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A Geometric Approach to Singular Perturbation Problems with Applications to Nerve Impulse Equations*

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INTRODUCTION

This paper develops a geometric approach to singular perturbation problems. Results are used to study a general model of a biological process (e.g., nerve impulse, heartbeat, muscle contraction) consisting of a differential equation coupled with l "slow" and m "fast" equations. The slow (fast) equations correspond to subprocesses whose rates are slow (fast) relative to the rate of the primary phenomenon.

For example, in the Hodgkin–Huxley model (0.1) of nerve impulse transmission one fast equation represents the entrance of Na^+ into the axon; and two slow equations represent K^+ exit and inhibition of Na^+ entrance.

In Section 1 the results are presented abstractly, in terms of isolating blocks [8, 11, 37, 38] for an autonomous system. The principal property of a block is that the map which sends a point u in the block to the first point of $u \cdot [0, \infty)$ in its exit set is continuous where defined (Fig. 2). Hypotheses (1.4, HET), (1.6, HOM), and (1.8, PER) give sufficient conditions for the existence of heteroclinic, homoclinic, and periodic solutions.

In Section 2 we examine a nonlinear diffusion equation (2.2) coupled with l "slow" equations. Hypotheses of Section 1 are recast as (2.4, HET′), (2.6, HOM′), and (2.8, PER′) in terms of singular solutions. (PER′) requires that $l = 1$, i.e., that the system include only one slow variable, as in (FN). Systems with $l = 2$ are treated provided that one slow variable is much slower than the others (plateau solutions). In [1] we redefine singular periodic solutions to include the case $l \geqslant 2$ in general.

The Hodgkin–Huxley (HH) [22] model of nerve impulse transmission is studied in detail in Section 3. (See [23, Sects. 33–34; 33, Chap. 10] for introductory discussions.) In this model, the nerve axon is a thin cylindrical membrane containing a fluid (axoplasm). When the nerve is at rest, concentration

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differences of Na^+ and K^+ between the axoplasm and the surrounding solution set up a potential difference across the membrane (membrane potential, in millivolts). When the nerve is stimulated above a threshold, the permeability of the membrane to Na^+ increases rapidly and sodium ions rush in (sodium activation) effecting a dramatic change in the membrane potential. Diffusion of electrons within the axon induces sodium activation farther along, and the resulting impulse proceeds in a wave-like manner. Two slower processes (sodium inactivation and potassium activation) inhibit Na^+ entrance and allow K^+ exit, and the axon returns to rest.

The Hodgkin–Huxley equations consist of a nonlinear diffusion equation coupled with one fast and two slow equations:

$$\begin{aligned}(1/R)(\partial^2 V/\partial x^2) &= C(\partial V/\partial t) + g(V, m, n, h),\\ \partial m/\partial t &= \delta^{-1}\gamma_m(V)(m_\infty(V) - m),\\ \partial n/\partial t &= \epsilon\gamma_n(V)(n_\infty(V) - n),\\ \partial h/\partial t &= \epsilon\gamma_h(V)(h_\infty(V) - h),\end{aligned} \tag{0.1}$$

where x is the distance from and t is the time since the stimulus. V denotes the displacement of membrane potential from rest ($V = 0$); m represents sodium activation; n potassium activation; and h sodium inactivation. R is the resistance of the axoplasm, and $(1/R)(\partial^2 V/\partial x^2)$ is the total current crossing the membrane (by Ohm's law). This membrane current is the sum of capacitance ($C(\partial V/\partial t)$) and ionic ($g(V, m, n, h)$) currents. g is the sum of sodium ($I_{Na}(V, m, h)$), potassium ($I_K(V, n)$), and leakage $I_L(V)$ currents, where $I_{Na} < 0$, $I_K > 0$, and I_L is small.

FitzHugh [17], noting the similarity between (0.1) and a van der Pol oscillator, set $m = m_\infty(V)$ and combined n, h into one slow variable, y.

$$\begin{aligned}(1/R)(\partial^2 V/\partial x^2) &= C(\partial V/\partial t) - f(V) + y,\\ \partial y/\partial t &= \epsilon(V - \gamma y).\end{aligned} \tag{0.2, FN}$$

Nagumo *et al.* [26] used (0.2) to model nerve transmission with a tunnel diode network.

