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CHAOTIC SPIKES ARISING FROM A MODEL OF BURSTING IN EXCITABLE MEMBRANES*

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Dedicated to the memory of Joseph Terman.

Abstract. A class of differential equations that model electrical activity in pancreatic beta cells is considered. It is demonstrated that these equations must give rise to both bursting solutions and, for different values of the parameters, continuous spiking. We also consider how the number of spikes per burst changes as parameters in the equations are varied. This transition may be continuous, in which case the period of the bursting solution increases significantly and then decreases. Hence, small perturbations may cause macroscopic changes in the bursting solution. This transition may also give rise to chaotic dynamics due to the existence of a Smale horseshoe.

Key words. bursting, excitable membranes, chaotic dynamics

AMS(MOS) subject classifications. 58F13, 34C35, 92A09

1. Introduction. In this paper, we study the qualitative behavior of solutions to mathematical models for electrical activity in pancreatic β-cells. These cells are responsible for the secretion of insulin. Atwater et al. [2] found that at certain levels of glucose concentration, the membrane potential of the beta cell underwent sustained oscillations of the burst type. Moreover, at higher glucose concentrations, the bursting gave way to continuous spiking or beating. The first theoretical model for this phenomena was given by Chay and Keizer [4]. This model consists of five first-order nonlinear differential equations of the Hodgkin-Huxley type. Later, Chay [3] simplified this model to a first-order system of three equations. Both the original and reduced Chay and Keizer models display many of the qualitative features observed in experiments. In particular, these models contain a parameter k_{Ca}, which increases with glucose concentration. Numerical studies of Chay and Keizer [4], Chay [3], and Chay and Rinzel [5] have demonstrated that both of these models exhibit bursting solutions, and, at higher values of k_{Ca}, these bursting solutions give rise to continuous spiking. The numerical and experimental results indicate that the transition from bursting to continuous spiking is a chaotic one.

In [12], Rinzel describes several mathematical mechanisms for burst generation. We consider one such mechanism; this includes the reduced Chay and Keizer model. See Rinzel [13]. We demonstrate, both analytically and numerically, that this type of model may give rise to chaotic solutions as parameters in the equations are varied. The chaotic solutions arise, mathematically, due to the existence of a Smale horseshoe.

The equations we consider are autonomous systems of ordinary differential equations. Following Rinzel [12], we say that a solution to the equations is bursting if it is a periodic solution whose behavior alternates between near steady state behavior (the passive phase) the trains of spike-like oscillations (the active phase). An example of a bursting solution is shown in Fig. 12. The system of equations consists of fast and slow subsystems. If we think of the variables of the slow subsystem as parameters, then the fast dynamics will have a branch of stable rest points and a branch of stable periodic solutions. The bursting solution will then be a closed orbit in phase space,

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which, in the passive phase, passes close to the branch of stable rest points. The trains of rapid spikes correspond to the closed-orbit passing close to the branch of periodic solutions.

We say that the system gives rise to continuous spiking if there exists a stable closed orbit that always lies close to the branch of periodic solutions.

We prove that these models must give rise to both bursting solutions and, for other values of the parameter k_{Ca}, must give rise to continuous spiking.

We also study how the number of spikes per burst changes as parameters in the slow subsystem change. We see that this can take place in two distinct ways depending on the structure of the slow dynamics. One possibility is that there is a smooth transition; for all values of the parameters, there exists a stable periodic solution whose trajectory in phase space changes in a continuous fashion as the parameters are varied. What is interesting about this type of transition is that as the number of spikes change, the period of each burst increases in size. Hence, small perturbations of the slow dynamics cause macroscopic changes in the bursting solution. See Fig. 13.

The transition from n to $n+1$ spikes need not be continuous; during this transition, the flow may give rise to a Smale horseshoe. We show in § 6 (see Remark 2 following Proposition 6.4.2) that the existence of the horseshoe implies that if $\{a_k\}$ is any biinfinite sequence of integers with $a_k \in \{n, n+1\}$, $-\infty < k < \infty$, then there must exist a burstlike solution of the equations such that the number of spikes in the kth burst pattern is a_k.

Our approach to this problem is quite geometrical. We prove the existence of a bursting solution by demonstrating that a certain Poincaré return map has a fixed point. The existence of chaotic solutions follow by showing that the Poincaré map gives rise to a Smale horseshoe. In order to define the Poincaré map and demonstrate that it has the correct properties, it is necessary to define various geometrical objects in phase space. It is important to understand how trajectories in phase space are mapped from one of these geometrical objects into another, and through which sides of the geometrical objects a trajectory may leave or enter.

This type of geometrical argument has been used by others to study singular perturbation problems arising from models for excitable membranes. See, for example, Cronin [6]. Aperiodic and chaotic solutions have also been studied for models in which the slow subsystem acts independently as a forcing function to the fast subsystem. For such models, Ermentrout and Kopell [8] and Alexander, Doedel, and Othmer [1] discuss the transition from n to $n+1$ spikes.

An outline of the paper is as follows. In § 2, we state precisely what assumptions we require for a bursting solution. In § 3, we define the basic geometrical objects in phase space. The existence of a bursting solution is proved in § 4. In § 5, we prove that for certain values of the parameters, the system must give rise to continuous spiking. In § 6, we study the transition from n to $n+1$ spikes. To do this we must introduce a notion of winding number. This corresponds to the number of spikes per burst for bursting solution. In § 7, we support our analytic results with numerical computations.

2. Assumptions.

We consider a system of ordinary differential equations of the form

$$
\begin{aligned}
v' &= f_1(v, w, y),\\
w' &= f_2(v, w, y), \qquad (2.1)\\
y' &= \varepsilon g(v, w, y, k).
\end{aligned}
$$

Here, ε is a small positive parameter, and f_1, f_2, and g are smooth functions. We consider y to be the slow variable. If we let $f(v, w, y) = (f_1, f_2)^T$, then by the fast subsystem we mean the equations

$$\text{(FS)} \qquad \begin{pmatrix} v \\ w \end{pmatrix}' = f(v, w, y).$$

Here, y is thought of as a parameter.

In the hope of keeping the notation somewhat manageable, we introduce the following conventions. Our first assumption will be that the set of rest points of (FS) is an S-shaped curve $\mathcal{S}$ in the three-dimensional (v, w, y) phase space. We denote the upper branch of $\mathcal{S}$ by UB, the middle branch by MB, and the lower branch by LB. the letters l, L, and $\mathcal{L}$ will be reserved for any object associated, in some way, with LB. Similar statements hold for MB and UB. The left and right knees of $\mathcal{S}$ also play a central role in our analysis. The letters λ and ρ will be reserved for any object associated with the left and right knees, respectively.

We have chosen the assumptions so that, for a specific system, they can be easily verified, numerically, using a standard ordinary differential equation solver. The first five assumptions are concerned with the two-dimensional system (FS), while the last two assumptions are concerned with the zero set of $g(v, w, y, k)$. The assumptions listed below are those required to prove the existence of a bursting solution. Further assumptions will be given later when we consider the existence of continuous spiking and horseshoes.

In what follows, the reader is referred to Fig. 1.

(A1) The rest points (FS) consist of a smooth, S-shaped, curve $\mathcal{S}$ in phase space. That is, there exists $\lambda < \rho$ such that
- (a) If $y < \lambda$, then (FS) has precisely one rest point, which we denote by l_y;
- (b) If $y > \rho$, then (FS) has precisely one rest point, which we denote by u_y;
- (c) If $\lambda < y < \rho$, then (FS) has precisely three rest points. These are denoted by l_y, m_y, and u_y;
- (d) The rest point at the "left knee," for $y = \lambda$, is denoted by K_λ, and the rest point at the "right knee," for $y = \rho$, is denoted by K_ρ;
- (e) The union of all the above rest points form a smooth curve, which we denote by $\mathcal{S}$.

(A2) Each of the rest points l_y is an attractor, as a solution of (FS). Each of the rest points m_y is a nondegenerate saddle. We denote the two trajectories in the unstable manifold of m_y by $M_y^+(t)$ and $M_y^-(t)$.

(A3) There exists $h \in (\lambda, \rho)$ such that $M_h^+(t)$ is homoclinic to m_h; that is, $\lim_{t\to\pm\infty} M_h^+(t) = m_h$. If $y \in (\lambda, \rho)$, then $\lim_{t\to\infty} M_y^-(t) = l_y$. If $y \in (\lambda, h)$, then $\lim_{t\to\infty} M_y^+(t) = l_y$.

(A4) There exists $\delta_0 > 0$ such that if $h < y < \rho + \delta_0$, then there exists an asymptotically stable periodic solution $p_y(t)$ of (FS). This periodic solution surrounds u_y, but not l_y or m_y. The union of these trajectories define a continuous branch of solutions, which terminate at $M_h^+(t)$ as $y \to h$. Let $\mathcal{P}$ be the union of all these periodic solutions.

Remark. In Fig. 2, we illustrate the phase planes corresponding to (FS) for three different values of the parameter y in order to demonstrate how the trajectory $M_y^+(t)$ changes as y passes through the critical value $y = h$. In each of these figures,

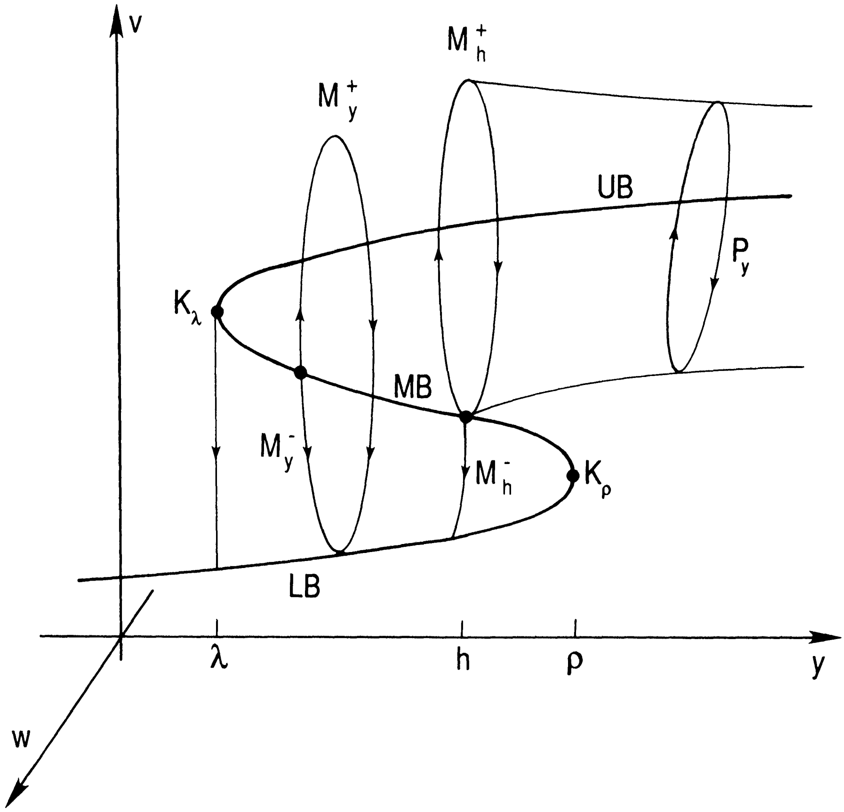


FIG. 1. LB, MB, *and* UB *are the branches of rest points of* (FS). *For* $y > h$ *there is a periodic solution* p_y *which surrounds* UB. *These periodic solutions terminate at the homoclinic orbit* M_h^+. *For* $\lambda < y < \rho$, *the trajectories in the unstable manifold of the middle branch are denoted by* M_y^- *and* M_y^+.

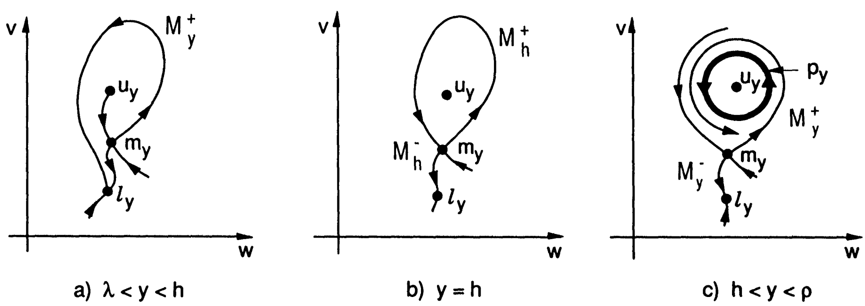


FIG. 2. *The phase plane of* (FS) *for three different values of* y. *If* $\lambda < y < h$, *then each trajectory in the unstable manifold of* m_y *approaches* l_y *as* $t \to \infty$. *If* $y = h$, *then one of these trajectories is a homoclinic orbit. If* $h < y < \rho$, *then this trajectory approaches the periodic solution* p_y *as* $t \to \infty$.

$\lim_{t\to\infty} M_y^-(t) = l_y$. In Fig. 2(a), we assume that $\lambda < y < h$. In this case $\lim_{t\to\infty} M_y^+(t) = l_y$. In Fig. 2(b), $y = h$, and $M_y^+(t)$ is the homoclinic orbit. Finally, in Fig. 2(c), $h < y < \rho$. In this case, $M_y^+(t)$ approaches the periodic orbit $p_y(t)$, as $t \to \infty$.

We now need an assumption which will allow us to conclude that for $0 < \varepsilon \ll 1$, solutions of (2.1) which pass close to the right knee must then pass close to the branch of periodic solutions, while solutions of (2.1) which pase close to the left knee must then pass close to the lower branch. In what follows, $\omega(\gamma_0)$ will be the omega limit set of the solution of (2.1) with $\varepsilon = 0$ which passes through γ_0.

(A5) There exists a neighborhood $\mathcal{U}_\rho$ of K_ρ such that if $\gamma_0 = (v_0, y_0, w_0) \in \mathcal{U}_\rho$, then either $\omega(\gamma_0) = m_{y_0}$, $\omega(\gamma_0) = l_{y_0}$, or $\omega(\gamma_0) = p_{\gamma_0}$. There exists a neighborhood $\mathcal{U}_\lambda$ of K_λ such that if $\gamma_0 \in K_y$, then either $\omega(\gamma_0) = m_{y_0}$, $\omega(\gamma_0) = l_{y_0}$, or $\omega(\gamma_0) = u_{y_0}$.

The final assumptions are concerned with the slow dynamics.

(A6) There exists $k_\rho < k_\lambda$ such that if $k_\rho < k < k_\lambda$, then there exists a smooth function $v = h(w, y, k)$ such that $g(v, w, y, k) = 0$ if and only if $v = h(w, y, k)$. Moreover, $g(v, w, y, k) < 0$ if and only if $v > h(w, y, k)$. If $M_k = \{(v, w, y)\colon v = h(w, y, k)\}$, then $M_k \cap \mathcal{S} = m_{y_k}$ for some $y_k \in (\lambda, \rho)$.

Remark. This assumption implies that for $k \in (k_\rho, k_\lambda)$ and $\varepsilon > 0$, there is precisely one fixed point of (2.1). This is the point m_{y_k} on the middle branch.

Let $\mathcal{M}_k^+ = \{(v, w, y)\colon v > h(w, y, k)\}$ and $\mathcal{M}_k^- = \{(v, w, y)\colon v < h(w, y, k)\}$.

(A7) If $k_\rho < k < k_\lambda$, then $LB \subset \mathcal{M}_k^-$. Moreover, there exists a unique $k_h \in (k_\rho, k_\lambda)$ such that $y_{k_h} = h$. If $k_\rho \leqq k \leqq k_h$, then $\mathcal{P} \subset \mathcal{M}_k^+$.

Remark. This last assumption implies that if $k \in (k_\rho, k_\lambda)$, $\varepsilon > 0$, and (v, y, w) lies near the lower branch, then $y' = \varepsilon g(v, y, w, k) > 0$. Moreover, if, $k_\rho < k < k_h$, $\varepsilon > 0$ and (v, y, w) lies near $\mathcal{P}$, then $y' < 0$. Note that if $k = k_h$ and $\varepsilon > 0$, then the fixed point of (2.1) is m_h. This is the homoclinic point for (2.1) with $\varepsilon = 0$.

Remarks. (1) These assumptions can be verified, at least numerically, for the β-cell models mentioned in the Introduction, if we make a suitable interpretation of the variables. Here, v corresponds to the potential difference between the inside and outside of the cell, w corresponds to the potasssium channel state variable, and y is related to the calcium concentration. In the original β-cell model variables, (2.1) gives rise to a "z-shaped" curve instead of our "S-shaped" curve. The parameter k corresponds to k_{Ca} mentioned in the Introduction.

(2) Note that we do not assume anything about the rest points u_y. This is because the periodic and chaotic solutions which we consider in the later sections do not ever approach the upper branch. It is possible, for example, that there exists $\bar{y} > h$ such that the rest points u_y are stable for $y > \bar{y}$ and undergo a Hopf bifurcation as the parameter y decreases past $\bar{y}$. This is what happens for the system (7.1.1).

