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Amitabha Bose

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SYMMETRIC AND ANTISYMMETRIC PULSES IN PARALLEL COUPLED NERVE FIBRES*

AMITABHA BOSE†

Abstract. Travelling wave solutions for equations that model two parallel coupled nerve fibres are found. The travelling wave here represents the action potential. It is shown that the introduction of weak coupling between the fibres induces either symmetry or antisymmetry of the action potentials. A symmetric pulse is a solution where both fibres fire simultaneously and the action potentials propagate locked in phase at the same wave speed along the length of each fibre; an antisymmetric pulse is a solution where one fibre fires, resulting in an action potential propagating along it, while the other remains at rest. Geometric singular perturbation theory and the exchange lemma are used to prove the existence of solutions. In addition, a technique which involves the use of differential forms for detecting transversalities of small order is introduced.

Key words. travelling wave, action potential, homoclinic, heteroclinic, singular solution, transversality, coupled fibres

AMS subject classifications. 34D15, 35K57

1. Introduction. Systems of singularly perturbed equations have long been used to successfully model the behavior of nerve impulses. Among the most important examples are the Hodgkin–Huxley equations [12]–[15] and a useful simplification of these equations known as the FitzHugh–Nagumo equations [10], [27]. The FitzHugh–Nagumo equations describe the shape and speed of a nerve impulse, or a so-called action potential, which propagates along the length of a single nerve fibre. Of natural interest is the propagation of action potentials along an array of coupled nerve fibres. For instance, in highly sensitive areas of the body such as the fingertips or tongue, the density of nerve fibres increases sharply.

Experiments of Katz and Schmitt [19]–[21] suggest that although an array of fibres physically constitutes a two- or three-dimensional medium, action potentials effectively propagate in well-defined one-dimensional paths. The preferred direction of these pulses is axial, along the length of a particular fibre, rather than between them. When adjacent fibres are simultaneously fired, the action potentials tend to behave as they would for a single fibre; i.e., the coupling has the effect of ensuring synchrony. Results of Sherman and Rinzel [30] suggest that under weak coupling, this in-phase solution may not be persistent to perturbations. As a consequence, perturbations may destroy the synchrony and lead to out-of-phase solutions.

Travelling waves represent the transport of information along one-dimensional paths. In this paper, we will be interested in existence results for travelling wave solutions of a system of equations that models voltage conduction along a pair of weakly coupled parallel, identical nerve fibres. We address the case of an array of an arbitrary, but finite, number of parallel nerve fibres in [3].

Appropriate stimulation of the nerve membrane creates an action potential which propagates along the length of the fibre. The potential is characterized by a sequence of transitions. First, when the fibre fires, the membrane depolarizes and a fast jump from a resting potential to an excited potential, called a travelling wave front, occurs. Next, a latent period ensues, following which a second fast jump occurs and the action

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 $^{^\}dagger$ Department of Mathematics, Boston University, 111 Cummington Street, Boston, Massachusetts 02215.

potential returns to near the resting state. This transition is called a travelling wave back. The mechanism which allows for the hyperpolarization is called membrane recovery. Recovery has the added effect of causing a second latent period, after which the nerve fibre returns to the resting state and becomes capable of supporting another action potential. Singularly perturbed systems capture this behavior.

When two fibres are coupled together, a relevant question to consider is whether an action potential on one fibre can induce the creation of an action potential on the other. Other important questions are the following. What effect does an action potential on one fibre have on the threshold of an adjacent fibre? How does the type of coupling, either excitatory or inhibitory, affect the propagation of voltage pulses? Does the coupling limit or increase the variety of action potentials that exist? Is the stability of relevant solutions dependent on the type of coupling?

The propagation of action potentials along a pair of fibres has been addressed by many authors. Arvanitaki [1] and Ramon and Moore [28] have conducted experimental investigations where they actually allow the fibres to touch one another. They were primarily interested in the possibility of ephaptic transmission of action potentials. Motivated by the work of Katz and Schmitt, Markin [24], [25] developed analytic models to study the problem of neighboring fibres. His results concern, among other things, changes in excitability of an adjacent fibre as an action potential passes by on another, the creation of so-called collective states, where pulses propagate individually on each fibre at a common wave speed, and the relation of collective wave speeds to uncoupled wave speeds. The specific model we use was studied by Keener [22]. In that work, he assumes that, when uncoupled, the action potential on each fibre can be described using the FitzHugh–Nagumo equations. The equations in question are

(1.1)
$$\begin{aligned} \epsilon u_{1_t} &= \epsilon^2 u_{1_{xx}} + f(u_1) - v_1 + d(u_2 - u_1), \\ \epsilon u_{2_t} &= \epsilon^2 u_{2_{xx}} + f(u_2) - v_2 + d(u_1 - u_2), \\ v_{1_t} &= (u_1 - \gamma v_1), \\ v_{2_t} &= (u_2 - \gamma v_2), \end{aligned}$$

where, for i=1,2, the variables u_i represent the voltage potential of each nerve fibre, the variables v_i are related to the recovery mechanism of the cell membrane, and f(u) is the bistable cubic which for convenience we choose to be f(u)=u(1-u)(u-a), 0 < a < 1/2. The parameter d is the coupling coefficient which is inversely proportional to resistance between the fibres. When d>0, the coupling is excitatory, and for d<0 it is inhibitory. Here $\epsilon \ll 1$ is the diffusion constant. Its smallness exaggerates the latent period between voltage transitions and introduces two time scales. The fast variables are u_i and the slow are v_i . By assumption, the coupling between adjacent fibres is electronic. The resulting current flow between them is proportional to the voltage difference between adjacent fibres. Note that when d=0 or when $u_1 \equiv u_2$, we recover two copies of the FitzHugh–Nagumo system; d=0 gives two uncoupled copies of the FitzHugh–Nagumo system, while $u_1 \equiv u_2$ gives one copy twice over. We are interested in the case where γ is small enough so that $v_i = u_i/\gamma$ and $v_i = f(u_i)$ have only (0,0) as a common solution for i=1,2. These solutions are the unique rest points of the d=0 subsystems.

For the one-fibre problem there are numerous existence results. Carpenter [5], Conley [7], Hastings [11], and Langer [23] have separately proved the existence of travelling wave pulses for $\epsilon \ll 1$. Keener [22] showed existence results for the two-fibre problem with a piecewise linear reaction term. Dockery [8] also has proved results for the two-fibre problem with a cubic nonlinearity. Other related work on coupled oscillators can be found in Somers and Kopell [31].

A solution for (1.1) of the form $(u_1, u_2, v_1, v_2) = (u_1(\xi), u_2(\xi), v_1(\xi), v_2(\xi))$ is a travelling wave where $\xi = \frac{x+\theta t}{\epsilon}$ and θ is the speed of the wave. As $\xi \to \pm \infty$, the travelling wave solutions of interest tend to the rest state of (1.1). Introducing the variable ξ , and recasting the resulting equations into a system of first-order equations by setting $u'_1 = w_1$ and $u'_2 = w_2$, we obtain

$$u'_{1} = w_{1},$$

$$w'_{1} = \theta w_{1} - f(u_{1}) + v_{1} - d(u_{2} - u_{1}),$$

$$u'_{2} = w_{2},$$

$$w'_{2} = \theta w_{2} - f(u_{2}) + v_{2} - d(u_{1} - u_{2}),$$

$$v'_{1} = \frac{\epsilon}{\theta}(u_{1} - \gamma v_{1}),$$

$$v'_{1} = \frac{\epsilon}{\theta}(u_{2} - \gamma v_{2}).$$

The mathematical object which corresponds to the earlier described physical situation is a homoclinic orbit, which is a solution to (1.2) that tends to the origin as $\xi \to \pm \infty$. We will consider all possible homoclinics that exist for d=0 and describe which solutions persist for d sufficiently small. Note that the symmetric solution, characterized by $u_1 \equiv u_2$, exists by the one-fibre results referred to above, since the coupling drops out.

We use geometric singular perturbation theory to carry out much of the analysis. At $\epsilon=0$, singular heteroclinic solutions are shown to exist for certain reduced problems. The heteroclinics connect rest points on different critical manifolds. These singular solutions are pieced together with curves on certain critical manifolds and constitute a so-called singular homoclinic orbit. A theorem of Jones and Kopell [17], which is based on the exchange lemma, is then used to conclude the existence of homoclinic solutions near the singular solutions for ϵ sufficiently small. The exchange lemma describes the behavior of tangent planes as they pass by a slow manifold. In particular, certain information about transversality of submanifolds of the $\epsilon=0$ reduced systems is exchanged during the passage near a slow manifold, and the exchange lemma quantifies this.

For d=0, there exist three possible types of homoclinic solutions. The first is a symmetric solution where both fibres fire simultaneously; i.e., the solution is phase-locked such that $u_1 \equiv u_2$. The second is an antisymmetric solution where one fibre fires while the other remains at rest. The third is an out-of-phase solution where both fibres fire concurrently, but the crest of an action potential on one fibre trails the crest of an action potential on the other fibre by a fixed distance. Within the class of out-of-phase solutions, we also will call an asymmetric solution a wave that is highly out-of-phase. The totality of all possible d=0 homoclinic solutions forms a two-dimensional family of solutions, which we denote Λ_H . For d small, we shall seek only single-pulse solutions, i.e., solutions which enter a neighborhood of the origin only when $\ell \to \pm \infty$.

One of the central results of this paper is that the introduction of weak diffusive coupling, for the most part, has the effect of forcing either symmetry or antisymmetry. Weak coupling ensures that except for the possibility of two asymmetric solutions, no other out-of-phase solutions exist in a neighborhood of Λ_H . We offer the interpretation that solutions which leave a neighborhood of Λ_H are random and are of relatively lesser importance than those which remain in a neighborhood of Λ_H .

Physically this implies that essentially only two types of behavior are seen: either both fibres simultaneously fire and the resulting action potentials propagate locked in-phase, or one fibre fires while the other must remain at rest. In other words, uncoupled pulses which initially exhibit phase differences, which may range in size from arbitrarily small to quite large, are destroyed by the introduction of weak coupling. Thus for identical fibres, this can be thought of as a mechanism for generating synchrony. Markin [25] shows an analogous result where travelling waves of initially different speeds, e.g., when $f(u_1) \neq f(u_2)$, synchronize in-phase at some common wave speed. Our results differ from those of Markin in that, due to the diffusive coupling, the wave speed for our symmetric solution coincides with the wave speeds of the individual uncoupled pulses. For his model, he shows that the wave speed of the collective pulse is slower than that of the individual pulses.

