Computing the Stable Manifold of a Saddle Slow Manifold

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Abstract

The behavior of systems with fast and slow time scales is organized by families of locally invariant slow manifolds. Recently, numerical methods have been developed for the approximation of attracting and repelling slow manifolds. However, the accurate computation of saddle slow manifolds, which are typical in higher dimensions, is still an active area of research. A saddle slow manifold has associated stable and unstable manifolds that contain both fast and slow dynamics, which makes them challenging to compute. We give a precise definition for the stable manifold of a saddle slow manifold and design an algorithm to compute it; our computational method is formulated as a two-point boundary value problem and uses pseudo-arclength continuation with AUTO. We explain how this manifold acts as a separatrix and determines the number of spikes in the transient response generated by a stimulus with fixed amplitude and duration in two different models.

1 Introduction

Ordinary differential equations (ODEs) are widely used to describe and predict the behavior and dynamics of natural phenomena. In many cases, one or more processes associated with a phenomenon evolve much faster than other processes in the system. For instance, the membrane voltage for a neuron typically changes much faster than the concentration of calcium ions in the neuron cytoplasm [12, 26]. Chemical reactions [3, 27, 32, 33, 37], laser dynamics [9, 13], electrical circuits [41, 42, 10] and food chains [5] are all examples of phenomena that can involve multiple time scales.

In mathematical models, time-scale separation in the evolution of the variables can be expressed by using *singularly perturbed* systems of differential equations. We consider the simplest possible case of a so-called *slow-fast* system with only two time scales:

$$\begin{cases} \frac{d\mathbf{x}}{dt} = f(\mathbf{x}, \mathbf{z}, \varepsilon), \\ \frac{d\mathbf{z}}{dt} = \varepsilon g(\mathbf{x}, \mathbf{z}, \varepsilon). \end{cases}$$
(1)

Here, $\mathbf{x} \in \mathbb{R}^m$, $\mathbf{z} \in \mathbb{R}^n$, and we assume that $f : \mathbb{R}^m \times \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^m$ and $g : \mathbb{R}^m \times \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^n$ are C^r -smooth functions with $r \geq 1$. We assume that $0 < \varepsilon \ll 1$, so that \mathbf{x} evolves significantly faster than \mathbf{z} . System (1) is written with respect to the fast time scale, denoted

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by t. If time is rescaled to $\tau = \varepsilon t$, we obtain a system with respect to the slow time scale, expressed as

$$\begin{cases} \varepsilon \frac{d\mathbf{x}}{d\tau} = f(\mathbf{x}, \mathbf{z}, \varepsilon), \\ \frac{d\mathbf{z}}{d\tau} = g(\mathbf{x}, \mathbf{z}, \varepsilon), \end{cases}$$
(2)

As long as $\varepsilon \neq 0$, systems (1) and (2) are equivalent but this is not the case in the limit $\varepsilon \to 0$. Taking the singular limit $\varepsilon \to 0$ in (1), one can treat the slow variables as parameters; the resulting *m*-dimensional system is called the fast subsystem or the layer problem. On the other hand, when system (2) is considered in the singular limit, as $\varepsilon \to 0$, the system becomes the reduced problem with dynamics restricted to the *n*-dimensional C^r -smooth critical manifold $f(\mathbf{x}, \mathbf{z}, 0) = 0$. Geometric singular perturbation theory (GSPT) utilizes these singular limits, and investigates the two lower-dimensional systems to deduce the behavior of the original (n+m)-dimensional system [16, 22, 24]. Note that the **z**-dependent equilibria of the fast subsystem together form the critical manifold.

For small enough ε , Fenichel theory [15, 16] guarantees that, far enough from singularities of the fast subsystem, the *n*-dimensional critical manifold perturbs to an *m*-parameter family of locally invariant *n*-dimensional slow manifolds. These slow manifolds could be attracting, repelling or of saddle type, depending on the stability of the equilibria on the critical manifold. In particular, a saddle slow manifold (SSM) is the perturbation of a family of saddle equilibria. Each saddle equilibrium in the family has stable and unstable manifolds. Fenichel theory also asserts that the union of these stable and unstable manifolds persists under a small perturbation [16] and the intersection of a pair of such persisting stable and unstable manifolds is an SSM [23].

In slow-fast systems, the slow manifolds together with invariant manifolds of equilibria and periodic orbits organize the local and global dynamics. For instance, it is well known that the interaction of attracting and repelling slow manifolds can lead to canard explosions [2, 30, 39]. More recently, it has been established that SSMs and their stable and unstable manifolds can play important roles in the dynamics of a system: the number of spikes in a bursting periodic orbit is organized by the intersection of the stable and unstable manifolds of an SSM [18]. In [35], the effect of changing a parameter on the number of spikes in the response of a system is investigated when a short-time stimulus is applied with fixed amplitude; a transition between solutions with different numbers of spikes occurs in an exponentially small parameter interval, and SSMs and their stable manifolds are an integral part of the mechanism for spike adding. Hence, the ability to compute accurate approximations to slow manifolds, including SSMs and their stable and unstable manifolds, is of significant interest.

Slow manifolds experience extremely strong attraction or repulsion because of the fast dynamics normal to the manifolds. Hence, their numerical approximation is a challenge, and shooting methods are often unhelpful, because small errors in the initial conditions grow exponentially quickly. The computation of SSMs is perhaps even more challenging because these manifolds have both repelling and attracting properties. There are well-established numerical methods for computing attracting and repelling slow manifolds [6, 17] but methods for the approximation of SSMs are scarce. The first method for the computation of an SSM and its associated (un)stable manifolds was presented in 2009 by Guckenheimer and Kuehn [18]. There, the SSM is approximated using a collocation method; the corresponding stable (unstable) manifolds are then computed as the union of trajectory segments integrated backward (forward) in time starting a small distance from the computed SSM in the direction of the stable (unstable) eigenvectors of the corresponding branch of equilibria of the fast subsystem. Kristiansen [29] introduces an iterative method for computing slow manifolds and particularly an SSM via enforcing the invariance condition of a slow manifold as an equation and solving it from an initial guess. The associated (un)stable manifold of an SSM is computed by another iterative method through a projection onto the SSM. Basically, the computations are split into two nonstiff parts: one on the SSM and the other as the connection to and from the SSM. The method has some advantages; for example, one only needs to know the vector field and its Jacobian, but its convergence is guaranteed only for small enough ε . In this paper, we compute an approximation of an SSM using pseudoarclength continuation in AUTO [7, 8] which is similar to the collocation method in [18]. However, we also extend this approach to the computation of the associated (un)stable manifolds of the SSM. Our method is fast and very accurate because of the setup in AUTO.

In this paper, we consider the case of systems with two fast variables (m = 2) and one slow variable (n = 1). The critical manifold is the one-dimensional C^r -smooth curve

$$C_0 := \{ (\mathbf{x}, z) \in \mathbb{R}^2 \times \mathbb{R} \mid f(\mathbf{x}, z, 0) = 0 \} \subseteq \mathbb{R}^3,$$
(3)

which we assume is folded twice, resulting in a middle branch that is of saddle type. Corresponding to this saddle branch, there will be a two-parameter family of one-dimensional SSMs with corresponding one-dimensional families of two-dimensional stable and unstable manifolds [16]. A trajectory started on such a stable manifold in a small neighborhood of the SSM converges very quickly toward the SSM, follows it for a time interval of $\mathcal{O}(1)$, and then diverges from the SSM, again very quickly [23]. We approximate the stable manifold of an SSM as a one-parameter family of trajectory segments. The method is implemented in the software package AUTO [7, 8] using pseudo-arclength continuation and a two-point boundary value problem (2PBVP) setup. We validate the accuracy of our algorithm by computing stable manifolds of SSMs in two models: a polynomial system introduced in [35] and a thalamic model adapted from [38].

