons, where $\gamma$ is the coupling strength; the synapse activates at a rate given by $\beta$ and decays at a rate given by $\delta$. The nonsmoothness of the Heaviside function $H(v)$ in (22) induces a separation of the phase space according to the sign of $v$ and also introduces a change in the timescale of the synapse $s$. Indeed, in the active phase, where $v>0, s$ is a fast variable, whereas it evolves slowly in the silent phase where $v<0$.

Drover et al. [19] reported a substantial decrease of the firing rate of the neuron (under constant current injection) when the self-coupling is activated ( $\gamma>0$ ) even though the synapse is excitatory. Indeed, the time series of the voltage potential for (20)-(22) exhibit consecutive action potentials that are separated by a number of small-amplitude (subthreshold) oscillations. These oscillations are an example of MMOs. Wechselberger [61] related this phenomenon to the presence of a foldednode singularity, which gives rise to canard orbits that organise the small-amplitude oscillations. The associated slow manifolds and canard orbits occur for $v<0$ when $H(v)=0$, so that they can be studied in the silent-phase system given by

$$
\begin{align*}
v^{\prime} & =h-\frac{v^{3}-v+1}{2}-\gamma s v,  \tag{23}\\
h^{\prime} & =-\varepsilon(2 h+2.6 v),  \tag{24}\\
s^{\prime} & =-\varepsilon \delta s \tag{25}
\end{align*}
$$

Note that (23)-(25) is a smooth slow-fast dynamical system in $\mathbb{R}^{3}$ with two slow variables of the form (4)-(6). Its critical manifold

$$
\begin{equation*}
S=\left\{(v, h, s) \in \mathbb{R}^{3} \left\lvert\, h=\frac{v^{3}+(2 \gamma s-1) v+1}{2}\right.\right\}, \tag{26}
\end{equation*}
$$

is folded with respect to the fast variable $v$ along the curve

$$
\begin{equation*}
F=\left\{(v, h, s) \in \mathbb{R}^{3} \left\lvert\, h=\frac{1}{2}-v^{3}\right., s=\frac{1-3 v^{2}}{2 \gamma}\right\} . \tag{27}
\end{equation*}
$$

The surface $S$ has a cusp at $(v, h, s)=\left(0, \frac{1}{2}, \frac{1}{2 \gamma}\right) \in F$ and it is divided by the fold curve $F$ into an attracting sheet $S^{a}$ and a repelling sheet $S^{r}$. Note that the cusp point does not play a role for the dynamics, because it does not lie in the region where $v<0$.

We now fix the parameters $\gamma$ and $\delta$ of (23)-(23) at $\gamma=0.5$ and $\delta=0.565$; furthermore, we initially set $\varepsilon=0.015$. Then there is a folded-node singularity on $F$ at $\mathbf{p}_{\mathrm{fn}} \approx(-0.4900,0.6176,0.2797)$, that is, in the relevant region where $v<0$. To


Figure 1. Panel (a) shows the slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ of (23)-(23) computed up to the section $\Sigma_{\mathrm{fn}}$; also shown are six secondary canards $\xi_{3}$ to $\xi_{8}$. Panel (b) shows the intersection curves of $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ in $\Sigma_{\mathrm{fn}}$ that are used to detect canard orbits.
detect canard orbits near this point we compute $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ as solutions to the BVPs given by (14)-(15) and (16)-(17), respectively, for the specific choices

$$
\begin{align*}
L^{a} & :=S \cap\{h=-6.0\}  \tag{28}\\
L^{r} & :=S \cap\{v=0.0\}  \tag{29}\\
\Sigma_{\mathrm{fn}} & :=\left\{(v, h, s) \in \mathbb{R}^{3} \mid s=0.2797\right\} \tag{30}
\end{align*}
$$

Initial orbit segments that satisfy the boundary conditions have been found with the homotopy method from [16].

The result of this computation is shown in figure 1. Panel (a) shows the computed parts of the attracting slow manifold $S_{\varepsilon}^{a}$ and the repelling slow manifold $S_{\varepsilon}^{r}$. Their intersection curves in $\Sigma_{\mathrm{fn}}$ are shown in panel (b), where canard orbits $\xi_{3}-\xi_{8}$ have been identified as points of transverse intersections. These canard orbits are also shown in panel (a) together with $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$; their index corresponds to the number of rotations (corresponding to small-amplitude oscillations) that each canard makes in the vicinity of the folded node before escaping the region of negative $v$. We remark that there is a maximal number of canard orbits that can be determined from the eigenvalue ratio $\mu$ of the folded node in the desingularized reduced flow. As the number of their


Figure 2. The canard orbit $\xi_{6}$ is represented in panel (a) by the two orbit segments $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ that match up in $\Sigma_{\mathrm{fn}}$, and in panel (b) by the single orbit segment $\mathbf{u}^{c}$ from $L^{a} \subset S^{a}$ to $L^{r} \subset S^{r}$.
rotations increases, canard orbits are increasingly closer to each other and accumulate onto the weak primary canard $\gamma_{w}$. Therefore, it becomes more and more difficult to detect canard orbits with large numbers of small oscillations; see also [15]. The six canard orbits $\xi_{3}-\xi_{8}$ in figure 1 have been identified reliably.

Figure 2(a) shows the two orbit segments $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ with $\mathbf{u}^{a}(1) \approx \mathbf{u}^{r}(0)$ that have been detected as a good approximation of the canard orbit $\xi_{6}$. The single orbit segment $\mathbf{u}^{c}$ that represents $\xi_{6}$ as a solution of the BVP defined directly by (18) and (19) is shown in figure 2(b).