We also prove the nonexistence of certain possible multiple jump pulses that contain more than two heteroclinic jumps in their singular limits. In particular, we show that it is not possible for one fibre to remain in an excited state while the other fibre excites. This does not rule out the possibility of an excited fibre and a resting fibre switching orientations; i.e., the excited fibre returns to rest, while concurrently the resting fibre becomes excited. In fact, Bose [2] has shown that for $\epsilon=0$ in (1.2) such situations arise.

The symmetric and antisymmetric solutions are found as transverse intersections of relevant manifolds. Asymmetric solutions are found by a bifurcation argument. In this paper, we do not actually prove the existence of asymmetric homoclinic solutions. Instead, we prove only that two asymmetric travelling wave fronts exist. In [6] and [26], it is shown that if there exists a heteroclinic orbit between points A and B and also between B and C, then under certain conditions, a bifurcating heteroclinic from A to C will also exist. Here, asymmetric travelling wave fronts are shown to exist as bifurcations of pairs of antisymmetric front solutions. In particular, the asymmetric solutions are not constructed as transverse intersections of manifolds.

This paper is organized as follows. In $\S 2$, we set up the geometry of the problem and state our main existence and nonexistence theorems. We also begin the proof of nonexistence of out-of-phase waves for the $\epsilon = 0$ system. In §3, we complete the nonexistence proof by proving that the singular symmetric front and back exist as transverse intersections of relevant manifolds, thus guaranteeing their local uniqueness. Moreover, their direction of transversality is an important aspect of the stability analysis of the symmetric solution; see Bose and Jones [4]. The symmetric solution exists as an O(d) transverse intersection of certain manifolds. In general, transversalities of such a small order are difficult to analyze. We introduce a technique which uses differential forms to greatly simplify the detection of such transversalities. In § 4, we show that various antisymmetric singular fronts and backs exist as transverse intersections of relevant manifolds. We also discuss the existence of asymmetric solutions here. In § 5, we construct solutions to the slow flow, which we piece together with the heteroclinic solutions of §§ 3 and 4 to form singular homoclinic solutions. We will then be in a position to use the aforementioned theorem of Jones and Kopell to conclude the existence of real homoclinic solutions. We conclude §§ 4 and 5 with discussions on the physical aspects of the problem.

2. Geometry and main theorems. In singularly perturbed systems, the smallness of a parameter, ϵ in our case, serves to naturally demarcate two distinct regions of interest. One of the regions is governed by a fast flow and the other by a slow flow. The equations which govern the fast flow are obtained by analyzing (1.2) when $\epsilon = 0$

and are given by

(2.1)
$$\begin{aligned} u_1' &= w_1, \\ w_1' &= \theta w_1 - f(u_1) + v_1 - d(u_2 - u_1), \\ u_2' &= w_2, \\ w_2' &= \theta w_2 - f(u_2) + v_2 - d(u_1 - u_2). \end{aligned}$$

Note that v_1 and v_2 act as parameters in (2.1). Equations for the slow flow are also obtained from (1.2) and are given by

(2.2)
$$v'_1 = \epsilon (u_1 - \gamma v_1)/\theta, \\ v'_2 = \epsilon (u_2 - \gamma v_2)/\theta,$$

where $u_i = u_i(v_1, v_2)$ for i = 1, 2 and is determined by solving (2.3) and (2.4) for u_1 and u_2 . At $\epsilon = 0$, solutions to

$$(2.3) v_1 = f(u_1) + d(u_2 - u_1),$$

$$(2.4) v_2 = f(u_2) + d(u_1 - u_2)$$

define manifolds of critical points of the system (1.2). For d fixed sufficiently small, solutions of (2.3) and (2.4) projected onto the u_1-v_1 and u_2-v_2 planes look like cubics, each with two branches of negative slope. Let u_{\min} be such that $f'(u_{\min}) = 0$ and $f''(u_{\min}) > 0$. Similarly, let u_{\max} be such that $f'(u_{\max}) = 0$ and $f''(u_{\max}) < 0$. Let σ be a small positive real number independent of d. Define for i = 1, 2

$$LB_i = \{(u_1, u_2, v_1, v_2) : (2.3) \text{ and } (2.4) \text{ hold }, u_i < u_{\min} - \sigma\},\ RB_i = \{(u_1, u_2, v_1, v_2) : (2.3) \text{ and } (2.4) \text{ hold }, u_i > u_{\max} + \sigma\}.$$

Next, following Keener's terminology, we define the critical manifolds as

$$\begin{aligned} & \text{manifold} & (0) = \{(u_1, u_2, v_1, v_2) : u_1 \in LB_1, u_2 \in LB_2\}, \\ & \text{manifold} & (1) = \{(u_1, u_2, v_1, v_2) : u_1 \in LB_1, u_2 \in RB_2\}, \\ & \text{manifold} & (2) = \{(u_1, u_2, v_1, v_2) : u_1 \in RB_1, u_2 \in LB_2\}, \\ & \text{manifold} & (3) = \{(u_1, u_2, v_1, v_2) : u_1 \in RB_1, u_2 \in RB_2\}. \end{aligned}$$

This is a base 2 representation, where the left branch corresponds to a 0 and the right branch corresponds to a 1. Physically, manifold (0) represents critical points for which both fibres are at rest. Manifold (3) represents critical points for which both fibres are excited. Manifolds (1) and (2) are cases for which one fibre is at rest and the other is excited.

Heteroclinic solutions which connect rest points on different critical manifolds are called solutions to the fast flow and are obtained by analyzing (2.1). Curves which connect rest points on the same critical manifold are called solutions to the slow flow and are obtained by analyzing (2.2).

We now define the singular homoclinic solutions which we will construct and then use to create real homoclinic solutions. Let θ^* be the wave speed at which a heteroclinic connection from (0,0,0,0) to (1,0,1,0) exists for $\epsilon=0$ and d=0 in (u_1,w_1,u_2,w_2) space. Here θ^* is the same value as the wave speed of the FitzHugh–Nagumo front. Let $v^*=f(u_R)=f(u_L)$. For the FitzHugh–Nagumo equations, (u_R,v^*) and (u_L,v^*) are the points on the right and left branches of the cubic between which the $\epsilon=0$ back travelling wave exists. The symmetric singular homoclinic

orbit consists of two fast jumps between manifolds (0) and (3) interspersed with two curves on each of these slow manifolds. Thus, we call it the symmetric 0-3-0 singular homoclinic orbit. It consists of the union of the following four objects:

- 1) a front heteroclinic jump from (0,0,0,0,0,0) on manifold (0) to (1,0,1,0,0,0) on manifold (3) at the wave speed $\theta = \theta^*$ in $(u_1, w_1, u_2, w_2, v_1, v_2)$ space;
- 2) a solution of the slow flow on manifold (3) which connects (1,0,1,0,0,0) to the point $(u_R, 0, u_R, 0, v^*, v^*)$;
- 3) a back heteroclinic jump from $(u_R, 0, u_R, 0, v^*, v^*)$ on manifold (3) to $(u_L, 0, u_L, 0, v^*, v^*)$ on manifold (0) at the wave speed $\theta = \theta^*$ in $(u_1, w_1, u_2, w_2, v_1, v_2)$ space;
- 4) a solution of the slow flow on manifold (0) which connects $(u_L, 0, u_L, 0, v^*, v^*)$ to the point (0, 0, 0, 0, 0, 0).

We next describe the 0-2-0 singular solution and observe that the 0-1-0 solution is analogous since (1.2) is invariant under the interchanging of u_1 and u_2 . For $d=0,\ v_2=0$, in (u_1,w_1,u_2,w_2,v_1) space, (1,0,0,0,0) is a fixed point on manifold (2). Using the implicit function theorem, it can be shown that for each d sufficiently small, there exists a unique nearby critical point on manifold (2) given by $(\tilde{u}_{1_R}(d),0,\tilde{u}_{2_R}(d),0,0)$. Also in (u_1,w_1,u_2,w_2,v_1) space, there exist unique critical points $(u_{1_R}(d),0,u_{2_R}(d),0,v_1(d))$ and $(u_{1_L}(d),0,u_{2_L}(d),0,v_1(d))$ which are close to $(u_R,0,0,0,v^*)$ and $(u_L,0,0,0,v^*)$ on manifolds (2) and (0) respectively. For d fixed sufficiently small, the 0-2-0 singular homoclinic solution consists of the following four pieces:

- 1) a front heteroclinic jump from (0,0,0,0,0) on manifold (0) to $(\tilde{u}_{1_R}(d),0,\tilde{u}_{2_R}(d),0,0)$ on manifold (2) at the wave speed $\theta=\theta(d)$ in (u_1,w_1,u_2,w_2,v_1) space;
- 2) a solution of the slow flow on manifold (2) between $(\tilde{u}_{1_R}(d), 0, \tilde{u}_{2_R}(d), 0, 0)$ and $(u_{1_R}(d), 0, u_{2_R}(d), 0, v_1(d))$;
- 3) a back heteroclinic jump from $(u_{1_R}(d), 0, u_{2_R}(d), 0, v_1(d))$ on manifold (2) to $(u_{1_L}(d), 0, u_{2_L}(d), 0, v_1(d))$ on manifold (0) at the wave speed $\theta = \theta(d)$ in $(u_1, w_1, u_2, w_2, v_1)$ space;
- 4) a solution of the slow flow on manifold (0) between $(u_{1_L}(d), 0, u_{2_L}(d), 0, v_1(d))$ and (0, 0, 0, 0, 0).

We will prove the following existence theorem.

THEOREM 1. a) If \hat{d} is sufficiently small, then for each $0 < |d| < \hat{d}$, there exists an $\epsilon > 0$ sufficiently small such that there exists a locally unique symmetric homoclinic solution Γ_{030} to (1.2), $O(\epsilon)$ close to the 0-3-0 singular solution. Moreover the wave speed at which the solution exists is within $O(\epsilon)$ of θ^* .

b) If d is sufficiently small, then for each 0 < |d| < d, there exists an $\epsilon > 0$ sufficiently small such that there exist two antisymmetric homoclinic solutions Γ_{010} and Γ_{020} to (1.2), which are each locally unique, where Γ_{010} (Γ_{020} , respectively) is $O(\epsilon)$ close to the 0-1-0 (0-2-0, respectively) singular solution. Moreover, the wave speeds at which these solutions exist are identical and are within $O(\epsilon)$ of $\theta(d)$.

A consequence of Theorem 3, found in § 5, is that Γ_{030} , Γ_{020} , and Γ_{010} all exist as the transverse intersection of relevant manifolds and are thus locally unique.

Recall Λ_H , the two-dimensional family of d=0 homoclinic solutions. Let N_H^6 be a neighborhood of a subset of Λ_H such that it does not contain manifolds (1) or (2). Also let N_H^6 contain only 0-3-0 homoclinic solutions for d=0 which are not asymmetric; i.e., N_H^6 does not contain 0-3-0 homoclinic solutions close to the 0-1, 0-2, 1-3, and 2-3 singular solutions for d=0. The following theorem addresses the nonexistence of out-of-phase pulses that are not asymmetric.