We shall examine traveling wave solutions of the (HH) and (FN) models. The simplification $m = m_\infty(V)$ is minor provided δ is small; however, the uncoupled n, h variables of (HH) yield a richer variety of solutions (finite wave train, plateau) than (FN). The principal condition (3.1, CUBIC, H) placed on (HH) is that $g(V, m_\infty(V), n, h)$ be a "cubic" function of V for fixed n, h (Fig. 13). Similarly, f is "cubic" for (FN) (Fig. 8). Mild qualitative conditions on each system imply the existence of a homoclinic traveling wave solution, that is, a waveform which travels at constant velocity and which returns to rest after the impulse has passed. A more specialized (but not uncommon) condition on

(HH) (3.5, WAVE TRAIN) implies the existence of finite wave train solutions of (HH) of any length where, for fixed $\epsilon > 0$, the number of waves increases as the wave speed θ increases. If γ_n/γ_h or γ_h/γ_n is large, (HH) admits homoclinic and periodic solutions with plateaus ([18, 34] and Fig. 18), corresponding to cardiac muscle and pacemaker activity. Periodic solutions of (FN) ($l = 1$) exist for all θ less than some $\bar{\theta}$; periodic solutions of (HH) ($l = 2$) are discussed in [1].[1]

In Section 4, we show that results of Sections 2 and 3 are valid for a system with fast variables whenever an associated system (setting $\delta = 0$) satisfies the appropriate hypotheses and δ is small.

Some parameter estimates for (HH) are given in Section 5. The set of all bounded solutions is shown to be in a compact subset of $\mathbb{R}^5$. In addition, a homoclinic solution does *not* exist if $\theta \geqslant \theta_{\max}$; $\theta \leqslant \epsilon\theta_{\min}$; $\epsilon \geqslant E$; or $\delta \geqslant D/\epsilon$, showing that some conditions on parameter values are necessary. Similar results hold for (FN).

Proofs are contained in Section 6.

Previous mathematical studies of the FitzHugh–Nagumo equations include [3, 7, 9, 21, 25, 29]. Conley [7, 9] uses isolating blocks to show the existence of a homoclinic solution of (FN). Rinzel and Keller [29] obtain existence and stability of a homoclinic solution with $f(V)$ piecewise linear. Hastings [21] shows the existence of a periodic solution. Casten, Cohen, and Lagerstrom [3], using a notion similar to our singular solution, show the existence of homoclinic and periodic solutions by numerical methods.

Hastings [20] shows the existence of a homoclinic solution of (HH) under particular conditions.

Isolating block methods have previously been used to study heteroclinic (shock) [12, 14, 31, 32], homoclinic [4, 14], and periodic [10, 11, 32] phenomena. In particular, Smoller and Conley [32] use isolating blocks about singular solutions to prove the existence of true solutions.

Notation

$\mathrm{dom}(f) \equiv$ domain of f,

$f \mid A \equiv f$ restricted to A,

$\partial A \equiv$ boundary of A,

$\mathrm{cl}(A) \equiv$ closure of A,

$\mathrm{int}(A) \equiv$ interior of A,

$x : y \equiv \sum_{i=1}^{n} x_i y_i$ (the usual inner product on $\mathbb{R}^n$), where

$$x = \langle x_1 \cdots x_n \rangle, \qquad y = \langle y_1 \cdots y_n \rangle,$$

$\nabla f \equiv \langle \partial f/\partial x_1 \cdots \partial f/\partial x_n \rangle$ where $f: \mathbb{R}^n \to \mathbb{R}$,

$DG \equiv (\partial G_i/\partial x_j)$ $(n \times n)$ where $G(x)$: $\mathbb{R}^n \to \mathbb{R}^n$,

[1] Recently, necessary and sufficient conditions for the existence of periodic bursting solutions of (HH) have been added to these results.

$D_u H \equiv (\partial H_i/\partial u_j)\ (k \times k)$ where $H(u, v)\colon \mathbb{R}^{k+l} \to \mathbb{R}^k$,

$\det(M) \equiv$ determinant of M,

$[B/A] \equiv$ the homotopy type of B with A identified to a point.

1. Heteroclinic, Homoclinic, and Periodic Solutions of an Autonomous System

In this section we consider a system

$$\dot{u} = G(u), \tag{1.1}$$

where $G \in C^1$ and $u \in \Omega \subseteq \mathbb{R}^n$.

Definitions. ($u \cdot t$, rest point, $U(\bar{u})$, $D(\bar{u})$, heteroclinic, homoclinic, periodic, block, $b^\pm$, transverse crossing, $T^\pm$, $\phi^\pm$, $D^\pm$). Let $u(t) \equiv \mathbf{u} \cdot \mathbf{t}$ be a solution of (1.1).

$\bar{u}$ is a *rest point* of (1.1) if $G(\bar{u}) = 0$.

If $\bar{u}$ is a rest point, let

$$\mathbf{U}(\mathbf{u}) \equiv \{u \in \Omega\colon u \cdot t \to \bar{u} \text{ as } t \to -\infty\},$$

$$\mathbf{S}(\mathbf{u}) \equiv \{u \in \Omega\colon u \cdot t \to \bar{u} \text{ as } t \to +\infty\}.$$

If $\det(DG(\bar{u})) \neq 0$ and $DG(\bar{u})$ has j eigenvalues with positive real part and $(n - j)$ with negative real part, $U(\bar{u})$ (the unstable manifold) is a j-manifold and $S(\bar{u})$ (the stable manifold) is an $(n - j)$-manifold [6, Chap. 13]. In Example 1.1 below, $U(\langle 0, 0\rangle) = \{x = y\}$ and $S(\langle 0, 0\rangle) = \{x = -y\}$. All rest points in this paper will be of this type.

