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Homoclinic Bifurcations in a Diffusively Coupled Excitable System

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Abstract. In this paper we consider the diffusively coupled system:

$$\begin{aligned} \dot{u}^1 &= f(u^1, \mu) + \nu D(u^2 - u^1) \\ \dot{u}^2 &= f(u^2, \mu) + \nu D(u^1 - u^2) \end{aligned} \tag{0.1}$$

where $u^j \in \mathbf{R}^2$ $(j = 1, 2)$, $f : \mathbf{R}^2 \times \mathbf{R}^1 \mapsto \mathbf{R}^2$ is sufficiently smooth, $D = \mathrm{diag}(d_1, d_2), d_j \geq 0 (j = 1, 2), d_1 + d_2 > 0$ and ν is a nonnegative parameter. The corresponding uncoupled system

$$\dot{u} = f(u, \mu) \tag{0.2}$$

models the force-length relationship in muscle cells and is shown to be excitable for $\mu < \mu_H$ and have a homoclinic bifurcation at $\mu = \mu_H$ from which stable periodic solutions emerge and persist for a range of $\mu > \mu_H$. A numerically computed global bifurcation diagram illustrates that, for some parameter values, the coupled system (0.1) has stable asymmetric periodic solutions which continue in some region of $\mu < \mu_H$, where no periodic solutions of (0.2) exist. Some degenerate codimension 2 bifurcations of equilibria are summarized after which we investigate conditions for asymmetric homoclinic and heteroclinic bifurcations to occur in (0.1). The role of such bifurcations in the whole bifurcation structure is discussed.

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1 Introduction

There are a variety of models which describe excitability in different systems. The literature is laden with examples and analyses of excitable systems describing the electrical activity of nerve and enodcrine cells. Some notable examples include the Hodgkin-Huxley model of electrical activity in the squid giant axon (Hodgkin and Huxley [1952]), and its analog version the FitzHugh-Nagumo model (FitzHugh [1961], Nagumo et al. [1962]). Less studied is the excitability exhibited in models based on the force-length relationship in the muscle system.

Here, we examine a minor variant of one such model developed by Murase [1992]. First we introduce the model, describing its biological interpretation and bifurcation structure. In subsequent sections we then examine bifurcations of equilibria and homoclinic solutions in a related coupled system. The theorem stated in the last section demonstrates that asymmetric homoclinic solutions of the coupled system can bifurcate from in-phase homoclinic solutions that are asymptotic to nonhyperbolic equilibria.

The original model of Murase is the 2-component system of ordinary differential equations

$$\gamma \frac{dx}{dt} = nF(x) - kx + z \quad , \tag{1.1}$$

$$\frac{dn}{dt} = g(x,n) = \begin{cases} b(1-n) & (x \le x_0) \\ -cn & (x > x_0) \end{cases} \quad , \tag{1.2}$$

where

$$F(x) = ax^2(1-x) \quad . \tag{1.3}$$

Here, x is the dimensionless sliding displacement of cross-bridges connecting thin and thick muscle filaments, n is the fraction of the active cross-bridges, z is the external shear force and the parameters $\lambda = (a, b, c, k, x_0, \gamma)$ have the interpretations:

a : the force constant of the active cross-bridges,
b : the activation rate constant,
c : the inactivation rate constant,
k : the force constant of the passive elastic component,
x_0 : activation region,
γ : the internal viscous shear resistance.

Equation (1.1) describes the balance of the external and elastic shear forces (right side), and the viscous force (left side). Equation (1.2) illustrates how the nonlinear shear force $F(x)$ is activated or inactivated depending on whether the cross-bridge displacement is below or above x_0. Thus, depending on the sliding displacement, the level of excitation n is driven to either $n = 0$ (a complete lack of excitability) or $n = 1$ (the maximal excitability) (see Murase [1992]) for details).

First, we briefly explain some characteristic features of this model. When $z = 0$, $(x, n) = (0, 0)$ is a rest point which is asymptotically stable. With an appropriate choice of λ the system (1.1)-(1.2) exhibits excitability, that is, a sufficiently large stimulus z (of short duration) causes a large excursion of x from and then back to its stable equilibrium. For constant external forces above a threshold, (1.1)-(1.2) exhibits periodic excitation. As z is increased, a bifurcation analysis shows (Murase [1992]) that these (stable) periodic solutions emerge through a homoclinic bifurcation. Hence large amplitude periodic motion suddenly appears as z is increased.