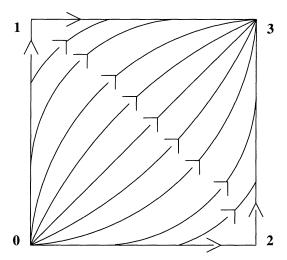


Fig. 2.1. The totality of d = 0 front heteroclinics.

THEOREM 2. If d is sufficiently small, then N_H^6 contains no homoclinic orbits from the origin to itself when $u_1 \not\equiv u_2$.

The proof of Theorem 2 will follow from Lemmas 1 and 3 below. Note that Theorem 1 does not address the question of multiple pulse/jump solutions, i.e., solutions that either pass near the origin more than once or contain more than two heteroclinic jumps in their singular limits. Dockery [8] has proved, using Lyapunov–Schmidt methods, that for each $\epsilon > 0$ sufficiently small, there exists a d sufficiently small such that a 0-1-0-2-0 and 0-2-0-1-0 solution exists. We refer the interested reader to his results.

2.1. Nonpersistence of certain out-of-phase fronts. We begin the proof of Theorem 1 by constructing solutions to the fast flow. Consider (2.1) with $v_1 = v_2 = 0$ and with the equation $\theta' = 0$ appended:

(2.5)
$$u'_{1} = w_{1}, w'_{1} = \theta w_{1} - f(u_{1}) - d(u_{2} - u_{1}), u'_{2} = w_{2}, w'_{2} = \theta w_{2} - f(u_{2}) - d(u_{1} - u_{2}), \theta' = 0,$$

These are the equations for the front part of the singular solution. When d=0, a two-dimensional family of travelling wave fronts exists which connects (0,0,0,0) to (1,0,1,0) at $\theta=\theta^*$. This family of waves is schematically depicted in Fig. 2.1. We will show that when weak coupling is introduced, only the symmetric 0-3 solution (which corresponds to the diagonal line in Fig. 2.1); the four antisymmetric 0-1, 0-2, 1-3, and 2-3 "edge" solutions; and for d>0, two highly out-of-phase asymmetric 0-3 solutions persist. For d<0, the asymmetric waves do not exist (see Figs. 2.2 and 2.3).

The critical point $(0,0,0,0,\theta)$ for (2.5) has a three-dimensional center-unstable manifold, $W^{cu}(0)$. The critical point $(1,0,1,0,\theta)$ has a three-dimensional center-stable manifold, $W^{cs}(3)$. For d=0 and $\theta=\theta^*$, the manifolds coincide, so $\dim(W^{cu}_0(0)\cap W^{cs}_0(3))=2$ where the subscript 0 refers to d=0. Since the ambient space is five-dimensional, the intersection is not transverse. Therefore when the vector field is perturbed, we expect this highly delicate situation to change.

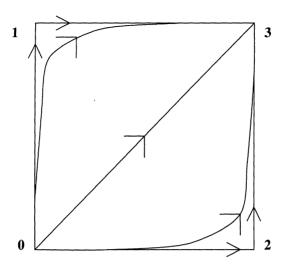


Fig. 2.2. Front heteroclinic solutions for d > 0 sufficiently small.

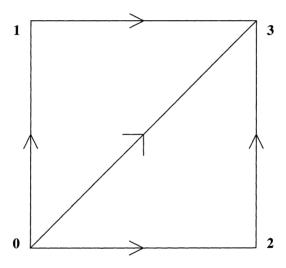


Fig. 2.3. Front heteroclinic solutions for d < 0 sufficiently small.

Restricting to $\theta = \theta^*$ and d = 0, we identify trajectories of the two-dimensional unstable manifold, $W^u(0)$, by the parameter $\alpha = 1/2 - u_2$. Note that $\alpha \in [-1/2, 1/2]$ and $\alpha < 0$ ($\alpha > 0$) above (below) the diagonal. Fix $\sigma_1 > 0$ sufficiently small. Define $K = \{\alpha : -1/2 + \sigma_1 \le \alpha \le 1/2 - \sigma_1\}$. Let M a compact subset of \mathbf{R}^2 . Consider a three-dimensional cross section to the flow defined by

$$\Sigma_1 = \{(u_1, w_1, u_2, w_2) : u_1 = 1/2, \alpha \in K, (w_1, w_2) \in M\}.$$

Note that Σ_1 is compact. For d=0 and $\theta=\theta^*$, $W^u(0)\cap W^s(3)\neq\emptyset$ and is a two-dimensional manifold. Let Γ^1_{03} be the subset of trajectories of this solution manifold which intersects Σ_1 ; i.e., Γ^1_{03} consists of the symmetric solution and out-of-phase solutions that are not asymmetric. In the following lemma, we show that only the diagonal trajectory of Γ^1_{03} persists for small d.

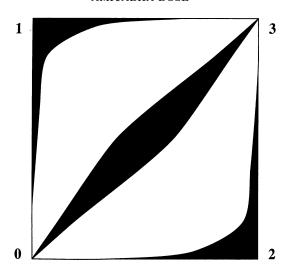


Fig. 2.4. The nonshaded regions depict the trajectories of Γ_{03}^2 .

LEMMA 1. There exists a neighborhood N_{03}^4 of Γ_{03}^1 and a d_0 sufficiently small such that if $0 < |d| < d_0$ and θ is sufficiently close to θ^* , then the only heteroclinic orbit from (0) to (3) contained in N_{03}^4 has $u_1 \equiv u_2$ and $\theta = \theta^*$. Moreover in \mathbf{R}^5 , $W^{cu}(0)$ transversely intersects $W^{cs}(3)$ at $u_1 \equiv u_2$ and $\theta = \theta^*$.

Remark. The reason we need to exclude neighborhoods of the edges of the square is that both the 0-2-3 pair and the 0-1-3 pair of heteroclinics, under certain conditions, bifurcate to produce 0-3 connections. In fact, if d>0, in § 4.1, it is shown that two asymmetric 0-3 wave fronts exist and each is locally unique. One is close to the 0-2-3, d=0 heteroclinic pair, and the other is close to the 0-1-3, d=0 heteroclinic pair.

Proof of Lemma 1. The proof of Lemma 1 has two main steps. One step is to prove that no solutions lie close to the symmetric front. This is achieved by proving that the symmetric front solution exists as a transverse intersection of $W^{cu}(0)$ and $W^{cs}(3)$ and is thus locally unique. The proof of this result is found in §3. Another step is to show that away from both the symmetric solution and the edges of the box in Fig. 2.1, there exist no out-of-phase solutions. This will be proved in Lemma 2 below, which will then conclude §2.

Consider a compact subset K_{σ_2} of K defined as follows. Fix σ_2 sufficiently small and let $K_{\sigma_2} = \{\alpha : \alpha \in K, |\alpha| \geq \sigma_2\}$. Now let

$$\Sigma_2 = \{(u_1, w_1, u_2, w_2) : u_1 = 1/2, \alpha \in K_{\sigma_2}, (w_1, w_2) \in M\}.$$

For d=0, let Γ_{03}^2 be the set of trajectories which satisfy $W_0^{cu}(0) \cap W_0^{cs}(3) \cap \Sigma_2 \neq \emptyset$. The nonshaded regions of Fig. 2.4 depict the set Γ_{03}^2 . We prove that none of these trajectories persist under perturbation.

LEMMA 2. There exists a neighborhood \tilde{N}_{03}^4 of Γ_{03}^2 and a d_f sufficiently small such that if $0 < |d| < d_f$ and θ is sufficiently close to θ^* , then $W^u(0) \cap W^s(3) \cap \Sigma_2 \cap \tilde{N}_{03}^4 = \emptyset$.

Proof of Lemma 2. Assume, without loss of generality, for solutions of the unperturbed system of (2.5) that $u_1 > u_2$; the treatment of $u_1 < u_2$ is identical. Let $q \in W_0^{cu}(0) \cap W_0^{cs}(3) \cap \Sigma_2$ such that, at $q, \xi = 0$. In a neighborhood of q, the perturbed manifolds are C^r -close to the unperturbed ones and are given by the graphs of appropriate functions. Denote anything associated with $W^{cu}(0)$ by the superscript + and

with $W^{cs}(3)$ by -. In a neighborhood of q, let $W^{cu}(0)$ and $W^{cs}(3)$ be the graphs of $(u_1, g^+(u_1, u_2, \theta, d), u_2, h^+(u_1, u_2, \theta, d), \theta)$ and $(u_1, g^-(u_1, u_2, \theta, d), u_2, h^-(u_1, u_2, \theta, d), \theta)$, respectively. Call

$$(\Delta g(u_1, u_2, \theta, d) = g^+(u_1, u_2, \theta, d) - g^-(u_1, u_2, \theta, d)), (\Delta h(u_1, u_2, \theta, d) = h^+(u_1, u_2, \theta, d) - h^-(u_1, u_2, \theta, d)).$$

Consider the function $F: \mathbf{R}^3 \to \mathbf{R}^2$ defined in a neighborhood of q and given by

$$F(u_2, \theta, d) = \begin{pmatrix} \Delta g \\ \Delta h \end{pmatrix}.$$

Since q is a point of intersection of the unperturbed manifolds, F(q) = 0. We will show that

(2.6)
$$\det D_{\theta,d}F(q) = \frac{\partial \Delta g(q)}{\partial \theta} \cdot \frac{\partial \Delta h(q)}{\partial d} - \frac{\partial \Delta h(q)}{\partial \theta} \cdot \frac{\partial \Delta g(q)}{\partial d} \neq 0.$$

The quantity det $D_{\theta,d}F(q)$ measures how $W^{cu}(0)$ and $W^{cs}(3)$ split when d is perturbed from 0.

For each $q \in W_0^{cu}(0) \cap W_0^{cs}(3) \cap \Sigma_2$, there corresponds a unique value of α , θ , and d. In particular, $\theta = \theta^*$, d = 0, and we will call $\alpha = \alpha^*$ for some chosen q. Assume (2.6) for a moment. Then by the implicit function theorem there exists a u_2 neighborhood, U, of α^* and a (θ, d) neighborhood, V, of $(\theta^*, 0)$ such that $\alpha^* \in U$, $(\theta^*, 0) \in V$, and for each $u_2 \in U$ there exists a unique $(\theta, d) \in V$ such that F = 0, where 0 denotes a two vector. Since for each u_2 near α^* , $(\theta, d) = (\theta^*, 0)$ implies F = 0, this must be the unique value of θ and d prescribed by the implicit function theorem. In other words, there are no other values of θ and d in V for which 0-3 heteroclinic connections exist.