If $\bar{u}$, $\bar{\bar{u}}$ are rest points, (1.1) admits a *heteroclinic* [*homoclinic*] solution from $\bar{\bar{u}}$ to $\bar{u}$ if $(S(\bar{u}) \cap U(\bar{\bar{u}})) - \{\bar{u}\} \neq \phi$ and $\bar{u} \neq \bar{\bar{u}}\,[\bar{u} = \bar{\bar{u}}]$.

$\mathbf{u} \cdot \mathbf{R}$ is a *periodic* solution of (1.1) if $u \cdot t = u$ for some $t \neq 0$.

B is a *block* for (1.1) if there exist C^1 functions $f_1 \cdots f_N\colon \mathbb{R}^n \to \mathbb{R}$ such that $B \equiv \bigcap_{i=1}^{N} f^{-1}([0, \infty))$ is homeomorphic to $[0, 1]^n$ and $f_i \equiv \nabla f_i : G \neq 0$ on ∂B.

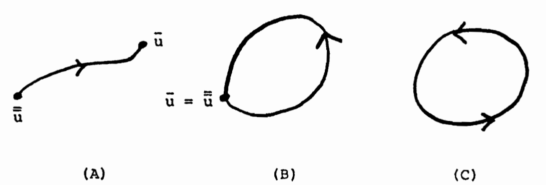

Fig. 1. (A) heteroclinic, (B) homoclinic, and (C) periodic solutions.

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some $T > 0$. If X, Y are compact subsets of $\mathbb{R}^n$, $d^*(X, Y) \equiv$ the Hausdorff distance from X to $Y \equiv$

$$\max\{\max_{x\in X} \min_{y\in Y} | x - y |, \max_{y\in Y} \min_{x\in X} | x - y |\}.$$

LEMMA 2. (A) *Let $\dot{\omega}_{\bar{u}}$ be a nontrivial solution segment of* (2.2). *Then for every $\gamma > 0$, $d^*(\omega_{\bar{u}}, \omega_{u,z}) < \gamma$ whenever $\langle u, z\rangle$ is near $\langle \bar{u}, z(\bar{u})\rangle$ and δ is small.*

(B) *Let $\bar{u}$ be a rest point of* (2.2) *whose eigenvalues have nonzero real part, and let $\bar{u} \in U(\bar{u})$ and $\gamma > 0$. Then $d^*(\text{cl}(\langle u, z\rangle \cdot (-\infty, 0]), \text{cl}(\bar{u} \cdot (-\infty, 0], z(\bar{u} \cdot (-\infty, 0])) \leqslant \gamma$ for some $\langle u, z\rangle \in U(\langle \bar{u}, z(\bar{u})\rangle)$ if δ is small.*

(5.1) The proof requires straightforward estimates which appear in [2].

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$\mathbf{b}^+$ (the *entrance set*) $\equiv \{u \in \partial B : f_i(u) = 0$ and $\dot{f}_i(u) > 0$ for some $i\}$. $\mathbf{b}^-$ (the *exit set*) $\equiv \{u \in \partial B : f_i(u) = 0$ and $\dot{f}_i(u) < 0$ for some $i\}$.

EXAMPLE 1.1 A block about a saddle point

$$\dot{x} = y, \quad \dot{y} = x. \tag{1.2}$$

Let $B \equiv \{| x | + | y | \leqslant 1\}$.

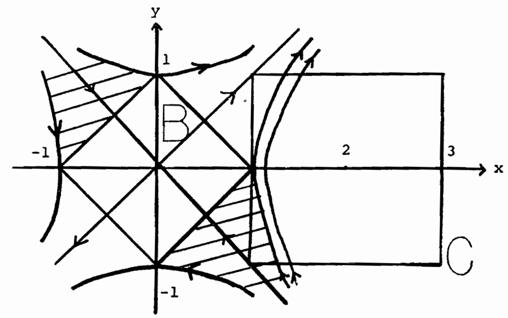

FIG. 2. B is a block for (1.2). D^+ is shaded.

B is a block, with $f_1(x, y) = 1 - x - y$; $f_2(x, y) = 1 + x - y$, etc. $\dot{f}_1(x, y) = -y - x = -1 < 0$ if $f_1(x, y) = 0$, so $b^- \supseteq f_1^{-1}(0) \cap B$. $\dot{f}_2(x, y) = y - x = 1$ if $f_2(x, y) = 0$, so $b^+ \supseteq f_2^{-1}(0) \cap B$.