This paper is organized as follows. In section 2, we define an approximation of an SSM and its stable and unstable manifolds. The implementation of the 2PBVP setup for the computation of the stable manifold of an SSM in AUTO is explained in section 3. The algorithm is used for two models in section 4, where we explain how the calculated stable manifold of an SSM organizes the number of spikes in a transient response and, hence, validate the accuracy of our method. Conclusions and a discussion of the results are included in section 5. Finally, A gives details for one of the models used in section 4.

2 Saddle slow manifolds and their (un)stable manifolds

By definition, a manifold is normally hyperbolic if the contraction and expansion normal to the manifold is stronger than the contraction and expansion tangent to the manifold [15, 19, 44]. Since C_0 is a manifold of equilibria, it is normally hyperbolic if and only if every point $(x, z) \in C_0$ is a hyperbolic equilibrium of the fast subsystem, that is, if and only if the associated Jacobian matrix $D_x f(x, z, 0)$ has no eigenvalues on the imaginary axis.

If C_0 is normally hyperbolic, Fenichel theory [15, 16] guarantees that C_0 perturbs to a family of locally invariant manifolds with compatible stability properties, each of which is C^r



Figure 1: (a) Sketch of a saddle equilibrium p_0 of the fast subsystem, together with its local stable (blue) and unstable (red) manifolds, denoted $W^s(p_0)$ and $W^u(p_0)$, respectively; (b) the union S_0 of such saddles with two-dimensional stable (blue) and unstable (red) manifolds, denoted $W^s(S_0)$ and $W^u(S_0)$, respectively. The double arrows indicate the direction of the flow.

and lies in an $\mathcal{O}(\varepsilon)$ -neighborhood of C_0 for ε sufficiently small. Typically, C_0 has folds with respect to z, which means that there exist values of z for which the fast subsystem exhibits a saddle-node bifurcation. At such points, C_0 is not normally hyperbolic, but we can divide C_0 into several isolated branches, so that each of these branches is normally hyperbolic and gives rise to a corresponding family of slow manifolds.

We are interested in branches of C_0 that are of saddle type. We define a compact, connected submanifold S_0 of C_0 extending from $z = z_{in}$ to $z = z_{out}$, such that each point on S_0 is a hyperbolic saddle equilibrium of the fast subsystem; here, we choose $z_{in} < z_{out}$ and assume that under (2) $\frac{dz}{d\tau} > 0$ along S_0 . The Jacobian matrix $D_x f(p_0, z_0, 0)$, for each equilibrium $p_0 \in S_0$ with fixed $z_0 \in [z_{in}, z_{out}]$, has exactly one negative and one positive eigenvalue. Hence, p_0 has a one-dimensional stable manifold, denoted $W^s(p_0)$, consisting of two trajectories that converge to p_0 in forward time. Similarly, p_0 has a one-dimensional unstable manifold, denoted $W^u(p_0)$, consisting of two trajectories that converge to p_0 in backward time; this is illustrated in Figure 1(a). The union of the (un)stable manifolds of all $p_0 \in S_0$ is a two-dimensional (un)stable manifold for S_0 , that is,

$$W^{s}(S_{0}) := \bigcup_{p_{0} \in S_{0}} W^{s}(p_{0}) \text{ and } W^{u}(S_{0}) := \bigcup_{p_{0} \in S_{0}} W^{u}(p_{0}).$$
 (4)

Figure 1(b) shows a sketch of S_0 , together with (local) manifolds $W^s(S_0)$ and $W^u(S_0)$. The Stable Manifold Theorem and the smoothness of system (2) guarantee that $W^s(S_0)$ and $W^u(S_0)$ are also C^r -smooth; see [15, 22, 24].

Associated with S_0 , provided ε is small enough, Fenichel theory guarantees the existence of a two-parameter family of saddle slow manifolds (SSMs) S_{ε} that are each locally invariant. Local invariance means that a solution started from a point in S_{ε} with z-coordinate $z_0 \in$ (z_{in}, z_{out}) stays in S_{ε} until $z = z_{out}$. While the theory does not guarantee uniqueness of S_{ε} , all manifolds in the family are exponentially close to one another [16, 31].

Fenichel theory [15, 16, 24, 31] also implies the existence of one-parameter families of locally invariant stable and unstable manifolds, denoted $W^s(S_{\varepsilon})$ and $W^u(S_{\varepsilon})$, associated



Figure 2: Sketch of a saddle slow manifold S_{ε} together with its stable manifold $W^{s}(S_{\varepsilon})$ (blue) and unstable manifold $W^{u}(S_{\varepsilon})$.

with $W^s(S_0)$ and $W^u(S_0)$, respectively. These manifolds lie in an $\mathcal{O}(\varepsilon)$ -neighborhood of their unperturbed counterparts. These stable and unstable manifolds of S_{ε} are C^r -diffeomorphic to $W^s(S_0)$ and $W^u(S_0)$, respectively. The (un)stable manifolds $W^s(S_{\varepsilon})$ and $W^u(S_{\varepsilon})$ are not unique and exist as families of manifolds that lie exponentially close to one another.

As mentioned in the introduction, each chosen pair $W^s(S_{\varepsilon})$ and $W^u(S_{\varepsilon})$ intersect in an SSM S_{ε} . Furthermore, there are trajectories which enter a small neighborhood of each S_{ε} close to $W^s(S_{\varepsilon})$, and follow S_{ε} for a certain length of time, after which they leave close to $W^u(S_{\varepsilon})$. We approximate $W^s(S_{\varepsilon})$ by selecting a one-parameter family from those trajectories that follow S_{ε} up to $z = z_{out}$; the unstable manifold $W^u(S_{\varepsilon})$ can be approximated in the same way by reversing time and considering $z = z_{in}$.

2 is a sketch of the stable and unstable manifolds of S_{ε} . These surfaces are perturbations of the stable and unstable manifolds of S_0 in Figure 1(b). For ease of visualization, we show just one sheet of each of $W^s(S_{\varepsilon})$ and $W^u(S_{\varepsilon})$. As shown, solutions on $W^s(S_{\varepsilon})$ approach S_{ε} very fast at different values of the slow variable z along S_{ε} . The same thing happens for trajectories on $W^u(S_{\varepsilon})$ in reverse time.

2.1 Selecting a saddle slow manifold

We first provide a suitable approximation of S_{ε} as a trajectory segment along S_0 . Let $B_{\delta}(z_0)$ denote a two-dimensional closed disk in the plane $z = z_0$ with radius δ and center $(x_0, z_0) \in S_0$. Here, δ is small, but it must be at least of order ε . We define

$$B_{\delta}(S_0) = \bigcup_{z_0 \in S_0} B_{\delta}(z_0), \tag{5}$$

which is a tubular compact set around S_0 ; see Figure 3(a).