We can extend this argument to all of the set Σ_2 . For each $\alpha \in K_{\sigma_2}$ there exist both u_2 and (θ, d) neighborhoods. Let us call these neighborhoods $\{U_i\}$ and $\{V_i\}$. Recall that K_{σ_2} is compact. Choose a finite number of sets U_1, U_2, \ldots, U_n that cover K_{σ_2} . We obtain associated neighborhoods V_1, V_2, \ldots, V_n . Each of these V neighborhoods has a radius for, in particular, the d component which we call $d_{r_1}, d_{r_2}, \ldots, d_{r_n}$. Now choose $d_f = \min\{d_{r_1}, d_{r_2}, \ldots, d_{r_n}\}$. Thus for all $0 < |d| < d_f$ the result of Lemma 2 holds.

We now show that (2.6) is true. Append d' = 0 to (2.5) and use the equation of variations:

(2.7)
$$u'_{1} = w_{1},
w'_{1} = \theta w_{1} - f(u_{1}) - d(u_{2} - u_{1}),
u'_{2} = w_{2},
w'_{2} = \theta w_{2} - f(u_{2}) - d(u_{1} - u_{2}),
\theta' = 0,
d' = 0.$$

The equation of variations associated with (2.7) is

$$\delta u_1' = \delta w_1,$$

$$\delta w_1' = \theta \delta w_1 + w_1 \delta \theta - \frac{\partial f_1}{\partial u_1} \delta u_1 - d(\delta u_2 - \delta u_1) - (u_2 - u_1) \delta d,$$

$$\delta u_2' = \delta w_2,$$

$$\delta w_2' = \theta \delta w_2 + w_2 \delta \theta - \frac{\partial f_2}{\partial u_2} \delta u_2 - d(\delta u_1 - \delta u_2) - (u_1 - u_2) \delta d,$$

$$\delta \theta' = 0,$$

$$\delta d' = 0.$$

We consider solutions to (2.8) that satisfy initial conditions associated with the center-stable and center-unstable manifolds. Note that the vector field of (2.7) is a tangent vector to both W^{cu} and W^{cs} , so it solves (2.8). Let

$$X_1(\xi) = (w_1, w_1', w_2, w_2', 0, 0),$$

$$X_2^{\pm}(\xi) = (\delta u_{12}^{\pm}, \delta w_{12}^{\pm}, \delta u_{22}^{\pm}, \delta w_{22}^{\pm}, 1, 0),$$

$$X_3^{\pm}(\xi) = (\delta u_{13}^{\pm}, \delta w_{13}^{\pm}, \delta u_{23}^{\pm}, \delta w_{23}^{\pm}, 0, 1)$$

be solutions to (2.8) which satisfy the following initial conditions

$$X_{1}(0) = (w_{1}, \theta^{*}w_{1} - f(u_{1}), w_{2}, \theta^{*}w_{2} - f(u_{2}), 0, 0),$$

$$X_{2}^{\pm}(0) = \left(0, \frac{\partial}{\partial \theta}g^{\pm}(q), 0, \frac{\partial}{\partial \theta}h^{\pm}(q), 1, 0\right),$$

$$X_{3}^{\pm}(0) = \left(0, \frac{\partial}{\partial d}g^{\pm}(q), 0, \frac{\partial}{\partial 0}dh^{\pm}(q), 0, 1\right).$$

Each of the coordinates $\delta u_1, \delta u_2$, etc. can be viewed as 1-forms. A differential form is a skew-symmetric linear functional on the cotangent bundle of a manifold. Thus 1-forms act on tangent vectors and take values in \mathbf{R} . Similarly, n-forms act on n-dimensional tangent spaces and take values in \mathbf{R} . We will be interested in 2-forms. The value of a 2-form acting on a plane will be given, up to normalization, by the area of the projection of that plane onto the plane of coordinates which constitute the 2-form.

The value of a 2-form is assigned as follows. The 2-form $P_{ij}^{lk} = i \wedge j(X_l, X_k)$ equals the 2×2 subdeterminant formed by the *i*th and *j*th components of the solutions X_l and X_k . For example, $P_{u_1w_1}^{12} = \delta w_{12} \cdot w_1 - \delta u_{12} \cdot w_1'$. These 2-forms are elements of the second exterior power of \mathbf{R}^6 , $\bigwedge^2 \mathbf{R}^6$. There are 15 linearly independent such 2-forms. Evolution equations for each are obtained using the product rule. For example, $P'_{u_1w_1} = \delta u'_1 \wedge \delta w_1 + \delta u_1 \wedge \delta w'_1$. However, in order to establish (2.6), we need only study $P_{u_1w_1}$ and $P_{u_2w_2}$ since

$$P_{u_1w_1}^{12^{\pm}}(0) = w_1 \cdot \frac{\partial}{\partial \theta} g^{\pm}(q), \qquad P_{u_2w_2}^{12^{\pm}}(0) = w_2 \cdot \frac{\partial}{\partial \theta} h^{\pm}(q),$$

$$P_{u_1w_1}^{13^{\pm}}(0) = w_1 \cdot \frac{\partial}{\partial d} g^{\pm}(q), \qquad P_{u_2w_2}^{13^{\pm}}(0) = w_2 \cdot \frac{\partial}{\partial d} h^{\pm}(q),$$

which implies

(2.9)
$$\Delta P_{u_1w_1}^{12}(0) = w_1 \cdot \frac{\partial}{\partial \theta} \Delta g(q), \qquad \Delta P_{u_2w_2}^{12}(0) = w_2 \cdot \frac{\partial}{\partial \theta} \Delta h(q),$$
$$\Delta P_{u_1w_1}^{13}(0) = w_1 \cdot \frac{\partial}{\partial d} \Delta g(q), \qquad \Delta P_{u_2w_2}^{13}(0) = w_2 \cdot \frac{\partial}{\partial d} \Delta h(q).$$

Note that w_1 and w_2 are strictly greater then zero along the front of both d = 0 subsystems, so in order to find the sign of the various right-hand sides in (2.9), we need only find the sign of the left-hand sides.

The equations of interest are

(2.10)
$$P'_{u_1w_1} = \theta P_{u_1w_1} + w_1 P_{u_1\theta} + dP_{u_2u_1} - (u_2 - u_1) P_{u_1d},$$

$$(2.11) P'_{u_2w_2} = \theta P_{u_2w_2} + w_2 P_{u_2\theta} - dP_{u_2u_1} - (u_1 - u_2) P_{u_2d}.$$

We first find $\frac{\partial}{\partial \theta} \Delta g(q)$. If we evaluate the relevant 2-forms at $X_1(\xi)$ and $X_2(\xi)$, we obtain $P_{u_1\theta}^{12^{\pm}} \equiv w_1$ and $P_{u_1d}^{12^{\pm}} \equiv 0$. At $d = 0, \theta = \theta^*$, (2.10) becomes

$$P_{u_1w_1}^{12'} = \theta^* P_{u_1w_1}^{12} + w_1^2.$$

Now, whenever $P_{u_1w_1}^{12}=0$, we have $P_{u_1w_1}^{12'}=w_1^2>0$. Moreover as $\xi\to \mp\infty$, $P_{u_1w_1}^{12^\pm}\to 0$ since they contain no vectors in the θ direction. This can also be seen by noting that the vector field equals 0 at $\pm \infty$. This implies $P_{u_1w_1}^{12^+} > 0$ and $P_{u_1w_1}^{12^-} < 0$ for all ξ . This then implies $\Delta P_{u_1w_1}^{12}(\xi) > 0$. Finally, it follows that

$$\frac{1}{w_1} \cdot \Delta P^{12}_{u_1 w_1}(0) = \frac{\partial}{\partial \theta} \Delta g(q) > 0.$$

Using $P_{u_2w_2}^{12}$, the calculation for $\frac{\partial}{\partial \theta}\Delta h(q) > 0$ is identical to the above. Now evaluate the 2-forms at $X_1(\xi)$ and $X_3(\xi)$:

$$P_{u_1\theta}^{13^{\pm}} \equiv 0, \qquad P_{u_2\theta}^{13^{\pm}} \equiv 0,$$
 $P_{u_1d}^{13^{\pm}} \equiv w_1, \qquad P_{u_2d}^{13^{\pm}} \equiv w_2$

At d = 0, $\theta = \theta^*$, (2.10) and (2.11) become

$$(2.12) P_{u_1w_1}^{13'} = \theta^* P_{u_1w_1}^{13} - w_1(u_2 - u_1),$$

(2.12)
$$P_{u_1w_1}^{13'} = \theta^* P_{u_1w_1}^{13} - w_1(u_2 - u_1),$$
(2.13)
$$P_{u_2w_2}^{13'} = \theta^* P_{u_2w_2}^{13} - w_2(u_1 - u_2).$$

Whenever $P_{u_1w_1}^{13} = 0$, we have that $P_{u_1w_1}^{13'} = -w_1(u_2 - u_1) > 0$, since $u_1(\xi) > u_2(\xi)$ for all ξ , by assumption, for the uncoupled system. Also whenever $P_{u_2w_2}^{13} = 0$, $P_{u_2w_2}^{13'} = -w_2(u_1 - u_2) < 0$. Noting, as before, that $P_{u_1w_1}^{13^{\pm}}$ and $P_{u_2w_2}^{13^{\pm}}$ tend to 0 as $\xi \to \mp \infty$ we obtain $P_{u_1w_1}^{13^{-}} < 0$, $P_{u_1w_1}^{13^{+}} > 0$, $P_{u_2w_2}^{13^{-}} > 0$ and $P_{u_2w_2}^{13^{+}} < 0$ for all ξ . This implies

$$\begin{split} \frac{1}{w_1} \cdot \Delta P^{13}_{u_1 w_1}(0) &= \frac{\partial}{\partial d} \Delta g(q) > 0, \\ \frac{1}{w_2} \cdot \Delta P^{13}_{u_2 w_2}(0) &= \frac{\partial}{\partial d} \Delta h(q) < 0. \end{split}$$

Substituting into the right-hand side of (2.6), we obtain det $D_{\theta,d}F(q) \neq 0$, which proves Lemma 2.

3. Transversality of symmetric solutions. We now turn our attention to proving that no solutions lie close to the symmetric front solution. This will be achieved by proving that the symmetric solution can be constructed as the transverse intersection of $W^{cu}(0)$ and $W^{cs}(3)$ when $d \neq 0$, but small. The transversality will be in terms of θ and is an O(d) transversality. In particular, when d=0, while $W^{cu}(0)$ and $W^{cs}(3)$ continue to intersect, they no longer do so transversely.