The canard orbit $\xi_{6}$, and indeed all detected canard orbits $\xi_{3}-\xi_{8}$ represented in the same way, can now be continued in system parameters. Figure 3 presents the results of a continuation with AUTO of $\xi_{3}-\xi_{8}$ in the time-scale parameter $\varepsilon$, where NTST $=200$ mesh intervals were used. Panel (a) shows the AUTO $L_{2}$-norm of the orbit segments representing the canard orbits as a function of $\varepsilon$. From the detected canard orbits for $\varepsilon=0.015$ the branches were computed for both increasing as well as decreasing $\varepsilon$. We first discuss the continuation for decreasing $\varepsilon$, where the canard orbits maintain the same number of small oscillations but move much closer to one another and to the strong singular canard $\hat{\gamma}_{s}$. This convergence process is illustrated in figure $3(\mathrm{~b})-(\mathrm{d})$, where $\xi_{3}-\xi_{8}$ are shown in projection onto the $(s, v)$-plane for $\varepsilon=0.015, \varepsilon=10^{-4}$ and $\varepsilon_{2}=10^{-6}$, respectively. Note that the singular canards $\widehat{\gamma}_{s}$ and $\widehat{\gamma}_{w}$ and the folded node $\mathbf{p}_{\mathrm{fn}}$ are the same in all three panels (since they correspond to the limiting case


Figure 3. Continuation of the canard orbits $\xi_{3}-\xi_{8}$ in $\varepsilon$. Panel (a) shows the branches $\xi_{3}-\xi_{8}$ represented by their AUTO $L_{2}$-norm as a function of $\varepsilon$; the black dots on the branch $\xi_{3}$ correspond to the specific canard orbits that are shown in figure 4. Panels (b)-(d) show all six canard orbits $\xi_{3}-\xi_{8}$ in projection onto the $(s, v)$-plane for the values of $\varepsilon$ as indicated; also shown are the strong singular canard $\widehat{\gamma}_{s}$ and the weak singular canard $\widehat{\gamma}_{w}$, which intersect at the folded node $\mathbf{p}_{\mathrm{fn}}$. See also the accompanying animation dko_a1.gif.
$\varepsilon=0$ ). For $\varepsilon=10^{-6}$ in panel (d) all canards are so close together that they can hardly be distinguished from one another and from $\widehat{\gamma}_{s}$. Our computations are in agreement with what is known from the literature [56, 61], and they illustrate numerically that the normal form of the folded-node singularity describes the dynamics accurately for sufficiently small $\varepsilon$; see also [15, Fig. 12].

While the theory of singular perturbation is valid only for "small" $\varepsilon$, the numerical representation of canard orbits as orbit segments satisfying (18) and (19) is valid also for "large" $\varepsilon$. This fact allows us to investigate canard orbits away from where theoretical information is available, and the branches of canard orbits in figure 3(a) continued from $\varepsilon=0.015$ for increasing $\varepsilon$ are an example. The branches $\xi_{3}-\xi_{8}$ run


Figure 4. Projection onto the $(s, v)$-plane of the canard orbit $\xi_{3}$ corresponding to the four consecutive black dots on the branch $\xi_{3}$ in figure $3(\mathrm{a})$; from panel (a) to (d) the value of $\varepsilon$ is as indicated. See also the accompanying animation dko_a2.gif.
roughly parallel up to a value of $\varepsilon \approx 0.031$ and then develop folds and loops (in this representation by the AUTO $L_{2}$-norm), which are seemingly aligned along some curves. We discuss the branch $\xi_{3}$ in more detail (it has the smallest number of oscillations). As $\varepsilon$ is increased, the branch $\xi_{3}$ has a minimum of the $L_{2}$-norm at $\varepsilon \approx 0.031$ and then moves through a number of folds before reaching a maximal value of the parameter $\varepsilon$ at a final fold for $\varepsilon \approx 0.00654$. When the branch $\xi_{3}$ passes through the minimum, the orbit segment $\mathbf{u}^{c}$ no longer satisfies that the $v$-component of $\mathbf{u}^{c}(t)$ is less than 0 for all $t \in[0,1]$. Furthermore, the $s$-component of thepoint $\mathbf{u}^{c}(0) \in L^{a}$ now lies to the left of $\mathbf{u}^{c}(1) \in L^{r}$ in the region of negative $s$. Figure 4 shows the canard orbit $\xi_{3}$ at the four successive black dots on the branch in figure 3(a). In figure 4(a) the three maxima of the oscillation are very large and all lie in the region of positive $v$. Further along the branch in figure $4(\mathrm{~b})$, the first oscillation is much smaller and
its maximum lies below $\{v=0\}$. Similarly, in panels (c) also the second oscillation is much smaller, until in panel (d) the entire orbit segment lies again in the region of negative $v$. In terms of an interpretation for the full self-coupled FitzHugh-Nagumo system (20)-(22), the canard orbits in figure 4 would correspond to a solution of (20)(22) that jumps before the first full oscillation for panel (a), after one full oscillation in panel (b), after two full oscillations in panel (c), and at the end point $\mathbf{u}^{c}(1)$ in panel (d). Notice also that the canard orbit in figure 4(d) may be of interest for the dynamics of the full FitzHugh-Nagumo system with self-coupling (since it lies entirely in the region where $v<0$ ). Overall, these calulations demonstrate that branches of canard orbits can indeed be continued readily over large ranges of a parameter.