For ε small enough, the intersection between $B_{\delta}(S_0)$ and the family of SSMs, which lies $\mathcal{O}(\varepsilon)$ from S_0 , is not empty. Moreover, we can choose δ such that there is a set of trajectories, including S_{ε} , that enter $B_{\delta}(S_0)$ at z_{in} , and leave $B_{\delta}(S_0)$ at z_{out} . This is illustrated in Figure 3(a), where two such trajectories are sketched inside $B_{\delta}(S_0)$. We approximate $S_{\varepsilon} \cap B_{\delta}(S_0)$ by the specific trajectory from this set that spends the longest time in $B_{\delta}(S_0)$; we denote this approximation by $S_{\varepsilon}^{\mathbf{x}}$. It is possible that there exists more than one trajectory with this property; we simply choose one of them. Note that, by definition, S_{ε} can be parameterized by $z \in [z_{in}, z_{out}]$.



Figure 3: Sketches of the neighborhoods $B_{\delta}(S_0)$ and $B_{\Delta}(S_{\varepsilon}^{\mathbf{x}})$ of S_0 and $S_{\varepsilon}^{\mathbf{x}}$, respectively, together with some nearby trajectories; (a) two representative trajectories that lie entirely in $B_{\delta}(S_0)$; (b) two trajectories in the family of $W^s(S_{\varepsilon})$ that enter $B_{\Delta}(S_{\varepsilon}^{\mathbf{x}})$ at z_0 and leave through z_{out} .

2.2 The (un)stable manifold of S_{ε}^{x}

We now proceed with defining the approximation $W^s(S_{\varepsilon}^x)$ of $W^s(S_{\varepsilon})$. Note that we only approximate one sheet of $W^s(S_{\varepsilon})$; the approximation of the other sheet is similar. As shown in Figure 3(b), we define a tubular neighborhood of S_{ε}^x similar to the way we defined $B_{\delta}(S_0)$. Specifically, we define

$$B_{\Delta}(S_{\varepsilon}^{\mathbf{x}}) = \bigcup_{z_{\varepsilon} \in [z_{in}, z_{out}]} B_{\Delta}(x_{\varepsilon}, y_{\varepsilon}, z_{\varepsilon}),$$
(6)

where $B_{\Delta}(z_{\varepsilon})$ is now a disk of radius Δ centered at a point $(\mathbf{x}_{\varepsilon}, z_{\varepsilon}) = (\mathbf{x}_{\varepsilon}(z_{\varepsilon}), z_{\varepsilon}) \in S_{\varepsilon}^{\mathbf{x}}$ and Δ is small.

We use ideas from [11, 45] for the definition of the stable manifold for a hyperbolic trajectory in a nonautonomous system to formulate a definition of $W^s(S_{\varepsilon}^{\mathbf{x}})$. The family of stable manifolds of $S_{\varepsilon}^{\mathbf{x}}$ corresponds to the set of trajectories that enter $B_{\Delta}(S_{\varepsilon}^{\mathbf{x}})$ (not necessarily from z_{in}) and, as long as they are in the Δ -neighborhood of $S_{\varepsilon}^{\mathbf{x}}$, come closer to $S_{\varepsilon}^{\mathbf{x}}$. In other words, a trajectory $\phi^t(z_{\varepsilon})$ that enters $B_{\Delta}(S_{\varepsilon}^{\mathbf{x}})$ at $z_{\varepsilon} \in [z_{in}, z_{out})$, lies on a member of the family of stable manifolds if $d_z(\varphi^t(z_{\varepsilon}), S_{\varepsilon}^{\mathbf{x}})$, the Euclidean distance between the intersections with the plane z = constant of $\varphi^t(z_{\varepsilon})$ and $S_{\varepsilon}^{\mathbf{x}}$, decreases in forward time (increasing z) until $\phi^t(z_{\varepsilon})$ reaches the disk $z = z_{out}$. We refer to such a trajectory as a converging trajectory. We emphasize that this definition also embraces all trajectories that enter $B_{\Delta}(S_{\varepsilon}^{\mathbf{x}})$ from z_{in} . Since we assume that the vector field is C^r -smooth, the distance function is also C^r -smooth, which is important for our definition of $W^s(S_{\varepsilon}^{\mathbf{x}})$.



Figure 4: The two-dimensional stable manifold $W^s(S_0)$ (blue) and unstable manifold $W^u(S_0)$ (red) of the middle branch S_0 (black dashed) of saddle equilibria of the fast subsystem (8). The manifolds $W^s(S_0)$ and $W^u(S_0)$ intersect at the homoclinic orbit Γ (green).

We approximate a representative $W^s(S^x_{\varepsilon})$ of the stable manifold family of S^x_{ε} as follows. We consider all the converging trajectories that enter $B_{\Delta}(S^x_{\varepsilon})$ at some fixed z-value, say $z = z_{\varepsilon}$, with $z_{in} < z_{\varepsilon} < z_{out}$. Of all these trajectories, $\phi^t(z_{\varepsilon})$ is chosen such that $d_z(\phi^t(z_{\varepsilon}), S^x_{\varepsilon})$ at $z = z_{out}$ is minimal, that is, at $z = z_{out}$, the converging trajectory $\phi^t(z_{\varepsilon})$ lies closest to S^x_{ε} . As for the definition of S^x_{ε} , it is possible that there is more than one trajectory with the minimum distance; here, we also select only one of them. At z_{in} , this comparison is made among the trajectories that enter $B_{\Delta}(z_{in})$ from the same radius r ($0 < r \leq \Delta$). The union of all of these trajectories over different values of z_{ε} and r gives our approximation $W^s(S^x_{\varepsilon})$. The C^r -smoothness of the vector field enables us to choose the minimum-distance trajectory for different z_{ε} - and r-values in a continuous manner. The extension of the selected trajectories the global stable manifold of S^x_{ε} .

Note that our definition of $W^s(S^x_{\varepsilon})$ considers only one sheet of the manifold; the other sheet can be approximated similarly and the two sheets meet at S^x_{ε} .

3 The algorithm

We compute an approximation to $W^s(S^x_{\varepsilon})$ with the pseudo-arclength continuation package AUTO [7, 8]. To this end, we set up a 2PBVP with boundary conditions based on the

definitions given in section 2.

We explain the steps in the algorithm by applying it to the following system of differential equations:

$$\begin{cases} \dot{x} = -1.1x^3 + 2x^2 - y - bz, \\ \dot{y} = x^2 - y, \\ \dot{z} = \varepsilon(2(x - z) + 0.1), \end{cases}$$
(7)

where we use $\varepsilon = 0.001 \ll 1$, so that the system has two fast variables x and y, and one slow variable z. This system was taken from [40]; see also [4, 14, 34, 35, 40]. Throughout this section, the parameter b is fixed at b = 0.9; we will vary b for the case study in subsection 4.1. The fast subsystem of system (7) is the two-dimensional system:

$$\begin{cases} \dot{x} = -1.1x^3 + 2x^2 - y - bz, \\ \dot{y} = x^2 - y, \end{cases}$$
(8)

where the slow variable z is now a parameter. The equilibria of system 8 form a Z-shaped curve that is the critical manifold:

$$C_0 = \left\{ (x, y, z) \in \mathbb{R}^3 \, \middle| \, z = \frac{-1.1x^3 + 2x^2 - y}{b} \text{ and } y = x^2 \right\}.$$