In what follows, fix $d \neq 0$ but sufficiently small. Choose $q \in W^{cu}(0) \cap W^{cs}(3)$, and without loss of generality take q to be the point along the solution where $\xi = 0$. $T_qW^{cu}(0)$, the tangent space of $W^{cu}(0)$ at q, is three-dimensional. Along the solution, at $\theta = \theta^*$, $u_1 = u_2$, $\xi = 0$, the following three vectors span $T_q W^{cu}(0)$.

$$\begin{pmatrix}
0, & \frac{\partial}{\partial \theta}g^{+}(q), & 0, & \frac{\partial}{\partial \theta}h^{+}(q), & 1
\end{pmatrix},$$

$$\begin{pmatrix}
1, & \frac{\partial}{\partial u_{1}}g^{+}(q), & 0, & \frac{\partial}{\partial u_{1}}h^{+}(q), & 0
\end{pmatrix},$$

$$\begin{pmatrix}
0, & \frac{\partial}{\partial u_{0}}g^{+}(q), & 1, & \frac{\partial}{\partial u_{0}}h^{+}(q), & 0
\end{pmatrix}.$$

Similarly the vectors

$$\begin{pmatrix}
0, & \frac{\partial}{\partial \theta}g^{-}(q), & 0, & \frac{\partial}{\partial \theta}h^{-}(q), & 1
\end{pmatrix},$$

$$\begin{pmatrix}
1, & \frac{\partial}{\partial u_{1}}g^{-}(q), & 0, & \frac{\partial}{\partial u_{1}}h^{-}(q), & 0
\end{pmatrix},$$

$$\begin{pmatrix}
0, & \frac{\partial}{\partial u_{2}}g^{-}(q), & 1, & \frac{\partial}{\partial u_{2}}h^{-}(q), & 0
\end{pmatrix}$$

span $T_qW^{cs}(3)$. Denote by R the 6×5 matrix formed by placing the above vectors as rows of R, i.e.,

$$R = \begin{pmatrix} 0 & \frac{\partial}{\partial \theta} g^{+}(q) & 0 & \frac{\partial}{\partial \theta} h^{+}(q) & 1 \\ 1 & \frac{\partial}{\partial u_{1}} g^{+}(q) & 0 & \frac{\partial}{\partial u_{1}} h^{+}(q) & 0 \\ 0 & \frac{\partial}{\partial u_{2}} g^{+}(q) & 1 & \frac{\partial}{\partial u_{2}} h^{+}(q) & 0 \\ 0 & \frac{\partial}{\partial \theta} g^{-}(q) & 0 & \frac{\partial}{\partial \theta} h^{-}(q) & 1 \\ 1 & \frac{\partial}{\partial u_{1}} g^{-}(q) & 0 & \frac{\partial}{\partial u_{1}} h^{-}(q) & 0 \\ 0 & \frac{\partial}{\partial u_{2}} g^{-}(q) & 1 & \frac{\partial}{\partial u_{2}} h^{-}(q) & 0 \end{pmatrix}.$$

 $W^{cu}(0)$ will intersect $W^{cs}(3)$ transversely if $T_qW^{cu}(0) \oplus T_qW^{cs}(3) = \mathbf{R}^5$. Thus $W^{cu}(0)$ will intersect $W^{cs}(3)$ transversely if the rank of R is equal to 5. Now consider the 5×5 matrix formed by dropping the last row from R. Call this new matrix T_F . To show that the rank of R is 5, it suffices to show the determinant of T_F is different from zero. After some elementary row operations, we obtain

(3.1)
$$\det T_F(d) = \frac{\partial \Delta h}{\partial \theta}(q) \cdot \frac{\partial \Delta g}{\partial u_1}(q) - \frac{\partial \Delta g}{\partial \theta}(q) \cdot \frac{\partial \Delta h}{\partial u_1}(q).$$

For the uncoupled wave, $\det T_F(0)=0$, since the tangent vectors along the solution from the stable and unstable manifolds are identical. Thus $\frac{\partial}{\partial u_1}\Delta g(q)=\frac{\partial}{\partial u_1}\Delta h(q)=0$.

We are interested in the case of d small. Since $W^{cu}(0)$ and $W^{cs}(3)$ depend smoothly on d, we can expand $\det T_F$ in a Taylor series about d=0 to obtain

(3.2)
$$\det T_F(d) = \det T_F(0) + \frac{\partial}{\partial d} \det T_F(0) \cdot d + O(d^2).$$

Therefore if

$$(3.3) \qquad \frac{\partial}{\partial d} \left[\frac{\partial \Delta h}{\partial \theta}(q) \cdot \frac{\partial \Delta g}{\partial u_1}(q) - \frac{\partial \Delta g}{\partial \theta}(q) \cdot \frac{\partial \Delta h}{\partial u_1}(q) \right] \neq 0,$$

then $\det T_F \neq 0$. Suppress the dependence on q to obtain

$$\frac{\partial}{\partial d} \left[\frac{\partial \Delta h}{\partial \theta} \cdot \frac{\partial \Delta g}{\partial u_1} - \frac{\partial \Delta g}{\partial \theta} \cdot \frac{\partial \Delta h}{\partial u_1} \right] = \frac{\partial}{\partial d} \frac{\partial \Delta h}{\partial \theta} \cdot \frac{\partial \Delta g}{\partial u_1} + \frac{\partial \Delta h}{\partial \theta} \left(\frac{\partial}{\partial d} \frac{\partial \Delta g}{\partial u_1} \right) - \left(\frac{\partial}{\partial d} \frac{\partial \Delta g}{\partial \theta} \cdot \frac{\partial \Delta h}{\partial u_1} + \frac{\partial \Delta g}{\partial \theta} \left(\frac{\partial}{\partial d} \frac{\partial \Delta h}{\partial u_1} \right) \right).$$
(3.4)

As mentioned above, at the point q, $\frac{\partial}{\partial u_1} \Delta g = \frac{\partial}{\partial u_1} \Delta h = 0$. Thus the first and third terms of (3.4) are equal to zero. Also by symmetry it is obvious that $\frac{\partial}{\partial \theta} \Delta g = \frac{\partial}{\partial \theta} \Delta h$. In $\S 2$, these terms were shown to be greater than zero. Thus

(3.5)
$$\frac{\partial}{\partial d} \det T_F(0) = \frac{\partial \Delta g}{\partial \theta} \left[\frac{\partial}{\partial d} \frac{\partial}{\partial u_1} (\Delta g - \Delta h) \right].$$

Use smoothness of the manifolds to switch the order of differentiation to obtain

$$\frac{\partial}{\partial d} \frac{\partial}{\partial u_1} (\Delta g - \Delta h) = \frac{\partial}{\partial u_1} \frac{\partial}{\partial d} (\Delta g - \Delta h).$$

Differentiate both sides of the last two equations of (2.9) with respect to u_1 to obtain

(3.6)
$$\frac{\partial}{\partial u_1} \Delta P_{u_1 w_1}^{13}(0) = w_1 \cdot \frac{\partial}{\partial u_1} \frac{\partial \Delta g(q)}{\partial d},$$

(3.7)
$$\frac{\partial}{\partial u_1} \Delta P_{u_2 w_2}^{13}(0) = w_2 \cdot \frac{\partial}{\partial u_1} \frac{\partial \Delta h(q)}{\partial d}$$

Next differentiate (2.12) and (2.13) with respect to u_1 and switch the order of differentiation to obtain the following evolution equations for $\frac{\partial}{\partial u_1} P_{u_1 w_1}^{13}$ and $\frac{\partial}{\partial u_1} P_{u_2 w_2}^{13}$:

$$\begin{split} &\left(\frac{\partial}{\partial u_1}P^{13}_{u_1w_1}\right){}'=\theta^\star\left(\frac{\partial}{\partial u_1}P^{13}_{u_1w_1}\right)+w_1,\\ &\left(\frac{\partial}{\partial u_1}P^{13}_{u_2w_2}\right){}'=\theta^\star\left(\frac{\partial}{\partial u_1}P^{13}_{u_2w_2}\right)-w_2. \end{split}$$

Note that $\frac{\partial}{\partial u_1} P_{u_1 w_1}^{13} = 0$ implies $(\frac{\partial}{\partial u_1} P_{u_1 w_1}^{13})' = w_1 > 0$ and $\frac{\partial}{\partial u_1} P_{u_2 w_2}^{13} = 0$ implies $(\frac{\partial}{\partial u_1} P_{u_2 w_2}^{13})' = w_2 < 0$. Furthermore, $\frac{\partial}{\partial u_1} P_{u_i w_i}^{13^{\pm}} \to 0$ as $\xi \to \mp \infty$ for i = 1, 2. This implies $\frac{\partial}{\partial u_1} P_{u_1 w_1}^{13+}(\xi) > 0$, $\frac{\partial}{\partial u_1} P_{u_1 w_1}^{13-}(\xi) < 0$, $\frac{\partial}{\partial u_1} P_{u_2 w_2}^{13+}(\xi) < 0$, and $\frac{\partial}{\partial u_1} P_{u_2 w_2}^{13-}(\xi) > 0$ for all ξ . Thus $\frac{\partial}{\partial u_1} \Delta P_{u_1 w_1}^{13}(0) > 0$, and $\frac{\partial}{\partial u_1} \Delta P_{u_2 w_2}^{13}(0) < 0$.

Along the symbol solution, $u_1 \equiv u_2$, which implies $w_1 \equiv w_2$. Therefore by subtracting $(2, \xi)$ and by factoring a symbol string $u_1 = u_2$.

subtracting (3.6) and (3.7) and by factoring a w_1 term, we obtain

$$(3.8) w_1 \cdot \frac{\partial}{\partial u_1} \left[\frac{\partial}{\partial d} (\Delta g - \Delta h)(q) \right] = \frac{\partial}{\partial u_1} (\Delta P_{u_1 w_1}^{13} - \Delta P_{u_2 w_2}^{13})(0) > 0.$$

Last, by (3.5), it follows that $\frac{\partial}{\partial d} \det T(0) > 0$, which implies $\det T_F(d) \neq 0$ for d sufficiently small. Therefore the rank of the matrix R is 5, which implies that $W^{cu}(0)$ transversely intersects $W^{cs}(3)$.

Denote by d_e the size of d for which the O(d) term is dominant in the above Taylor expansion. Choose $d_0 = \min\{d_f, d_e\}$. Now for all $0 < |d| < d_0$ the result of Lemma 1 holds. This concludes the proof of Lemma 1.

Remark. In both Lemmas 1 and 2, we have not required that d be positive. Indeed the results established hold for d both positive and negative. However, since $\det T_F(d) = \beta d + O(d^2)$ where $\beta > 0$, it is important to note that a change in the sign of the coupling implies a change in the sign of $\det T_F$. This has an important consequence for the stability of the symmetric solution. For further details see Bose and Jones [4].