## 4. Canard orbits in a 3D reduced Hodgkin-Huxley model

The Hodgkin-Huxley equations [33] describe the evolution of the membrane potential of the giant axon of a squid. This famous nonlinear model displays very interesting dynamics but its phase-space dimension makes it difficult to analyse the behaviour both numerically and analytically. Since it was derived in the early 1950s, several reductions were developed to try to simplify the analysis. In particular, the FitzHugh-Nagumo system (without self-coupling) is a two-dimensional reduction of the Hodgkin-Huxley equations. We consider here a three-dimensional reduction of a non-dimensionalized version of the Hodgkin-Huxley equations; see [36, 53] for more details. It is obtained by equilibrating the fastest of the gating variables - the activation of the sodium channels - and takes the form

$$
\begin{align*}
\varepsilon \frac{d v}{d \tau} & =V(v, n, n) \\
& :=\bar{I}-m_{\infty}^{3}(v) h\left(v-\bar{E}_{\mathrm{Na}}\right)-\bar{g}_{k} n^{4}\left(v-\bar{E}_{\mathrm{K}}-\bar{g}_{l}\left(v-\bar{E}_{\mathrm{L}}\right)\right)  \tag{31}\\
\frac{d h}{d \tau} & =\frac{1}{\tau_{h} t_{h}(v)}\left(h_{\infty}(v)-h\right)  \tag{32}\\
\frac{d n}{d \tau} & =\frac{1}{\tau_{n} t_{n}(v)}\left(n_{\infty}(v)-n\right) \tag{33}
\end{align*}
$$

Here, the equilibrium and relaxation functions are given by

$$
\begin{align*}
x_{\infty}(v) & =\frac{\alpha_{x}(v)}{\alpha_{x}(v)+\beta_{x}(v)}  \tag{34}\\
t_{x}(v) & =\frac{k_{t}}{\alpha_{x}(v)+\beta_{x}(v)} \tag{35}
\end{align*}
$$

where $x \in\{m, h, n\}$ and $k_{t}=1 \mathrm{~ms}$, such that each $t_{x}$ is dimensionless. The opening and closing functions, associated with the dynamics of the ionic channels, are given

| $\varepsilon$ | $\bar{g}_{k}$ | $\bar{g}_{l}$ | $\bar{E}_{\mathrm{Na}}$ | $\bar{E}_{\mathrm{K}}$ | $\bar{E}_{\mathrm{L}}$ | $\tau_{h}$ | $\tau_{n}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0.0083 | 0.3 | 0.0025 | 0.5 | -0.77 | -0.544 | 6.0 | 1.0 |

Table 1. Parameters values as used in (31)-(33).
by

$$
\begin{align*}
\alpha_{m}(v) & =\frac{\left(k_{v} v+40\right) / 10}{\left.\left.1-\exp \left(-\frac{1}{10}\right) k_{v} v+40\right)\right)} \\
\beta_{m}(v) & =4 \exp \left(-\frac{1}{18}\left(k_{v} v+65\right)\right) \\
\alpha_{h}(v) & =0.07 \exp \left(-\frac{1}{20}\left(k_{v} v+65\right)\right)  \tag{36}\\
\beta_{h}(v) & =\frac{1}{1+\exp \left(-\frac{1}{10}\left(k_{v} v+35\right)\right)} \\
\alpha_{n}(v) & =\frac{\left(k_{v} v+55\right) / 100}{1-\exp \left(-\frac{1}{10}\left(k_{v} v+55\right)\right)} \\
\beta_{n}(v) & =0.125 \exp \left(-\frac{1}{80}\left(k_{v} v+65\right)\right) .
\end{align*}
$$

Finally, $\tau=t / k_{t}$ where $t$ is the time variable in the original Hodgkin-Huxley model. Throughout this section, we study (31)-(33) for the (classical) parameter values given in table 1. The main free parameter is the applied current $I$ (in units of $\mu \mathrm{A} / \mathrm{cm}^{2}$ ) in the original Hodgkin-Huxley model, which enters (31) as $\bar{I}=I / k$ where $k=k_{v} \cdot 120 \mathrm{mS} / \mathrm{cm}^{2}$ with $k_{v}=100 \mathrm{mV}$.

We consider the 3D reduced Hodgkin-Huxley model (31)-(33) for a number of reasons. It is a more realistic neuronal system with an explicit separation of time scales, which is known to produce mixed-mode oscillations, for example for $\tau_{n}=1$ and $\tau_{h}>1[53,54]$. Moreover, (31)-(33) possesses a folded node in a relevant range of the parameters and a natural reinjection mechanism. This is in contrast to the self-coupled FitzHugh-Nagumo system, where the reinjection mechanism is realized, rather artificially, by a Heaviside function. Hence, (31)-(33) avoids having to consider a silent-phase system with the need to worry about irrelevant parts of phase space.

### 4.1. Bifurcations of periodic solutions with the applied current $I$

As a starting point of our investigation we present in figure 5 a bifurcation study, performed with the package AUTO, of (mixed-mode) periodic orbits in dependence on the injected current $I$. Panel (a) shows an overview over a large range of $I$ and panel (b) an enlargement. There is a unique fixed point that forms the lower branch; it is stable for small and for large values of $I$ and unstable in between two Hopf bifurcation points at $I \approx 7.78047$ and $I \approx 265.365$. The two Hopf points are connected by a branch of periodic orbits. The left Hopf point at $I \approx 7.78047$ is subcritical, so that the emanating branch of periodic solutions is initially of saddle type. The stable Floquet direction loses stability at a first saddle-node of limit cycle bifurcation $S L$ at $I \approx 6.46194$, but then again is of saddle type after a period-doubling bifurcation $P D$ at $I \approx 7.17374$; see figure $5(\mathrm{~b})$. After further bifurcations, the branch stabilizes at a last saddle-node of limit cycle bifurcation $S L$ at $I \approx 14.9747$ and then remains stable until it disappears in the right Hopf bifurcation at $I \approx 265.365$.