The middle branch S_0 of C_0 is bounded by fold points at z = 0, denoted SN_1 , and z = $\frac{4}{27b(1.1)^2} \approx 0.13604$ when b = 0.9, denoted SN₂. Each equilibrium on S_0 is of saddle type with one-dimensional stable and unstable manifolds. The union of these one-dimensional stable and unstable manifolds forms two-dimensional surfaces $W^{s}(S_{0})$ and $W^{u}(S_{0})$, respectively. We computed $W^{s}(S_{0})$ and $W^{u}(S_{0})$ with AUTO via continuation of a z-dependent family of orbit segments as suggested in [35]. Figure 4 shows $W^{s}(S_{0})$ (blue) and $W^{u}(S_{0})$ (red) for $z_{in} = 0.001 \le z \le z_{out} = 0.13276$, together with S_0 (black dashed) as part of C_0 (black, solid when stable and dashed when unstable). Note that the bottom branch of C_0 is attracting while the top branch changes from attracting to repelling via a Hopf bifurcation. Also shown is a homoclinic orbit Γ (green) of the fast subsystem that exists for $z = z_{\Gamma} \approx 0.04091$, at which $W^{s}(S_{0})$ and $W^{u}(S_{0})$ intersect. One sheet of $W^{s}(S_{0})$ (the "lower" sheet) extends directly to infinity in the direction of $x \to -\infty$. The other sheet (the "upper" sheet) behaves differently: for $z_{in} < z \leq z_{\Gamma}$, the one-dimensional manifolds fold only once around C_0 before extending to infinity as $x \to -\infty$ while for $z_{\Gamma} < z \leq z_{out}$, they spiral around the upper branch of C_0 . For the unstable manifold, one sheet of $W^u(S_0)$ (the "lower" sheet) directly accumulates onto the lower attracting branch of C_0 as x decreases. The other sheet (the "upper" sheet) behaves again differently on each side of z_{Γ} : for $z_{in} < z \leq z_{\Gamma}$, the one-dimensional manifolds fold only once around the upper branch of C_0 before accumulating on the attracting branch of C_0 , while for $z_{\Gamma} < z \leq z_{out}$ they spiral around the upper branch of C_0 . The manifolds $W^{s}(S_{0})$ and $W^{u}(S_{0})$ provide information about the dynamics of the full system close to the singular limit $\varepsilon \to 0$, but their geometry does not consider the effect of the slow drift in z when $\varepsilon \neq 0$. Hence, they can only be used to predict behavior locally; see also [35].

In order to gain information about the global dynamics for the full system with $\varepsilon = 0.001$, we compute $W^s(S^x_{\varepsilon})$ as a family of orbit segments that, together, form a surface in a region of interest. Each orbit segment, defined as a set $\{u(s) \in \mathbb{R}^3 \mid 0 \le s \le 1\}$, is a solution of the rescaled system

$$\dot{u} = TF(u). \tag{9}$$



Figure 5: Illustration of how the boundary conditions are modified during the setup of the 2PBVP for the computation of $W^s(S_{\varepsilon}^{\mathbf{x}})$ for (7). Each panel shows the critical manifold (black) that contains S_0 with the fold points SN_1 and SN_2 (grey); panel (a) shows the stationary solution p_0 with start point on Σ_{01} and (the same) last point on L_{11} ; panel (b) shows the orbit segment with the start point on $\Sigma_{01} \cap \{z = 0\}$ and the end point on L_{11} ; panel (c) shows the first approximate orbit segment on $W^s(S_{\varepsilon}^{\mathbf{x}})$; and panel (d) shows another orbit segment on $W^s(S_{\varepsilon}^{\mathbf{x}})$.

Here, F is the right-hand side of (7) and T is the total integration time of u(s). The computation is done in three steps. First, we use homotopy to obtain a first orbit segment in $W^s(S^x_{\varepsilon})$.

Step 1: Homotopy starting from a point on S_0

We start the computation by choosing $\mathbf{p}_0 = (\mathbf{x}_0, z_0) \in S_0$ close to SN_2 with $z_0 = z_{out} = 0.13276$, because z increases with the flow from SN_1 to SN_2 . Hence, $\mathbf{x}_0 = (x_0(z_0), y_0(z_0)) \approx$

 $(0.55, 0.55^2)$ and $\mathbf{p_0}$ lies just to the left of SN_2 ; see Figure 5(a). We define the line L_{11} through p_0 that is parallel to the eigenvector associated with the stable eigenvalue of p_0 with respect to fast subsystem (8). We also need to define the plane

$$\Sigma_{01} := \{ (x, y, z) \in \mathbb{R}^3 \mid x = 0.55 \},\$$

transverse to L_{11} and the stable eigenvectors of S_0 ; the value 0.55 is chosen such that $p_0 \in \Sigma_{01}$. Near p_0 , this choice for Σ_{01} is transverse to the flow on $W^s(S_{\varepsilon})$ for $\varepsilon = 0.001$.

The orbit segment $\{u(s) = p_0 \mid 0 \le s \le 1\}$, is a solution of the rescaled system (9) with T = 0 and boundary conditions

$$u(0) \in \Sigma_{01}$$
 and $u(1) \in L_{11}$.

Figure 5(a) shows this initial setup with the point p_0 as the first orbit segment. We now vary the end point u(1) along L_{11} and let T increase while u(0) changes on Σ_{01} . For $\varepsilon = 0.001$, S_{ε}^{x} has moved away from S_0 with the result that the line L_{11} intersects one of the two sheets of $W^u(S_{\varepsilon}^{x})$. Moving u(1) along L_{11} toward $W^u(S_{\varepsilon}^{x})$ causes the solution segment to remain close to S_0 for increasingly large T. Therefore, u(0) moves toward smaller z-values. Figure 5(b) shows the final orbit segment, where we stopped the continuation as soon as the z-coordinate of u(0) reached 0, which is the value of z at SN_1 .

The final orbit segment consists of two parts; a fast segment that approaches S_0 and a slow segment that follows S_0 for $\mathcal{O}(1)$ time. It perhaps lies on $W^s(S_{\varepsilon}^x)$ to a good approximation, but its end point is determined by an eigendirection of the fast subsystem. More precisely, $u(1) = u_1^x \approx 0.54809$.

Step 2: Approximating an orbit on $W^s(S_{\varepsilon}^x)$

In the second step, we find a better approximation of an orbit segment on $W^s(S^{\mathbf{x}}_{\varepsilon})$, namely, an orbit segment that stays close to $S^{\mathbf{x}}_{\varepsilon}$ for the longest integration time. Here, we swap the dimensions of the boundary conditions at either end. We define the line segment

$$L_{02} := \{(x, y, z) \in \mathbb{R}^3 \mid x = 0.55 \text{ and } z = 0\} \subseteq \Sigma_{01},$$

transverse to $W^{s}(S_{0})$ and the plane

$$\Sigma_{12} := \{ (x, y, z) \in \mathbb{R}^3 \mid x = u_1^{\mathsf{x}} \},\$$

parallel to Σ_{01} and transverse to $W^u(S_0)$. Note that the final orbit segment calculated in step 1 is also a solution of system (9) with boundary conditions

$$u(0) \in L_{02}$$
 and $u(1) \in \Sigma_{12}$.

We now vary the start point u(0) along L_{02} such that T increases. This means that u(0) moves closer to $W^s(S^x_{\varepsilon})$ and the z-coordinate of u(1) increases so that the orbit segment follows S^x_{ε} for a longer time. We continue the orbit segment until a maximum in T is reached, which AUTO detects as a fold with respect to T. Figure 5(c) shows the orbit segment at the moment of maximal T. We use this orbit segment as a good approximation of an orbit segment on $W^s(S^x_{\varepsilon})$, even though it is also defined for a small z-interval beyond $z = z_{out}$.