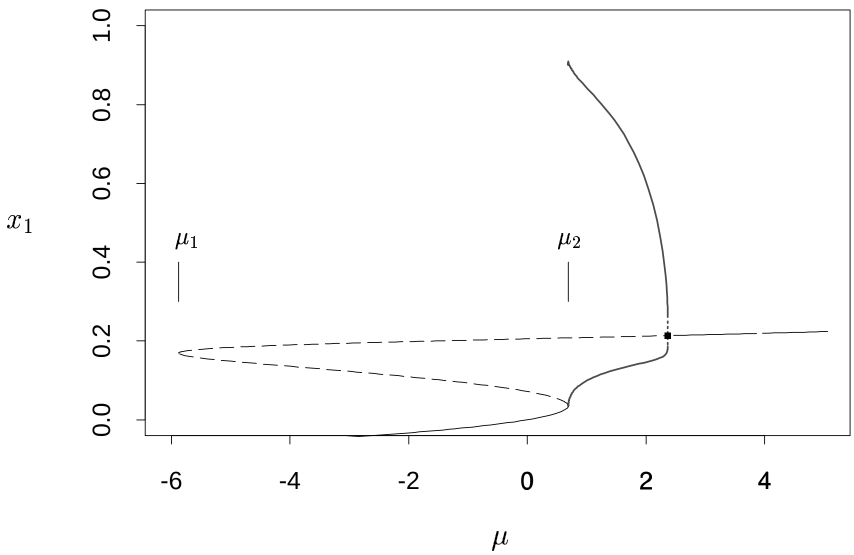

Figure 1 Bifurcation diagram of the modified Murase model. Thick and thin lines indicate periodic solutions and equilibria, respectively. Solid lines indicate stable solutions whereas dashed lines indicate unstable solutions. Note the emergence of periodic solutions ¿from a Hopf point (solid square) which terminate at a homoclinic bifurcation at $\mu = \mu_H$.

For convenience, we modify the model (1.1)-(1.2) by smoothing the discontinuity in $g(x, n)$ as follows:

$$\dot{u} = f(u, \mu) = \begin{pmatrix} \gamma^{-1}(nF(x) - kx + \mu/100) \\ G(x) - cn \end{pmatrix} \quad , \tag{1.4}$$

where $u = (x, n)^T \in \mathbf{R}^2$ and

$$G(x) := \frac{b}{2}\left\{1 + \tanh\left(\frac{x_0 - x}{\delta}\right)\right\} \quad . \tag{1.5}$$

With these definitions $G(x) - cn \to g(x, n)$ as $\delta \to 0^+$ if $b = c$. In this manner, the modified system (1.4) is an approximation of the original model provided $0 < \delta << 1$. Henceforth, we fix the parameters $\lambda = (6, 1, 1, 2/5, 1/5, 1/10)$, $\delta = 3/100$, and $b = c = 1$, leaving μ as a bifurcation parameter in later analyses.

In Figure 1, AUTO (Doedel [1981]) was used to numerically generate a bifurcation diagram for (1.4). The qualitative features depicted in this figure are identical to those found by Murase [1992] for (1.1)-(1.2). Stated precisely, the bifurcation structure is:

1) There are three branches of equilibria $u = u_K(\mu) = (x_K(\mu), n_K(\mu))^T, K = 0, +, -$ of (1.4):

$$\begin{array}{ll} (a) & C_+ := \{u = u_+(\mu) : \mu_1 < \mu\} \\ (b) & C_0 := \{u = u_0(\mu) : \mu_1 < \mu < \mu_2\} \\ (c) & C_- := \{u = u_-(\mu) : \mu < \mu_2\} \end{array}$$

for μ_1, μ_2 with $\mu_1 < 0 < \mu_2$. A saddle-node bifurcation occurs at $\mu = \mu_1$ and μ_2. Then the two branches C_+ (resp. C_-) and C_0 join at $\mu = \mu_1$ (resp. $\mu = \mu_2$), hence

$$\lim_{\mu\to\mu_1+} u_+(\mu) = \lim_{\mu\to\mu_1+} u_0(\mu), \qquad \lim_{\mu\to\mu_2-} u_-(\mu) = \lim_{\mu\to\mu_2-} u_0(\mu) \quad .$$