An important feature of the bifurcation diagram in figure $5(\mathrm{a})$ and (b) is a family of isolas of mixed-mode periodic orbits of type $1^{\ell}$ (having one large oscillation followed by $\ell$ small ones). We computed 15 of these closed branches; they intersect one another


Figure 5. Panel (a) shows branches of solutions of (31)-(33) as a function of the applied current $I$, and panel (b) is an enlargement of isolas of mixed-mode periodic orbits; all other parameters are as given in table 1. Stable branches are solid thick curves and unstable branches are solid dashed curves; the isolas of MMOs are plotted as thin curves (without stability information) that alternate between dark and light; also shown are points of Hopf $(H)$, saddle-node of limit cycle ( $S L$ ) and period-doubling bifurcation ( $P D$ ). Panels (c) and (d) show the time profiles of two mixed-mode periodic attractors, on the right-most isolas (at $I=12.51$ ) and on the left-most isola (at $I=8.761$ ), respectively.
and lie in between the period-doubling point $P D$ and the unstable part of the branch of periodic orbits bifurcating from the Hopf points. We do not show the stability of the periodic orbits on the isolas since it varies substantially along each branch, but note that for certain values of $I$ several coexisting stable MMOs can be found (which is how the continuation runs were started). The profile of the periodic orbit belonging to a particular isola, that is, its pattern as a mixed-mode periodic orbit, changes as one moves in parameter space around the isola, but the overall number of oscillations remains constant. The MMO isolas appear to accumulate for increasing $\ell$ onto a curve to the left. Furthermore, the left-most isola correspond to mixed-mode periodic orbits that are increasingly close to a homoclinic bifurcation. Two time profiles of MMOs are shown in figure 5 (c) and (d). The mixed-mode periodic orbit in panel (c) is from the right-most isola, and it is of type $1^{4}$. By contrast, the mixed-mode periodic orbit in panel (d) is from the left-most isola; it indeed appears to be very close to a homoclinic bifurcation and displays so many and so small oscillations that they are hard to count.

We remark that we found numerically many more isolas of mixed-mode oscillations of even more complicated type in terms of large and small oscillations. A detailed study of the bifurcation structure of MMO periodic orbits (also in dependence on other parameters) remains a challenging task for future research. Instead, we use figure 5 as a guide and now concentrate on how the slow-fast dynamics is organized by a folded node in the region of mixed-mode periodic orbits of type $1^{\ell}$ - in the $I$-range around $I=12.0$.

### 4.2. Detection of secondary canards

The 3D reduced Hodgkin-Huxley model (31)-(33) is a smooth slow-fast dynamical system in $\mathbb{R}^{3}$ with two slow variables of the form (1)-(3). Its critical manifold is given by

$$
\begin{equation*}
S=\left\{(v, h, n) \in \mathbb{R}^{3} ; V(v, h, n)=0\right\} \tag{37}
\end{equation*}
$$

where $V(v, h, n)$ is the right-hand side of (31). The critical manifold $S$ is folded along the curve

$$
\begin{equation*}
F=\left\{(v, h, n) \in S ; \frac{\partial}{\partial v} V(v, h, n)=0\right\} . \tag{38}
\end{equation*}
$$

For $I=12.0$ and the other parameters as in table 1 one finds a folded-node singularity $\mathbf{p}_{\mathrm{fn}}=(-0.5927,0.2817,0.4858)$ on $F$. To compute the attracting and repelling slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ near $\mathbf{p}_{\mathrm{fn}}$ with the method from section 2, we consider the specific choices

$$
\begin{align*}
L^{a} & :=S \cap\{v=-0.75\}  \tag{39}\\
L^{r} & :=S \cap\{v=-0.55\}  \tag{40}\\
\Sigma_{\mathrm{fn}} & :=\left\{(v, h, n) \in \mathbb{R}^{3} \mid n=0.2817\right\} \tag{41}
\end{align*}
$$

Initial orbit segments $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ satisfying the boundary conditions (14)-(15) and (16)-(17), respectively, have been found with the homotopy method from [16], and they are shown in figure 6 (a). Continuation with AUTO then yields the slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ as surfaces shown in figure $6(\mathrm{~b})$. Nine canard orbits $\xi_{4}-\xi_{12}$ have been identified reliably as transverse intersection points of the curves $S_{\varepsilon}^{a} \cap \Sigma_{\mathrm{fn}}$ and $S_{\varepsilon}^{r} \cap \Sigma_{\mathrm{fn}}$; see panel (c). After concatenation, each canard orbit is then represented directly as an orbit segment $\mathbf{u}^{c}$ that satisfies boundary conditions (18) and (19). The canard orbits $\xi_{4}-\xi_{12}$ are also shown in figure $6(\mathrm{~b})$, where they can be seen to connect the line $L^{a} \subset S^{a}$ with the line $L^{r} \subset S^{r}$. As before the labeling is such that the canard orbit $\xi_{i}$ completes $i$ full rotations in the vicinity of the folded node.