(3) The essential reason why a burst-like solution exists is the following (see Fig. 3(a)). Suppose that $\gamma(t)$ is a solution of (2.1) with $0 < \varepsilon \ll 1$, $k \in (k_\rho, k_h)$, and assume that $\gamma(0)$ lies close to the lower branch. Because $y' > 0$ near the lower branch, $\gamma(t)$ will travel slowly to the right, up the lower branch. This corresponds to the passive phase of the burst. $\gamma(t)$ will travel up the lower branch until it is pushed past the right knee. At this point, the fast dynamics take over the $\gamma(t)$ quickly travels close to $\mathcal{P}$, the branch of periodic solutions. Because $y' < 0$ near the periodic solutions, $\gamma(t)$ will loop around $\mathcal{P}$, slowly moving to the left. This corresponds to the spike train or active phase of the burst. The spiking will continue until $\gamma(t)$ is pushed to the left of the homoclinic trajectory. It is not clear, at this point, how $\gamma(t)$ behaves once it passes the homoclinic trajectory. However, it is reasonable to expect that eventually the fast dynamics force $\gamma(t)$ back to the lower branch, and the whole process starts over again. A key step in finding the chaotic solutions is in understanding how $\gamma(t)$ behaves as it passes the homoclinic trajectory. We see that $\gamma(t)$ must, at some point, lie close to one of the unstable trajectories $M_y^+(t)$ or $M_y^-(t)$ defined in (A2). This is illustrated in Fig. 3(b).

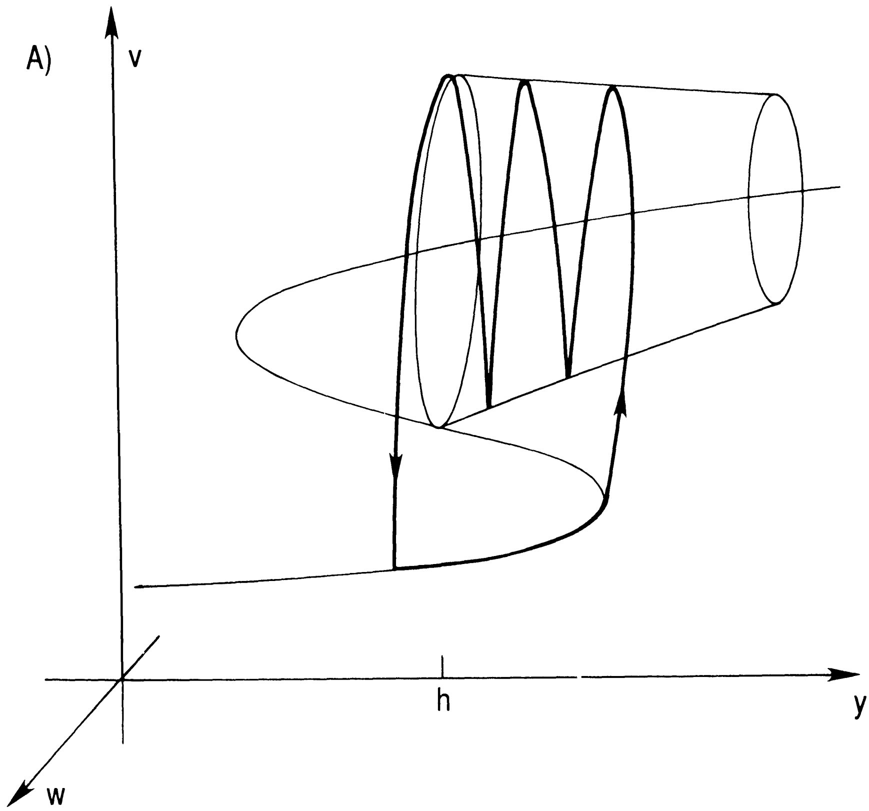


FIG. 3(a). *The trajectory of a bursting solution in phase space. In the passive phase, the solution lies close to the lower branch. The trains of rapid spikes correspond to the solution passing close to the branch of periodic solutions.*

3. Pillboxes, tubes, etc. We now define various neighborhoods in phase space. These neighborhoods will allow us to keep track of trajectories as they loop around in phase space. The basic idea is to put "pill boxes" about the left and right knees, "tubes" about the lower and middle branches, and annuluslike regions about the periodic solutions. Of course, these neighborhoods must be defined with care so that they fit together properly. Moreover, we must make sure that trajectories enter and exit them in a proper fashion. Throughout this section, we assume that $k_p < k < k_h$.

The pill boxes and tubes will be homeomorphic images of the unit cube

$$C = \{(x, s, z): |x| \leqq 1, |s| \leqq 1, |z| \leqq 1\}.$$

We denote the open sides of C by

$$C_L = \operatorname{int}\{(x, s, z) \in C: s = -1\}, \qquad C_R = \operatorname{int}\{(x, s, z) \in C: s = +1\},$$

$$C_{BT} = \operatorname{int}\{(x, s, z) \in C: z = -1\}, \qquad C_T = \operatorname{int}\{(x, s, z) \in C: z = +1\},$$

$$C_{BK} = \operatorname{int}\{(x, s, z) \in C: x = -1\}, \qquad C_F = \operatorname{int}\{(x, s, z) \in C: x = +1\}.$$

Let E^3 be the (v, w, y) phase space. Let $\pi_y: E^3 \to E^1$ be the projection map given by $\pi_y(v, w, y) = y$.

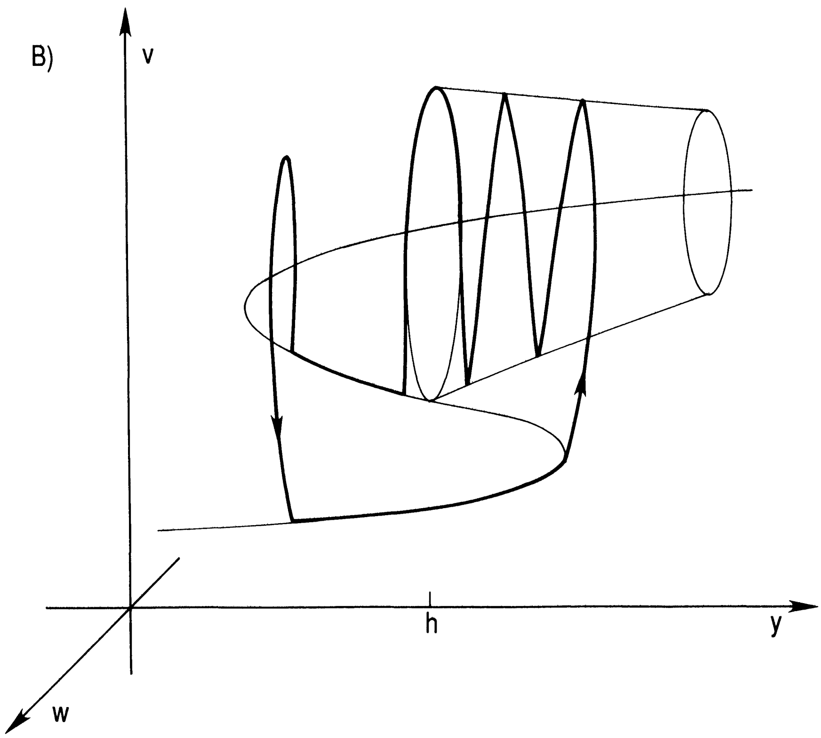


FIG 3(b). *A bursting solution may lie close to the middle branch for a long time before leaving it. This gives rise to the plateau region in a bursting solution.*

DEFINITION. Suppose that $\mathcal{U} \in R^3$ and $\Phi: \mathcal{U} \to E^3$. We say that Φ is a y-homeomorphism from $\mathcal{U}$ into E^3 if

(a) Φ is a homeomorphism from $\mathcal{U}$ onto its image.

(b) If $(x_1, s_1, z_1) \in \mathcal{U}$ and $(x_2, s_2, z_2) \in \mathcal{U}$ with $s_1 \leqq s_2$, then

$$(\pi_y \circ \Phi)(x_1, s_1, z_1) \leqq (\pi_y \circ \Phi)(x_2, s_2, z_2).$$

All of the maps considered in this section will be y-homeomorphisms. Condition (b) is natural, because y is the slow variable which is considered as a parameter when $\varepsilon = 0$. In what follows, δ will be a small positive constant which may decrease in size.

3.1. The right knee and lower branch. The following two propositions follow easily from the assumptions stated in the previous section. In the first proposition, we define a neighborhood N_ρ of the right knee. In the second proposition, we define a neighborhood N_L of the lower branch. It will be attracting in the sense that for $\varepsilon = 0$, solutions of (2.1) which lie on ∂N_L must enter N_L in forward time. These sets are constructed so that the right side of N_L is contained in the interior of the left side of N_ρ. When ε is small, trajectories which lie in N_L must eventually enter N_ρ and then leave N_ρ through its top side. See Fig. 4

PROPOSITION 3.1.1. *There exists a y-homeomorphism $\Phi_\rho: C \to E^3$ such that*

(a) $K_\rho \in \operatorname{int}(\Phi_\rho(C))$.

(b) $\Phi_\rho(C) \subset \mathcal{M}^- \cap \{(v, w, y): y < \rho + \delta_0\}$ *where δ_0 was defined in* (A4).

(c) *If $\varepsilon = 0$ and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in \operatorname{int}(\Phi_\rho(C))$, then $\gamma(t)$ can only leave $\Phi_\rho(C)$ through $\Phi_\rho(C_T)$. If $\gamma(t)$ does leave $\Phi_\rho(C)$, then $\omega(\gamma(t)) \subset \mathcal{P}$, the manifold of periodic solutions defined in* (A4).

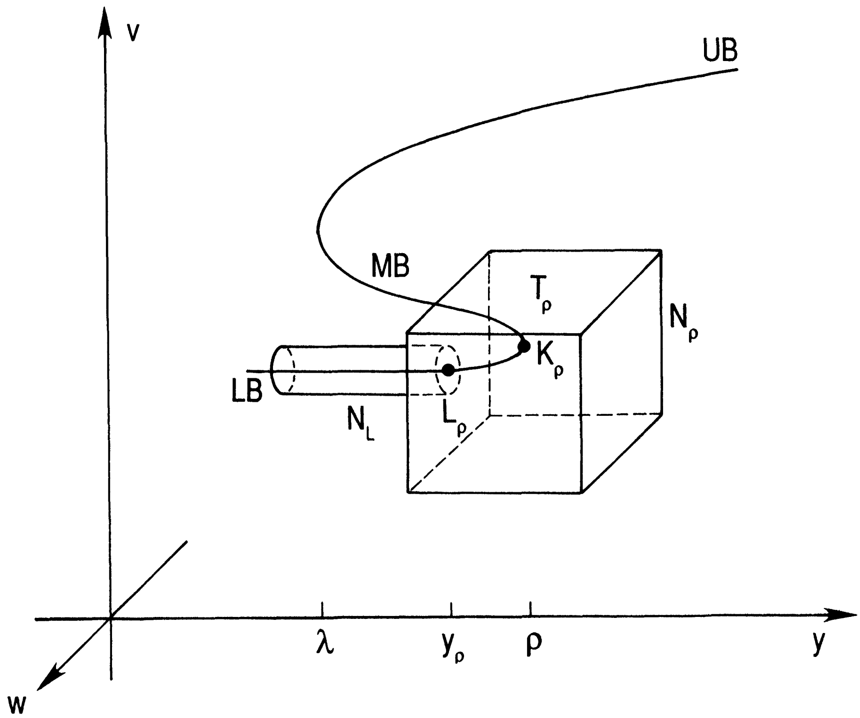


FIG. 4. *If $\varepsilon > 0$, then solutions of* (2.1) *which lie in N_L must enter N_ρ through L_ρ and can only leave N_ρ through T_ρ.*

(d) *If $\varepsilon = 0$ and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in \partial\Phi_\rho(C)$, then $\gamma'(t_0)$ is not tangent to $\partial\Phi_\rho(C)$.*

Let $N_\rho = \Phi_\rho(C)$, $T_\rho = \Phi_\rho(C_T)$, $L_\rho = \Phi_\rho(C_L)$, and $y_\rho = (\pi_y \circ \Phi_\rho)(C_L)$. Note that y_ρ is well defined, because Φ_ρ is a y-homeomorphism.

Our next result follows from the previous proposition and the continuous dependence of solutions to an ordinary differential equation on a parameter. It states that if ε is sufficiently small, then any solution of (2.1) which crosses the left side L_ρ of N_ρ must enter N_ρ and then leave N_ρ through its top side T_ρ.

COROLLARY 3.1.2. *If $\varepsilon > 0$ is sufficiently small and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in L_\rho$, then there exists $t_1 > t_0$ such that $\gamma(t) \in N_\rho$ for $t_0 < t < t_1$ and $\gamma(t_1) \in T_\rho$.*

We now consider the lower branch. The following results follow easily from the assumptions.

PROPOSITION 3.1.3. *There exists a y-homeomorphism $\Phi_L : C \to E^3$ such that if $N_L = \Phi_L(C)$, then*

(a) $l_y \in N_L$ *for* $\lambda - \delta \leqq y \leqq y_\rho$;

(b) $N_L \subset \mathcal{M}^-$;

(c) $(\pi_y \circ \Phi_L)(C_L) = \lambda - \delta$;

(d) $(\pi_y \circ \Phi_L)(C_R) = y_\rho$ *and* $\Phi_L(C_R) \subset L_\rho$;

(e) *If $\varepsilon = 0$, and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(0) \in \partial(N_L) \cap \{(v, w, y) : \lambda - \delta < y < y_\rho\}$, then $\gamma(t)$ enters N_L, transversely, in forward time.*

COROLLARY 3.1.4. *If $\varepsilon > 0$ is sufficiently small and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in N_L$, then there exists $t_1 \geqq t_0$ such that $\gamma(t) \in N_L$ for $t \in (t_0, t_1)$ and $\gamma(t_1) \in \Phi_L(C_R) \subset L_\rho$.*

Combining Corollaries 3.1.2 and 3.1.4 we obtain the next result.

COROLLARY 3.1.5. *If $\varepsilon>0$ is sufficiently small and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0)\in N_L$, then there exists $t_2>t_1>t_0$ such that $\gamma(t)\in N_L$ for $t\in(t_0,t_1)$, $\gamma(t_1)\in L_\rho$, $\gamma(t)\in N_\rho$ for $t_1<t<t_2$, and $\gamma(t_2)\in T_\rho$.*

3.2. The left knee. We now define a neighborhood of the left knee in a manner similar to what we did for the right knee. The following result follows easily from our assumptions.

PROPOSITION 3.2.1. *There exists a y-homeomorphism $\Phi_\lambda: C\to E^3$ such that if $N_\lambda=\Phi_\lambda(C)$, then*

(3.2.1)

(a) $K_\lambda\in N_\lambda$;

(b) $N_\lambda\subset\mathcal{M}^+$;

(c) *If $\varepsilon=0$ and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0)\in\partial N_\lambda$, then $\gamma'(t_0)$ is not tangent to ∂N_λ;*

(d) *If $\varepsilon=0$ and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0)\in N_\lambda$, then for $t>t_0$, $\gamma(t)$ can only leave N_λ through $\Phi_\lambda(C_{BT})$. In this case, there exists $t_1>t_0$ such that $\gamma(t_1)\in N_L$.*

Let $B_\lambda=\Phi_\lambda(C_{BT})$, $R_\lambda=\Phi_\lambda(C_R)$, and $y_\lambda=(\pi\circ\Phi_\lambda)(C_R)$.

The next result follows from the previous proposition and the continuous dependence of solutions on a parameter.

COROLLARY 3.2.2. *If $\varepsilon>0$ is sufficiently small, and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0)\in R_\lambda$, then there exists $t_2>t_1>t_0$ such that $\gamma(t)\in N_\lambda$ for $t\in(t_0,t_1)$, $\gamma(t_1)\in B_\lambda$, and $\gamma(t_2)\in N_L$.*

3.3. The middle branch. We now construct a "tube" N_M, which contains the middle branch for $y_\lambda\leqq y\leqq h+\delta_1$ for some $\delta_1>0$. It will be important to keep track of which sides of N_M trajectories may leave or exit, and where trajectories go once they do leave N_M.