2) Equilibria on C_- are asymptotically stable node points, while equilibria on C_0 are saddle points. The stability of the equilibria on C_+ changes through a Hopf bifurcation at $\mu_c (> \mu_2)$. Indeed, these equilibria are asymptotically stable for $\mu > \mu_c$ and unstable for $\mu \in (\mu_1, \mu_c)$.
3) There is a $\mu_H, \mu_1 < \mu_H < \mu_2$ such that a homoclinic orbit asymptotic to the equilibrium u_0 appears at $\mu = \mu_H$. For $\mu > \mu_H$, an asymptotically stable periodic orbit bifurcates from the homoclinic orbit. This branch of periodic solutions terminate at the Hopf bifurcation at $\mu = \mu_c$.

We note that the numerics indicate $\mu_H < \mu_2$ only in closeups of Figure 1 (the numerical values are, to three significant figures, $\mu_H = 0.689, \mu_2 = 0.691$). Here, we have presented a view where the bistability of equilibria in the range $\mu \in (\mu_1, \mu_2)$ and the emergence of periodic solutions from the Hopf point are more clearly visible.

In terms of the Jacobians

$$A_K(\mu) := D_u f(u_K(\mu), \mu), \qquad K = 0, +, -, \tag{1.6}$$

the stability criteria embodied in the description above are realized by the conditions

$$\begin{aligned} &\mathrm{tr}A_+(\mu) \begin{cases} > 0 & (\mu_1 < \mu < \mu_c) \\ = 0 & (\mu = \mu_c) \\ < 0 & (\mu_c < \mu) \end{cases} , \\ &\det A_+(\mu) > 0 \qquad (\mu_1 < \mu) \quad , \\ &\det A_0(\mu) < 0 \qquad (\mu_1 < \mu < \mu_2) \quad , \\ &\mathrm{tr}A_-(\mu) < 0,\ \det A_-(\mu) > 0 \qquad (\mu < \mu_2) \quad , \end{aligned} \tag{1.7}$$

where it is understood that the limiting values of $detA_K(\mu)$ and $trA_K(\mu)$ are assumed to be the same near the knees at $\mu = \mu_1, \mu_2$.

Moreover, stable periodic solutions can bifurcate from the homoclinic orbit at μ_H only if

$$\mathrm{tr}A_0(\mu) < 0 \quad \text{at } \mu = \mu_H, \tag{1.8}$$

which in turn implies the modulus of the negative eigenvalue of $A_0(\mu_H)$ is greater than the positive one.

We are now in a position to define a related coupled system

$$\begin{aligned} \dot{u}^1 &= f(u^1, \mu) + \nu D(u^2 - u^1) \quad , \\ \dot{u}^2 &= f(u^2, \mu) + \nu D(u^1 - u^2) \quad , \end{aligned} \tag{1.9}$$

where $\nu > 0$ and $D = \mathrm{diag}(d_1, d_2), d_1, d_2 \geq 0, d_1 + d_2 > 0$. Taking account the background of the model, we assume $d_2 = 0$, hence we may set $d_1 = 1$ without any loss of generality. With these values, the parameter ν can be regarded as an elastic coupling strength between two different regions on the filaments. In later discussions of this system we assume the description 1)-3), the conditions (1.7)-(1.8) (all of which are supported by the numerical results in Figure 1) and these values of d_i.

In sections 2 and 3, we discuss the following problems for the system (1.9):

(i) existence of stable periodic solutions for some region of $\mu < \mu_H$; in other words, the existence of periodic orbits induced by the coupling for which (1.4) exhibits no oscillation;
(ii) classification of degenerate bifurcation points;
(iii) existence of asymmetric homoclinic/heteroclinic orbits.

2 Bifurcations in the coupled system

In this section, we consider bifurcations of the coupled system indicating some codimension 2 bifurcations of the equilibria. To begin, we clearly define some terminology. Firstly, by in-phase periodic solutions we shall mean any periodic solution having the form $(u^1, u^2) = (p(t), p(t))$, where $p(t)$ is a periodic solution of (1.4). By anti-phase (periodic) solutions of (1.9) we shall mean a solution which can be written as $(u^1, u^2) = (\tilde{p}(t), \tilde{p}(t + T/2))$ where $\tilde{p}(t)$ is some T-periodic function. Note that under the reflection $(u^1, u^2) \mapsto (u^2, u^1)$, both the in-phase and anti-phase solutions are symmetric (up to phase shift for the anti-phase solutions). Lastly, by asymmetric periodic solutions we mean any periodic solution of (1.9) which is neither in-phase nor anti-phase but can be written in the form $(u^1, u^2) = (p^1(t), p^2(t))$ where $p^k(t), k = 1, 2$, are periodic functions of commensurate periods. Note that for any asymmetric periodic solution $(p^1(t), p^2(t))$, there also exists the reflected one $(p^2(t), p^1(t))$.