Figure 6: The stable manifold (blue) of a saddle slow manifold superimposed with the critical manifold (black).

Step 3: Continuation of the two-dimensional surface $W^s(S_{\varepsilon}^x)$

We are now ready to compute $W^s(S^x_{\varepsilon})$ as a one-parameter family of orbit segments. We obtain a large portion of $W^s(S^x_{\varepsilon})$ by changing boundary conditions for a third time; see Figure 5(d). We define the plane

$$\Sigma_{03} := \{ (x, y, z) \in \mathbb{R}^3 \mid z = 0 \},\$$

that contains L_{02} and is transverse to $W^{s}(S_{0})$, and we also define

$$\Sigma_{13} := \Sigma_{12} = \{ (x, y, z) \in \mathbb{R}^3 \mid x = u_1^{\mathsf{x}} \},\$$

where $u_1^{\rm x} \approx 0.54809$ is as before, which means that Σ_{13} contains u(1) in step 2. Hence, the last computed orbit segment from step 2 is a solution of system (9) with boundary conditions

$$u(0) \in \Sigma_{03}$$
 and $u(1) \in \Sigma_{13}$.

We seek solutions of system (9) with $u(0) \in \Sigma_{03}$ such that T is maximal. All of the trajectories on $W^s(S^x_{\varepsilon})$ follow S^x_{ε} for the longest time and leave S^x_{ε} exponentially close to $W^u(S^x_{\varepsilon})$ at SN_2 . Accordingly, by continuing the detected fold with respect to T in the previous step, a oneparameter family of orbit segments sweeps $W^s(S^x_{\varepsilon})$ in such a way that each orbit segment in this family tracks the slow manifold up to SN_2 and leaves S^x_{ε} exponentially close to $W^u(S^x_{\varepsilon})$. Figure 5(d) shows a representative orbit segment on $W^s(S^x_{\varepsilon})$.

Figure 6 shows the approximation $W^s(S_{\varepsilon}^x)$ (blue) of $W^s(S_{\varepsilon})$ calculated with the algorithm described above. Also shown is the critical manifold C_0 (black). We generate both sheets of



Figure 7: The stable manifold $W^s(S^x_{\varepsilon})$ (blue) together with the transient response of system (10) for b = 0.9. The first segment (cyan) of the response starts at equilibrium E_1 (brown dot, which lies behind $W^s(S^x_{\varepsilon})$ from this view point), and ends at the point with $t = T_{\rm on}$ (red dot) between the layers of $W^s(S^x_{\varepsilon})$. The response makes two more oscillations for $t > T_{\rm on}$ (orange), before converging back to E_1 .

 $W^s(S^{\mathbf{x}}_{\varepsilon})$ in a single continuation run with AUTO, because $S^{\mathbf{x}}_{\varepsilon} \subseteq W^s(S^{\mathbf{x}}_{\varepsilon})$ is an orbit segment in the solution family, so the continuation simply proceeds past $S^{\mathbf{x}}_{\varepsilon}$ to the other side of $W^s(S^{\mathbf{x}}_{\varepsilon})$. Some orbit segments on the lower part of $W^s(S^{\mathbf{x}}_{\varepsilon})$ are tangent to Σ_{03} , which means that we miss part of the surface. In order to complete the entire surface $W^s(S^{\mathbf{x}}_{\varepsilon})$ for $z \ge 0$, we use the section

$$\Sigma'_{03} := \{ (x, y, z) \in \mathbb{R}^3 \mid x = -0.3 \},\$$

which is transverse to the orbit segments on $W^s(S_{\varepsilon}^{\mathbf{x}})$ that have a tangency with Σ_{03} .

One sheet of the stable manifold $W^s(S^{\mathbf{x}}_{\varepsilon})$ spirals around the upper branch of C_0 and accumulates on the repelling slow manifold associated with the repelling branch of C_0 . The other sheet of $W^s(S^{\mathbf{x}}_{\varepsilon})$ goes straight down to infinity as $x \to -\infty$.

4 Numerical examples

We illustrate the accuracy of our method for the computation of the stable manifold of a saddle slow manifold with two examples.



Figure 8: Two different slices of $W^s(S_{\varepsilon}^x)$ and the transient response shown in Figure 7, namely, $z \approx 0.01174$ in panel (a), and x = 1 in panel (b). The black dot in panel (a) corresponds to the upper branch of the critical manifold C_0 and the red dot shows the transient response when $t = T_{\text{on}}$; in panel (b), the cyan symbol \odot represents the point of the transient response with $0 \leq t \leq T_{\text{on}}$ and x increases; the orange symbols \odot and \otimes represent the points of the transient response transient response when $t > T_{\text{on}}$ as x increases and decreases, respectively.

4.1 A polynomial model

The polynomial model (7) from section 3 was used in [14, 34, 35, 40] to study spike adding of a transient response as parameters are varied. The transient response is triggered by a short-time fixed amplitude perturbation (current) that is applied when the system is at steady state. The system considered here is a slight variation of system (7), where we add a



Figure 9: The stable manifold $W^s(S^x_{\varepsilon})$ (blue) together with the transient response of system (10) for b = 0.75. The transient response starts at E_1 . The cyan segment represents the transient response when $0 \le t \le T_{\rm on}$ while orange represents the segment when $t > T_{\rm on}$.

product of two Heaviside functions to model the applied current. The system then becomes

$$\begin{cases} \dot{x} = -1.1x^3 + 2x^2 - y - bz + I_{app}H(T_{on} - t)H(t), \\ \dot{y} = x^2 - y, \\ \dot{z} = \varepsilon(2(x - z) + 0.1), \end{cases}$$
(10)

where b is the free parameter and we fix $I_{app} = 0.02$ and $T_{on} = 15$. Without the perturbation, system (10) is the same as system (7), so it has a Z-shaped curve of equilibria which is also the critical manifold of the system; see also section 3. In addition the z-nullcline of the system is a plane which does not depend on the free parameter b [14]. For an interval of b far from 0, the critical manifold and the z-nullcline intersect exactly once at a globally attracting equilibrium E_1 on the lower attracting branch of C_0 .

Let us first consider b = 0.9 fixed as in section 3. Figure 7 illustrates how the perturbation induces a transient response. Shown are $W^s(S^x_{\varepsilon})$ and the critical manifold (black curve) of system (7) together with the transient response of system (10) (cyan and orange curves). We assume that the system is initially at rest, that is, the initial condition is set at E_1 (brown dot). The product of the two Heaviside functions is 1 only when $0 \le t \le T_{\text{on}}$. During this time interval, the initial condition moves along the cyan curve from E_1 to the red dot. After the perturbation is turned off, the orbit is represented by the orange curve: it makes two more oscillations around C_0 before returning to the rest state at E_1 . The number of spikes in the transient response at $t = T_{\text{on}}$ with respect to $W^s(S^x_{\varepsilon})$ [14, 35]. As soon as $t > T_{\text{on}}$, system (10) equals system (7) and $W^s(S^x_{\varepsilon})$ acts as a separatrix that prevents the



Figure 10: The same slices through $W^s(S_{\varepsilon}^x)$ as in Figure 8, except now with b = 0.77835 in panels (a1) and (b1), and b = 0.75 in panels (a2) and (b2), respectively. Here, $z \approx 0.01226$ in panel (a1) and $z \approx 0.01239$ in panel (a2).

response from returning to E_1 immediately. When the perturbation is removed at $t = T_{\rm on}$, the transient response lies between the layers of the stable manifold of $S_{\varepsilon}^{\mathrm{x}}$. Accordingly, the solution of (7) passing through this point cannot cross $W^s(S_{\varepsilon}^{\mathrm{x}})$. Therefore, the solution has to start oscillating between the layers. Figure 7 shows that the response exhibits three spikes before returning to E_1 .