PROPOSITION 3.3.1. *There exists a $\delta_1>0$, and a y-homeomorphism $\Phi_M: C\to E^3$ such that if $N_M=\Phi_M(C)$, and $\gamma(t)$ is a solution of* (2.1) *with $\varepsilon=0$, then*

(a) *$m_y\in N_M$ for $y_\lambda\leqq y\leqq h+\delta_1$;*

(b) $N_M\subset\mathcal{M}^+$;

(c) *$\Phi_M(C_L)\subset R_\lambda$ and $(\pi_y\circ\Phi_M)(C_R)=h+\delta_1$;*

(d) *If $\gamma(t_0)\in\Phi_M(C_T)\cup\Phi_M(C_{BT})$, then $\gamma(t)$ enters N_M, transversely, in forward time;*

(e) *If $\gamma(t_0)\in\Phi_M(C_F)\cup\Phi_M(C_{BK})$, then $\gamma(t)$ leaves N_M, transversely, in forward time. Moreover, there exists $t_1>t_0$ such that $\gamma(t)\notin N_M$ for $t\in(t_0,t_1)$, and either $\gamma(t_1)\in N_M$, or $\gamma(t_1)\in N_L$.*

(f) *If $h<y\leqq h+\delta_1$, then each of the periodic solutions $p_y(t)$ enters N_M and crosses $\Phi_M(C_{BK})$.*

Proof. Throughout this proof we consider solutions of (2.1) with $\varepsilon=0$. We change coordinates so that near the middle branch, (2.1) becomes

$$\begin{aligned}p'&=\lambda_1(y)p+g_1(p,q,y),\\ q'&=-\lambda_2(y)q+g_2(p,q,y),\\ y'&=0.\end{aligned}\tag{3.3.1}$$

These equations hold for, say, $|p|\leqq\delta$, $|q|\leqq\delta$, and $y_\lambda\leqq y\leqq h+\delta$. Here $\lambda_1(y)$ and $-\lambda_2(y)$ are, respectively, the positive and negative eigenvalues of (FS) linearized at the rest points m_y. The functions $g_1(p,q,y)$ and $g_2(p,q,y)$ are both $o(|p|+|q|)$ and satisfy

(a) $g_1(0,q,y)=0$ for $|q|\leqq\delta$ and $y_\lambda\leqq y\leqq h+\delta$;

(b) $g_2(p,0,y)=0$ for $|p|\leqq\delta$ and $y_\lambda\leqq y\leqq h+\delta$.

Therefore, the local stable manifold at m_{y_1}, $y_\lambda \leqq y_1 \leqq h+\delta$, is given by $\{(p, q, y): p=0, y=y_1\}$, and the local unstable manifold is given by $\{(p, q, y): q=0, y=y_1\}$. The unstable manifold at m_y consists of two trajectories, which, as in § 2, we denote by $M_y^+(t)$ and $M_y^-(t)$. We assume that the local coordinates are chosen so that for $y_\lambda \leqq y \leqq h+\delta$,

$$M_y^-(0)=(-\delta, 0, y) \quad \text{and} \quad M_y^+(0)=(\delta, 0, y).$$

Assume that q_1, q_2, and δ_1 are positive constants with $\max\{q_1, q_2, \delta_1\} \leqq \delta$. Consider the rectangular neighborhood given by

$$R \equiv R(q_1, q_2, \delta_1)=\{(p, q, y): |p| \leqq \delta, -q_2 \leqq q \leqq q_1, y_\lambda < y < h+\delta_1\}.$$

We denote the sides of R by

$$R_F=\{(p, q, y) \in R: p=-\delta, -q_2 < q < q_1\},$$

$$R_B=\{(p, q, y) \in R: p=\delta, -q_2 < q < q_1\},$$

$$R_T=\{(p, q, y) \in R: |p| < \delta, q=q_1\},$$

$$R_{B \circ T}=\{(p, q, y) \in R: |p| < \delta, q=-q_2\}.$$

By choosing δ smaller, if necessary, we may assume that $R \in \mathcal{M}^+$, trajectories enter R through $R_T \cup R_{B \circ T}$, and leave R through $R_F \cup R_B$. Note that $M_y^-(t)$ leaves R through R_F, and $M_y^+(t)$ leaves R through R_B.

Let $\Phi_M: C \to R^3$ be a y-homeomorphism such that $\Phi_M(C)=R(q_1, q_2, \delta_1)$, $\Phi_M(C_T)=R_T$, $\Phi_M(C_{BT})=R_{B \circ T}$, $\Phi_M(C_F)=R_F$, and $\Phi_M(C_{BK})=R_B$. This map satisfies (a)-(d) of the proposition. We now show that it is possible to choose the constants q_1, q_2, and δ_1 so that Φ_M satisfies (e) and (f).

In order to verify (e), we must demonstrate that each trajectory which leaves R must eventually either return to R or enter N_L. Note that trajectories can only leave R through R_F or R_B. Suppose that $y \in [y_\lambda, h+\delta_1]$ and $\gamma_q(t)$ is the solution of (2.1) with $\varepsilon=0$ and $\gamma_q(0)=(-\delta, q, y) \in R_F$. Since $\gamma_0(t)=M_y^-(t) \to l_y$ as $t \to \infty$, it follows that if $|q|$ is sufficiently small, then $\gamma_q(t) \in N_L$ for some $t>0$. Therefore, if q_1 and q_2 are sufficiently small, then every trajectory which leaves R_F must eventually enter N_L.

We now consider trajectories which leave R through R_B. For $y \in [y_\lambda, h+\delta_1]$, let $\gamma_q(t)$ now be the solution of (2.1) with $\varepsilon=0$ and $\gamma_q(0)=(\delta, q, y) \in R_B$. If $y \in [y_\lambda, h)$, then $\gamma_0(t)=M_y^+(t) \to l_y$ as $t \to \infty$. It follows that given δ_1, q_0 can be chosen so that if $y_\lambda < y < h-\delta_1$ and $|q| < q_0$, then $\gamma_q(t) \in N_L$ for some $t \geqq 0$.

Now suppose that $|y-h| < \delta_1$. If q and δ_1 are sufficiently small, then $\gamma_q(0)$ lies close to $M_h^+(0)$. The trajectory $M_h^+(0)$ returns to R for some $t>0$ no matter how the constants q_1, q_2, and δ_1 are chosen. It is not hard to see that q_1, q_2, and δ_1 can be chosen so that if $|h-y| < \delta_1$ and $-q_1 < q < q_2$, then $\gamma_q(t)$ must also return to R. See Fig. 5. This verifies (e) of the proposition.

Finally, consider the periodic solutions $p_y(t)$. These trajectories approach $M_h^+(t)$ as $y \to h$. Recall that $M_h^+(t)$ leaves R through $R_B=\Phi_M(C_{BK})$. Therefore, choosing δ_1 smaller, if necessary, we can guarantee that if $h<y<h+\delta_1$, then $p_y(t)$ crosses R_B. $\square$

We conclude this section by considering solutions of (2.1), with $\varepsilon>0$, which pass close to MB.

COROLLARY 3.3.2. *If ε is sufficiently small and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in N_M$ for some t_0, then there exists $t_1 > t_0$ such that $\gamma(t_1) \in N_L$. Moreover, $\gamma(t)$ can only leave N_M through $\Phi_M(C_F)$, $\Phi_M(C_{BK})$, or $\Phi_M(C_L)$.*

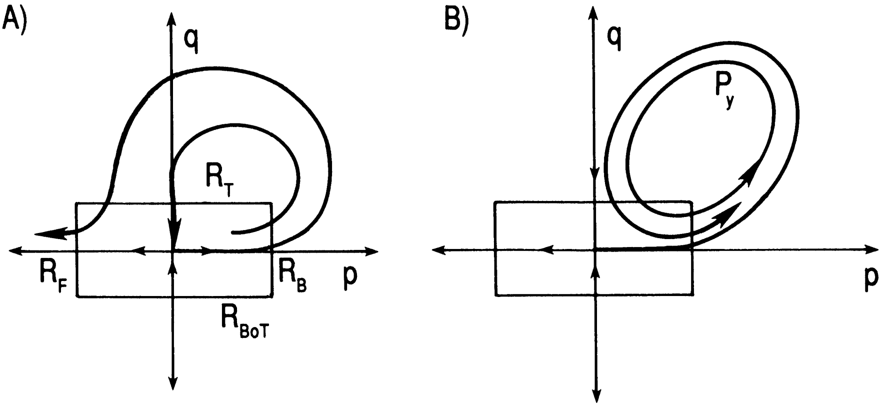


FIG. 5. *Various objects used in the proof of Proposition* 3.3.1. *In* (a), $h-\delta_1<y<h$, *while in* (b), $h<y<h+\delta_1$. *In both cases, solutions which leave R through R_B must, at some later time, enter R through R_T.*

Proof. Since $y'<0$ in N_M, $\gamma(t)$ must certainly leave N_M. From the preceding proposition, continuous dependence of solutions on a parameter, and the fact that $y'<0$ in N_M, it follows that if ε is sufficiently small, then $\gamma(t)$ can only leave N_M through $\Phi_M(C_F)$, $\Phi_M(C_{BK})$, or $\Phi_M(C_L)$. If $\gamma(t)$ leaves N_M through $\Phi_M(C_L)$, then it follows from Corollary 3.2.2 that $\gamma(t_1)\in N_L$ for some $t_1>t_0$. If $\gamma(t)$ leaves N_M through $\Phi_M(C_F)\cup\Phi_M(C_{BK})$, then from the preceding proposition, either $\gamma(t)$ returns to N_M or $\gamma(t_1)\in N_L$ for some $t_1>t_0$. However, for $\varepsilon>0$, $\gamma(t)$ can certainly only return to N_M a finite number of times without crossing through N_L. □

3.4. The periodic solutions. Recall from (A4) that each of the periodic solutions, $p_y(t)$, is asymptotically stable as a solution of (FS). Hence, for each $y\in(h,\rho+\delta_0)$ there exists a compact neighborhood of $p_y(t)$ in (v,w) phase space which is attracting. For this reason, the following proposition follows easily. For the statement of the result we let

$$A=\{(x,s,z): \tfrac{1}{2}\leqq x^2+z^2\leqq 2, -1\leqq s\leqq 1\},$$

$$\Sigma_P=\{(x,s,z)\in A: x=0, z<0\},$$

$$A_L=\{(x,s,z)\in A: s=-1\},$$

$$A_R=\{(x,s,z)\in A: s=+1\},$$

$$A_B=\{(x,s,z)\in\partial A: |s|<1\},$$

$$\Sigma_L=A_L\cap\Sigma_P.$$

PROPOSITION 3.4.1. *There exists a y-homeomorphism $\Phi_P: A\to E^3$ such that if $N_P=\Phi_P(A)$, and $\gamma(t)$ is a solution of* (2.1) *with $\varepsilon=0$, then*

(3.4.1)
(a) $N_P\subset\mathcal{M}^+$;
(b) *If $\gamma(t_0)\in\Phi_P(A_B)$, then $\gamma(t)$ enters N_P, transversely, in forward time*;
(c) $(\pi_y\circ\Phi_P)(A_L)=h+\delta_1$, *and* $(\pi_y\circ\Phi_P)(A_R)=\rho+\delta_0$;
(d) $\Phi_P(\Sigma_L)\subset\Phi_M(C_{BK})$.

The reason we can choose Φ_P so that (3.4.1)(d) holds is because of Proposition 3.3.1(f). From continuous dependence, it follows that if ε is sufficiently small, then every solution of (2.1) which lies in $\Phi_P(A_L)$ must enter N_M. Moreover, if $\varepsilon>0$, then $y'<0$ in N_P. Therefore, if ε is sufficiently small, then every solution of (2.1) which lies in N_P, must leave N_P through $\Phi_P(A_L)$ and then enter N_M. By choosing ε small we can guarantee that when this trajectory enters N_M it does so at a point whose y-coordinate satisfies $y > h$. This is because of (3.4.1)(c). We summarize this last paragraph in the next corollary.

COROLLARY 3.4.2. *If ε is sufficiently small and $\gamma(t)$ is a solution of* (2.1) *with $\gamma(t_0) \in N_P$, then there exists $t_2 > t_1 > t_0$ such that $\gamma(t) \in N_P$ for $t_0 \leqq t \leqq t_1$, $\gamma(t_1) \in \Phi_P(A_L)$, $\gamma(t) \in \mathcal{M}^+$ for $t \in (t_0, t_2)$, and $\gamma(t_2) \in N_M$. Moreover, $\pi_y(\gamma(t_2)) > h$.*

4. Existence of a bursting solution. We now use a fixed point argument to show that there must exist a periodic solution of (2.1) if $k_\lambda < k < k_h$ and ε is sufficiently small. This corresponds to the bursting solution. We demonstrate that for ε sufficiently small, the set T_ρ, which was defined following Proposition 3.1.1, is mapped continuously into itself by the flow. The existence of a periodic solution then follows from the Brouwer fixed point theorem. See Fig. 6.

Fix $\gamma_0 \in T_\rho$, and let $\gamma_\varepsilon(t)$ be the solution of (2.1) with $\gamma(0) = \gamma_0$. If $\varepsilon = 0$, then $\gamma(t)$ approaches one of the periodic solutions $p_y(t)$ as $t \to \infty$. Therefore, if ε is sufficiently small, then $\gamma(t_1) \in N_P$ for some $t_1 > 0$. We now apply Corollaries 3.1.5, 3.3.2, and 3.4.2 to conclude that there exists ε_0 such that if $0 < \varepsilon < \varepsilon_0$, then there exists $t_4 > t_3 > t_2 > t_1$ such that $\gamma(t_2) \in N_M$, $\gamma(t_3) \in N_L$, and $\gamma(t_4) \in T_\rho$. Let $\Gamma(\gamma_0) = \gamma(t_4)$. Certainly, ε_0 can be chosen independently of γ_0, and Γ is continuous. Hence, Γ must have a fixed point. This fixed point, of course, corresponds to a periodic solution of (2.1).

5. Continuous spiking. In this section we consider the existence of continuous spiking. Recall that this corresponds to a stable periodic solution of (2.1) which always

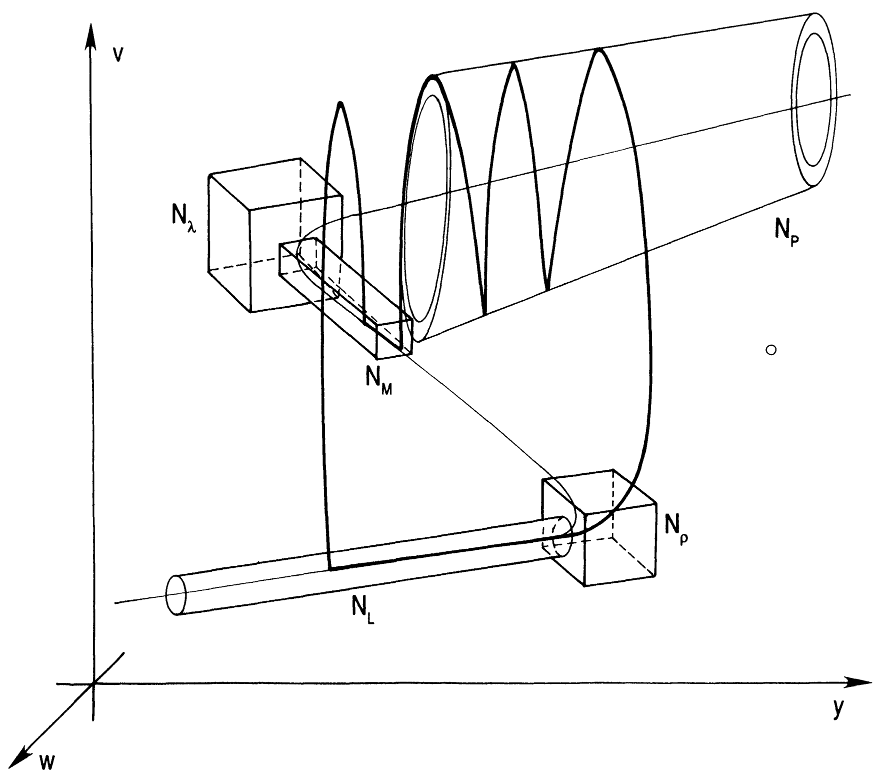


FIG. 6. *Various sets used to prove the existence of a bursting solution. Every solution of* (2.1) *which lies in N_L must, at some later time, lie in N_ρ, N_P, N_M, and then return to N_L.*

lies near the manifold $\mathcal{P}$. For our result, it will be necessary to make two additional assumptions concerning the nonlinear functions in (2.1). The first assumption is concerned with the periodic solutions $p_y(t)$ of (FS). Since (FS) is two-dimensional, each solution $p_y(t)$ can have only one Floquet multiplier, say β_y, which is not unity. We assumed, in (A4), that each trajectory $p_y(t)$ is asymptotically stable. Hence, $|\beta_y| \leqq 1$. We now make the following additional assumption.

(A8) There exists α, $h < \alpha < \rho$, such that if $h < y < \alpha$, then $|\beta_y| < 1$.

This assumption will allow us to conclude that the two-dimensional, invariant manifold $\mathcal{P}$ perturbs for ε small.

For our second additional assumption, we recall the notation defined in (A6).

(A9) If $k_h < k < k_\lambda$, then $\partial g/\partial k(v, w, y, k) > 0$ in some neighborhood of the homoclinic orbit $M_y^+(y)$.

Remark. This last assumption is satisfied for the β-cell models mentioned in the Introduction. For those models, $\partial g/\partial k > 0$ everywhere.

In (A7), we assumed that if $k = k_h$, then $\mathcal{P} \subset M_k^+$. In particular, $p_\alpha(t) \in M_{k_h}^+$ for all t. Choose $k_0 \in (k_h, k_\lambda]$ so that if $k \in [k_h, k_0]$, then $p_\alpha(t) \in M_k^+$ for all t. We can now state the main result of this section.