In Figure 2 we present bifurcation diagrams for (1.9) generated using AUTO. The parameter values for the simulations are as described in the previous section with the coupling strength set at $\nu \simeq 0.089$. As is evident from this figure, the in-phase periodic solution of (1.9) exists for $\mu > \mu_H$ until it disappears at the Hopf bifurcation point of the branch C_+. Furthermore, we observe that there are two branches of asymmetic periodic solutions connecting the anti-phase solutions with the in-phase periodic solutions. These asymmetric periodic solutions are certainly stable for an interval containing μ_H (approximately (0.4, 1.05)). We note that these numerical results include those of the corresponding coupled Murase equations (Tsuruzoe [1995]) and that is similar to bifurcation structures found in other excitable systems (Sherman [1994]).

Next we consider codimension 2 bifurcations of the coupled system (1.9). First note that for any ν the system (1.9) has three symmetric (homogeneous) equilibria

$$(u_K(\mu), u_K(\mu)), \quad K = 0, +, - \quad .$$

By defining

$$y = \frac{u^1 + u^2}{2}, \qquad z = \frac{u^1 - u^2}{2} \quad , \tag{2.1}$$

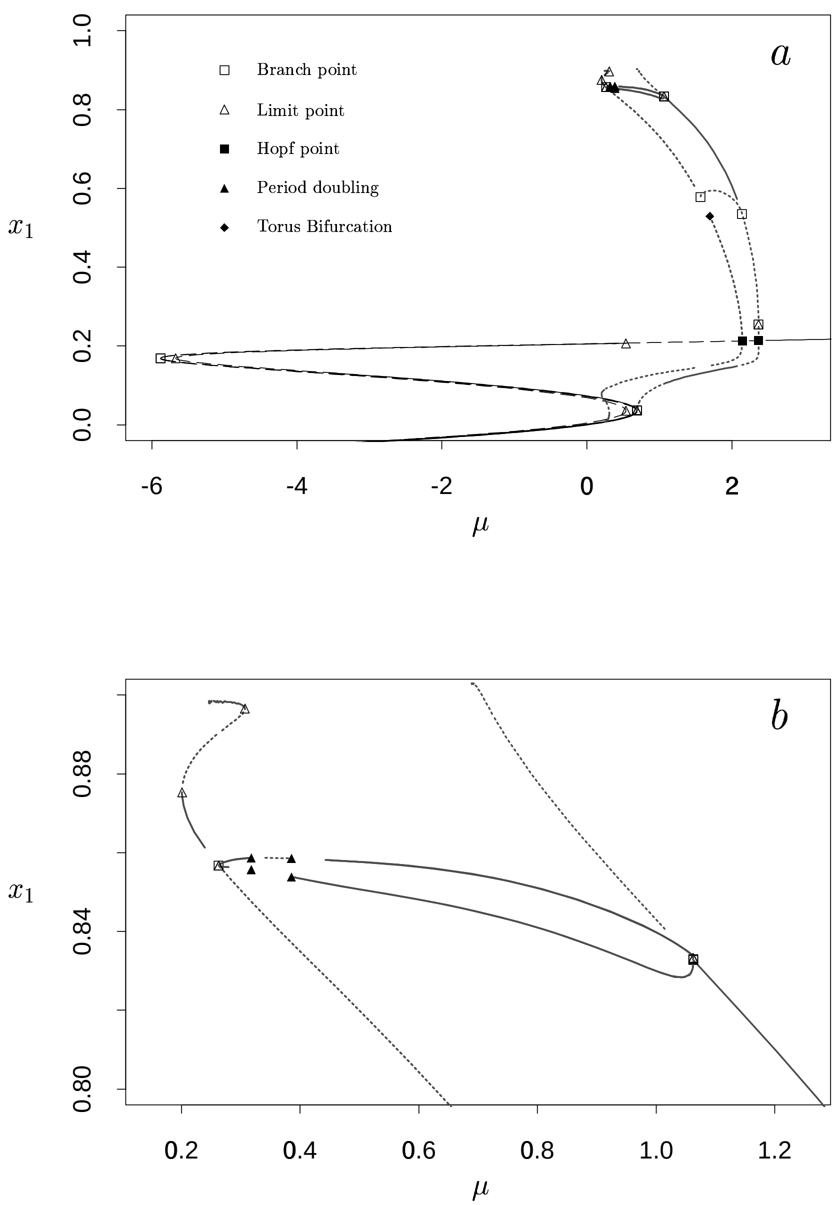

Figure 2 Bifurcation diagrams for the coupled system: (a) Shows the overall bifurcation structure. Periodic solutions emanating ¿from the right Hopf point are in-phase, (b) shows a closeup of the stable asymmetric periodic solutions connecting periodic branches.

the system (1.9) can be transformed into

$$\begin{aligned} \dot{y} &= F_1(y,z,\mu) := \frac{1}{2}\{f(y+z,\mu)+f(y-z,\mu)\} \quad , \\ \dot{z} &= F_2(y,z,\mu,\nu) := \frac{1}{2}\{f(y+z,\mu)-f(y-z,\mu)\} - 2\nu D z \quad . \end{aligned} \tag{2.2}$$

In this form, it is easy to see that a local stability analysis of the symmetric equilibria of (1.9) reduces to finding the eigenvalues of the matrices

$$A_K(\mu) \quad \text{and} \quad A_K(\mu) - 2\nu D, \qquad K = 0, +, -.$$

Now, we determine conditions which imply $A_K(\mu) - 2\nu D$ has either a zero eigenvalue or a pair of purely imaginary eigenvalues. Given $d_1 = 1$ and $d_2 = 0$, it follows from (1.4)-(1.6) that