$C \equiv \{| x - 2 | \leqslant 1$ and $| y | \leqslant 1\}$ is not a block. Note that the map which sends u to the first point of $u \cdot [0, \infty)$ in ∂C is *not* continuous in C.

This definition of a block is more limited than usual [11]; the C^1 isolating-block-with-corners of [38] could be used instead. Defined in this way, a block B for (1.1) has the property that if $| G - \tilde{G} |$ is small, then B is a block for the system

$$\dot{u} = \tilde{G}(u),$$

with $b^\pm$ remaining invariant.

If f is a C^1 function from Ω to $\mathbb{R}$ and $\bar{u} \in \Omega$, $\bar{u}$ *crosses* $\{f(u) = c\}$ *transversely* if $T \equiv \inf\{t > 0 : f(\bar{u} \cdot t) = c\} < \infty$ and $\dot{f}(u \cdot T) \neq 0$.

$\mathbf{T}^\pm(\mathbf{u})$ (the time needed for u to reach $b^\pm$) $\equiv$

$$\begin{cases} 0 & \text{if } u \in b^\pm \\ \sup\{t > 0 : u \cdot (0, t) \cap b^\pm = \phi\} & \text{if } u \notin b^\pm \end{cases}.$$

$\boldsymbol{\phi}^\pm(\mathbf{u}) \equiv u \cdot T^\pm(u)$ if $0 \leqslant T^\pm(u) < \infty$. $\phi^\pm$ is the first point of $u \cdot [0, \infty)$ in $b^\pm$. $\mathbf{D}^\pm = \{u : 0 < T^\pm(u) < \infty$ and $\phi^\pm(u) \notin b^\mp\}$. $D^\pm$ contains the set on which $\phi^\pm$

is defined and continuous. If $\bar{u} \in D^{\pm}$, $\bar{u}$ crosses $\{f_i(u) = 0\}$ transversely at $\phi^{\pm}(\bar{u})$ for some i.

In example 1.1,

$$D^{+} = \{x^2 - y^2 < 1\} \cap \{x < 0 \text{ and } y > 0, \text{ or } x > 0 \text{ and } y < 0\} - B$$

(shaded in Fig. 2), and

$$D^{-} = (D^{+} \cup B) - (b^{-} \cup S(\langle 0, 0 \rangle)).$$

If $\{B_\alpha\}$ is a family of blocks, $T_\alpha^{\pm}$, $\phi_\alpha^{\pm}$, $D_\alpha^{\pm}$ denote the corresponding functions and sets.

In Lemmas 1.2 and 1.3 we construct blocks containing a given rest point or solution segment of (1.1) and verify the principal continuity property of blocks.

LEMMA 1.2. (Canonical blocks). (A) *Let $\bar{u}$ be a rest point of* (1.1). *The eigenvalues of $\bar{u}$ have j positive and $(n - j)$ negative real parts iff every neighborhood of $\bar{u}$ contains a block B such that:*

(i) $[B/b^{+}]$ *is the pointed $(n - j)$ sphere;*

(ii) $[B/b^{-}]$ *is the pointed j sphere; and*

(iii) $u \cdot \mathbb{R} \subset B$ *iff* $u = \bar{u}$.

(iii) *implies that* $u \in S(\bar{u})$ *if* $u \cdot [0, \infty) \subseteq B$.

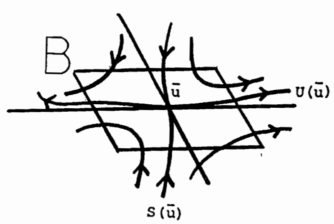

FIG. 3. B is a block for (1.1) with $n = 2, j = 1$.

(B) *If $\bar{u} \cdot t \neq \bar{u}$ for $0 < t \leqslant T$, there exist blocks B_1, B_2 and $f: \Omega \to \mathbb{R}$ such that:*

(i) $B_1, B_2 \subseteq f^{-1}(0) \cdot [0, T]$;

(ii) $B_1^{+} \subseteq f^{-1}(0)$;

(iii) $B_2^{-} \subseteq f^{-1}(0) \cdot T$; *and*

(iv) *no positive half solution is contained in B_1 or B_2.*

For $\eta > 0$, B_1, B_2 may be chosen so that $|u \cdot t - \bar{u} \cdot t| < \eta$ if $u \in B_i \cap f^{-1}(0)$ and $0 \leqslant t \leqslant T$ $(i = 1, 2)$.