THEOREM 5.1. *Assume that $k_h < k < k_0$. If ε is sufficiently small, then* (2.1) *gives rise to continuous spiking.*

Remark. The range of ε for which the theorem holds depends on the choice of k.

Proof. Fix $k \in (k_h, k_0)$. For $\delta < (\alpha - h)/10$, let $S_\delta = \{(v, w, y) : h + \delta < y < \alpha - \delta\}$. We use assumption (A8) and Fenichel [9] to conclude that $\mathcal{P} \cap S_\delta$ perturbs, for ε sufficiently small, to a smooth, two-dimensional invariant manifold, which we denote by $\mathcal{P}_\varepsilon$. The constant δ will be specified later. We will show that δ can be chosen so that if ε is sufficiently small then there must exist a periodic solution which lies on $\mathcal{P}_\varepsilon$. The proof will use a fixed point argument. To set things up, we first consider the case $\varepsilon = 0$.

Let Σ be a two-dimensional section which contains each of the points $p_y(0)$, $h + \delta < y < \alpha - \delta$, and is transverse to the flow given by (2.1) with $\varepsilon = 0$. We may assume that $p_y(0)$ depends continuously on y. Hence, $\Sigma \cap \mathcal{P}$ is a continuous curve on Σ. If ε is small, the Σ will still be transverse to the flow. Moreover, $\mathcal{P}_\varepsilon \cap \Sigma$ will be a continuous curve which is the homeomorphic image of some function $\psi_\varepsilon : [-1, 2] \to \Sigma$. Let π_y be the projection map defined in § 3. We may assume that $\pi_y(\psi_\varepsilon(-1)) = h + \delta$, $\pi_y(\psi_\varepsilon(0)) = h + 2\delta$, $\pi_y(\psi_\varepsilon(1)) = \alpha - 2\delta$, $\pi_y(\psi_\varepsilon(2)) = \alpha - \delta$, and if $-2 < s_1 < s_2 < 1$, then $\pi_y(\psi_\varepsilon(s_1)) < \pi_y(\psi(s_2))$.

Let $\gamma_{\varepsilon,s}(t)$ be the solution of (2.1) with $\gamma_{\varepsilon,s}(0) = \psi_\varepsilon(s)$. If $\varepsilon = 0$, then for each $s \in [-1, 2]$, $\gamma_{0,s}(t)$ is periodic. Hence, there exists t_s such that $\gamma_{0,s}(t) \notin \Sigma$ for $0 < t < t_s$ and $\gamma_{0,s}(t_s) = \gamma_{0,s}(0) \in \Sigma$. If ε is small, and $0 \leqq s \leqq 1$, then there exists $t_{\varepsilon,s}$ such that $\gamma_{\varepsilon,s}(t) \notin \Sigma$ for $0 < t < t_{\varepsilon,s}$ and $\gamma_{\varepsilon,s}(t_{\varepsilon,s}) \in \Sigma$. Of course, $t_{\varepsilon,s} \to t_s$ as $\varepsilon \to 0$. Moreover, since $\mathcal{P}_\varepsilon$ is invariant, $\gamma_{\varepsilon,s}(t_{\varepsilon,s}) \in \mathcal{P}_\varepsilon \cap \Sigma$. Hence, for $s \in [0, 1]$, $\Phi_\varepsilon(s) = \psi_\varepsilon^{-1}(\gamma_{\varepsilon,s}(t_{\varepsilon,s}))$ is a well-defined continuous map from $[0, 1]$ into $[-1, 2]$. We will prove that for ε small, Φ_ε has a fixed point. That is, there exists an $s_0 \in [0, 1]$ such that $\gamma_{\varepsilon,s_0}(t_{\varepsilon,s_0}) = \psi_\varepsilon(s_0) = \gamma_{\varepsilon,s_0}(0)$. This implies that $\gamma_{\varepsilon,s_0}(t)$ must be a periodic solution. To prove that Φ_ε has a fixed point we will prove that if ε is sufficiently small, then $\Phi_\varepsilon(0) > 0$ and $\Phi_\varepsilon(1) < 1$. This is equivalent to proving that δ can be chosen so that for ε sufficiently small,

$$\text{(5.1)} \quad \begin{aligned} &\text{(a)} \quad \pi_y(\gamma_{\varepsilon,0}(t_{\varepsilon,0})) > h + 2\delta, \\ &\text{(b)} \quad \pi_y(\gamma_{\varepsilon,1}(t_{\varepsilon,1})) < \alpha - 2\delta. \end{aligned}$$

To prove (5.1)(b), we use the assumption that if $k \in [k_h, k_0]$ then $p_\alpha(t) \in M_k^+$ for all t. This implies that if δ is sufficiently small, then $p_{\alpha-2\delta}(t) \in \{(v, w, y): g(v, w, y, k) < 0\}$ for all t. Therefore, if $\gamma_{\varepsilon,1}(t) = (v_{\varepsilon,1}(t), w_{\varepsilon,1}(t), y_{\varepsilon,1}(t))$ and ε is sufficiently small, then $y'_{\varepsilon,1}(t) < 0$ for $|t| < 2t_{\varepsilon,1}$. Hence, $\pi_y(\gamma_{\varepsilon,1}(t_{\varepsilon,1})) = y_{\varepsilon,1}(t_{\varepsilon,1}) < y_{\varepsilon,1}(0) = \alpha - 2\delta$.

It remains to prove (5.1)(a). We must be careful with our notation because the trajectory $\gamma_{\varepsilon,0}(t)$ and the constant $t_{\varepsilon,0}$ depend on the parameters ε and δ. We will now write

$$\gamma(\varepsilon, \delta, t) = (v(\varepsilon, \delta, t), w(\varepsilon, \delta, t), y(\varepsilon, \delta, t))$$

for $\gamma_{\varepsilon,0}(t)$, and $t(\varepsilon, \delta)$ for $t_{\varepsilon,0}$. Note that $\gamma(0, \delta, t) = p_{h+2\delta}(t)$. Therefore, the trajectories $\gamma(0, \delta, t)$ approach the homoclinic trajectory $M_h^+(t)$ as $\delta \to 0$, and $t(0, \delta) \to \infty$ as $\delta \to 0$. Now (5.1)(a) will follow from the following result.

LEMMA 5.3. *Fix $k \in (k_h, k_0)$. Then δ_0 can be chosen so that if $0 < \delta < \delta_0$, then there exists $\varepsilon(\delta)$ such that if $0 < \varepsilon < \varepsilon(\delta)$, then $y(\varepsilon, \delta, t(\varepsilon, \delta)) > y(\varepsilon, \delta, 0)$.*

From the last equation in (2.1) we find that this lemma will follow if we can choose ε and δ so that

$$\int_0^{t(\varepsilon,\delta)} g(\gamma(\varepsilon, \delta, t), k)\, dt > 0. \tag{5.2}$$

In what follows, we let k_δ be such that $y_{k_\delta} = h + 2\delta$. Here we are using the notation defined in (A6). Then

$$\int_0^{t(\varepsilon,\delta)} g(\gamma(\varepsilon, \delta, t), k)\, dt = A(\delta) + B(\delta) + C(\varepsilon, \delta), \tag{5.3}$$

where

$$A(\delta) = \int_0^{t(0,\delta)} g(p_{h+2\delta}(t), k_\delta)\, dt,$$

$$B(\delta) = \int_0^{t(0,\delta)} [g(p_{h+2\delta}(t), k) - g(p_{h+2\delta}(t), k_\delta)]\, dt,$$

$$C(\varepsilon, \delta) = \int_0^{t(\varepsilon,\delta)} g(\gamma(\varepsilon, \delta, t), k)\, dt - \int_0^{t(0,\delta)} g(p_{h+2\delta}(t), k)\, dt.$$

We claim that $A(\delta)$ is uniformly bounded. That is, there exists a constant K_0 such that

$$|A(\delta)| < K_0 \quad \text{for all } \delta. \tag{5.4}$$

To prove this, recall that the trajectories $p_{h+2\delta}(t)$ approach the homoclinic orbit $M_h^+(t)$ as $\delta \to 0$. Hence, (5.4) will follow if we can prove that $\int_{-\infty}^{\infty} g(M_h^+(t), k_h)\, dt$ is bounded. This last statement holds because $M_h^+(t) \to m_h$ exponentially as $|t| \to \infty$, $g(m_h, k_h) = 0$, and g is a smooth function.

We next consider $B(\delta)$. From the mean value theorem,

$$B(\delta) = \int_0^{t(0,\delta)} \frac{\partial g}{\partial k}(p_{h+2\delta}(t), \eta(t))(k - k_\delta)\, dt \tag{5.5}$$

for some function $\eta(t) \in (k_\delta, k)$, $t \in (0, t(0, \delta))$. From assumption (A9), we can choose $\eta_0 > 0$ so that

$$\frac{\partial g}{\partial k}(p_{h+2\delta}(t), \eta(t)) > \eta_0 \quad \text{for } t \in (0, t(0, \delta)). \tag{5.6}$$

We assume that δ_0 is chosen so that if $0<\delta<\delta_0$, then

$$k_\delta < \frac{k+k_h}{2}. \tag{5.7}$$

It then follows that if $0<\delta<\delta_0$, then

$$B(\delta) > \eta_0\left(\frac{k-k_h}{2}\right) t(0,\delta). \tag{5.8}$$

Recall that $t(0,\delta)\to\infty$ as $\delta\to 0$. We assume that δ_0 is chosen so that

$$\eta_0\left(\frac{k-k_h}{2}\right) t(0,\delta) > 4K_0 \tag{5.9}$$

for $\delta\in(0,\delta_0)$.

Now fix $\delta\in(0,\delta_0)$ and consider $C(\varepsilon,\delta)$. Note that $\gamma(\varepsilon,\delta,t)\to p_{h+2\delta}(t)$ as $\varepsilon\to 0$, uniformly for $t\in(0,t(\varepsilon,\delta))$. Moreover, $t(\varepsilon,\delta)\to t(0,\delta)$ as $\varepsilon\to 0$. Therefore, there exists $\varepsilon(\delta)$ such that if $0<\varepsilon<\varepsilon(\delta)$, then

$$|C(\varepsilon,\delta)| \leqq \eta_0\left(\frac{k-k_h}{4}\right) t(0,\delta). \tag{5.10}$$

Combining (5.3), (5.4), (5.8), (5.9), and (5.10), we conclude that (5.2) holds

This completes the proof of Lemma 5.3, which in turn implies that ε and δ can be chosen so that (5.1)(a) holds. From our previous remarks, this demonstrates that there must exist a periodic solution on $\mathcal{P}_\varepsilon$. Using (A8) and the fact that the flow on $\mathcal{P}_\varepsilon$ is two-dimensional, it is not hard to see that there must, in fact, exist a stable periodic solution on $\mathcal{P}_\varepsilon$. □

6. The transition from n to $n+1$ spikes.

6.1. Introduction. Throughout this section we assume that $k_\rho<k<k_h$. In § 4 we proved that, in this case, there must exist a bursting solution for ε sufficiently small. By one "burst" of the bursting solution, we mean one period of the solution. It is easy to see that as ε approaches zero, the number of spikes per burst becomes unbounded. This is because the bursting solution spends an increasing amount of time near the branch of periodic solutions $\mathcal{P}$. We consider how the number of spikes per burst increases as ε decreases. To do this we must first define a notion of winding number for each bursting solution. This corresponds to the number of spikes per burst. It is equal to the number of times the solution winds around the upper branch during one period. There are actually two ways in which a solution $\gamma(t)$ of (2.1) can wind around the upper branch; either $\gamma(t)$ lies close to one of the periodic solutions $p_y(t)$, or it lies close to one of the trajectories $M_y^+(t)$. The key to locating the Smale horseshoe will be to understand how this winding number changes as ε is varied. We demonstrate that the winding number can change only if $\gamma(t)$ passes close to the left knee K_λ. This implies that the width of each burst increases during the process of adding one spike. In order to make this precise we first need to understand the set of all trajectories which pass close to the left knee.

6.2. The "stable manifold" of the left knee. Consider (2.1) with $\varepsilon=0$. For each $y\in(\lambda,\rho)$, m_y is a saddle with two trajectories in its stable manifold. Let W_M be the union of all of these trajectories. Then W_M is an invariant, two-dimensional manifold; it is in the center stable manifold of the middle branch. Because each of the rest points m_y, $\lambda<y<\rho$, is hyperbolic, W_M perturbs, for small ε, to an invariant, two-dimensional manifold which we denote by $W_M(\varepsilon)$. See Fenichel [9].

Note that W_M divides N_M into two closed regions. Therefore, if ε is sufficiently small, then $W_M(\varepsilon)$ divides N_M into two closed regions, which we denote by N_M^+ and N_M^-. We assume, without loss of generality, that each of the trajectories $M_y^+(t)$ leaves N_M through N_M^+, and each of the trajectories $M_y^-(t)$ leaves N_M through N_M^-. Let $\Sigma_\lambda = N_M^+ \cap \Phi_M(C_L)$. This is the "left side" of N_M^+, which lies close to the left knee K_λ.

Suppose that ε is sufficiently small, and $\gamma(t)$ is a solution of (2.1) with $\gamma(t_0) \in W_M(\varepsilon) \cap N_M$. Then, from Corollary 3.3.2 there exists $t_1 > t_0$ such that

$$\gamma(t) \in N_M \quad \text{for } t \in (t_0, t_1) \quad \text{and} \quad \gamma(t_1) \in \Phi_M(C_F) \cup \Phi_M(C_{BK}) \cup \Phi_M(C_L).$$

Since $W_M(\varepsilon)$ lies close to W_M, and $W_M \cap (\Phi_M(C_F) \cup \Phi_M(C_{BK})) = \varnothing$, we conclude that $\gamma(t_1) \in \Phi_M(C_L)$, the left side of N_M. Therefore, each trajectory in $W_M(\varepsilon)$ must intersect N_M and leave N_M through its left side $\Phi_M(C_L)$.

6.3. The winding number. Throughout this section we assume that $\varepsilon > 0$ is sufficiently small. Fix $\gamma_0 \in N_L \cup N_\rho$ and let $\gamma_\varepsilon(t)$ be the solution of (2.1) with $\gamma_\varepsilon(0) = \gamma_0$. We now define what we mean by the winding number $\omega_\varepsilon(\gamma_0)$ of this trajectory with respect to γ_0.

In § 3 we saw that there exists $t_2 > t_1 > 0$ such that $\gamma_\varepsilon(t) \in N_L \cup N_\rho$ for $0 \leqq t \leqq t_1$, $\gamma_\varepsilon(t) \notin N_L \cup N_\rho$ for $t_1 < t < t_2$, and $\gamma_\varepsilon(t_2) \in N_L \cup N_\rho$. Let $\Sigma = \Phi_P(\Sigma_P) \cup \Phi_M(C_{BK}) \cup \Sigma_\lambda$, where $\Phi_P(\Sigma_P)$ was defined in § 3.4, $\Phi_M(C_{BK})$ was discussed in § 3.3, and Σ_λ was defined in § 6.2. Let $\omega_\varepsilon(\gamma_0)$ equal to the number of times $\gamma_\varepsilon(t)$ intersects Σ for $0 < t < t_2$. Note that $\gamma_\varepsilon(t)$ can only intersect Σ transversely. Hence, $\omega_\varepsilon(\gamma_0)$ depends continuously on ε and γ_0.

In our next result we study how the winding number changes as ε is varied.

PROPOSITION 6.3.1. *Suppose that* $0 < \varepsilon_1 < \varepsilon_2$ *are sufficiently small,* $\gamma_0 \in N_L \cup N_\rho$ *and* $\omega_{\varepsilon_1}(\gamma_0) \neq \omega_{\varepsilon_2}(\gamma_0)$. *Then there exists* $\varepsilon \in (\varepsilon_1, \varepsilon_2)$ *such that* $\gamma_0 \in W_M(\varepsilon)$.

Proof. Because the trajectories $\gamma_\varepsilon(t)$ cross Σ transversely, there must exist $\varepsilon \in (\varepsilon_1, \varepsilon_2)$ and $t_0 > 0$ such that $\gamma_\varepsilon(t_0) \in \partial\Sigma$. From Corollary 3.3.2 and the fact that N_P is attracting it follows that $\gamma(\varepsilon)(t_0) \notin \partial(\Phi_M(C_{BK}) \cup \Phi_P(\Sigma_P))$. Therefore, $\gamma_\varepsilon(t_0) \in \partial(\Sigma_\lambda) \backslash \partial(\Phi_M(C_{BK}))$. From the definitions, this last set is contained in $W_M(\varepsilon)$, so the proof is complete. $\square$

Remarks. (1) It follows easily from our constructions that when the winding number changes it does so by exactly one.