3.1. Back travelling waves. We now state the analogous transversality and nonpersistence results for back travelling waves. Such waves are heteroclinic orbits which start at $-\infty$ on manifold (3) and end up on manifold (0) at $+\infty$. Theorem 3, which is used to create $\epsilon \neq 0$ homoclinics, requires that the singular homoclinic solution contain heteroclinic jumps which all occur at the same wave speed. We have established that the wave speed of the symmetric front is $\theta = \theta^*$. To achieve the same speed for the back, it is necessary that the jump corresponding to the back occurs at appropriate values of v_1 and v_2 along manifolds (3) and (0). In the one-fibre problem, this occurs at $v = v^*$. In the present situation, because of the diffusive coupling, i.e., because $u_1 \equiv u_2$ renders two copies of the one-fibre problem, in order to have $\theta = \theta^*$, it is also necessary that $v_1 = v_2 = v^*$.

The equations for the back restricted to $\theta = \theta^*$ and $v = v_1 = v_2$ are

(3.9)
$$u'_{1} = w_{1}, w'_{1} = \theta^{*}w_{1} - f(u_{1}) + v - d(u_{2} - u_{1}), u'_{2} = w_{2}, w'_{2} = \theta^{*}w_{2} - f(u_{2}) + v - d(u_{1} - u_{2}), v' = 0.$$

The critical point $(u_R, 0, u_R, 0, v^*)$ has a three-dimensional $W^{cu}(3)$, and the critical point $(u_L, 0, u_L, 0, v^*)$ has a three-dimensional $W^{cs}(0)$. As before, for d = 0, dim $(W_0^{cu}(3) \cap W_0^{cs}(0)) = 2$, which in \mathbf{R}^5 is not a transverse intersection. Analogous to Σ_1 , let Σ_3 be a three-dimensional cross section to this solution manifold. Also let Γ_{30}^1 be the subset of trajectories which intersects Σ_3 . The counterpart to Lemma 1 appropriate for the back is the following lemma.

LEMMA 3. There exists a neighborhood N_{30}^4 of Γ_{30}^1 and a d_1 sufficiently small such that if $0 < |d| < d_1$ and v is sufficiently close to v^* , then the only heteroclinic orbit from (3) to (0) contained in N_{30}^4 has $u_1 \equiv u_2$ and $v = v^*$. Moreover in \mathbb{R}^5 , $W^{cu}(3)$ transversely intersects $W^{cs}(0)$ at $u_1 \equiv u_2$ and $v = v^*$.

We omit the proof of Lemma 3 since it is similar to that of Lemma 1. We do note that the transversality of the front with respect to the parameter θ has been exchanged for transversality of the back with respect to the parameter v. We also remark that analogous to $\det T_F(d)$, there corresponds $\det T_B(d)$ which is a function associated with the transversality of $W^{cu}(3)$ and $W^{cs}(0)$. In particular, for d sufficiently small, $\det T_B(d) = \nu d + O(d^2)$, where $\nu > 0$. For more details see [2].

Imbed N_{03}^4 and N_{30}^4 in ${\bf R^6}$ and call the resulting neighborhoods N_{03}^6 and N_{30}^6 , respectively. In Theorem 2, the neighborhood N_H^6 can now be taken as the union of

 N_{03}^6 , N_{30}^6 , manifold (0), and manifold (3). Together, Lemmas 1 and 3 prove Theorem 2, thus proving the nonexistence of out-of-phase pulses that are not asymmetric.

4. Antisymmetric and asymmetric heteroclinics. In §§ 2 and 3, we showed that, excluding neighborhoods of the edges of Fig. 2.1, the only 0-3, d=0 heteroclinic solution which persists for small d is the symmetric one. We next show that the eight antisymmetric 0-1, 0-2, 1-3, 2-3, 1-0, 2-0, 3-1, and 3-2 heteroclinics persist under perturbation. Recall that antisymmetric solutions represent the situation where one fibre fires while the other remains at rest. Concurrently, we will show that near the edges of the box, for d>0 sufficiently small, there exist exactly two 0-3 asymmetric fronts. One of these solutions lies O(d) close to the 0-1-3, d=0 heteroclinic pair, and the other lies O(d) close to the 0-2-3, d=0 heteroclinic pair. The asymmetric solutions will be obtained by using the theory of Chow, Deng, and Terman [6], which is applicable to situations such as ours. It should be noted that McCord and Mischaikow [26] also address situations such as ours. The analysis will show that the wave speeds of the antisymmetric and asymmetric solutions differ not only from one another but also from the symmetric solution. Thus it will be possible to piece together only certain singular homoclinic solutions for use in Theorem 3.

Specifically, we next construct the 0-2 and 2-0 heteroclinic jumps. It is of importance that we can construct both solutions, using the same values of θ and d, as transverse intersections of appropriate manifolds. By symmetry considerations, results for the 0-1 and 1-0 solutions will also follow. The system of equations under consideration is

$$u'_{1} = w_{1},$$

$$w'_{1} = \theta w_{1} - f(u_{1}) + v_{1} - d(u_{2} - u_{1}),$$

$$u'_{2} = w_{2},$$

$$w'_{2} = \theta w_{2} - f(u_{2}) - d(u_{1} - u_{2}),$$

$$v'_{1} = 0,$$

$$\theta' = 0.$$

We first prove the transversality of the 0-2 heteroclinic at d = 0. The calculations are quite similar to earlier ones, so we omit most of the details.

LEMMA 4. In $(u_1, w_1, u_2, w_2, \theta)$ space, for d = 0, $W^{cu}(0, 0, 0, 0, \theta)$ transversely intersects $W^{cs}(1, 0, 0, 0, \theta)$ at $\theta = \theta^*$.

Proof of Lemma 4. Consider (4.1) with $v_1=0$ and no $v_1'=0$ equation. When d=0, the subsystems uncouple. In effect, there are no dynamics in the u_2-w_2 subsystem. The saddle structure at (0,0) of this subsystem gets carried by the flow and persists for d small. Let $q \in W^{cu}(0) \cap W^{cs}(2)$. In a neighborhood of q let $W^{cu}(0)$ be given by the graph of $(u_1, m^+(u_1, \theta), u_2, n^+(u_2, \theta), \theta)$. Also let $W^{cs}(2)$ be the graph of $(u_1, m^-(u_1, \theta), u_2, n^-(u_2, \theta), \theta)$. $T_q W^{cu}(0)$ is spanned by the following three vectors:

$$\left(1, \frac{\partial}{\partial u_1} m^+(q), 0, 0, 0\right),$$

$$\left(0, \frac{\partial}{\partial \theta} m^+(q), 0, 0, 1\right),$$

$$\left(0, 0, 1, \lambda_u, 0\right).$$

Similarly $T_q W^{cs}(2)$ is spanned by

$$\left(1, \frac{\partial}{\partial u_1} m^-(q), 0, 0, 0\right),$$

$$\left(0, \frac{\partial}{\partial \theta} m^-(q), 0, 0, 1\right),$$

$$\left(0, 0, 1, \lambda_s, 0\right),$$

where $\lambda_u = \frac{\theta}{2} + \frac{1}{2}\sqrt{\theta^2 + 4a}$, $\lambda_s = \frac{\theta}{2} - \frac{1}{2}\sqrt{\theta^2 + 4a}$ correspond to the unstable and stable eigenvalues on manifold (0) for the $u_2 - w_2$ subsystem.

Form the 6×5 matrix by using the above vectors as rows. Drop the first row and call the resulting matrix T_E . Then after some easy manipulations

(4.2)
$$\det T_E = \frac{\partial}{\partial \theta} \Delta m \cdot (\lambda_u - \lambda_s).$$

Since $\lambda_u \neq \lambda s$ and $\frac{\partial}{\partial \theta} \Delta m > 0$, det $T_E \neq 0$, which implies that $W^{cu}(0)$ intersects $W^{cs}(2)$ transversely.

Remarks. (1) This is an example of an O(1) transversality. Note that it differs fundamentally from the transversality of the symmetric solutions.

(2) By symmetry, the above proof can be used to prove the existence of 0-1, 2-3, and 1-3 heteroclinics.

Let Γ_{02} denote the 0-2 heteroclinic at d=0. A direct consequence of Lemma 4 is the following corollary.

COROLLARY 1. There exists a neighborhood N_{02}^4 of Γ_{02} such that if d is sufficiently small and θ is sufficiently close to θ^* , then there exists a unique heteroclinic solution in N_{02}^4 which connects the rest point (0,0,0,0) to $(\tilde{u}_{1_R}(d),0,\tilde{u}_{2_R}(d),0)$. Moreover in \mathbf{R}^5 , $W^{cu}(0,0,0,0,\theta)$ transversely intersects $W^{cs}(\tilde{u}_{1_R}(d),0,\tilde{u}_{2_R}(d),0,\theta)$ at $\theta=\theta(d)$.

The same procedure can be applied to find heteroclinics along the back of each individual subsystem. Recall that $v^* = f(u_L) = f(u_R)$ is the value at which the 2-0 heteroclinic exists for d = 0.

LEMMA 5. In $(u_1, w_1, u_2, w_2, v_1)$ space, for d = 0, $W^{cu}(u_R, 0, 0, 0, v_1)$ transversely intersects $W^{cs}(u_L, 0, 0, 0, v_1)$ at $v_1 = v^*$.

The proof of Lemma 4 carries through for this case with the parameter v_1 replacing θ . Also note that here $\lambda_u = \theta/2 + \frac{1}{2}\sqrt{\theta^2 - 4f'(u_R)}$, $\lambda_s = \theta/2 - \frac{1}{2}\sqrt{\theta^2 - 4f'(u_L)}$. As in the remarks following Lemma 4, this proof can be used to show the existence of 1-0, 3-2, and 3-1 heteroclinics.

Let Γ_{20} denote the 2-0 heteroclinic at d=0. A direct consequence of Lemma 5 is the following corollary.

COROLLARY 2. There exists a neighborhood N_{20}^4 of Γ_{20} such that if d is sufficiently small and $v_1(d)$ is sufficiently close to v^* , then there exists a unique heteroclinic solution in N_{02}^4 which connects the rest point $(u_{1_R}(d), 0, u_{2_R}(d), 0, v_1(d))$ to $(u_{1_L}(d), 0, u_{2_L}(d), 0, v_1(d))$. Moreover, $W^{cu}(u_{1_R}(d), 0, u_{2_R}(d), 0, v_1)$ transversely intersects $W^{cs}(u_{1_L}(d), 0, u_{2_L}(d), 0, v_1)$ in \mathbf{R}^5 at $v_1 = v_1(d)$.

We next show that the 0-2 front and the 2-0 back can be constructed at the same wave speed. We know that $W^{cu}(0) \cap W^{cs}(2)$ at d=0. This transversality is with respect to the parameter θ . Also at d=0, $W^{cu}(2) \cap W^{cs}(0)$ with respect to v_1 . Essentially we want to solve for θ and v_1 simultaneously as functions of d. We use the

implicit function theorem and the transversality results of Lemmas 4 and 5 restated in the context of distance functions to achieve this.