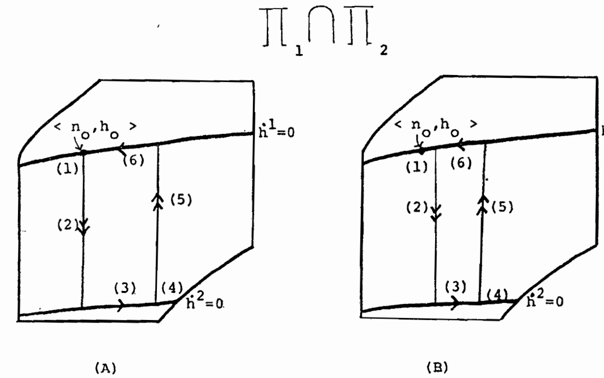

FIG. 26. (A) Singular plateau homoclinic solution. (B) Singular plateau periodic solution.

(B) Plateau periodic singular solutions are constructed similarly (Fig. 26 B). The existence of plateau periodic solutions of (3.3) follows as in Theorem 2.9.

(4.2) follows from Lemmas 1 and 2 below.

Lemma 1 constructs a block for (4.1, δ) given a block for the associated system (2.2) ($\delta = 0$). Lemma 2 states that a solution segment or the unstable manifold of (4.1, δ) stays close to the corresponding object of (2.2) when δ is small. Let $u \equiv \langle V, W, y \rangle$.

LEMMA 1. *Let A be a block for* (2.2).

(A) *Every neighborhood of $\{\langle u, z(u) \rangle : u \in A\}$ contains a block B for* (4.1, δ) *when δ is small. Moreover, for $u \in A$ $B_u \equiv \{z : \langle u, z \rangle \in B\}$ is a block for*

$$\dot{z} = q(u, z);$$

$b^{+} = \{\langle u, z \rangle \in \partial B : u \in a^{+}$ *or* $z \in \partial B_u\}$; *and* $b^{-} = \{\langle u, z \rangle \in \partial B : u \in a^{-}\}$.

(B) *If no set $u \cdot [0, \infty) \subseteq A$, B may be chosen so that no set $\langle u, z \rangle \cdot [0, \infty) \subseteq B$.*

(C) *If $\bar{u}$ is a rest point of* (2.2) *whose eigenvalues have nonzero real part, and $u \cdot \mathbb{R} \subseteq A$ iff $u = \bar{u}$, then if δ is small the eigenvalues of $\langle \bar{u}, z(\bar{u}) \rangle$ have nonzero real part and $\langle u, z \rangle \cdot \mathbb{R} \subseteq B$ iff $\langle u, z \rangle = \langle \bar{u}, z(\bar{u}) \rangle$. Moreover* $\dim(U(\langle \bar{u}, z(\bar{u}) \rangle)) = \dim(U(\bar{u}))$.

Let ω_u be a *solution segment of* (2.2) if $\omega_u = \{\langle u \cdot t, z(u \cdot t) \rangle : t \in [0, T]\}$ for some $T > 0$. $\omega_{u,z}$ is a *solution segment of* (4.1, δ) if $\omega_{u,z} = \langle u, z \rangle \cdot [0, T]$ for

Then $A, B, C, D > 0$; $(\mathrm{H})_1$ linearized about $\langle n_0, h_0\rangle$ is the system

$$\begin{pmatrix}\dot n\\ \dot h\end{pmatrix}^i = \begin{pmatrix}\gamma_n(0) & 0\\ 0 & \gamma_h(0)\end{pmatrix}\begin{pmatrix}-A(n_0, h_0) & B(n_0, h_0)\\ C(n_0, h_0) & -D(n_0, h_0)\end{pmatrix}\begin{pmatrix}n - n_0\\ h - h_0\end{pmatrix},$$

and the eigenvalues of $\langle n_0, h_0\rangle$ are negative.

(B) Let $f(n, h) = n_\infty(V_1(n, h)) - n$. Since $\partial f/\partial h = B > 0$, there exists $h_a(n)$ such that $f(n, h) = 0$ iff $h = h_a(n)$, and $h_a' = A/B > 0$. Since $0 < n_\infty < 1$, $\mathrm{dom}(h_a) \subseteq (0, 1)$ and $h_a(n) = 0$ for some n. h_b is defined similarly with $h_b' = C/D > 0$.

(C) $h_a' - h_b' = (AD - BC)/BD > 0$. Also, no solution leaves $\{\dot n^1 \geqslant 0$ and $\dot h^1 \geqslant 0\} \cup \{\dot n^1 \leqslant 0$ and $\dot h^1 \leqslant 0\}$. The result follows from a computation of the eigenvectors.

(D) follows from the fact that $V > 0$ if $G = \partial G/\partial V = 0$ and $\partial^2 G/\partial V^2 > 0$ (so $V = V_2(n, h)$ and $\langle n, h\rangle \in \partial\Pi_2$) since $\partial V_2/\partial n < 0$ and $\partial V_2/\partial h > 0$.

(E) follows from (D) since $V = 0$ at a rest point.