(2) Note that for each $\gamma_0 \in N_L \cup N_\rho$ $\omega_\varepsilon(\gamma_0) \to \infty$ as $\varepsilon \to 0$. This is because for ε small, $\gamma_\varepsilon(t)$ will at some time lie arbitrarily close to one of the periodic solutions $p_y(t)$. Each of these periodic solutions crosses Σ infinitely often. Therefore, the number of times $\gamma_\varepsilon(t)$ crosses Σ will become unbounded as $\varepsilon \to 0$.

(3) Fix $\gamma_0 \in N_L \cup N_\rho$. The previous two remarks imply that there exists a positive integer N_0 such that for each integer $N > N_0$ there exists ε_N such that $\gamma_0 \in W_M(\varepsilon_N)$ and $\omega_{\varepsilon_N}(\gamma_0) = N$.

6.4. The Smale horseshoe. In the Introduction, we stated that it is possible for a Smale horseshoe to exist for the flow defined by (2.1). Whether or not a Smale horseshoe exists depends in a crucial way on the structure of the slow dynamics. We now elaborate on these statements. We first prove a proposition which gives a sufficient condition for the flow to give rise to a Smale horseshoe. As we show in § 7, this sufficient condition can be easily tested numerically for a specific set of equations. In § 6.5, we prove, analytically, that there do exist functions $f_1(v, w, y)$, $f_2(v, w, y)$, and $g(v, w, y, k)$ which satisfy (A1)-(A9) so that this sufficient condition is satisfied. In § 6.6, we discuss when (2.1) does not give rise to a Smale horseshoe. In this case, the process of adding one spike will be continuous.

The Smale horseshoe will arise from a certain return map defined by the flow. We now define certain subsets of phase space which will allow us to define and describe the important properties of this map.

Consider the trajectories $M_y^+(t)$ and $M_y^-(t)$ which were defined in (A3). Recall that for each $y \in (\lambda, h)$, $\lim_{t\to\infty} M_y^-(t) = l_y$ and $\lim_{t\to\infty} M_y^+(t) = l_y$. Therefore, $M_y^+(t)$ and $M_y^-(t)$ must lie in N_L for t sufficiently large. That is, if $\lambda < y < h$, then there exists t_y^+ and t_y^- such that $M_y^-(t) \in N_L$ if and only if $t \geqq t_y^-$, and $M_y^+(t) \in N_L$ if and only if $t \geqq t_y^+$. If $y = h$, then it is still true that $\lim_{t\to\infty} M_h^-(t) = l_y$. Choose t_h so that $M_h^-(t) \in N_L$ if and only if $t \geqq t_h$.

We now assume that the trajectories $M_y^+(t)$ and $M_y^-(t)$ coalesce as $y \to \lambda$ to form one trajectory $M_\lambda(t)$. This assumption may not follow from our previous assumptions, however all of the solutions we are actually interested in are bounded away from the set where $y = \lambda$. For this reason, we may redefine the flow in a smooth fashion in the set where $y < \lambda + \delta$, for δ small, without changing the solutions of interest. Choose t_λ so that $M_\lambda(t) \in N_L$ if and only if $t \geqq t_\lambda$. Note that $t_\lambda = \lim_{y \searrow \lambda} t_y^+ = \lim_{y \searrow \lambda} t_y^-$.

Now let S equal to the union of the points:

(a) $M_y^+(t_y^+)$ for $\lambda < y < h$;

(b) $M_y^-(t_y^-)$ for $\lambda < y < h$;

(c) $M_\lambda(t_\lambda)$;

(d) $M_y^-(t_h)$.

Note that $S \subset \partial N_L$. For convenience, we assume that $S \subset \Phi_L(C_T) \equiv N^T$, where we are using notation defined in § 3.1. Since S is homeomorphic to a circle, there exists a y-homeomorphism Φ_S from the unit circle S^1 into N^T such that $\Phi_S(S^1) = S$. Let

$$\begin{aligned} &\mathcal{A} = \{(x, s): \tfrac{1}{2} < x^2 + s^2 < 2\}, && \mathcal{D} = \{(x, s): x^2 + s^2 < 2\}, \\ &\mathcal{D}_1 = \{(x, s): x^2 + s^2 < \tfrac{1}{2}\}, && \mathcal{H}_r = \{(x, s) \in \mathcal{D}: s < r\}. \end{aligned} \tag{6.4.1}$$

Clearly, we can extend Φ_S to a y-homeomorphism $\Phi_H : \mathcal{D} \to N^T$. Let $D = \Phi_H(\mathcal{D})$, $D_1 = \Phi_H(\mathcal{D}_1)$, $H = \Phi_H(\mathcal{A})$, and for $|r| < \frac{1}{2}$, $H_r = \Phi_H(\mathcal{H}_r)$.

These sets are illustrated in Fig. 7. Note that H is an open neighborhood of S in N^T.

LEMMA 6.4.1. *If ε is sufficiently small, then the flow given by* (2.1) *defines a continuous map $\Phi_\varepsilon : D \to H$.*

Proof. Fix $\gamma_0 \in D$ and let $\gamma(t)$ be the solution of (2.1) with $\gamma(0) = \gamma_0$. We need to prove that there exists $t_0 > 0$ such that $\gamma(t) \notin D$ for $0 < t < t_0$, and $\gamma(t_0) \in H$.

From the discussion in § 3, we know that there exists $t_0 > 0$ such that $\gamma(t) \notin \partial N_L$ for $0 < t < t_0$ and $\gamma(t_0) \in \partial N_L$. It only remains to prove that if ε is sufficiently small, then $\gamma(t_0) \in H$. However, when $\gamma(t)$ leaves N_M, the neighborhood of the middle branch, it must do so close to one of the trajectories M_y^+ or $M_y^-(t)$ for $\lambda \leqq y \leqq h$. We can see that this is true by choosing the constants q_0 and δ_1 in the proof of Proposition 3.3.1 to be very small. Now each of the trajectories M_y^+, $\lambda < y < h$, and M_y^-, $\lambda < y \leqq h$, enter N_L through H. Since H is open, it follows that if ε is sufficiently small, then $\gamma(t)$ must also enter N_L through H, and the result follows. The map Φ_ε is illustrated in Fig. 8. □

We now give sufficient conditions for Φ_ε to give rise to a Smale horseshoe. See Fig. 10. In what follows we always assume that ε is sufficiently small.

PROPOSITION 6.4.2. *Suppose that there exists $\gamma_1 \in D_1$ and $\gamma_2 \in D_1$ such that $|\omega_\varepsilon(\gamma_1) - \omega_\varepsilon(\gamma_2)| > 2$. Then Φ_ε gives rise to a Smale horseshoe.*

Proof. The proof of this result is broken up into a number of steps. In what follows, we say that C *is a curve in* D if there exists a continuous function $\mathcal{C} : [0, 1] \to D$

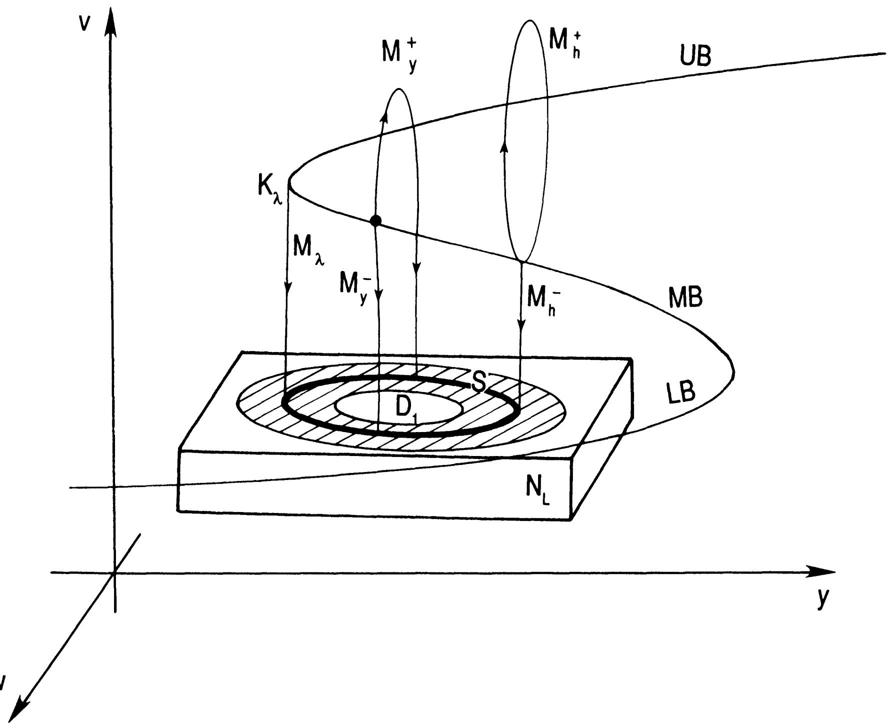


FIG. 7. *Various subsets of N_L. S is where the unstable manifold of the middle branch, $\lambda < y < h$, enters N_L. H is a neighborhood of S on ∂N_L. Every bursting solution must enter N_L through H.*

such that C is the image of $\mathscr{C}$. We say that C *crosses* D if there exists a continuous function $\mathscr{C}:[0,1]\to \text{cl } D$ such that C is the image of $\mathscr{C}$, $\mathscr{C}(s)\in D$ for $s\in(0,1)$, $\mathscr{C}(0)\in\partial D$, and $\mathscr{C}(1)\in\partial D$.

Let $C=\text{Im } \mathscr{C}(s)$, $0\leqq s\leqq 1$, be any curve in D such that $\mathscr{C}(0)=\gamma_1$ and $\mathscr{C}(1)=\gamma_2$. Because $\omega_\varepsilon(\gamma_1)\neq\omega_\varepsilon(\gamma_2)$, there must exist $s_1\in(0,1)$ such that $\mathscr{C}(s_1)\in W_M(\varepsilon)$. This follows from an argument similar to the proof of Proposition 6.3.1. Moreover, $\omega_\varepsilon(\mathscr{C}(s))$ can change by at most one at a time as s is varied. This, together with the assumption that $|\omega_\varepsilon(\gamma_1)-\omega_\varepsilon(\gamma_2)|>2$, implies that there exists s_1 and s_2 such that for $i=1$, 2, $\mathscr{C}(s_i)\in W_M(\varepsilon)$, and $\omega_\varepsilon(\mathscr{C}(s_1))=\omega_\varepsilon(\mathscr{C}(s_2))+2$.

We have now shown that $W_M(\varepsilon)$ intersects D in at least two distinct points. However, $W_M(\varepsilon)$ is a two-dimensional manifold which intersects D transversely. Therefore, $W_M(\varepsilon)$ must intersect D in at least two curves which cross D. We denote these curves by C_1 and C_2. They have the property that $\mathscr{C}(s_i)\in C_i$, $i=1$, 2, and the winding number is constant along each curve.

Let M be the subset of D bounded by C_1, C_2, and ∂D. See Fig. 9. We claim that the map $\Phi_\varepsilon: M\to H$ satisfies the conditions necessary for a Smale horseshoe. To prove this, we let $\hat{C}=\text{Image } \hat{\mathscr{C}}(s)$, $0\leqq s\leqq 1$, be any curve in D which satisfies $\hat{\mathscr{C}}(0)\in C_1$, $\hat{\mathscr{C}}(1)\in C_2$, and $\hat{\mathscr{C}}(s)\in M$ for $0\leqq s\leqq 1$. Then $\Phi_\varepsilon(\hat{C})$ is a curve which lies in H. Now H is topologically an annulus. Because $|\omega_\varepsilon(\hat{\mathscr{C}}(0))-\omega_\varepsilon(\hat{\mathscr{C}}(1))|=2$, it follows that $\Phi_\varepsilon(\hat{\mathscr{C}})$ is a curve which wraps around (in the obvious sense) H twice. See Fig. 9. Since $\hat{C}$ was an arbitrary curve in M which connects C_1 with C_2, it follows that $\Phi_\varepsilon(M)$ intersects M in such a way that it gives rise to a Smale horseshoe, and the proof is complete. □

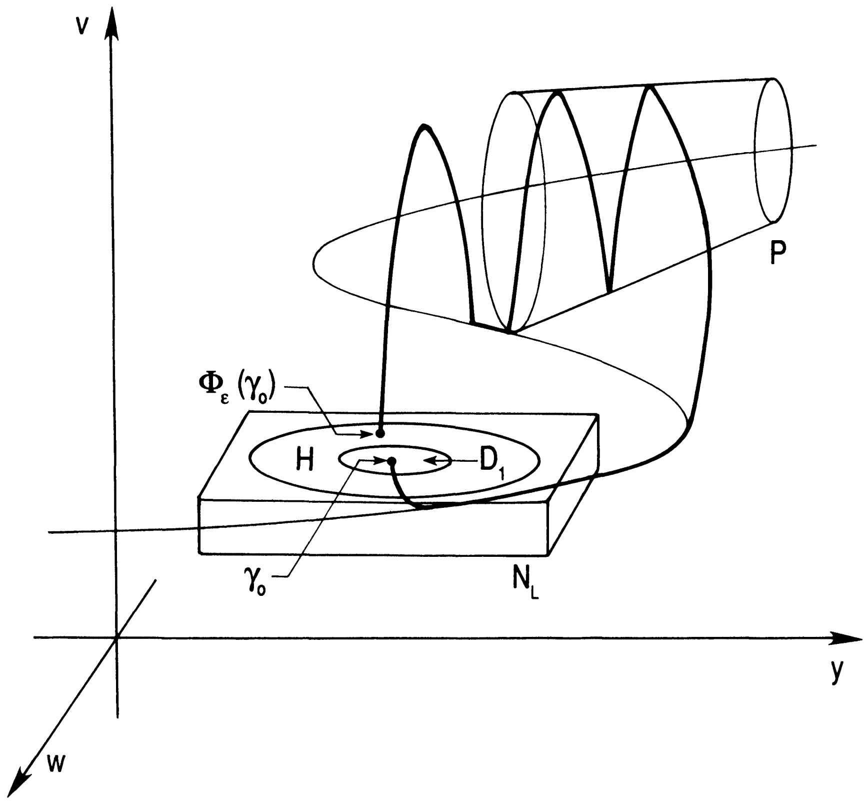


FIG. 8. *The return map used in the construction of a Smale horseshoe. Every trajectory which starts in D must, at some later time, cross H. This defines a continuous map $\Phi_\varepsilon : D \to H$.*

Remark 1. With additional assumptions one can prove that the horseshoe just described is hyperbolic. Sufficient additional assumptions which guarantee this are the following. Each of these assumptions is concerned with solutions of the fast subsystem (FS).

(H1) The eigenvalues of the fixed points l_y on the lower branch form two continuous functions $\lambda_1(y)$ and $\lambda_2(y)$ for $\lambda < y < \rho$. These functions can be chosen so that $\lambda_2(y) < \lambda_1(y) < 0$ for each y. Moreover, each of the trajectories $M_y^+(t)$ and $M_y^-(t)$, $\lambda < y < h$, approach l_y tangent to an eigenvector corresponding to $\lambda_1(y)$.

(H2) Near K_ρ the fixed points of (FS) can be parametrized as a curve $(v(s), w(s), y(s))$ such that $(v(0), w(0), y(0)) = K_\rho$. Our previous assumptions imply that $y'(0) = 0$. We now require that $y''(0) \neq 0$.

(H3) The homoclinic orbit $M_h^+(t)$ arises from a transverse intersection of the center stable and center unstable manifolds of the middle branch. Note that each of these manifolds is two-dimensional. The center unstable manifold of the middle branch is the union of trajectories $M_y^+(t)$ and $M_y^-(t)$ for $\lambda < y < \rho$. The center stable manifold of the middle branch is the manifold W_M described in § 6.2.

With these assumptions we are able to define local coordinates near each "piece" of phase space. That is, (H1) allows us to define local coordinates near the lower

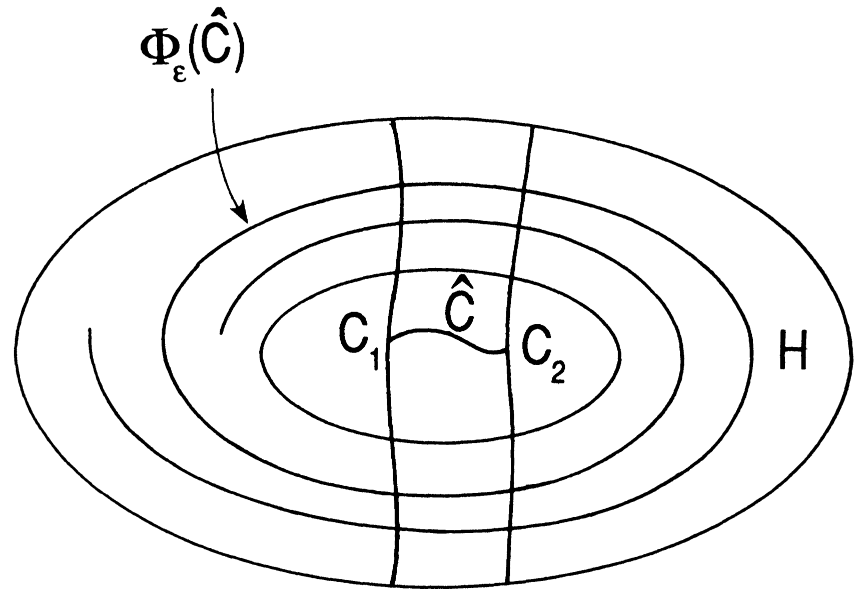


FIG. 9. *Various sets used in the proof of Proposition* 6.4.2. *The winding number ω_ε is constant along each curve C_1 and C_2 with $\omega_\varepsilon(C_1) = \omega_\varepsilon(C_2) + 2$. If $\hat{C}$ is any curve which connects C_1 with C_2, then $\Phi_\varepsilon(\hat{C})$ must wind around H twice.*

branch, (H2) allows us to define local coordinates near the right knee K_ρ, (A8) allows us to define local coordinates near $\mathcal{P}$, and (A2) allows us to define local coordinates near the middle branch. (H3) allows us to carefully keep track of trajectories which pass close to the homoclinic orbit $M_h^+(t)$. With these local coordinates we can compute $D\Phi_\varepsilon$, the linearization of the return map Φ_ε. It is properties of this linearized map which allows us to conclude that the Smale horseshoe is hyperbolic. See Guckenheimer and Holmes [10, p. 241].