The fact that there are three spikes in the transient response is better illustrated in Figure 8, which shows the intersections of $W^s(S^x_{\varepsilon})$ and the system response with two different planes. Figure 8(a) shows the intersection of $W^s(S^x_{\varepsilon})$ with the plane fixed at z = 0.01174, which is the z-coordinate of the response when $t = T_{on}$. The inset shows an enlargement

of the box indicated on the main panel. The red dot indicates the location of the transient response at $t = T_{on}$. The inset shows that two (blue) intersection curves of $W^s(S_{\varepsilon}^x)$ with z = 0.01174 lie to the left of the red dot, which means that the response must make two further oscillations as it spirals out from $W^s(S_{\varepsilon}^x)$ before it can return to E_1 . Figure 8(b) shows a slice of the manifold at x = 1, together with all intersection points of the response with this plane. The cyan point shows an intersection for $0 \le t \le T_{on}$ and the orange points show successive intersections for $t > T_{on}$; the symbols \odot and \otimes indicate intersections that occur as x increases or decreases, respectively. The cyan \odot gives no information about the number of spikes, but the relative position of the first orange \otimes indicates that two oscillations must occur as the orbit spirals out of $W^s(S_{\varepsilon}^x)$ before convergence to E_1 .

If we now vary b, the number of oscillations (or spikes) in the response of the system can vary. Figure 9 shows $W^s(S_{\varepsilon}^{\mathbf{x}})$ for b = 0.75 when the transient response of system (10) has four spikes. The system is perturbed from the equilibrium E_1 (brown dot) and generates the response represented by the cyan curve for $t \leq T_{\rm on}$, and the orange curve for $t \geq T_{\rm on}$. Just as for the three-spike case, the invariance of $W^s(S^x_{\varepsilon})$ means that the transient response solution must oscillate between the spiraling layers of $W^s(S^x_{\varepsilon})$ before coming back to E_1 . The transition from three to four spikes occurs when b is such that the response at $t = T_{on}$ lies on $W^s(S^x_{\epsilon})$, which is approximately at b = 0.77835. Figure 10 shows the same slices as in Figure 8; here, the slices in panels (a1) and (a2) are chosen such that they contain the transient response at $t = T_{\rm on}$, that is, $z \approx 0.01226$ in panel (a1) and $z \approx 0.01239$ in panel (a2). Panels (a1) and (b1) are for b = 0.77835 almost at the moment of the transition from three to four spikes. When $t = T_{on}$, the transient response lies on $W^s(S_{\varepsilon}^x)$ which means that the response without the perturbation $(t \ge T_{\text{on}})$ is an orbit segment in $W^s(S_{\varepsilon}^{\mathbf{x}})$. Panels (a2) and (b2) are for b = 0.75 and show that an additional layer of $W^s(S_{\varepsilon}^x)$ has appeared to the right of the location of the transient response when $t = T_{on}$, which forces the response to exhibit an extra spike before returning to E_1 . Note that layers of $W^s(S^x_{\varepsilon})$ are very closely packed for large x, so that it is virtually impossible to predict the number of spikes from panel (a2). The insets in panels (a1) and (a2) are enlargements of the area inside the box around the red dot, but even with the help of these enlargements, distinguishing the two outer layers from each other is not possible.

We remark that system (7) has an explicit separation of time scales with $\varepsilon = 0.001$. In other models, the difference in the time scales is often not explicit. For the computation of the stable manifold of an SSM with the algorithm introduced in section 3, we do not rely on there being an explicit time-scale separation; we only need to know that there exists a significant time-scale difference and we must have identified a globally defined slow variable in the system. In the next example, we implement the algorithm on a model with an implicit time-scale separation and one slow variable.

4.2 A thalamic neuron model

The second example is a slight variation of a model taken from [38], which is a simplified version of a thalamic neuron model originally introduced in [43]. The system is three dimensional and given by

$$\begin{cases} \dot{V} = I_{\text{base}} - I_{\text{T}}(V, h) - I_{\text{AP}}(V, n) - I_{\text{L}}(V), \\ \dot{n} = (n_{\infty}(V) - n)/\tau_{n}(V), \\ \dot{h} = (h_{\infty}(V) - h)/\tau_{h}(V), \end{cases}$$
(11)



Figure 11: Bifurcation diagram of system (12). The curve of equilibrium solutions (black) has five branches, separated by the four saddle-node bifurcations denoted SN_1 to SN_4 . The saddle branches are denoted by S_0^t and S_0^b . The family of attracting periodic orbits emanating from a supercritical Hopf bifurcation HB₁ terminates at a homoclinic bifurcation on S_0^t . The subcritical Hopf bifurcation HB₂ generates a family of repelling period orbits terminating at a homoclinic bifurcation on S_0^t . The inset shows an enlargement of S_0^t .

where V represents the membrane potential, n the activation of the delayed rectifier potassium current, and h the inactivation of the calcium current. We use the same steady-state kinetics of the gating variables and parameter values as in [38] but modify one of the parameters in the model to reduce the time-scale separation between the variables and improve visualization of the manifold; for completeness, the full details of the model are given in A.

As reported in [38], the variable h evolves much slower than V and n. Hence, the fast subsystem of (11) is

$$\begin{cases} \dot{V} = I_{\text{base}} - I_{\text{T}}(V, h) - I_{\text{AP}}(V, n) - I_{\text{L}}(V), \\ \dot{n} = (n_{\infty}(V) - n)/\tau_{n}(V), \end{cases}$$
(12)

where the slow variable h is treated as a parameter. Figure 11 shows the bifurcation diagram of the fast subsystem (12). The black and green curves are the h-dependent sets of equilibria and periodic orbits of (12), respectively. The equilibria of (12) form a double S-shaped curve consisting of five branches separated by fold bifurcation points, denoted SN_1 , SN_2 , SN_3 and SN_4 . The inset enlarges the details occurring close to SN_1 and SN_2 . There are two saddle branches, namely, the branch S_0^t ending at SN_1 and SN_2 , and the branch S_0^b ending at SN_3 and SN_4 . The equilibria on the upper branch are attracting for large values of h, and change to repelling at a supercritical Hopf bifurcation, denoted HB_1 . The periodic orbits emanating from the Hopf bifurcation are attracting and terminate at a homoclinic bifurcation on S_0^t . The equilibria on the branch between SN_2 and SN_3 are stable for small values of h and change to sources after a subcritical Hopf bifurcation HB_2 close to SN_2 . The periodic orbits created by HB_2 are repelling and also terminate at a homoclinic bifurcation on S_0^t . The lower branch is stable for all h.