$$\begin{aligned} \det(A_K(\mu) - 2\nu D) &= \det A_K(\mu) + 2\nu c, \\ \operatorname{tr}(A_K(\mu) - 2\nu D) &= \operatorname{tr} A_K(\mu) - 2\nu \quad . \end{aligned} \tag{2.3}$$

Considering the conditions (1.7), there are three curves in the (μ,ν)-plane on which the eigenvalues of $A_K(\mu) - 2\nu D$ are either zero or $\pm\alpha i$:

$$\begin{aligned} B_c &:= \{(\mu,\nu) : \nu = \operatorname{tr} A_+(\mu)/2,\ \mu_1 < \mu < \mu_c\} \quad , \\ B_0 &:= \{(\mu,\nu) : \nu = -\tfrac{1}{2c}\det A_0(\mu),\ \mu_1 < \mu < \mu_2\} \quad , \\ B_a &:= \{(\mu,\nu) : \nu = \operatorname{tr} A_0(\mu)/2,\ \nu > -\tfrac{1}{2c}\det A_0(\mu)\} \quad , \end{aligned} \tag{2.4}$$

On B_c anti-phase periodic solutions bifurcate from a Hopf point on C_+ while on B_0 a pair of asymmetric equilibria bifurcate from $u_0(\mu)$. On B_a anti-phase periodic solutions also bifurcate but from $u_0(\mu)$ on C_0.

With these definitions, codimension 2 bifurcations can occur at points where any two of the six curves $B_c, B_0, B_a, \mu = \mu_1, \mu = \mu_2$ and $\mu = \mu_c$ intersect. In Figure 3, all six of these curves are plotted in the (μ,ν)-plane and it is seen that there are two such intersection points $(\bar{\mu}_0, \bar{\nu}_0)$ and (μ_1, ν_1):

$$\{(\bar{\mu}_0,\bar{\nu}_0)\} = B_0 \cap B_a, \qquad \{(\mu_1,\nu_1)\} = B_c \cap \{(\mu,\nu) : \mu = \mu_1\},$$

where

$$\bar{\nu}_0 = \operatorname{tr} A_0(\bar{\mu}_0)/2 = -\frac{1}{2c}\det A_0(\bar{\mu}_0), \qquad \nu_1 := \operatorname{tr} A_+(\mu_1)/2.$$

At $(\bar{\mu}_0, \bar{\nu}_0)$, the matrix $A_0(\bar{\mu}_0) - 2\bar{\nu}_0 D$ has a zero eigenvalue with double algebraic multiplicity while $A_0(\bar{\mu}_0)$ has two nonzero eigenvalues with opposite signs on account of (1.7). For the other point (μ_1, ν_1) the former matrix has a pair of pure imaginary eigenvalues and the latter one has a simple zero eigenvalue. At both of these points, the corresponding equilibria have one-dimensional unstable directions. We remark that around each of these singularities, a classification of bifurcations were locally investigated by Guckenheimer and Holmes [1983] using normal form calculations. We do not perform these tedious computations here.