The analysis just described is very technical and will be presented, in detail, in a later paper.

Remark 2. Suppose that Φ_ε does give rise to a hyperbolic horseshoe, and assume that Λ is the maximal invariant set of Φ_ε. It is well known that on Λ, Φ_ε is topologically equivalent to the shift map on the set of biinfinite sequences of two symbols. We now discuss what this implies about the nature of bursting solutions of (2.1).

The set Λ is contained in a set of the form $M \cap \Phi_\varepsilon(M)$ where M is as in the proof of the proposition. Now $M \cap \Phi_\varepsilon(M) = M_1 \cup M_2 \subset H$, where $M_1 \cap M_2 = \emptyset$. See Fig. 10. Since H lies close to where the trajectories $M_y^-(t)$ and $M_y^+(t)$, $\lambda < y < h$, enter N_L, we may choose M_1 and M_2 so that M_1 lies close to where the trajectories $M_y^-(t)$ enter N_L, and M_2 lies close to where the trajectories $M_y^+(t)$ enter N_L. This implies that if γ_1 and γ_2 are two points in Λ, such that $\Phi_\varepsilon(\gamma_1) \in M_1$ and $\Phi_\varepsilon(\gamma_2) \in M_2$, then $\omega_\varepsilon(\gamma_2) = \omega_\varepsilon(\gamma_1) + 1$. Another way to say this is that if $\gamma_1(t)$ and $\gamma_2(t)$ are the solutions of (2.1) with $\gamma_1(0) = \gamma_1$ and $\gamma_2(0) = \gamma_2$, and t_1, t_2 are chosen so that $\gamma_1(t_1) = \Phi_\varepsilon(\gamma_1)$, $\gamma_2(t_2) = \Phi_\varepsilon(\gamma_2)$, then $\gamma_1(t)$ has one less spike during its burst, $0 < t < t_1$, than $\gamma_2(t)$ has during its burst, $0 < t < t_2$.

Let n be the positive integer such that if $\Phi_\varepsilon(\gamma_1) \in M_1$, then $\omega_\varepsilon(\gamma_1) = n$, and let Γ be the set of all biinfinite sequences $\{a_i\}$, where $a_i \in \{n, n+1\}$. Let $\sigma: \Lambda \to \Gamma$ be the map defined by $\sigma(\gamma_0) = \{a_i\}$, where $a_i = n$ if $\Phi_\varepsilon^i(\gamma_0) \in M_1$ and $a_i = n+1$ if $\Phi_\varepsilon^i(\gamma_0) \in M_2$. This map is a bijection. Therefore, if $\{a_i\}$ is any element of Γ, there exists a point $\gamma_0 \in \Lambda$

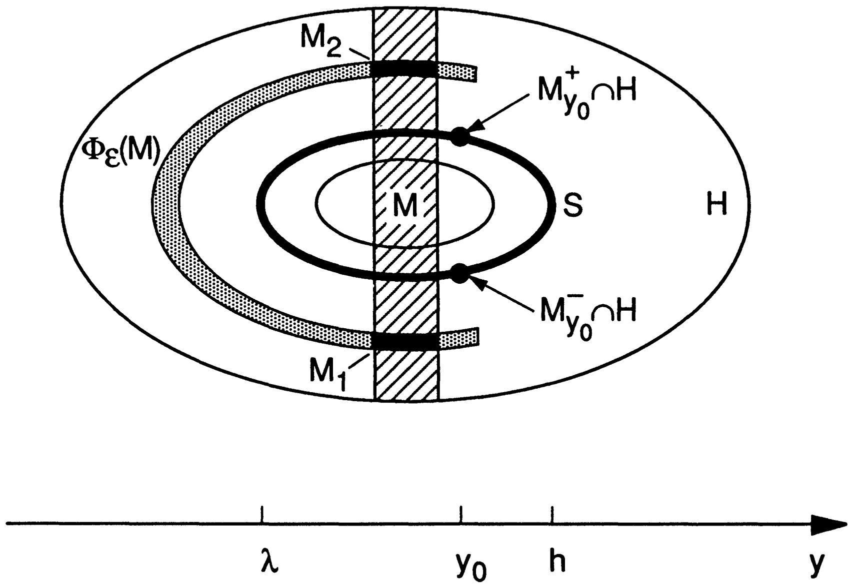


FIG. 10. *In this case, Φ_ε gives rise to a Smale horseshoe.*

such that $\sigma(\gamma_0) = \{a_i\}$. Let $\gamma(t)$ be the solution of (2.1) with $\gamma(0) = \gamma_0$ and choose $\{t_i\}$ so that $\gamma(t_i) = \Phi^i_\varepsilon(\gamma_0)$. Our previous discussion implies that $\omega_\varepsilon(\gamma(t_i)) = a_i$, or the number of spikes in the ith burst, $t_{i-1} < t < t_i$, is a_i.

Remark 3. We may expect that the proposition remains valid if $|\omega_\varepsilon(\gamma_1) - \omega_\varepsilon(\gamma_2)| = 2$. This will indeed be the case if (H1)-(H3) are satisfied. It is also possible that a Smale horseshoe exists even though $|\omega_\varepsilon(\gamma_1) - \omega_\varepsilon(\gamma_2)| \leqq 1$ for all $\gamma_1, \gamma_2 \in D$. An example of this is demonstrated numerically in § 7.

Remark 4. Suppose that there exist $\gamma_1, \gamma_2 \in D$ such that $|\omega_\varepsilon(\gamma_1) - \omega_\varepsilon(\gamma_2)| = k > 2$. Then M can be chosen so that $\Phi_\varepsilon(M)$ wraps around H, k times. Hence, Φ_ε gives rise to a Smale horseshoe which wraps around at least $k-1$ times. An example of this, with $k = 4$, is presented in § 7.

6.5. Nonlinearities which give rise to a Smale horseshoe. We now demonstrate that it is possible to choose the nonlinearities in (2.1) so that the corresponding map Φ_ε gives rise to a Smale horseshoe. In fact, we will prove the following stronger result. For this result we assume that $g(v, w, y) = g(v, w, y, k)$ for some fixed $k \in (k_p, k_h)$.

PROPOSITION 6.5.1. *Assume that the functions $f_1(v, w, y)$ and $f_2(v, w, y)$ satisfy* (A1)-(A5) *and fix K. Then there exists a function $g(v, w, y)$ which satisfies* (A6) *and* (A7), *so that if ε is sufficiently small, then $|\omega_\varepsilon(\gamma_1) - \omega_\varepsilon(\gamma_2)| = K$ for some $\gamma_1, \gamma_2 \in D_1$.*

Proof. Recall the sets N_L, N_p, and T_p which were defined in § 3. We assume that $g(v, w, y) = 1$ in $N_L \cup N_p$. Each trajectory which passes through a point in D_1 must enter N_L, then enter N_p, and then leave N_p through T_p. Fix $\gamma_1 \in D_1$, $\gamma_2 \in D_1$, and let $\gamma_i(t) = (v_i(t), w_i(t), y_i(t))$ be the solution of (2.1) which satisfies $\gamma_i(0) = \gamma_i$, $i = 1, 2$. Choose t_1 and t_2 so that for $i = 1, 2$, $\gamma_i(t_i) \in T_p$ and $\gamma_i(t) \notin T_p$ for $0 < t < t_i$. Suppose that $y_i = \pi_y(\gamma_i(t_i))$. We assume that $y_1 \neq y_2$. For this to be true it may be necessary to change γ_1 and γ_2 or adjust T_p. Without loss of generality we assume that $y_1 < y_2$.

We now follow $\gamma_1(t)$ and $\gamma_2(t)$ forward in time. Each of these trajectories will enter N_P, the neighborhood of the periodic solutions. Suppose that, for $i = 1, 2$, $\gamma_i(t)$ enters N_P at $t = \hat{t}_i$. By choosing $g(v, w, y)$ appropriately we may assume that for some $\delta > 0$,

$$\max \{y_1(t): t_1 < t < \tilde{t}_1\} \equiv y_0 < y_0 + 2\delta = y_2(\tilde{t}_2).$$

In what follows we assume that

$$g(v, w, y) = -\tau \quad \text{in } N_P \cap \{(v, w, y): y > y_0 + \delta\},$$

where τ is a small positive constant, to be determined. Outside of this region we assume that $g(v, w, y)$ is chosen so that (A6) and (A7) are satisfied. In particular, we assume that g is fixed in the region $\{(v, w, y): y \leqq y_0\}$. Hence, $\omega_\varepsilon(\gamma_1)$ is now well defined. We show that it is possible to choose τ so that $\omega_\varepsilon(\gamma_2) > \omega_\varepsilon(\gamma_1) + K$.

Let $t_0 = \hat{t}_2 + \delta/\varepsilon\tau$. Then $y_2(t_0) = y_0 + \delta$ and $y_2(t) > y_0 + \delta$ for $\hat{t}_2 < t < t_0$. Because $t_0 \to \infty$ as $\tau \to 0$, we may choose τ so small that for $\hat{t}_2 < t < t_0$, $\gamma_2(t)$ winds around in N_P as many times as we please. Therefore, by choosing τ small we may assume that $\omega_\varepsilon(\gamma_2)$ is as large as we please. In particular, we may choose τ so small that $\omega_\varepsilon(\gamma_2) > \omega_\varepsilon(\gamma_1) + K$. □

6.6. Smooth transition from *n* to *n*+1 spikes. We now discuss one way in which it is possible that (2.1) does not give rise to a Smale horseshoe. In this case the transition from n to $n+1$ spikes is continuous. As ε is adjusted, there always exists a stable periodic solution of (2.1) which varies continuously with ε. As ε is varied the period of the bursting solution increases. This is because the periodic solution travels up the middle branch an increasing amount of time. The new spike is added at the value of ε for which the periodic solution travels all the way up the middle branch until it reaches close to the left knee. We wish to give conditions on the nonlinearities in (2.1), which guarantee that this happens. In what follows we assume that the fast dynamics f_1 and f_2 is fixed. We show that a smooth transition takes place if g is chosen so that the slow dynamics in the passive phase is much slower than the slow dynamics in the active phase.

For $|r| < \frac{1}{2}$, let H_r be the set defined in (6.4.1). Suppose that for each r, $\Phi_\varepsilon(H_r) \subset H_r$. This implies that Φ_ε has a fixed point in each H_r. This fixed point, of course, corresponds to a periodic, or bursting, solution of (2.1). For r close to $-\frac{1}{2}$, this bursting solution must travel up the middle branch close to the left knee. It therefore corresponds to a bursting solution with a long period. We now find conditions on the slow dynamics which guarantee that $\Phi_\varepsilon(H_r) \subset H_r$ for $|r| < \frac{1}{2}$. In this case, we do not expect that Φ_ε gives rise to a Smale horseshoe.

The essential idea of this analysis is the following. For $h \in H_r$, let $\gamma(h)(t)$ be the solution of (2.1) with $\gamma(h)(0) = h$. As $\gamma(H_r)$ passes near the lower branch, it contracts in size at an exponential rate. Later, when it passes near the middle branch, it stretches at an exponential rate. In order for H_r to be mapped into itself, we must have that the contraction near the lower branch be greater than the stretching near the middle branch. This can be accomplished by choosing the rate of the slow dynamics near the lower branch to be much less than the rate of the slow dynamics near the middle branch.

In order to simplify the discussion we assume that (2.1) is linear near the lower and middle branches. That is, in N_L, we assume that (2.1) is given by

$$\begin{aligned} v' &= -\lambda_1(v - v_l), \\ w' &= -\lambda_2(w - w_l), \qquad (6.6.1) \\ y' &= \varepsilon_1, \end{aligned}$$

while in N_M, (2.1) is given by

$$
\begin{aligned}
v' &= -\gamma_1(v - v_m),\\
w' &= \gamma_2(w - w_m), \qquad (6.6.2)\\
y' &= -\varepsilon_2.
\end{aligned}
$$

We also take N_L and N_M to be rectangular boxes. That is, there exists (v_l, w_l), (v_m, w_m), and $\beta > 0$ such that

$$N_L = \{(v, w, y): |v - v_l| \leqq \beta, |w - w_l| \leqq \beta, \lambda - \delta \leqq y \leqq y_\rho\},$$

$$N_M = \{(v, w, y): |v - v_m| \leqq \beta, |w - w_m| \leqq \beta, y_\lambda \leqq y \leqq h + \delta_1\}.$$

Choose $r_0 \in (\lambda, h)$ such that $H_r \subset \{(v, w, y): \lambda - \delta \leqq y \leqq r_0\}$.

We now follow H_r in forward time until it crosses L_ρ. Fix $\gamma_0 = (v_0, w_0, y_0) \in H_r$, and let $\gamma(t) = \gamma(h_0)(t)$. Choose t_0 so that $\gamma(t_0) \in L_\rho$. From (6.6.1), and the definition of L_ρ, we have that $y(t_0) = y_0 + \varepsilon_1 t_0 = y_\rho$, or $t_0 = (y_\rho - y_0)/\varepsilon_1$. We then conclude from (6.6.1) that

$$|v(t_0) - v_l| = |v(0) - v_l|\, e^{-\lambda_1 t_0} \leqq \beta \exp\left[-\lambda_1\left(\frac{y_\rho - y_0}{\varepsilon_1}\right)\right],$$

$$|w(t_0) - w_l| = |w(0) - w_l|\, e^{-\lambda_2 t_0} \leqq \beta \exp\left[-\lambda_2\left(\frac{y_\rho - y_0}{\varepsilon_1}\right)\right].$$

Now if $\gamma_0 \in H_r$, then $\lambda - \delta \leqq y_0 \leqq r_0$. Assume, without loss of generality, that $\lambda_1 < \lambda_2$. It therefore follows that

$$
\begin{aligned}
\beta \exp\left[-\lambda_2\left(\frac{y_\rho - \lambda + \delta}{\varepsilon_1}\right)\right] &\leqq \|(v(t_0), w(t_0)) - (v_l, w_l)\| \qquad (6.6.3)\\
&\leqq 2\beta \exp\left[-\lambda_1\left(\frac{y_\rho - r_0}{\varepsilon_1}\right)\right].
\end{aligned}
$$

This gives us an estimate of how much $\gamma(H_r)$ is contracted by the flow as it passes near the lower branch.

We now wish to estimate how much $\gamma(H_r)$ is stretched as it passes near the middle branch. Recall that we are trying to find conditions on the parameters so that $\Phi_\varepsilon(H_r) \subset H_r$. What we will do is follow H_r backward in time and estimate how much it is contracted by the backward flow as it passes through N_M. Fix $\gamma_0 = (v_0, w_0, y_0) \in H_r$ and let $\gamma(t)$ be the solution of (2.1) with $\gamma(0) = \gamma_0$. We assume, as before, that $\lambda - \delta < y_0 < r_0$ for $\gamma_0 \in H_r$. Choose $t_2 < t_1 < 0$ so that $\gamma(t) \notin N_L \cup N_M$ for $t \in (t_1, 0)$, $\gamma(t_1) \in \partial N_M$, $\gamma(t) \in N_M$ for $t \in (t_2, t_1)$, and $\gamma(t_2) \in \partial N_M$. Let $\gamma(t_1) = (v_1, w_1, y_1)$ and $\gamma(t_2) = (v_2, w_2, y_2)$. For $t \in (t_1, 0)$, $\gamma(t)$ is determined by the fast dynamics. We may assume that ε is sufficiently small so that $\lambda - \delta < y_1 < r_0$.

Now $\gamma(t)$ enters, in forward time N_M at $t = t_2$. It follows from Corollary 3.4.2 that $h < y_2 < h + \delta_1$. Therefore, if $\delta_2 = \delta + \delta_1$, then

$$h - r_0 < y_2 - y_1 < h - \lambda + \delta_2. \qquad (6.6.4)$$

We assume, without loss of generality, that $\gamma(t)$ enters N_M at $t = t_2$ through the side $v = v_m + \beta$ and leaves N_M at $t = t_1$ through the side $w = w_m + \beta$.