### 4.3. Properties of the secondary canards and their continuation in $\varepsilon$

Figure $7(\mathrm{a})$ and (b) show the nine detected secondary canards $\xi_{4}-\xi_{12}$ from figure 6 in two different projections together with numerical computations of the strong singular canard $\widehat{\gamma}_{s}$ and the weak primary canard $\gamma_{w}$. The strong singular canard $\widehat{\gamma}_{s}$ has been obtained as the limit of canards continued for decreasing $\varepsilon$; compare with figure 3 . The weak primary canard $\gamma_{w}$ was identified during the computation of $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$, where we used the fact that orbit segments on the slow manifolds spiral around $\gamma_{w}$ and accumulate onto it. Notice the particular shape of the right-most part of $\gamma_{w}$ further away from the folded node. We find that there is a saddle-focus equilibrium nearby. The weak canard $\gamma_{w}$ appears to follow its one-dimensional stable manifold


Figure 6. Panel (a) shows the initial orbit segments $\mathbf{u}^{a}$ and $\mathbf{u}^{r}$ from $L^{a}$ and $L^{r}$ to $\Sigma_{\mathrm{fn}}$. The attracting and repelling slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ together with the detected canard orbits $\xi_{4}-\xi_{12}$ are shown in ( $v, h, n$ )-space panel (b), and in $\Sigma_{\mathrm{fn}}$ in panel (c). Here $I=12.0$ and all other parameters are as given in table 1.
extremely closely towards the saddle-focus, and then spirals out by following its unstable manifold. For increasing $i$ the secondary canards $\xi_{i}$ accumulate onto $\gamma_{w}$, so that they also accumulate on the invariant manifolds of the saddle-focus. These observations clearly indicate a close connection between the folded-node singularity and the saddle-focus attractor of the system. As a result, when this attractor


Figure 7. Panels (a) and (b) show the nine canard orbits $\xi_{4}-\xi_{12}$ from figure 6 in projection onto the $(n, v)$-plane and the $(h, v)$-plane, respectively; also shown are the strong singular canard $\widehat{\gamma}_{s}$ and the weak primary canard $\gamma_{w}$. Panels ( c 1 ) and (c2) show the branches of canard orbits $\xi_{4}-\xi_{8}$ that are obtained when $\varepsilon$ is varied for fixed $I=12.0$.
undergoes a Hopf bifurcation (upon variation of $I$ ) the canard orbits generated by the folded singularity interact with the emanating periodic orbit; this will be discussed in section 4.4.

Figure $7(c 1)$ shows the branches of the five secondary canards $\xi_{4}-\xi_{8}$ that were obtained by continuation with AUTO for increasing and decreasing $\varepsilon$, where NTST $=$ 300 intervals points were used. As was the case for the self-coupled FitzHughNagumo system (compare with figure 3), all canards converge for $\varepsilon \rightarrow 0$ to the same orbit segment, which corresponds to the strong singular canard $\widehat{\gamma}_{s}$. When $\xi_{4}-\xi_{8}$ are continued in the direction of increasing $\varepsilon$, a fold in $\varepsilon$ is detected for each branch at $\varepsilon \approx 0.0211$; that is, the $\varepsilon$-values of all fold points as computed with AUTO agree up to four decimal places. This suggest an underlying dynamical phenomenon that affects all secondary canards. We verified that the coincidence of folds for all branches of


Figure 8. Panel (a) shows the branch of the secondary canard $\xi_{6}$ from figure $7(\mathrm{c} 1)$, along which five points are marked. Panels (b) to (f) show the canard orbit $\xi_{6}$ in projection onto the $(n, v)$-plane at these five different locations along the branch, together with the fold curve $F$, the strong singular canard $\widehat{\gamma}_{s}$ and the folded node $\mathbf{p}_{\mathrm{fn}}$. See also the accompanying animation dko_a3.gif.
canard orbits is robust in the sense that it is independent of the particular boundary conditions that we imposed to compute the slow manifolds $S_{\varepsilon}^{a}$ and $S_{\varepsilon}^{r}$ and, hence, the canards orbits. When we modify the boundary conditions and recompute slow manifolds and canards, the continuation of the resulting canard orbits features a fold in $\varepsilon$ at the same value up to four decimal places. Past the fold in $\varepsilon$, each branch of canard orbits can be continued in the direction of decreasing $\varepsilon$, all the way towards $\varepsilon=0$; see figure $7(\mathrm{c} 1)$. The line $\varepsilon=0$ is shown in grey in this panel to emphasise that the limit is reached in both directions of the continuation.

Figure 8 illustrates how the canard orbit $\xi_{6}$ changes along the branch; it is qualitatively representative for any of the other detected secondary canards of system (31)-(33). For orientation purposes, panel (a) reproduces the $\xi_{6}$-branch in dependence on $\varepsilon$ from figure $7(\mathrm{c} 1)$. Five black dots, marked (b) to (f), are chosen along the branch, and figure $8(\mathrm{~b})-(\mathrm{f})$ display the corresponding canard orbit $\xi_{6}$ in projection onto the $(h, v)$-plane; also shown are $F, \mathbf{p}_{\mathrm{fn}}$ and $\widehat{\gamma}_{s}$ (which was extended by continuation over a larger $v$-range from the computed limit of $\xi_{6}$ for $\varepsilon \rightarrow 0$ ). A number of interesting observations can be made. The detected canard orbit $\xi_{6}$ is shown in panel (c); as $\varepsilon$ is decreased to 0 it maintains the same number of small oscillations (six for this particular canard) but their $v$-amplitude and width in the $h$-direction shrink to zero; see figure $8(\mathrm{c})$. This agrees with what is known from theory; compare with figure 3 . When the detected canard orbit $\xi_{6}$ in figure $8(\mathrm{c})$ is continued in the direction of increasing $\varepsilon$, the amplitude of all six small oscillations increases up to the critical value of $\varepsilon=0.0211$, which corresponds to the fold point; see panel (d). As is shown in panels (e) and (f), past the fold only the left-most oscillation (a full rotation around the weak canard) continues to grow slightly up to a certain limit, whilst the five remaining small oscillations start to shrink in amplitude. Finally, figure 8(f) reveals that, as the branch is continued towards $\varepsilon=0$ past the fold, the first oscillation of $\xi_{6}$ develops into a relaxation-type loop. The orbit segment starting at $\mathbf{u}^{c}(0)$, follows the strong singular canard $\widehat{\gamma}_{s}$ well past the fold curve $F$ and then has a fast segment that is is almost vertical, that is, in the direction of the fast variable $v$. The canard orbit $\xi_{6}$ past the fast segment continues on with five more (now quite small) oscillations. Hence, in this limit of $\varepsilon \rightarrow 0$ of the branch past the fold point, the canard orbit $\xi_{6}$ 'splits off' one large canard-type oscillation, meaning that $\xi_{6}$ resembles the concatenation of a canard periodic orbit with $\xi_{5}$. As was mentioned earlier, $\xi_{6}$ is representative: we found the new phenomenon that, when continued past the fold, any of the detected canard orbits $\xi_{i}$ converges to a concatenation of a relaxation oscillation with $\xi_{i-1}$.