(F) h_c, h_d are defined as in (B). (F) follows from the fact that if $V = V_2(n, h) > 0$ then $0 < h_\infty(V) < h_0$ and $n_0 < n_\infty(V) < 1$.

(G) No solution of $(\mathrm{H})_2$ leaves $\{\dot n^2 \geqslant 0$ and $\dot h^2 \geqslant 0\} \cup \{\dot n^2 \leqslant 0$ and $\dot h^2 \leqslant 0\}$ so all solutions run to $\{\partial G/\partial V = 0\}$ in finite time.

(3.4) Lemma 3.2(A) implies (2.6, HOM′) (A) with $y = \langle n_0, h_0\rangle$; 3.1(C) implies (B); 3.3(A) implies (C); and 3.3(B) and 3.2(C) imply (D). Thus (3.1) satisfies hypotheses (2.2, CUBIC) and (2.6, HOM′) and the result follows from Theorem 2.7.

(3.6) (A) A singular wave train solution of length k is constructed as in Fig. 16. The existence of a wave train solution of (3.1, H) follows from Theorem 2.7 as in 3.4. The fact that $\theta_{\epsilon l} < \cdots < \theta_{\epsilon k}$ follows from the proof, noting that a solution may jump back to Π_2 at a smaller value of θ than would be needed for the solution to continue back to rest.

(B) If $j \leqslant (J - 1)$, a wave train solution exists as in (A).

(3.8) (A) A plateau homoclinic singular solution of (H) is shown in (Fig. 26 A). (1) represents a solution of $(\mathrm{H}, \bar\theta, 0, 0)$ from $\langle 0, 0, n_0, h_0\rangle$ to $\langle V_2(n_0, h_0), 0, n_0, h_0\rangle$; (2) is a solution of $(\mathrm{H})_2$ with $\tau = 0$ from $\langle n_0, h_0\rangle$ to $\langle n_0, h_d(n_0)\rangle$. (1) and (2) form a heteroclinic singular solution from Π_1 to Π_2. Similarly, (4) and (5) form a heteroclinic singular solution from Π_2 to Π_1. The corresponding heteroclinic solutions of (H) are then joined in Π_2 and Π_1 by (3) and (6). The existence of a homoclinic solution of (3.3) follows as in Theorem 2.7. The plateau phases correspond to (3) (excited) and (6) (near rest).

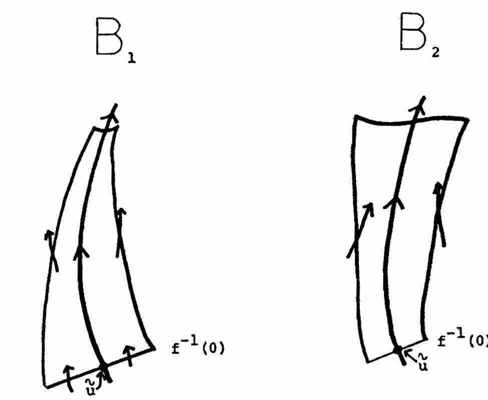

FIG. 4.

LEMMA 1.3. (Continuity of maps defined by a block). *If B is a block, $T^\pm$ and $\phi^\pm$ are continuous on $D^\pm$.*

For the rest of Section 1 we shall consider a system parameterized by $\sigma \in \mathbb{R}^k$:

$$\dot u = G(u, \sigma). \tag{1.3, σ}$$

If B is a block for $(1.3, \bar\sigma)$ then B is a block for $(1.3, \sigma)$ if σ is near $\bar\sigma$. $b^\pm$ remains invariant under small perturbation of σ. Let $T^\pm(u; \sigma)$ denote the time needed for u to reach $b^\pm$ in $(1.3, \sigma)$ and $\phi^\pm(u; \sigma)$ denote $u \cdot T^\pm(u; \sigma)$ in $(1.3, \sigma)$.

Hypotheses (1.4, HET), (1.6, HOM), and (1.8, PER) give sufficient conditions for the existence of heteroclinic, homoclinic, and periodic solutions of $(1.3, \sigma)$.

HYPOTHESIS (1.4, HET). There exists a block B for $(1.3, \sigma)$ $(\sigma \in \Sigma)$ with properties (A)–(C):

(A) $\bar u, \bar{\bar u}$ are rest points of $(1.3, \sigma)$, and $u \in S(\bar u)$ if $u \cdot [0, \infty) \subseteq B$.

(B) There exists a path $\{\langle u_s, \sigma_s\rangle : 0 \leqslant s \leqslant 1\} \subseteq D^+ \times \Sigma$ such that $u_s \in U(\bar{\bar u})$ in $(1.3, \sigma_s)$; $u_0, u_1 \in D^-$; and $\phi^- \circ \phi^+(u_0; \sigma_0)$, $\phi^- \circ \phi^+(u_1, \sigma_1)$ are contained in distinct components of b^-.