It follows from (6.6.2) that for $t \in (t_1, t_2)$, $\gamma(t)$ is given by

$$\text{(6.6.5)} \qquad \begin{aligned} &\text{(a)} \;\; v(t) = \beta\, e^{-\gamma_1(t-t_2)} + v_m, \\ &\text{(b)} \;\; w(t) = (w_2 - w_m)\, e^{\gamma_2(t-t_2)} + w_m, \\ &\text{(c)} \;\; y(t) = y_2 - \varepsilon_2(t - t_2). \end{aligned}$$

Therefore, (6.6.4) and (6.6.5)(c) imply that

$$\text{(6.6.6)} \qquad \frac{h - r_0}{\varepsilon_2} < t_1 - t_2 = \frac{y_2 - y_1}{\varepsilon_2} < \frac{h - \lambda + \delta_2}{\varepsilon_2}.$$

From (6.6.5)(b) we conclude that

$$|w_2 - w_m| \exp\left[\frac{\gamma_2(h - r_0)}{\varepsilon_2}\right] < |w(t_1) - w_m| < |w_2 - w_m| \exp\left[\frac{\gamma_2(h - \lambda + \delta_2)}{\varepsilon_2}\right].$$

Since $|w(t_1) - w_m| = \beta$, we conclude that

$$\text{(6.6.7)} \qquad \beta \exp\left(-\frac{\gamma_2(h - \lambda + \delta_2)}{\varepsilon_2}\right) < |w_2 - w_m| < \beta \exp\left(\frac{-\gamma_2(h - r_0)}{\varepsilon_2}\right).$$

This gives bounds on the size of $\gamma(H_r)$ as it passes through N_M in backward time. On the other hand, (6.6.3) gives an estimate of how much $\gamma(H_r)$ is contracted in forward time as it passes though N_L. We assume that the change in size of $\gamma(H_r)$ as it travels from N_L to N_M is $O(1)$ with respect to the parameters. Therefore, if we require that $\Phi_\varepsilon(H_r) \subset H_r$, then we must have that for a sufficiently large constant C,

$$\text{(6.6.8)} \qquad \exp\left[-\lambda_1\left(\frac{y_p - r_0}{\varepsilon_1}\right)\right] < C \exp\left(-\frac{\gamma_2(h - \lambda + \delta_2)}{\varepsilon_2}\right).$$

Recall that a smooth transition will take place if $\Phi_\varepsilon(H_r) \subset H_r$ for each $r \in (-\frac{1}{2}, \frac{1}{2})$. Therefore, we expect that a smooth transition takes place if $\varepsilon_1 \ll \varepsilon_2$. In this case we do not expect a Smale horseshoe to exist. On the other hand, we demonstrated in the previous section that a Smale horseshoe will exist if the slow dynamics in the active phase, that is ε_2, is much smaller than the slow dynamics in the passive phase, that is ε_1.

Remark. Suppose that $k_p < k < k_h$ and $(k - k_p)$ is small. Then the fixed point of (2.1) will lie close to the lower branch. If $(k_h - k)$ is small, then the fixed point will lie close to the middle branch and branch of periodic solution $\mathcal{P}$. This implies that if $(k - k_p)$ is small then the slow dynamics in the passive phase (lower branch) is smaller than the slow dynamics in the active phase. On the other hand, if $(k_h - k)$ is small, then the slow dynamics in the active phase will be smaller than the slow dynamics in the passive phase. These considerations lead us to predict that if $(k - k_p)$ is small, then the transition from n to $n+1$ spikes will be continuous. If $(k_h - k)$ is small then this transition will be chaotic in the sense that Smale horseshoes will arise. In the next section, we demonstrate numerically that this is precisely what happens.

7. Numerical results. We now describe the results of numerical computations we performed in order to test the results of the previous sections. The system we considered was

$$\text{(7.1)} \qquad \begin{aligned} v' &= y - .5(v + .5) - 2w(v + .7) - m_\infty(v)(v - 1), \\ w' &= 1.15(w_\infty(v) - w)\tau(v), \\ y' &= \varepsilon(k - v), \end{aligned}$$

where

$$w_\infty(v) = \frac{1}{2}\left[1 + \tanh\left(\frac{v - .1}{.145}\right)\right],$$

$$m_\infty(v) = \frac{1}{2}\left[1 + \tanh\left(\frac{v + .01}{.15}\right)\right],$$

$$\tau(v) = \cosh\left(\frac{v - .1}{.29}\right).$$

This system was introduced by Morris and Lecar [11] as a model for electrical activity in the barnacle muscle fiber. We can verify, numerically, that this system satisfies the basic assumptions (A1)-(A9) and (H1)-(H3). See Rinzel and Ermentrout [14]. In Fig. 11 we show that the set of rest prints for the fast subsystem together with the maximum and minimum values of the v-coordinate along each periodic solution. Stable rest points and periodic solutions are drawn with solid curves while unstable solutions are drawn with dashed curves. This bifurcation diagram was drawn using AUTO [7]. Note that for these equations,

$$k_h \approx -.186 \quad \text{and} \quad k_p \approx -.245. \tag{7.2}$$

From the remark in the preceding section, we expect that the transition from n to $n+1$ will be continuous if $k - k_p$ is small, and will be chaotic if $k_h - k$ is small.

In Fig. 12, we show that v components of three solutions of (7.1) with $k = -.22$. These computations demonstrate that (7.1) gives rise to chaotic dynamics in the transition from two to three spikes. Figure 12(a) illustrates the v component of the solution of (7.1) with $\varepsilon = .007$ and initial data

$$(v(0), w(0), y(0)) = (-.2, .015, .059).$$

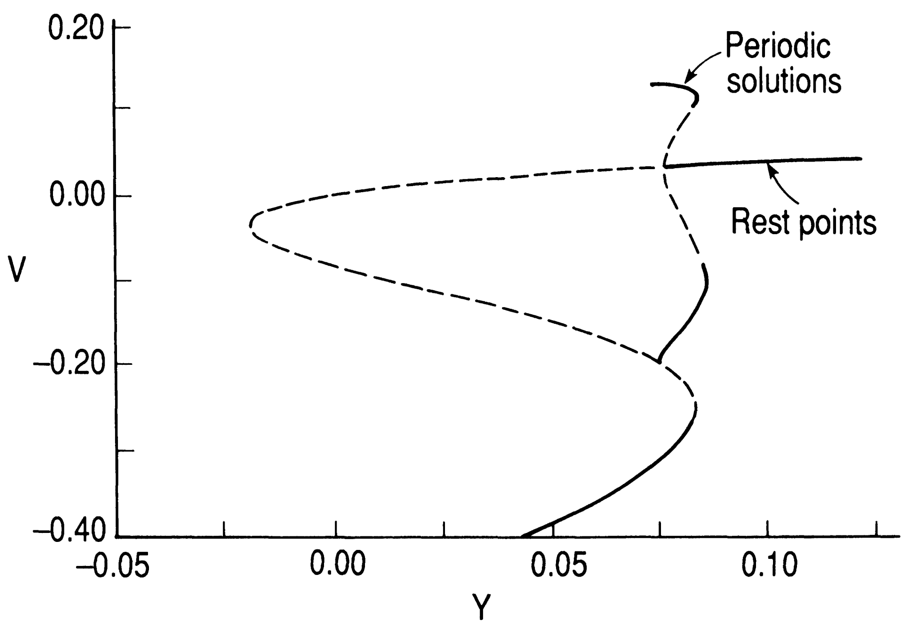
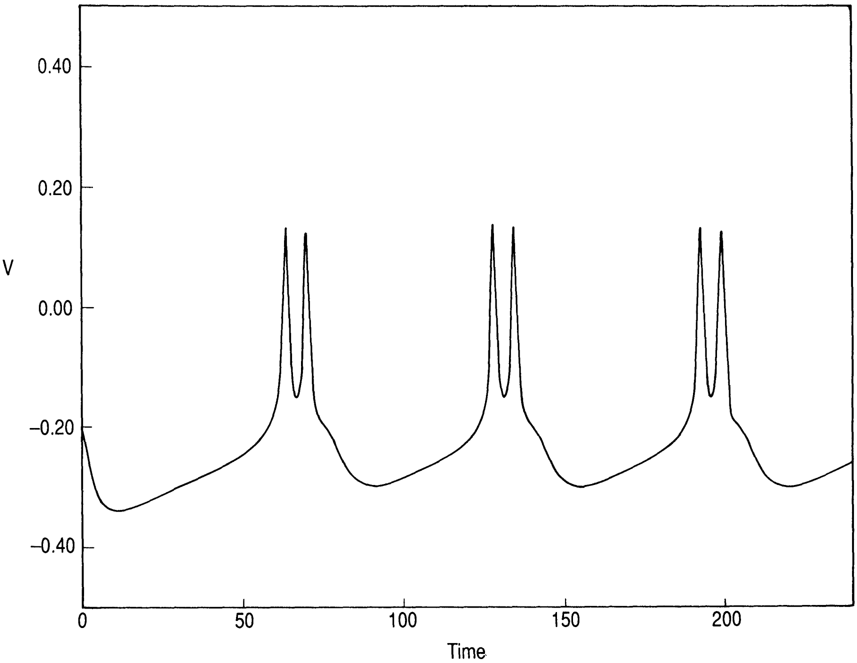


FIG. 11. *The bifurcation diagram for the steady state and periodic solutions of* (7.1) *with* $\varepsilon = 0$. *The solid curves correspond to stable solutions and the dashed curves correspond to unstable solutions.*



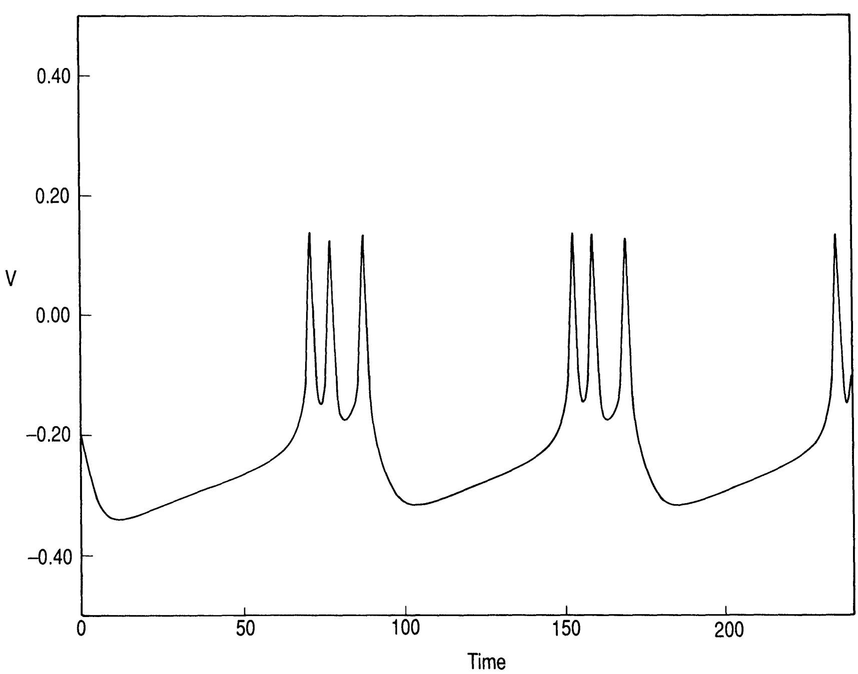
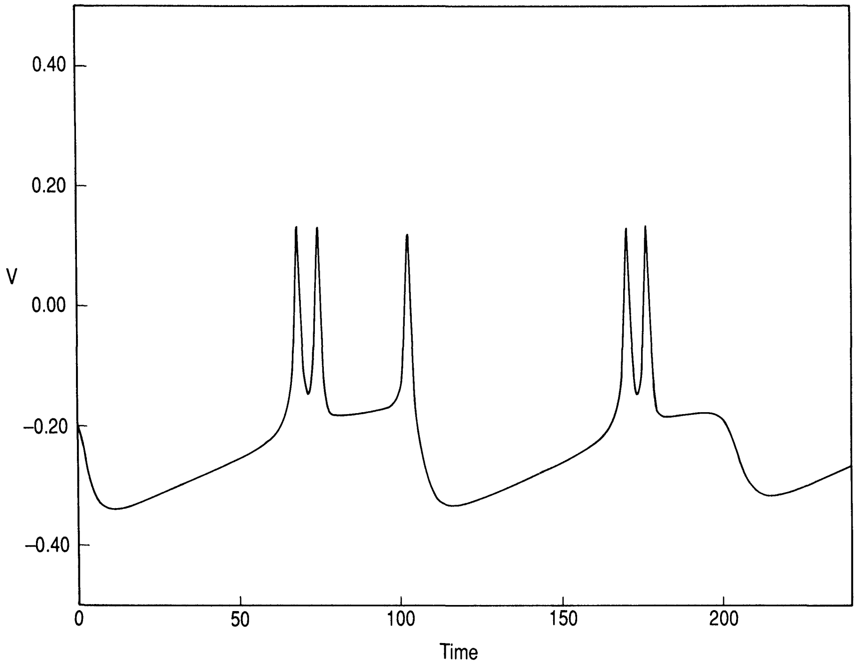


FIG. 12. *Solutions of* (7.1) *with* $k = -.22$ *and* (a) $\varepsilon = .007$, (b) $\varepsilon = .006$, *and* (c) $\varepsilon = .006368$. (d) *shows the preimage and image of a return map when* $\varepsilon = .006368$. *This map gives rise to a Smale horseshoe.*



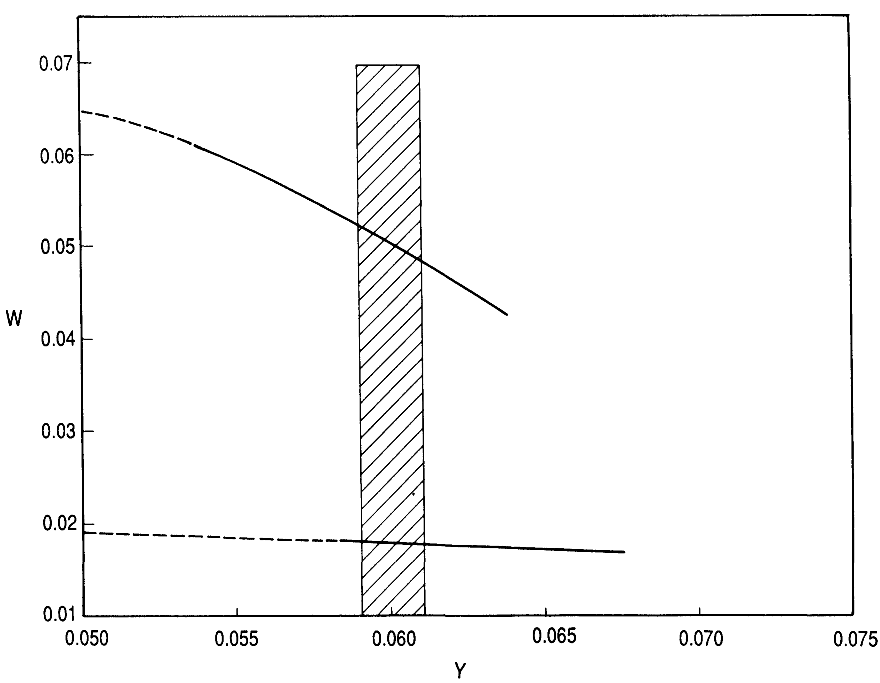
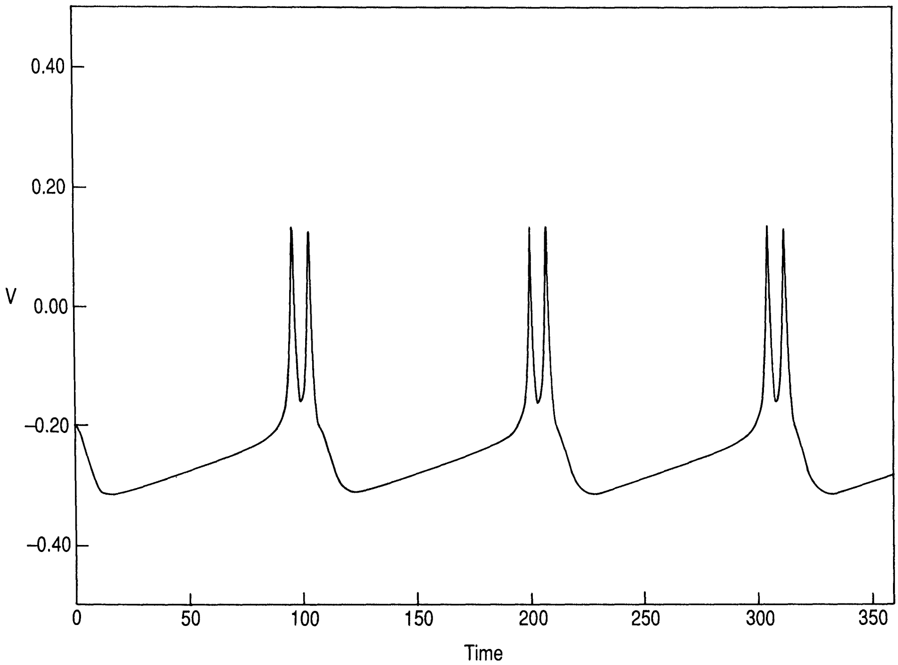