### 4.4. Continuation of canard orbits in I for $\varepsilon=10^{-6}$

Once they are detected, canard orbits can be continued in any system parameter of interest. As an example, we now consider the dependence of the canards $\xi_{4}-\xi_{8}$ on the injection current $I$ of the 3D reduced Hodgkin-Huxley model (31)-(33), where we fix the time-scale parameter at $\varepsilon=10^{-6}$. This choice for $\varepsilon$ is motivated by the fact that Rubin and Wechselberger [54] give numerical evidence that the theory of a folded node singularity in conjunction with a reinjection mechanism [14] explains MMOs of type $1^{\ell}$ of (31)-(33) only when $\varepsilon \in\left[0,10^{-5}\right)$. A second motivation is to demonstrate that continuation in a system parameter can be performed reliably even for quite small values of $\varepsilon$. The result of the continuation of the five canard orbits $\xi_{4}-\xi_{8}$ is shown in figure 9 (a) over a large range of $I$ and represented by the AUTO $L_{2}$-norm. Continuation runs for both decreasing and increasing $I$ were started from the canard


Figure 9. Panel (a) shows the branches of the secondary canards $\xi_{4}-\xi_{8}$ for $\varepsilon=10^{-6}$ as a function of the injected current $I$; panel (b) is an enlargement near where they end in limit points $L P$ at $I^{*} \approx 4.83411$. The canard orbit $\xi_{6}$ for $I=I^{*}$ is shown in panels (c1) and (c2) as a time profile of $v$. Panel (d) shows the branch of the folded singularity, which changes type at $\widehat{I} \approx 4.83378$ from folded node (solid curve) to folded saddle (dashed curve).
orbits for fixed $I=12.0$ that were found at $\varepsilon=10^{-6}$ (when $\varepsilon$ was decreased from the classical value $\varepsilon=0.0083$; see section 4.3); for these computations NTST $=400$ mesh intervals were used. The branches of canard orbits $\xi_{4}-\xi_{8}$ run almost parallel in this projection over the entire shown range of $I \in[4,34]$. The difference in the $L_{2}$-norm from $\xi_{i}$ to $\xi_{i+1}$ is due to the fact that the respective orbit segments differ by exactly one small oscillation.

We first discuss the continuation in the direction of increasing $I$, where we find that each of the branches $\xi_{4}-\xi_{8}$ stops close to $I=32$; see figure 9(a). Increasing $I$ corresponds to decreasing the eigenvalue ratio $\mu$ of the folded node. Theory predicts that the secondary canards rapidly (exponentially in $\mu$ ) approach the weak canard $\gamma_{w}$, where they terminate at integer values of $\mu$ (that correspond to the number of rotations around $\gamma_{w}$ ) [61]. We found in [15] for the normal form of the folded node that the continuation of secondary canards is numerically so delicate that a canard with more than a few rotations around $\gamma_{w}$ can generally not be continued all the way to its expected end point. This numerical sensitivity for decreasing $\mu$ also arises here:
a numerical computation of $\mu=\mu(I)$ shows that the continuation of the branches $\xi_{4^{-}}$ $\xi_{8}$ stops well before their expected end points are reached. The fact that our choice $\varepsilon=10^{-6}$ is very small is likely to make matters worse compared to computations in the normal form. In any case, the continuation in $I$ is inconclusive as far as the suggested validity range [54] of the normal form for secondary canards near the folded node of (31)-(33) is concerned.

We now consider the continuation for decreasing $I$, and figure 9 (b) shows an enlargement of the branches of $\xi_{4}-\xi_{8}$ near their left end points. The behaviour of the five branches is indeed very similar: they run parallel and are offset by practically the same amount in the $L_{2}$-norm. Each branch $\xi_{4}-\xi_{8}$ ends at a limit point bifurcation, labelled $L P$, which corresponds to a fold with respect to $I$. We found that it is not possible to continue branches past the detected limit point. What is more, the associated numerical $I$-value of the detected limit point $L P$ was found to be the same value of $I^{*} \approx 4.83411$ for all five branches up to five decimal places (with EPSS $=10^{-5}$ as the relative convergence criterion for the detection of special solutions in AUTO). The agreement of the left end points of the branches $\xi_{4}-\xi_{8}$ is emphasized in figure 9 (b) by the grey vertical line at $I^{*}$. Figure $9(\mathrm{c} 1)$ is the time profile of the $v$-variable of the orbit segment $\mathbf{u}^{c}$ representing $\xi_{6}$ at the final point where $I=I^{*}$. As the enlargement in panel (c2) shows, at $I^{*}$ we find that $\xi_{6}$ makes six small oscillations of effectively the same amplitude; this is again representative, meaning that at $I^{*}$ any of the computed orbits $\xi_{i}$ has $i$ small oscillations with practically identical amplitudes.