Figure 12: The stable manifold $W^s(S^b_{\varepsilon})$ together with the critical manifold of system (11). The two sheets of $W^s(S^b_{\varepsilon})$ extend like a plane near the critical manifold and then go on directly to infinity in the direction of $V \to \infty$ such that the upper branch of the critical manifold lies between the two sheets.

The parameters of system (11) are chosen slightly differently to those in [38] so that there exists exactly one equilibrium on the lower attracting branch. The unique equilibrium E_1 of the system lies at $(V, n, h) \approx (-84.93047, 0.02725, 0.99999)$ and is a global attractor for the parameter values specified in A.

As we did in the example studied in subsection 4.1, we assume that the model is in the rest state (at E_1) and perturb the system by applying a fixed current of strength 0.2 (μ A/cm²) and duration 70 (ms); this is modeled in the same way as in subsection 4.1, using a multiplication of two Heaviside functions, where the parameters are now $T_{\rm on} = 70$ and $I_{\rm app} = 0.2$.

As discussed in sections 1 and 2, the two saddle branches S_0^b and S_0^t give rise to SSMs, denoted S_{ε}^b and S_{ε}^t , of the full system (11) provided ε is small enough. Let us first focus on S_{ε}^b , for which the flow is in the direction of decreasing h. Starting from the fast subsystem equilibrium $p_0 = (-66.4645, 0.12227) \in S_0^b$ for h = 1, we approximate $W^s(S_{\varepsilon}^b)$ with the setup explained in section 3. Figure 12 shows $W^s(S_{\varepsilon}^b)$ (the light blue surface) with the critical manifold (black curve) of system (11). The manifold $W^s(S_{\varepsilon}^b)$ is a simple U-shaped bowl that encloses S_0^t . Hence, we expect that it also contains $W^s(S_{\varepsilon}^t)$. We approximate $W^s(S_{\varepsilon}^t)$ starting from $p_0 = (-25.889, 0.67651) \in S_0^t$ with h = 0.3; as for S_{ε}^b , the flow is in the direction of decreasing h. Figure 13 shows part of $W^s(S_{\varepsilon}^t)$ together with the critical manifold. The geometry of $W^s(S_{\varepsilon}^t)$ is much more complicated than $W^s(S_{\varepsilon}^b)$ because it spirals around the upper branch of the critical manifold. In fact, $W^s(S_{\varepsilon}^t)$ accumulates in backward time on a one-dimensional repelling slow manifold associated with the repelling branch of the critical manifold which lies in between SN_1 and HB_1 .



Figure 13: The stable manifold $W^s(S^t_{\varepsilon})$ together with the transient response from E_1 (brown dot). The cyan curve is the response of (11) for $0 \leq t < T_{\rm on}$ and the orange curve represents the solution for $t > T_{\rm on}$. The red dot indicates the transient response with $t = T_{\rm on}$.

To explain the geometry of $W^s(S^t_{\varepsilon})$ and its interaction with $W^s(S^b_{\varepsilon})$, we consider the intersections of both manifolds with a sequence of planes defined by h = 0.86, h = 0.867, h = 0.869, h = 0.871, h = 0.872 and h = 0.92; these h-values are chosen to visualize the creation of the right most layer of $W^s(S^t_{\varepsilon})$ in Figure 13. Figure 14 shows these six corresponding intersection sets, denoted $W^s(S^t_{\varepsilon})$, and we also include the intersection curves $\widehat{W}^{s}(S^{b}_{\varepsilon})$ of $W^{s}(S^{b}_{\varepsilon})$; see also Figures 12 and 13. The outer U-shaped curve (light blue) is the intersection $\widehat{W}^{s}(S^{b}_{\varepsilon})$, and the dark-blue curves are $\widehat{W}^{s}(S^{t}_{\varepsilon})$. The black dot is the intersection with the repelling upper branch of the critical manifold of system (11), denoted \widehat{S}_0^r . For h = 0.86, shown in panel (a), $\widehat{W}^s(S^t_{\varepsilon})$ lies very close to $\widehat{W}^s(S^b_{\varepsilon})$ on the left and accumulates onto $\widehat{S_0^r}$ on the right. The inset shows an enlargement of $\widehat{W^s}(\check{S_{\varepsilon}^t})$ around $\widehat{S_0^r}$, illustrating that the accumulation occurs in a spiraling manner. As h increases, that is, while we follow the flow backward in time, the small bump on the bottom right of $W^s(S^t_{\varepsilon})$ grows, moving up toward the right as shown in panel (b) for h = 0.867 and in panel (c) for h = 0.869. The bump then gets fatter and its top segment is not visible in the bottom panels of Figure 14. Note how the second curve of $\widehat{W}^{s}(S_{\varepsilon}^{t})$ in panel (d), when h = 0.871, starts moving left toward the first intersection curve in $\widehat{W}^{s}(S_{\varepsilon}^{t})$, while it remains almost fixed on the right, as h increases to h = 0.872 in panel (e). Here, $\widehat{W}^s(S^t_{\varepsilon})$ consists of two layered intersection curves that accumulate on $\widehat{W}^s(S^b_{\varepsilon})$ on the left side as h increases. Only the top curve in $\widehat{W}^s(S^t_{\varepsilon})$



Figure 14: A sequence of intersection curves $\widehat{W}^s(S^b_{\varepsilon})$ and $\widehat{W}^s(S^b_{\varepsilon})$ of $W^s(S^b_{\varepsilon})$ (light blue curves) and $W^s(S^t_{\varepsilon})$ (dark blue curves), respectively, with the planes h = 0.86 (a), h = 0.867 (b), h = 0.869 (c), h = 0.871 (d), h = 0.872 (e) and h = 0.92 (f). The black dot indicates the upper branch of the critical manifold, denoted S^r_0 . Insets in panels (a) and (f) show enlargements of $\widehat{W}^s(S^t_{\varepsilon})$ around S^r_0 .

accumulates on the repelling slow manifold associated with \widehat{S}_0^r . In the plane h = 0.92, shown in panel (f), the new curve in $\widehat{W}^s(S_{\varepsilon}^t)$ spirals tightly around \widehat{S}_0^r , as illustrated in the enlargement near \widehat{S}_0^r . This process continues for larger *h*-values and more and more intersection curves appear. In the full phase space, $W^s(S_{\varepsilon}^t)$ starts from ∞ in V and makes some very large oscillations, after which it spirals closely around the repelling slow manifold associated with S_0^r . As *h* increases, the number of oscillations around S_0^r along with the number of large layers increases. Figures 12 and 14 show that the shape and position of $W^s(S_{\varepsilon}^b)$ remains almost unchanged for this variation in *h*.

Figures 13 and 14 show that $W^s(S^t_{\varepsilon})$ includes layers that appears to divide the space into different regions. However, the regions are connected to each other through the spiraling nature of the manifold. As we saw in subsection 4.1, the location with respect to $W^s(S^t_{\varepsilon})$ of the transient response at time $t = T_{on}$ (red dot), when the applied perturbation is removed, determines the number of spikes that must occur for $t > T_{on}$ (orange) before the transient response returns to E_1 . As shown in Figure 13, two layers of $W^s(S^t_{\varepsilon})$ lie to the right of the red dot, which means that the transient response must oscillate twice before converging to E_1 .

Note that $\widehat{W}^s(S^t_{\varepsilon})$ accumulates very tightly on $\widehat{W}^s(S^b_{\varepsilon})$; see Figure 14. Even though $\widehat{W}^s(S^t_{\varepsilon})$ and $\widehat{W}^s(S^b_{\varepsilon})$ are computed separately, their numerical approximations never intersect. This confirms that our method is consistent and provides evidence that the numerics are accurate.