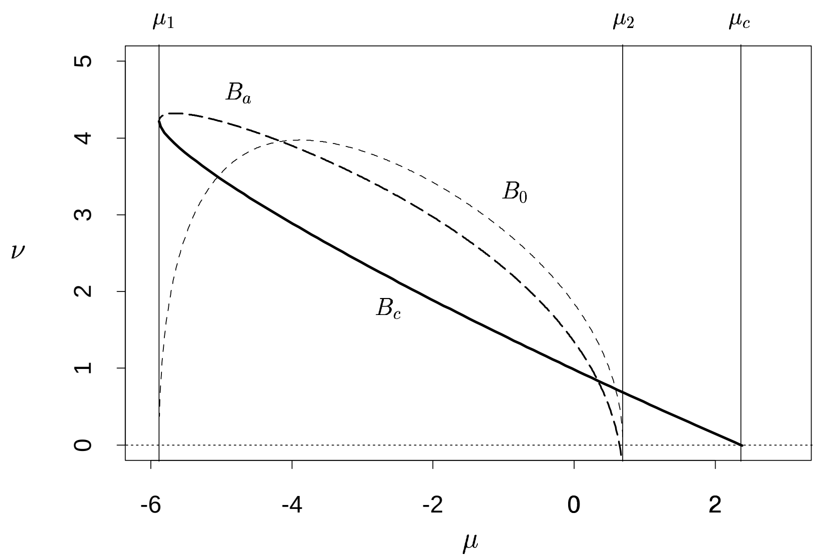

Figure 3 Bifurcation curves in (μ, ν)-plane.

3 Existence of asymmetric homoclinic orbits

In the previous section we demonstrated the existence of some locally degenerate bifurcations of equilibria occuring in the coupled system. In this section we examine a degenerate bifurcation which depends on global information. Specifically, we consider bifurcations of the in-phase homoclinic solution $(u_h(t), u_h(t))$ for parameters (μ, ν) local to the intersecting point (μ_H, ν_H) of $\mu = \mu_H$ and B_0. At this point the in-phase homoclinic solution is degenerate in the sense it is asymptotic to an equilibrium $(u_0(\mu), u_0(\mu))$ which is not hyperbolic. Under certain generic conditions we can prove that a pair of asymmetric homoclinic (or heteroclinic) solutions bifurcate from $(u_h(t), u_h(t))$ and its respective bifurcation curve in the (μ, ν)-plane emerges from (μ_H, ν_H). We outline our assumptions, then state the main theorem and lastly present numerical evidence for the existence of the aforementioned bifurcation curve in the (μ, ν)-plane.

First, consider the linear variational equation of the single equation (1.4) about the homoclinic solution $u_h(t)$:

$$\dot{v} = A(t)v, \qquad A(t) := D_u f(u_h(t), \mu_H) \quad , \tag{3.1}$$

and its respective adoint equation:

$$\dot{y} = -A(T)^T y \quad , \tag{3.2}$$

Equation (3.1) has a bounded solution $v = \dot{u}_h(t)$ over $\mathbf{R}$. Therefore, the adjoint equation (3.2) also has a bounded solution $q(t)$ for $t \in \mathbf{R}$. Letting α be the modulus of the negative eigenvalue of $A_0(\mu_H)$, it can be shown with the normalization

$$q(t)^T \dot{u}_h(t) = 1 \quad \text{and} \quad \lim_{t\to\infty} q(-t)^T \dot{u}_h(t) e^{2\alpha t} = 1 \quad ,$$

the condition

$$\alpha_1 = \int_{-\infty}^{\infty} q(t)^T D_\mu f(u_h(t), \mu_H) dt < 0 \tag{3.3}$$

implies a bifurcation of a stable periodic solution from $u_h(t)$ occurs in the direction $\mu > \mu_H$. This is easily computed from the definition of the Melnikov function (see Chow and Yamashita [1992]). We assume this condition is satisfied.