(C) $\bar u \neq \bar{\bar u}$.

THEOREM 1.5 (Heteroclinic solutions of (1.3)). *Hypothesis (1.4, HET) implies that $(1.3, \sigma_s)$ admits a heteroclinic solution from $\bar{\bar u}$ to $\bar u$ for some σ_s.*

Remark. If (1.4, HET) (C) is replaced by

(C′) $\bar u = \bar{\bar u}$,

(1.4, HET) implies that $(1.3, \sigma)$ admits a homoclinic solution. This observation will be used in the proof of Theorem 1.7.

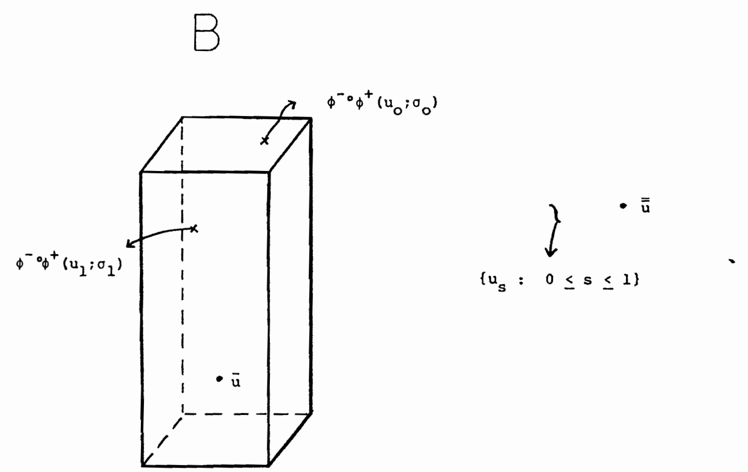

FIG. 5. B satisfies (1.4, HET), with b^- = front and back.

HYPOTHESIS (1.6, HOM). There exist blocks B_1, B_2 for (1.3, σ) ($\sigma \in \Sigma$) with properties (A)–(D):

(A) $\bar{u}$ is a rest point of (1.3, σ), and $u \in S(\bar{u})$ if $u \cdot [0, \infty) \subseteq B_1$.

(B) No positive half solution is contained in B_2.

(C) There exists Δ, an open subset of b_2^-, such that $\Delta \subseteq D_1^+$ and $(b_2^- - \Delta)$ consists of two components, β_0 and β_1. In addition, if $\delta_0 \equiv \beta_0 \cap \mathrm{cl}(\Delta)$ and and $\delta_1 \equiv \beta_1 \cap \mathrm{cl}(\Delta)$, then $\delta_0 \cup \delta_1 \subseteq D_1^-$; and $\phi_1^- \circ \phi_1^+(\delta_0)$ and $\phi_1^- \circ \phi_1^+(\delta_1)$ are contained in distinct components of b_1^-.

(D) There exists a path $\{\langle u_s, \sigma_s\rangle : 0 \leqslant s \leqslant 1\} \subseteq D_2^+ \times \Sigma$ such that $u_s \in U(\bar{u})$ in (1.3, σ_s); $\phi_2^- \circ \phi_2^+(u_0; \sigma_0) \in \beta_0$; and $\phi_2^- \circ \phi_2^+(u_1; \sigma_1) \in \beta_1$.

THEOREM 1.7 (Homoclinic solutions of (1.3)). *Hypothesis* (1.6, HOM) *implies that* (1.3, σ_s) *admits a homoclinic solution for some* σ_s.

Remark. The proof of 1.7 generalizes immediately to the case in which $U(\bar{u})$ passes through any number of blocks $B_2 \cdots B_N$ before returning to $\bar{u}$. In particular, we say that $U(\bar{u})$ is a *wave train of length* k if $U(\bar{u})$ passes through B_2 k times.

Periodic solutions of (1.3, σ) will be found for fixed σ using the notion of topological degree [13, 30].

HYPOTHESIS (1.8, PER). There exist B_1, B_2, disjoint blocks for (1.3, σ), with properties (A)–(C):

Choose $y_1, y_4, y_5, y_8 \in \mathbb{R}$ such that

(A) $y_1 < \bar{y} < y_4 < y_5 < \bar{\bar{y}} < y_8$,

(B) $[y_1, y_8] \subseteq \Pi_1 \cap \Pi_2$, and

(C) $H(V_1(y), 0, y) < 0 < H(V_2(y), 0, y)$ for every $y \in [y_1, y_8]$.

A construction similar to that of B_2 in 2.7 yields disjoint blocks $P_1 = P_1(C_1)$, $B_2 = B_2(C_2)$ for (2.2, θ, ϵ) (when C_1, C_2, $|\theta - \tilde{\theta}|$, ϵ are small) such that

(A) no positive half solution is contained in P_1, B_2,

(B) $P_1 \cap \{y = y_1\} \subseteq p_1^-$ and $B_2 \cap \{y = y_8\} \subseteq b_2^-$,

(C) $p_1^- - \{y = y_1\}$ and $b_2^- - \{y = y_8\}$ each has two components, one in $\{W \geqslant 0\}$, one in $\{W \leqslant 0\}$.