These numerical results clearly suggest an underlying dynamical phenomenon, which we now explore further. Figure 9(d) shows the branch of the folded singularity of system (31)-(33), as a true equilibrium of the desingularized reduced system (11)(12) for $\varepsilon=0$. It is a folded node $\mathbf{p}_{\mathrm{fn}}$ for larger values of $I$, but changes stability at $I=\widehat{I} \approx 4.83378$ where one of its eigenvalues goes through 0 . This means that at $I=\widehat{I}$ the folded singularity is a folded saddle-node, and for $I<\widehat{I}$ it is a folded saddle. Theory predicts that, as the folded saddle-node is approached by decreasing $I$ down to $I=\widehat{I}$, the number of secondary canards that exist for $\varepsilon>0$ goes to infinity; for $I<\widehat{I}$, on the other hand, there will be a single canard orbit when the folded saddle is perturbed for $\varepsilon>0$; see [56, 61]. Hence, for $0<\varepsilon \ll 1$ one would expect that the branches of canard orbits $\xi_{4}-\xi_{8}$, found near $\mathbf{p}_{\mathrm{fn}}$ and followed for decreasing $I$, terminate in some way in the vicinity of $\widehat{I}$. Note that $\widehat{I}$ (which is determined from the limit $\varepsilon=0$ ) is only about $10^{-3}$ from $I^{*}$ (which was found numerically for $\varepsilon=10^{-6}$ ).

System (31)-(33) with $\varepsilon=10^{-6}$ has an actual equilibrium very close to the folded singularity (for $\varepsilon=0$ ). Associated with this equilibrium is a sequence of bifurcations that is qualitatively just what we found for $\varepsilon=0.0083$; compare with figure $5(\mathrm{~d})$. Namely, for $\varepsilon=10^{-6}$ the equilibrium loses its stability in a Hopf bifurcation $H$, which takes place exactly at $I_{H}=I^{*}$ up to the numerical precision of our computation. Figure 10(a) shows the bifurcating ( $I$-dependent) family of periodic orbits as a surface in $(v, h, n)$-space for $I_{S L} \leq I \leq 4.83653$. Past the Hopf bifurcation $H$ the periodic orbits are initially of saddle type. They undergoes a saddle-node of limit cycle bifurcation already at $I_{S L} \approx 4.83394$, where the surface turns around towards increasing values of $I$ and $h$; the correpsonding fold in the surface of periodic orbits is not visible in figure 10(a) because it occurs very close to the Hopf point $H$. For $I>I_{S L}$ the periodic orbits are repelling until a period-doubling bifurcation is reached at $I_{P D} \approx 4.83422$. The periodic orbit $\Gamma_{P D}$ at the moment of period-doubling bifurcation divides the surface: periodic orbits to the right of $\Gamma_{P D}$ are of saddle type, and periodic orbits to the left of $\Gamma_{P D}$ are repelling (for $I>I_{S L}$ ). Notice from the


Figure 10. Panel (a) shows the canard orbit $\xi_{6}$ in $(v, h, n)$-space for $I=I_{2}=$ 4.83607, for $I=I_{1}=4.83508$ and for $I=4.83411 \approx I^{*}$; also shown are the corresponding periodic orbits $\Gamma_{2}, \Gamma_{1}$ and $\Gamma^{*}$ as they lie on the surface of periodic orbits that emerges from the Hopf point $H$. The peridic orbit labelled $\Gamma_{P D}$ is that at the moment of the period-doubling bifurcation for $I_{P D} \approx 4.83422$. Panels (b) and (c) show projections onto the ( $v, n$ )-plane of $\Gamma_{2}$ and $\xi_{6}$ for $I=I_{2}$, and $\Gamma^{*}$ and $\xi_{6}$ for $I=I^{*}$, respectively. See also the accompanying animation dko_a4.gif.
axes scales in figure 10(a) that the family of periodic orbits exists in a very small region of $(v, h, n)$-space, where it depends extremely sensitively on the parameter $I$; furthermore, the family consists of canard periodic orbits with a single fast segment, very much like those that one finds near the begining of a classical canard explosion [12, 30].

The purpose of figure 10 is to show how the canard orbit $\xi_{6}$ terminates when $I^{*}$ is approached along the branch shown in figure $9(\mathrm{~b})$. To this end, $\xi_{6}$ is shown in figure 10(a) at three different values of $I$, namely at $I_{2}=4.83607$, at $I_{1}=4.83508$ and at $I=I^{*} \approx 4.83411$. (Due to the very small scale of figure 10(a), these canard orbits have been computed with NTST $=800$ mesh intervals.) Highlighted on the surface of periodic orbits are the associated periodic orbits $\Gamma_{2}, \Gamma_{1}$ and $\Gamma^{*}$ that exist at these values of $I$. Overall, we see that, as $I$ is decreased, the size of the periodic orbit and its $h$-distance from the canard orbit $\xi_{6}$ decreases. At the end point $I=I^{*}$ the canard orbit $\xi_{6}$ appears to spiral very close to the (repelling) periodic orbit $\Gamma^{*}$. This convergence process is also shown in panels (b) and (c) in projections onto the $(v, n)$-plane for $I=I_{2}=4.83607$ and $I=I^{*} \approx 4.83411$, respectively. We checked that the canard orbit $\xi_{6}$ is again representative. All canard orbits $\xi_{4}-\xi_{8}$ show the same convergence behaviour towards $\Gamma^{*}$.