Next, consider the linear variational equation of (1.9) about the in-phase homoclinic orbit $(u^1, u^2) = (u_h(t), u_h(t))$. By means of the transformation (2.1) this linearization can be decomposed into the system

$$\dot{v}^1 = A(t)v^1, \qquad \dot{v}^2 = (A(t) - 2\nu D)v^2 \quad , \tag{3.4}$$

where $v_k \in \mathbf{R}^2$. The equation for v_1 is the same as (3.1). The latter equation has a bounded solution when $\nu = \nu_H$. Indeed, if $p_0(t)$ is this bounded solution, its asymptotics as $t \to \pm\infty$ can be characterized in the following way:

$$\lim_{t \to -\infty} p_0(t) = \zeta_0 \qquad , \quad \lim_{t \to \infty} p_0(t) = \hat{c}\zeta_0 \quad , \tag{3.5}$$

where ζ_0 is in the nullspace of $A_0 - 2\nu_H D$ and $\hat{c}$ is some constant.

Given these assumptions and definitions we can now state the main theorem which shows the existence of a pair of asymmetric homoclinic orbits bifurcating from the homogeneous one.

Theorem 3.1. *Assume (3.3), and that $\hat{c} > 0$ in (3.5). Then there is a curve $(\mu(\varepsilon), \nu(\varepsilon)), 0 < \varepsilon < \varepsilon_1$, emerging from (μ_H, ν_H) such that for each $(\mu, \nu) = (\mu(\varepsilon), \nu(\varepsilon))$ Equation (1.9) has a pair of asymmetric homoclinic orbits bifurcating from the in-phase homoclinic solution $(u_h(t), u_h(t))$ and $\lim_{\varepsilon \to 0^+}(\mu(\varepsilon), \nu(\varepsilon)) = (\mu_H, \nu_H)$. Each asymmetric homoclinic orbit is asymptotic to one of the equilibria which bifurcate from the homogeneous equlibrium $(u_0(\mu), u_0(\mu))$. Moreover, $\mu(\epsilon)$ solves a bifurcation equation which is expanded as*

$$H(\mu, \epsilon) = \alpha_1(\mu - \mu_H) + \frac{\beta_1}{2}\epsilon^2 + h.o.t = 0, \tag{3.6}$$

where the coefficients α_1 and β_1 are given by (3.3) and

$$\beta_1 := \int_{-\infty}^{\infty} q(t)^T D_{uu} f(u_h(t), \mu_H) \circ (p_0(t), p_0(t)) dt \quad , \tag{3.7}$$

respectively. Hence if in addition β_1 is positive (resp. negative), then $\mu(\varepsilon) - \mu_H$ is positive (resp. negative) for ε sufficiently small.

The last assertion of the theorem implies that the direction of the bifurcation curve, $\mu(\varepsilon) > \mu_H$ or $\mu(\varepsilon) < \mu_H$, can be determined by the sign of α_1 and β_1 in (3.3) and (3.7).

In Figure 4 we present numerical results where the bifurcation curve $(\mu(\varepsilon), \nu(\varepsilon))$ in the theorem was computed and continued using AUTO (Champneys et al. [1995]). Parameter values in the computation were the same as before except with $b = c = 2$ and $a = 4$. The figure indicates a branch of asymmetric (dashed curve) homoclinic solutions of (1.9) bifurcating from the symmetric (solid vertical line) homoclinic points at the point (μ_H, ν_H). Note that the theorem predicts such a bifurcation local to (μ_H, ν_H). Figure 4a clearly demonstrates that the numerically continued homoclinics away from (μ_H, ν_H) are asymmetric.

Finally, we remark that if $\hat{c} < 0$ in Theorem 3.1, asymmetric heteroclinic orbits rather than homoclinic orbits, bifurcate from the in-phase homoclinic solution. See Morita et al. [1997] for details and the proof of Theorem 3.1.