5 Conclusions

We have developed a new algorithm for computing an accurate approximation to the stable manifold of a saddle slow manifold (SSM). We restricted our attention to the case of slow-fast systems with one slow and two fast variables. In this context, we defined a particular candidate from the family of SSMs and similarly for its stable and unstable manifolds. For the definition of a stable manifold of an SSM, we relied on the theory for nonautonomous systems [11, 45].

To compute the stable manifold of an SSM, we formulated a two-point boundary value problem two-point boundary value problem in the software package AUTO [7, 8]. The manifold was then approximated by a one-parameter family of orbit segments. To find a first orbit segment in the family, we used a homotopy approach in three steps, switching between different sets of well-chosen boundary conditions. The collocation setup of AUTO is capable of computing such a family, even in the presence of the strong simultaneous attraction and repulsion along an SSM and the extreme sensitivity due to the difference in the time scales.

We applied the algorithm to compute stable manifolds of SSMs in two models, and used the geometry of the manifolds to explain delicate transitions in the dynamics of the systems. In both models, we were specifically interested in explaining the number of spikes seen in the transient model response to a particular type of stimulus. We found that the precise location of the transient response relative to the stable manifold of the SSM, at the time at which the stimulus is removed, determined the number of spikes in the response; these findings are in line with predictions given in [35], and provide indirect but strong evidence for the accuracy of our algorithm. The computational accuracy is also evident from the results in the second example, where the stable manifolds of two SSMs accumulate on each other.

There is an important difference between the two models presented in section 4: in the first model, there is an explicit parameter ε that shows the significant differences in the time scales of variables, but the time-scale separation is implicit in the second model. This is not an issue for our algorithm because it suffices to identify the slow variable and the saddle branch of the critical manifold. In this paper, we assume that the slow variable is always increasing (or decreasing) along the SSM. This assumption fails as soon as saddle equilibria of the full system appear on the saddle branch of the critical manifold. In this case the SSM splits into different segments that include heteroclinic connections between the equilibria. In such a situation, the equilibria are always part of the SSM and the (un)stable manifold of an SSM is contained in the invariant (un)stable manifolds of the saddle equilibria, which can be calculated with different methods; see, e.g. [28].

There are computational methods for the so-called (un)stable fibre bundles of a hyperbolic trajectory in a nonautonomous system [20, 21, 25, 46] that are specifically designed for finite-time invariance. Our numerical approach utilizes the difference in time scales and is not directly amenable for use in the nonautonomous context; see also [1, 36] for an approach that computes stable manifolds in systems with a slowly varying time-dependent parameter.

At present, our algorithm has been implemented for the relatively restricted class of systems with two fast and one slow variables. We anticipate that this algorithm can be generalized to higher-dimensional settings. For example, it is relatively straightforward to compute a two-dimensional (un)stable manifold of an SSM for a system with one slow and more than two fast variables. The adaptation to higher-dimensional manifolds and higherdimensional SSMs will pose more of a challenge; the visualization of such manifolds is also a major obstacle. We expect that stable manifolds of SSMs also control the spike-adding behavior of bursting periodic orbits, e.g., in [34], but such computations are left for future work. It would be worthwhile to consider the interaction of an SSM and its associated (un)stable manifolds with globally invariant manifolds of saddle equilibria or periodic orbits, for example, to investigate whether the stable manifold of an SSM plays a role in separating the basins of attraction of a bistable system.

A Detailed expressions and parameters for the thalamic model

The thalamic neuron model from subsection 4.2 is presented here, in full detail. The model is the same as in [38], except that we used slightly different values for four of the parameters; see 1. Recall from system (11) that the equation for V involves the functions $I_{\rm T}(V, h)$, $I_{\rm AP}(V, n)$, and $I_{\rm L}(V)$. We used

$$I_{\mathrm{T}}(V,h) = g_{\mathrm{T}} s_{\infty}^{3}(V) h(V - V_{\mathrm{Ca}}),$$

where

$$s_{\infty}(V) = 1/\{1 + \exp[(V - \theta_s)/k_s]\}$$

The function $I_{AP}(V, n)$ is defined as

$$I_{\rm AP}(V,n) = g_{\rm Na} m_{\infty}^3(V)(0.85 - n)(V - V_{\rm Na}) + g_{\rm K} n^4(V - V_{\rm K}),$$

where

$$m_{\infty}(V) = \alpha_m(V) / [\alpha_m(V) + \beta_m(V)],$$

with

$$\alpha_m = 0.1(V + 35 - \sigma_m) / \{1 - \exp[-0.1(V + 35 - \sigma_m)]\},\$$

and

$$\beta_m = 4 \exp[-0.05(V + 60 - \sigma_m)]\}.$$

The function $I_{\rm L}(V)$ is defined as $g_{\rm KL}(V - V_{\rm k}) + g_{\rm NaL}(V - V_{\rm Na})$.

In the differential equation for n, we use

$$n_{\infty}(V) = \alpha_n(V) / [\alpha_n(V) + \beta_n(V)],$$

with

$$\alpha_n = 0.01(V + 50 - \sigma_n) / \{1 - \exp[-0.1(V + 50 - \sigma_n)]\},\$$

and

$$\beta_n = 0.125 \exp[-0.0125(V + 60 - \sigma_n)]\};$$

the function $\tau_n(V)$ is defined by

$$\tau_n(V) = 0.05/[\alpha_m(V) + \beta_m(V)].$$

The equation for h is specified by

$$h_{\infty}(V) = 1/\{0.5 + \sqrt{0.25 + \exp[(V - \theta_h)/k_h]}\},\$$

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Parameter	Value	Unit	Parameter	Value	Unit
θ_s	-63.0	mV	$g_{ m Na}$	105.0	$\rm mS/cm^2$
k_s	-7.8	mV	$g_{ m K}$	10.0	$\mathrm{mS/cm^2}$
θ_h	-72	mV	$g_{ m NaL}$	0.01429	$\mathrm{mS/cm^2}$
k_h	1.1	mV	$g_{ m KL}$	0.08571	$\mathrm{mS/cm^2}$
			g_{T}	0.17	$\mathrm{mS/cm^2}$
$I_{\rm base}$	-2	$\mu A/cm^2$	$V_{\rm Na}$	55.0	mV
σ_m	10.3	mV	$V_{\rm K}$	-85.0	mV
σ_n	9.3	mV	$V_{\rm Ca}$	120.0	mV

Table 1: The parameter values used for the thalamic model (11).

and

$$\tau_h(V) = \exp[(V+150)/w]/\{1.5+\sqrt{0.25}+\exp[(V-80)/4]\}+30,$$

where w = 180.

Almost all parameters used are the same as in [38], and given in Table 1. The only differences are that we changed g_{Na} and i_{base} to ensure the existence of a unique attracting equilibrium; modified g_{T} to control the number of spikes, and changed w in the numerator of $\tau_h(V)$ from w = 18 in [38] to w = 180 to decrease the difference in the time scales and make the visualisation of the manifold simpler.

Acknowledgments

We thank John Guckenheimer for providing the details of the computational methods in [18]. We also acknowledge Bernd Krauskopf, Martin Wechselberger and Mathieu Desroches for their helpful discussions and comments on this manuscript.

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