The picture that emerges is that the dynamics we find near $I=I^{*}$ can be viewed as a "slow passage through a canard explosion"; recall the canard-type nature of the family of periodic orbits in figure 10 and its extremely sensitive dependence on $I$. This phenomenon has recently been studied in [35, 40, 41] in the context of systems with three different time scales, where it was shown to exist near a folded saddle-node. Indeed, we find for $\varepsilon=0$ the transition of the folded singularity from folded node, via a folded saddle-node, to folded saddle when $I$ is changed through $I=\widehat{I} \approx 4.83378$. Our evidence suggests that the saddle-node is of type II in the terminology of [56, 61], which means that at a distance of $O(\varepsilon)$ of the folded node one finds a Hopf bifurcation. This type of Hopf bifurcation is generally referred to as a singular Hopf bifurcation [3, 4, 10, 31]. Recently, Guckenheimer [31] developed a generic model vector field of a singular Hopf bifurcation in the context of slow-fast systems with one fast and two slow variables, and showed that singular Hopf bifurcation gives rise to canard orbits that organize associated MMOs. Furthermore, he investigated the geometry of slow manifolds for the case that the Hopf bifurcation occurs near a folded saddle, in which case there is a single canard orbit nearby. The scenario we find here is consistent with what one would expect near a singular Hopf bifurcation. However, it is evident from figure 10 that we are dealing with a more complicated case, the "unfolding" of which by a normal form is yet unknown. In particular, we find that the canard orbits interact with a repelling periodic orbit that is connected to the Hopf bifurcation via a nearby saddle-node of limit cycle bifurcation. Overall, our numerical investigations suggest that there is an underlying bifurcation structure that involves the interaction of a folded saddle-node with a singular Hopf bifurcation near a higher-order degeneracy. The study of this (type of) bifurcation in the 3D reduced Hodgkin-Huxley model, as well as in simpler generic model systems, such as that in [31], is a very interesting topic for future research.

## 5. Discussion

We introduced and demonstrated a numerical method for the computation of branches of canard orbits of slow-fast ordinary differential equations in system parameters. It has at its core the continuation of solution families of suitably defined two-point boundary value problems. This setup allows for efficient and accurate computations and, in particular, it deals effectively with the challenge of strong attraction to and repulsion from canard orbits. We introduced the associated boundary value condition for slow-fast systems in $\mathbb{R}^{3}$ with two slow and one fast variables, where canard orbits are structurally stable and isolated because they arise as transverse intersections of two-dimensional attracting and repelling slow manifolds. As we have demonstrated, once they have been detected, such canard orbits can be continued in system parameters, including the time-scale parameter $\varepsilon$. In particular, we find that fold points on the branches bound the maximal range of $\varepsilon$ where canard orbits can be found and, hence, may give an estimate of the validity range of theoretical existence results (that are typically obtained near $\varepsilon=0$ ). Notice further that a fold of a branch corresponds geometrically to a (quadratic) tangency of the associated slow manifolds. Our method was explained here for the case that the equations are in the standard form where $\varepsilon$ appears explicitely as a factor. Nevertheless, it is possible to compute slow manifolds and canard orbits in much the same way also in certain situations where the separation of time scales is not immediately apparent from the equations; see [17] for an example.

The two examples presented here not only demonstrate how the method works in practice, but also illustrate how the continuation of canard orbits can contribute to an understanding of dynamical phenomena in a given slow-fast system. In particular, we found in a reduced 3D Hodgkin-Huxley model that branches of canard orbits end near a folded saddle-node (of type II) and the associated singular Hopf bifurcation. A more detailed case study of this phenomenon under variation of other system parameters emerges as an promising project for future research. In fact, investigation of folded singularities, singular Hopf bifurcation and their interactions is ongoing and not complete. We expect that the continuation of canard orbits may also contribute to the study of different generic cases in representative models [31, 40, 61] (that play the roles of normal forms). In particular, it will be of great interest to consider how slow manifolds interact with stable and unstable manifolds of equilibria and periodic orbits of saddle type, which can be computed with similar methods $[38,39]$.

More generally, folded singularities and singular Hopf bifurcation may give rise to mixed-mode oscillations if a reinjection mechanism is present. The self-coupled FitzHugh-Nagumo system [16, 61] and the 3D reduced Hodgkin-Huxley model [53, 54] considered here are examples of systems with these type of singularities and associated MMOs. As we demonstrated, the computation of the associated slow manifolds and branches of canard orbits for such systems is a helpful tool for the investigation of how different patterns of MMOs arise; other examples of systems where the continuation of canards may prove fruitful include [1, 41, 46, 62]. Similarly, canard orbits may play a role in models of neurons to explain the transition between different types of bursting (for example, between square-wave, elliptic or parabolic bursting [50]), or between bursts with different numbers of spikes in the active phase [32, 58]. Therefore we expect that numerical methods as presented here may also contribute to the analysis of bursting phenomena.

Finally, it appears feasible to generalize and extend the BVP approach taken
here so that it can also be used for the investigation of slow-fast systems with higherdimensional phase spaces. A geometric theory of multiple times-scale systems in higher dimensions is not yet available, but it is natural next step to consider canard orbits in the locus of intersection of two slow manifolds of a slow-fast systems in $\mathbb{R}^{n}$ for any $n \geq 3$. Generically, the intersection locus consists of structurally stable and isolated (one-dimensional) canard orbits if and only if the sum of the dimensions of attracting and repelling slow manifolds adds up to $n+1$. However, the intersection locus may be of higher dimension or of higher codimension; the case of a $k$-dimensional intersection locus for $k>1$ is also refereed to as a "black swan" [55]. We believe that, in combination with ideas from [38] and [39], the approach taken here may also be used to detect and then continue (families of) canard orbits in such more general situations.

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