We first form the distance function for the 0-2 connection along the front using the notation of [6]. At d=0, $W^u(0)$ is two-dimensional, as is $W^s(2)$. Note that both W^u and W^s depend smoothly on d and θ . Choose a three-dimensional cross section to the flow as $\Sigma_4 = \{u_1 = 1/2\}$. Therefore dim $(W^u \cap \Sigma_4) = 1$ and dim $(W^s \cap \Sigma_4) = 1$. Let $M^u(\theta, d)$ and $M^s(\theta, d)$ be connected components of $W^u \cap \Sigma_4$ and $W^s \cap \Sigma_4$, respectively, satisfying that they vary continuously in θ and d and

$$d_{02}(\theta, d) = \inf |z_1 - z_2|, z_1 \in M^u, z_2 \in M^s.$$

Now $d_{02}(\theta^{\star},0)=0$. The transversality result of Lemma 4 implies that $\frac{\partial}{\partial \theta}d_{02}(\theta^{\star},0)\neq 0$. A similar procedure is applied to the 2-0 back heteroclinic. Define $d_{20}(v_1,d)$ such that $d_{20}(v^{\star},0)=0$. The transversality result of Lemma 5 implies that $\frac{\partial}{\partial v_1}d_{20}(v^{\star},0)\neq 0$. Next define

(4.3)
$$R(\theta, v_1, d) = \begin{pmatrix} d_{02}(\theta, d) \\ d_{20}(v_1, d) \end{pmatrix}.$$

From above, $R(\theta^*, v^*, 0) = 0$. Also

$$(4.4) D_{\theta,v_1}R(\theta^{\star}, v^{\star}, 0) = \begin{pmatrix} \frac{\partial}{\partial \theta} d_{02}(\theta^{\star}, v^{\star}) & 0\\ 0 & \frac{\partial}{\partial v_1} d_{20}(\theta^{\star}, v^{\star}) \end{pmatrix}.$$

This implies det $D_{\theta,v_1}R(\theta^*,v^*,0)=\frac{\partial}{\partial v_1}d_{20}(\theta^*,v^*)\cdot\frac{\partial}{\partial \theta}d_{02}(\theta^*,v^*)\neq 0$ by the above transversality conditions. Therefore for each d sufficiently small, there exist unique values of θ and v_1 such that $R(\theta(d),v_1(d),d)=0$ with $(\theta(0),v_1(0))=(\theta^*,v^*)$. Thus for each d sufficiently small, we can choose a unique wave speed θ and back parameter v_1 to obtain both a 0-2 and a 2-0 heteroclinic connection, what we call a 0-2-0 heteroclinic pair. We can carry out similar constructions to obtain 0-1-0, 2-3-2, and 1-3-1 heteroclinic pairs for d sufficiently small.

4.1. Asymmetric solutions. We have now determined the fate of all of the trajectories of Fig. 2.1, except for those that lie close to the edges of the box. We now discuss such trajectories and simultaneously answer a question about the possible existence of certain multiple-jump solutions. As mentioned earlier, in order to create $\epsilon \neq 0$ homoclinic solutions using the techniques of this paper, it is essential that the heteroclinic jumps, which in part constitute the singular homoclinic solution, all occur at the same wave speed. Thus it is of interest to see whether a 0-1-3 or 0-2-3 connection exists at a given value of θ and d. Such connections represent the situation where one fibre is stimulated, reaches an excited state, and is then followed by the excitation of the second fibre. A 0-2-3 connection will exist if the implicit functions $\theta_{02}(d)$ and $\theta_{23}(d)$ locally coincide in (θ,d) parameter space. Here $\theta_{02}(d)$ and $\theta_{23}(d)$ are the respective wave speeds at which the 0-2 and 2-3 heteroclinic solutions exist for d small. We next show that these curves intersect transversely, and as a result it will be impossible to create a 0-1-3 or 0-2-3 connection at any local value of (θ, d) other than $(\theta^*, 0)$. Moreover, it follows from [6] since the two curves intersect transversely in (θ, d) , parameter space that there exists a third curve of wave speeds, $\theta_{03}^{A}(d)$, for which

a locally unique bifurcating 0-3 asymmetric front exists. For each d > 0 sufficiently small, this front solution lies O(d) close to the 0-2-3, d = 0 heteroclinic pair. Since the equations are invariant under interchanging of u_1 and u_2 , there also exists an asymmetric solution O(d) close to the 0-1-3, d = 0 heteroclinic pair.

To show that $\theta_{02}(d)$ transversely intersects $\theta_{23}(d)$, we calculate $\theta'_{02}(0)$ and $\theta'_{23}(0)$, where ' denotes the derivative with respect to the coupling coefficient d. In particular, it is shown that $\theta'_{02}(0) < 0$ while $\theta'_{23}(0) > 0$ (see Fig. 4.1). First, consider $\theta_{02}(d)$. Define $J(\theta,d,u_2) = \Delta m(\theta,d,u_2)$ which measures the distance between $W^{cu}(0)$ and $W^{cs}(2)$ in the cross section $\{u_1 = 1/2\}$, where Δm is the same as before. Since we are interested in the case of d=0 and in calculating the change in $\theta_{02}(d)$ as d varies, we suppress the dependence of J on u_2 . From above, $J(\theta^*,0) = 0$ and $\frac{\partial}{\partial \theta}J(\theta^*,0) = \frac{\partial}{\partial \theta}\Delta m(\theta^*,0) > 0$. This result, using the implicit function theorem, locally establishes $\theta_{02} = \theta_{02}(d)$. Moreover, it also follows from the implicit function theorem that

(4.5)
$$\theta'_{02}(0) = -\left[\frac{\partial}{\partial \theta} \Delta m(\theta^*, 0)\right]^{-1} \cdot \frac{\partial}{\partial d} \Delta m(\theta^*, 0).$$

As in § 2, using differential forms and the equation of variations, $w_1 \cdot \frac{\partial}{\partial d} \Delta m(\theta^*, 0) = \Delta P_{u_1 w_1}^{13}(0)$ evaluated at d = 0, $u_2 = 0$, and $\theta = \theta^*$. The evolution equation for $P_{u_1 w_1}^{13}$ was calculated in § 2 and is given by

$$(4.6) P_{u_1w_1}^{13'} = \theta P_{u_1w_1}^{13} + w_1 P_{u_1\theta}^{13} - dP_{u_1u_2}^{13} - (u_2 - u_1) P_{u_1d}^{13}.$$

At $\theta = \theta^*$, d = 0, $u_2 = 0$, (4.6) becomes

(4.7)
$$P_{u_1w_1}^{13'} = \theta^* P_{u_1w_1}^{13} + w_1u_1.$$

Since $w_1 > 0$ along the front, it follows from the decay properties of these 2-forms that $\Delta P_{u_1w_1}^{13}(0) > 0$, from which $\frac{\partial}{\partial d}\Delta m(\theta^*,0) > 0$. Substituting into (4.5), we obtain $\theta'_{02}(0) < 0$.

Working similarly with quantities associated with the 2-3 heteroclinic solution, we obtain $\theta'_{23}(0) > 0$.

Therefore the signs of the derivatives at d=0 of the implicit functions verify that the curves $\theta_{02}(d)$ and $\theta_{23}(d)$ do intersect transversely at $\theta=\theta^{\star}$, d=0 as shown in Fig. 4.1. The wave speeds $\theta_{02}(d)$ and $\theta_{23}(d)$ do not locally coincide, which proves that 0-1-3 and 0-2-3 connections do not exist for parameter values close to $\theta=\theta^{\star}$ and d=0. It now follows from [6] that a bifurcating family of 0-3 heteroclinic solutions exists at some wave speed $\theta_{03}^A(d)$. Furthermore, a consequence of the theory of [6] and [32] is that the 0-3 asymmetric front exists only when $\theta_{23}(d)$ exceeds $\theta_{02}(d)$. From Fig. 4.1, $\theta_{23}(d) > \theta_{02}(d)$ when d>0. We do not attempt to construct asymmetric back or asymmetric homoclinic solutions at this time. In theory, it appears entirely likely that a 3-0 asymmetric back should exist. Whether a 0-3-0 asymmetric homoclinic solution exists requires further investigation of the slow flow.

To conclude, we have now determined the fate of all trajectories of Fig. 2.1.

4.2. Physical consequences of asymmetric fronts. Bifurcating asymmetric solutions exist only for stimulatory coupling between the fibres. Physically, this observation implies that under weak coupling, one fibre fires causing a transition from the rest state to begin. As the front approaches the excited voltage threshold, the second fibre has either been sufficiently depolarized or its threshold for excitability

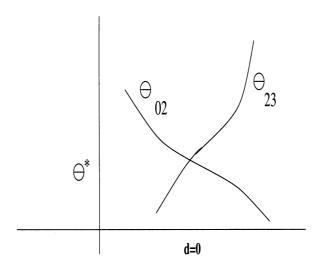


FIG. 4.1. The transverse intersection of the wave speed curves in parameter space.

has been lowered, or both, such that it too fires and also begins a transition to an excited state. The second fibre then tends to have the effect of forcing the first fibre to remain at an excited state. A different interpretation of this situation is that the action potential on the first fibre is sufficiently translated along the length of the fibre so as to not affect the stimulation of the second fibre. Another interesting physical aspect is that the coupling has an opposite effect on both of the fibres. The wave speed $\theta_{02}(d)$ is locally a decreasing function of d. Thus stimulatory coupling has the effect of slowing down the wave speed. In this case, the fibre at rest acts as a current sink and causes this reduction in speed. However, the wave speed $\theta_{23}(d)$ is locally an increasing function of d. So for stimulatory coupling, the excited fibre, which remains inactive, acts as a current source and tends to increase the wave speed.

5. Homoclinic solutions. Having completed a detailed study of reduced solutions, we are now in a position to determine what type of homoclinic orbits exist. There are two distinct types of homoclinic solutions that we consider. The first represents the situation where one fibre fires and then returns to rest while the other fibre remains entirely silent. The second represents the situation where both fibres fire simultaneously.

In particular, we will establish the existence of three homoclinic orbits which are close to the 0-1-0, 0-2-0, and 0-3-0 singular solutions, respectively. The idea behind their construction will be to apply the theorem of Jones and Kopell to the singular solutions that were shown to exist in §§ 2-4. We state their theorem in its given general form [17] and note that the work of §§ 2-4 place the present problem within the context of the hypothesis of the theorem.