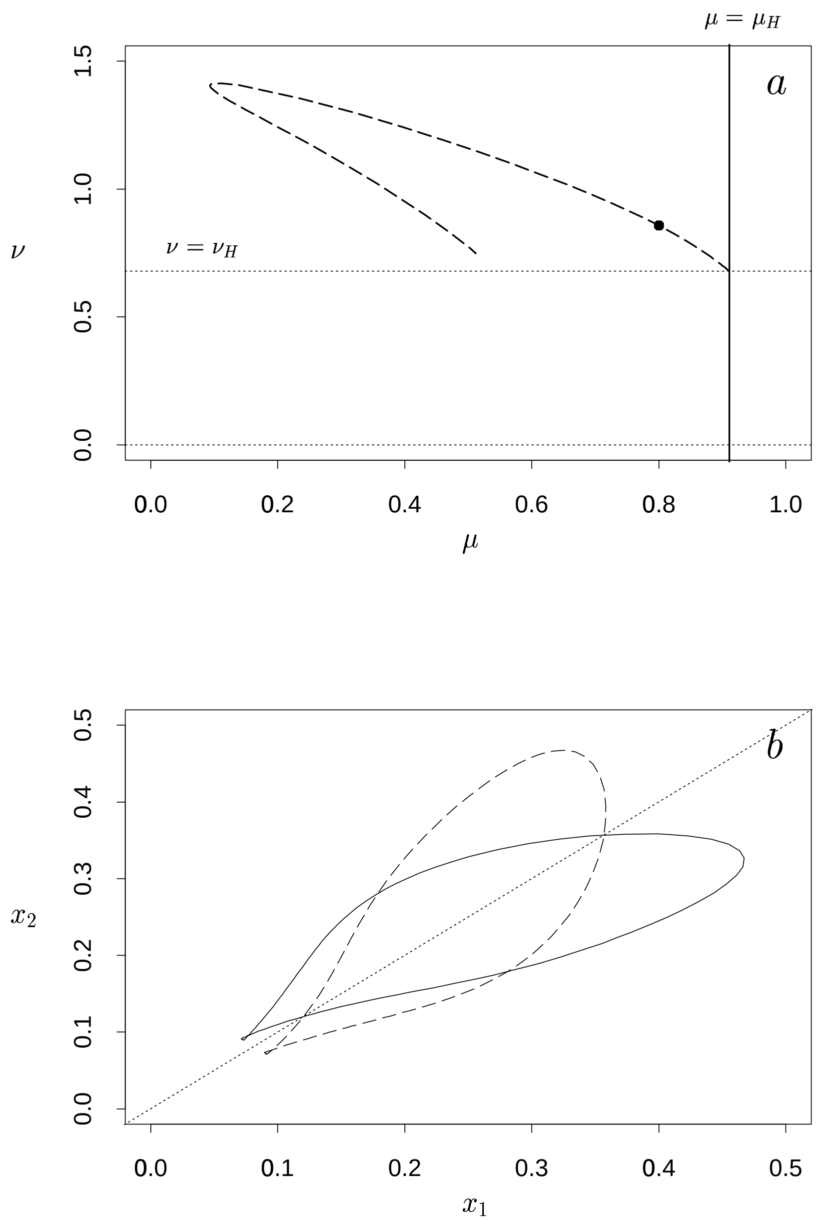

Figure 4 Bifurcation curves of symmetric and asymmetric homoclinic orbits: a) vertical line $\mu = \mu_H$ and dark dashed curve indicate parameter values where symmetric and asymmetric homoclinics exist, respectively. b) the projection of an asymmetric homoclinic orbit of (1.9) onto $x_1 - x_2$ plane for parameter values indicated by solid dot in a)

4 Discussion

We conclude with a few remarks addressing the relevance of our results. Firstly, we note that it is possible that asymmetric periodic solutions could bifurcate from the asymetric homoclinics in the theorem. An example of a similar situation occurring can be found in Lin [1996]. The stability of any such asymmetric periodic solutions would become especially relevant in the application being examined. If stable, then other periodic mechanical oscillations in muscle fibers may be induced by heterogeneities within the region (through ν).

Secondly, it is often practical to numerically continue homoclinic solutions by finding a large period periodic orbit continued from a Hopf point. For our model this procedure failed to find the asymmetric homoclinic orbit of the theorem. As pointed out in the first remark, periodic solutions may bifurcate from these asymmetric homoclinics. Thus, it may not always be possible to find all periodic motion in coupled musle fiber (and excitable cell) models by continuing periodic solutions from Hopf points. We point this out as a cautionary reminder to those researchers interested in such problems.

Finally it is a very interesting but hard problem to reveal the whole bifurcation strucure in (μ, ν) plane. Indeed, to perform it, we will not only need precise local bifurcation diagrams of all the degenerate equilibria, but also have to investigate the existence of other asymptotic behaviors such as quasi-periodic motion which have not been examined. Those will perhaps be the subject of a later study.

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