FIG. 12—continued



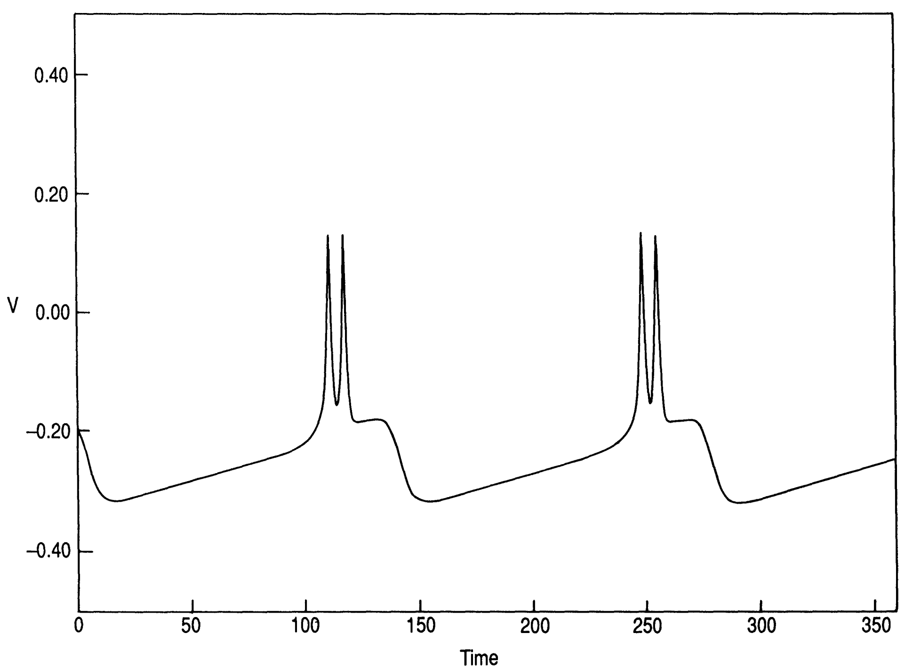


FIG. 13. *Solutions of* (7.1) *with* $k = -.24$ *and* (a) $\varepsilon = .005$, (b) $\varepsilon = .004123$, (c) $\varepsilon = .004122$, *and* (d) $\varepsilon = .004$. *In this case the transition from two to three spikes is continuous.*

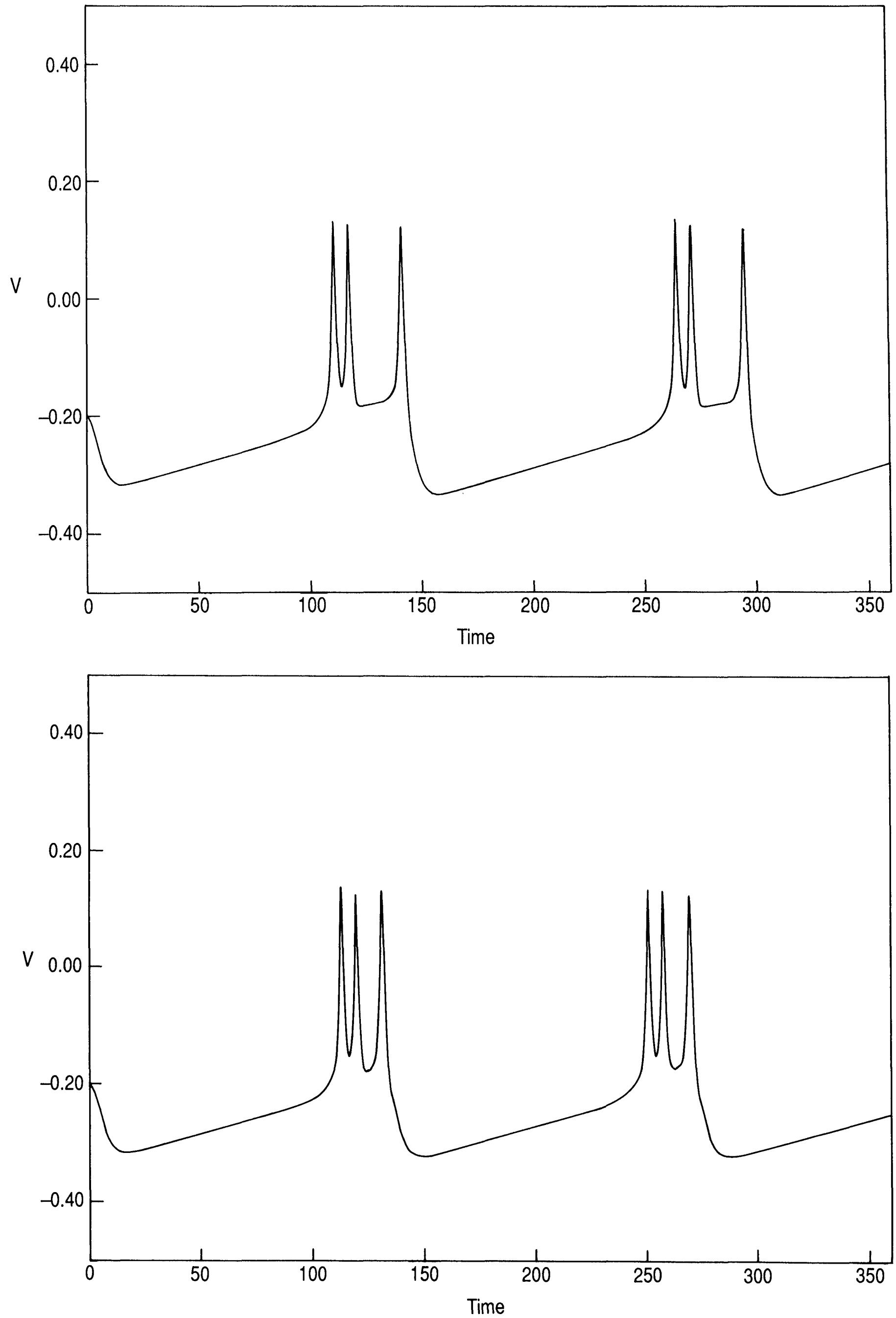


FIG. 13—continued

In this case, there are two spikes per burst. In Fig. 12(b), we solved (7.1) with $\varepsilon = .006$ and the same initial data. Now there are three spikes per burst. In Fig. 12(c), we solved (7.1) with $\varepsilon = .006368$ and the same initial data. Note that there are three spikes in the first burst and two in the second. Moreover, there is a wide plateau region in each burst. In order to verify that (7.1) gives rise to a Smale horseshoe for some values of

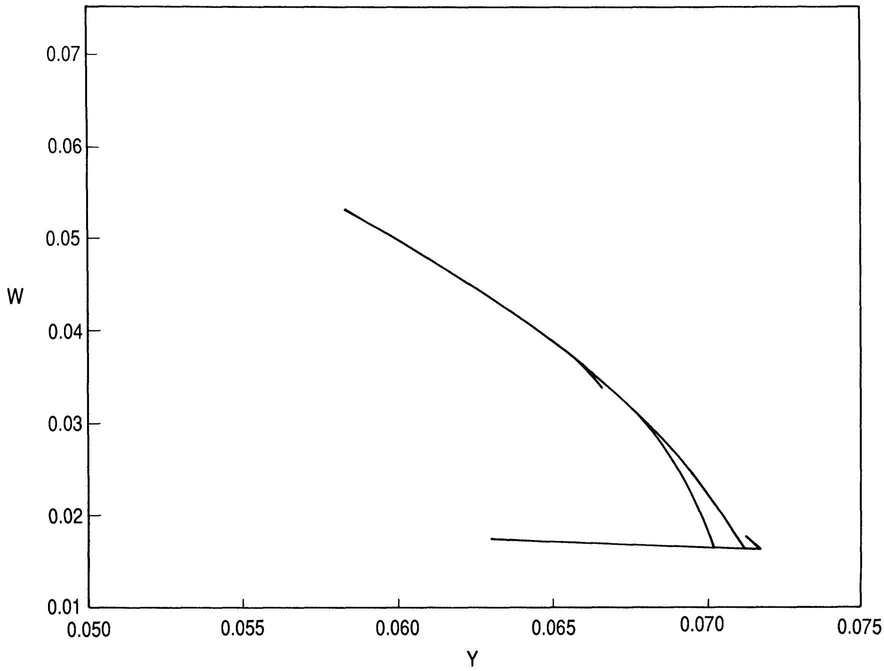


FIG. 14. *The image of one line segment of the return map* Φ_ε *corresponding to solutions of* (7.1) *with the last equation replaced with* (7.3). *Here* $\varepsilon = .0585$ *and* $\delta = .1$. *This map gives rise to a Smale horseshoe which winds around four times.*

ε between .006 and .007, we numerically computed a Poincaré map similar to that considered in § 6. The Poincaré map is defined as follows. Let

$$\Sigma = \{(v, w, y): v = -.2\}$$

and

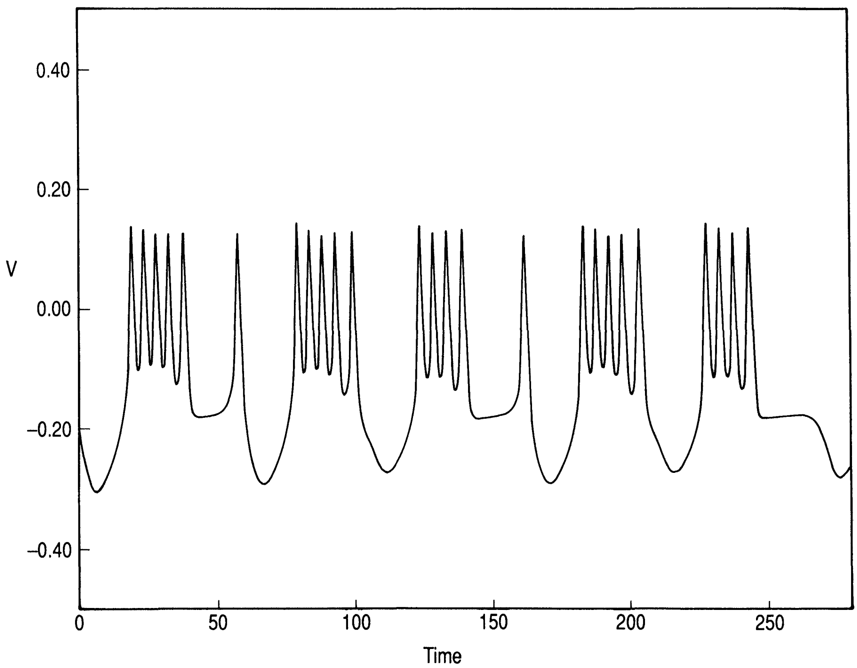
$$M = \{(v, w, y): v = -.2, 0 < w < .007, .059 < y < .061\}.$$

For $m \in M$, let $\gamma_\varepsilon(t)$ be the solution of (7.1) with $\gamma(0) = m$. We then let $\Phi_\varepsilon(m) = \gamma_\varepsilon(t_0)$, where t_0 is chosen so that $\gamma_\varepsilon(t_0) \in \Sigma$, and $\gamma_\varepsilon(t) \notin \Sigma$ for $0 < t < t_0$. In Fig. 12(d) we show, in the plane $v = -.2$, the rectangle M and the image of M under Φ_ε for $\varepsilon = .006368$. Note that $\Phi_\varepsilon(M)$ must lie close to the unstable manifold of the middle branch. The dashed curves in Fig. 12(d) are not numerically computed points. Rather, they are simply extensions of the solid curves which were numerically computed. The range of parameter values for which points in Σ are mapped by Φ_ε close to the left knee is extremely narrow.

In Fig. 13, we show that v components of four solutions of (7.1) with $k = -.24$. Our computations demonstrate that the transition from two to three spikes is continuous. In each of these four solutions we solved (2.1) with initial data

$$(v(0), w(0), y(0)) = (-.2, .004, .07).$$

This point lies very close to the lower branch. The values of ε in Figs. 13(a), 13(b), 13(c), and 13(d) are .005, .004123, .004122, and .004, respectively. The numerical computations indicate that each of the solutions quickly approaches a stable periodic solution. We see in Figs. 13(b) and 13(c) that during the transition from two to three spikes the solution spends an increased amount of time in the excited state. This is



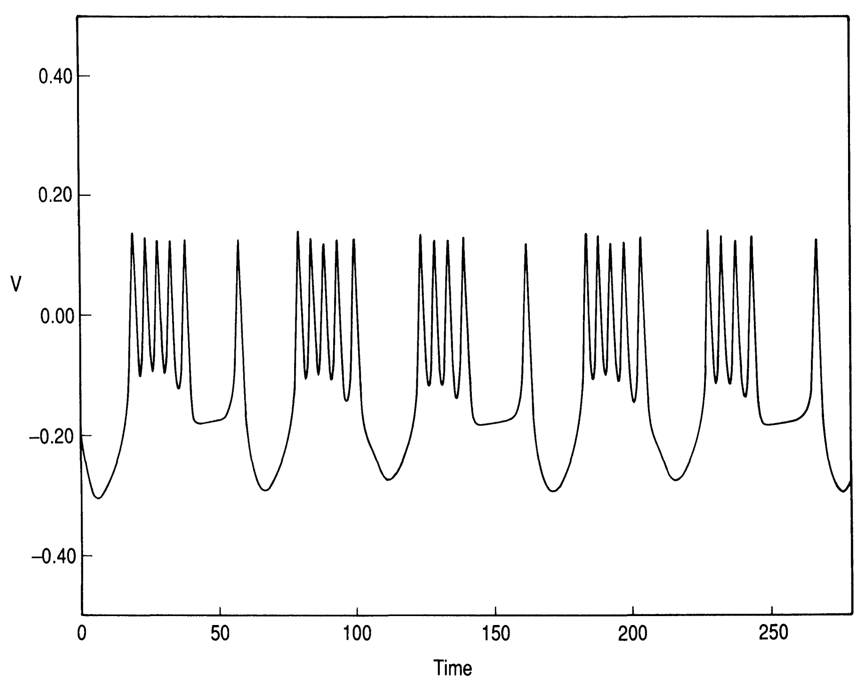


FIG. 15. *Solutions of* (7.1) *where the last equation is replaced with* (7.3). *The number of spikes per burst varies from four, five, and six. This reflects the existence of the Smale horseshoe.*

because the corresponding trajectory in a phase space spends an increased amount of time near the middle branch.

Our final example illustrates the results described in § 6.5. In that section we demonstrated that if the slow dynamics in the active phase is much smaller than the slow dynamics in the passive phase, then (2.1) may give rise to Smale horseshoes with a large winding number. We consider the system (7.1) with the last equation replaced by

$$y' = -\varepsilon[.22+v]\left[\left(\frac{1+\delta}{2}\right) - \left(\frac{\delta-1}{2}\right)\tanh\left(\frac{v+.23}{.005}\right)\right], \tag{7.3}$$

where $\delta = .1$.

The parameter δ measures the ratio of the rate of the slow dynamics in the active phase divided by the rate of the slow dynamics in the passive phase. On the lower branch, $v < -.23$, so $\tanh((v+.23)/.005) \approx -1$. Hence, on the lower branch, $y' \approx -\varepsilon(.22+v)$. On the other hand, in the active phase, $v > .23$. Hence, $\tanh((v+.23)/.005) \approx +1$, so $y' \approx -\delta\varepsilon(.22+v)$. If we take $\delta = .1$ then we should expect the system to give rise to chaotic dynamics.

In Fig. 14, we set $\varepsilon = .0585$ and consider the map Φ_ε described earlier in this section. Figure 14 shows the image of the line segment

$$l = \{(v, w, y) \colon v = -.2,\ w = .03,\ .03 < y < .075\}. \tag{7.4}$$

Note that $\Phi_\varepsilon(l)$ winds around four times. Further computations demonstrate that Φ_ε gives rise to a Smale horseshoe which winds around four times.

In Fig. 15(a) we show the v component of the solution of the equations with $\varepsilon = .0585$ and initial conditions

$$(v(0), w(0), y(0)) = (-.2, .015, .05900043). \tag{7.5}$$

Note that the number of spikes per burst varies between four, five, and six. Moreover, some bursts have a plateau region, while others do not.

The solution is extremely sensitive to changes in the parameters. For example, if instead of (7.5) we took initial conditions

$$(v(0), w(0), y(0)) = (-.2, .015, .059000429),$$

then the v component of the solution is as shown in Fig. 15(b). The only significant difference between Figs. 15(a) and 15(b) is the last spike.

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