Theorem 3 (Jones, Kopell). Consider

(5.1)
$$x' = f(x, y, \theta, \epsilon), y' = \epsilon g(x, y, \theta, \epsilon), \theta' = 0,$$

where $x \in \mathbf{R^{k+l}}, y \in \mathbf{R^n}$. Assume that for each θ and $\epsilon \neq 0$, there is a locally unique hyperbolic equilibrium point $P(\theta)$ with k unstable directions and l + n stable

directions; of the eigenvalues associated to the latter, n tend to zero with ϵ . Let $\{S^i\}$, $i=1,\ldots,N$ denote a family of slow manifolds for the $\epsilon=0$ equation (with the equilibrium point for $\epsilon\neq 0$ in S^0) and assume that for each i, S^i is normally hyperbolic with splitting k stable, l unstable. Assume further that there is a singular homoclinic orbit, with finitely many jumps, each from S^i to S^{i+1} for some i (where the $\{S^i\}$ are not necessarily disjoint, so the singular orbit may visit the same slow manifold more that once). Finally, assume that the following transversality conditions hold for the $\epsilon=0$ system: Let $W^s(S^i)$ and $W^u(S^i)$ denote the stable and unstable manifolds of the S^i as above and $[P(\theta), \theta]$ the graph as θ is varied of the $\epsilon=0$ limit of the $\epsilon\neq 0$ equilibrium point. We require that

$$\begin{array}{ll} \left.W^u(S^0)\right|_{[P(\theta),\theta]} \ \ transversely \ intersects \ W^s(S^1) \ \ in \ (x,y,\theta) space, \\ \left.W^u(S^i)\right|_{sing. \ orbit} \ \ transversely \ intersects \ W^s(S^{i+1}) \ \ in \ (x,y,\theta) space. \end{array}$$

Then for ϵ sufficiently small, there is a locally unique homoclinic solution to (5.1) near the singular solution.

In particular, the solution obtained exists as the transverse intersection of manifolds.

5.1. The structure of the slow flow. In order to apply Theorem 3, we need to establish the following two facts. First, for each singular solution, there must be a curve on the appropriate slow manifold which connects the point at which the singular orbit enters the slow manifold to the point at which the singular solution leaves this manifold. This is the point on each of the slow manifolds at which a back jump exists at the same wave speed as the reduced front jump. Similarly, for each of the singular solutions, there must exist a connecting curve on manifold (0) between the point at which the back enters (0) and the origin. Second, we need to verify that the transversality results of §§ 3 and 4 do in fact imply the transversality requirements of Theorem 3.

Consider first the 0-3-0 symmetric solution. For d fixed and small, the reduced 0-3 heteroclinic jump, which occurs at $\theta = \theta^*$, lands on manifold (3) at the critical point (1,0,1,0,0,0). In §3, a 3-0 jump was shown to occur at $\theta = \theta^*$ when v_1 and v_2 were restricted to v^* . This 3-0 jump leaves manifold (3) from the critical point $(u_R, 0, u_R, 0, v^*, v^*)$. We need to verify that for the slow flow, an orbit connecting (0,0) to (v^*, v^*) exists.

The equations which govern the slow flow on manifold (3) are given by

(5.2)
$$v'_1 = \epsilon \left(u_1(v_1, v_2) - \gamma v_1 \right) / \theta, \\ v'_2 = \epsilon \left(u_2(v_1, v_2) - \gamma v_2 \right) / \theta.$$

Here u_1 and u_2 are functions of v_1 and v_2 which satisfy (2.3) and (2.4). For the symmetric solution, we restrict to $u_1 \equiv u_2$ and, as a result, $v_1 \equiv v_2$. Thus (5.2) becomes

(5.3)
$$v'_1 = \epsilon \ (u_1(v_1) - \gamma v_1)/\theta, v'_2 = \epsilon \ (u_2(v_1) - \gamma v_2)/\theta,$$

where $v_i = f(u_i)$ for i = 1, 2. Recall that γ is chosen small enough so that $u_i = \gamma v_i$ and $v_i = f(u_i)$ have only the (0,0) solution in common for i = 1, 2. As a result,

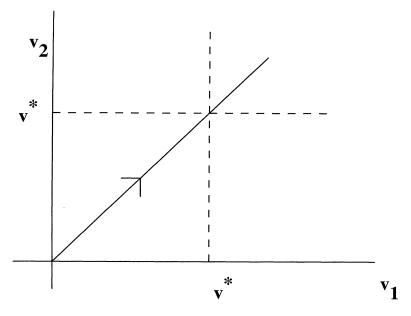


Fig. 5.1. Evolution of the symmetric slow flow on manifold (3).

there will be a flow on the slow manifold. Moreover, on manifold (3), $u_i > \gamma v_i$, which implies $v_i' > 0$ for i = 1, 2, since $\epsilon > 0$. Finally, $v_1' = v_2' > 0$ implies the flow on the slow manifold (3) will cross (v^*, v^*) as is depicted by the solid line in Fig. 5.1.

We next verify that there exists a trajectory on manifold (0) which connects (v_1, v_2) to (0,0). Excluding a neighborhood of u_{\min} , the left branch of each cubic can be approximated by the linear function $v_i = -\eta u_i$, where $\eta > 0$. Substituting into (5.3), we obtain

(5.4)
$$v_1' = \epsilon \left(-1/\eta - 1/\gamma\right)v_1/\theta, \\ v_2' = \epsilon \left(-1/\eta - 1/\gamma\right)v_2/\theta.$$

The above approximation allows us to easily linearize about the rest point (0,0). Since the eigenvalues of the resulting linearization matrix both equal $(-1/\eta - 1/\gamma) < 0$, the point (0,0) is attracting for the slow flow. Since $v'_1 = v'_2 < 0$, we have verified that on manifold (0), there exists an orbit which connects (v^*, v^*) to (0,0).

We next check that the transversality requirements of Theorem 3 are satisfied. We define certain objects associated with the $\epsilon=0$ flow. Let S_{R_3} be a compact portion of manifold (3) which contains $-\delta \leq v_1 \leq v^* + \delta$ and $-\delta \leq v_2 \leq v^* + \delta$. Let $I_{\delta} = [\theta^* - \delta, \theta^* + \delta]$. Let $W^u(S_3 \times I_{\delta})$ and $W^s(S_3 \times I_{\delta})$ be the five-dimensional unions of stable and unstable manifolds of $S_3 \times I_{\delta}$ for $\epsilon=0$. Let $W^u(A_3)$ be the three-dimensional restriction of $W^u(S_3 \times I_{\delta})$ to the singular orbit and $\theta=\theta^*$. Note that A_3 is a subset of the slow manifold (3), where $v_1=v_2=v$ and $v^*-\delta \leq v \leq v^*+\delta$. Also $W^u(A_3)$ contains $W^{cu}(u_R,0,u_R,0,v)$ of §3. Analogously to $W^s(S_3 \times I_{\delta})$, define $W^s(S_0 \times I_{\delta})$ to be the five-dimensional union of stable manifolds over $-\delta \leq v_1 \leq v^* + \delta$, $-\delta \leq v_2 \leq v^* + \delta$, $\theta \in I_{\delta}$, associated with the critical points on manifold (0) at $\epsilon=0$. To apply Theorem 3 to the 0-3-0 symmetric solution,

we need

- 1) $W^{cu}(0,0,0,0,0,0,\theta) \cap W^s(S_3 \times I_{\delta})$ in $(u_1, w_1, u_2, w_2, v_1, v_2, \theta)$ space at $\theta = \theta^*$.
- 2) $W^{u}(A_{3}) \cap W^{s}(S_{0} \times I_{\delta})$ in $(u_{1}, w_{1}, u_{2}, w_{2}, v_{1}, v_{2}, \theta)$ space.

Lemma 1 proves that $W^{cu}(0,0,0,\theta) \cap W^{cs}(1,0,1,0,\theta)$ in (u_1,w_1,u_2,w_2,θ) space. It is not hard to establish that $W^{cu}(0,0,0,0,0,0,\theta)$ in fact transversely intersects $W^s(S_3 \times I_{\delta})$ in $(u_1,w_1,u_2,w_2,v_1,v_2,\theta)$ space, thus verifying 1). Lemma 3 proves that $W^u(A_3)$ transversely intersects $W^{cs}(u_L,0,u_L,0,v)$ in \mathbf{R}^5 at $v=v^*$. Again, it is easy to establish that $W^u(A_3)$ and $W^s(S_0 \times I_{\delta})$ transversely intersect in $(u_1,w_1,u_2,w_2,v_1,v_2,\theta)$ space as needed, thus proving the existence of the $\epsilon \neq 0$ 0-3-0 homoclinic solution. Note that in Theorem 1a), $\hat{d} = \min(d_0,d_1)$ where d_0,d_1 are defined in Lemmas 1 and 3, respectively.

Verification that Theorem 3 can be applied to the 0-2-0 and 0-1-0 antisymmetric solutions is qualitatively similar to the one just presented, so we omit the details. Note that for these solutions, \tilde{d} is chosen so that Corollaries 1 and 2 hold.

5.2. Physical conclusions. The introduction of weak coupling between parallel fibres has been shown to have a pronounced organizational effect. It forces either symmetry or antisymmetry, thus severely limiting allowable types of behavior. It has also been shown that uncoupled action potentials which were initially slightly out-ofphase are destroyed by the introduction of weak coupling. Here the coupling can be thought of as a synchronizing agent. Except for the case of the symmetric solution and for the possibility of two asymmetric solutions, weak coupling ensures that only one fibre at a time can be excited. In this case, the coupling forces the second fibre to remain inactive at rest until the first fibre returns to a resting potential. In our notation, this proves that homoclinic orbits whose singular limit is 0-1-3-1-0 or 0-2-3-2-0 can not exist. In particular, homoclinics whose singular limits visit both manifolds (3) and either (2) and/or (1) cannot exist. This suggests that under appropriate types of stimulation, pathways of propagation are isolated from one another. According to Keener, this observation may help to explain the onset of fibrillation, where precisely this type of isolating behavior is observed. For the symmetric solution, the fibres effectively decouple. However, for the antisymmetric solutions, the weak coupling has a strong locking effect, thereby excluding the creation of most out-of-phase solutions.

At the level of this investigation, the type of coupling, either excitatory or inhibitory, was seen to be of relevance only for the creation of asymmetric fronts, which were shown to exist only for excitatory coupling. Symmetric and antisymmetric solutions exist for both types of coupling. It turns out, however, that the type of coupling is the determining factor in the stability of the symmetric solution. The symmetric pulse is stable for excitatory coupling, and unstable for inhibitory coupling. See [4] for the exact details.

We have not ruled out the possibility of a solution near to a 0-1-2-0 or 0-2-1-0 singular orbit. Further study in this direction is merited, as Bose [2] has shown that 1-2 and 2-1 heteroclinics exist for $\epsilon = 0$. Thus it is possible for one fibre to depolarize while the other is simultaneously hyperpolarizing. Mathematically it remains to be seen whether a mimicking singular orbit can be constructed and then used to create an actual $\epsilon \neq 0$ homoclinic orbit.

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