Now, for $s \in (0, 1]$, $y \in [y_1, y_8]$, let $c(s, y)$ be a nondecreasing C^1 function such that

$$c(s, y) = \begin{Bmatrix} sC_1 & \text{if } y \in [y_1, y_4] \\ C_1 & \text{if } y \in [y_5, y_8] \end{Bmatrix}.$$

Let $P_s \equiv \{\langle V, W, y\rangle : y \in [y_1, y_8]$ and $|W \pm (\tilde{\theta} + 1)(V - V_2(y))| \leqslant (\tilde{\theta} + 1)\, c(y, s)\}$ (see Fig. 7).

Let $D^\pm$, $\phi^\pm$ refer to P_1. There exist y_6, y_7 such that $y_5 < y_6 < \bar{\bar{y}} < y_7 < y_8$ and some negative half solution of $A(y, -\tilde{\theta})$ (see 2.3) is contained in D^+ for every $y \in [y_6, y_7]$. Shrinking C_2 if necessary, then $B_2 = B_2(C_2)$ has the property that if $\Delta \equiv b_2^- \cap \{W \leqslant 0$ and $y \in (y_6, y_7)\}$, $\delta_0 \equiv \mathrm{cl}(\Delta) \cap \{y = y_6\}$ and $\delta_1 \equiv \mathrm{cl}(\Delta) \cap \{y = y_7\}$, then $\Delta \subseteq D^+$, $\phi^- \circ \phi^+(\delta_0) \subseteq \{W < 0\}$, $\phi^- \circ \phi^+(\delta_1) \subseteq \{W > 0\}$, and $\phi^- \circ \phi^+(\delta_0 \cup \delta_1) \cdot (-\infty, 0] \subseteq \{y > y_5\}$. In a similar way, we now choose $y_2 < \bar{y} < y_3$; $B_1 = P_s$; and $\Gamma \subseteq b_1^-$ such that Hypothesis (1.8, PER) is satisfied.

(3.2) Recall that $n_\infty' > 0$, $\partial V_i/\partial n < 0$, $h_\infty' < 0$, $\partial V_i/\partial h > 0$, and $\gamma_n, \gamma_h > 0$.

(A) If $V = V_1(n, h)$ and $\langle n, h\rangle$ is a rest point of $(\mathrm{H})_1$, $G(V, n, h) = G(V, n_\infty(V), h_\infty(V)) = 0$, so $V = 0$, $n = n_0$, and $h = h_0$.

Let

$$A(n, h) \equiv 1 - n_\infty'(V_1(n, h))(\partial V_1/\partial n)(n, h),$$
$$B(n, h) \equiv n_\infty'(V_1(n, h))(\partial V_1/\partial h)(n, h),$$
$$C(n, h) \equiv h_\infty'(V_1(n, h))(\partial V_1/\partial n)(n, h),$$

and

$$D(n, h) \equiv 1 - h_\infty'(V, (n, h))(\partial V_1/\partial h)(n, h).$$

Let $\lambda(\bar\theta, 0)$ be the negative eigenvalue of $(2.2, \bar\theta, 0)$. For small $|\theta - \bar\theta|$, ϵ, let $\lambda(\theta, \epsilon)$ be the negative eigenvalue of $(2.2, \theta, \epsilon)$ near $\lambda(\bar\theta, 0)$.

Fix small $\epsilon, \tau > 0$. For $-1 \leqslant s \leqslant 1$ let $\Lambda(s)$ be that branch of $U(\langle V_2(\bar y), 0, \bar y\rangle)$ in $(2.2, \bar\theta + \tau s, \epsilon)$ tangent to the eigenvector of $\lambda(\bar\theta + \tau s, \epsilon)$ and beginning in $\{W < 0\}$ (Fig. 24D). Let $\Pi = \{U_s = \langle V_s, W_s, y_s\rangle\}$ be a path with $U_s \in \Lambda(s)$ near $\langle V_2(\bar y), 0, \bar y\rangle$. If τ, ϵ are small $\Pi \subseteq D^+$; and $\phi^- \circ \phi^+(U_{-1}; \bar\theta - \tau, \epsilon)$, $\phi^- \circ \phi^+(U_1; \bar\theta + \tau, \epsilon)$ are contained in distinct components of b^-. Thus (1.4, HET) is satisfied and Theorem 1.5 implies that $(2.2, \theta_\epsilon, \epsilon)$ admits a heteroclinic solution with $\theta_\epsilon = \bar\theta + \tau s$ for some s. The proof implies that θ_ϵ may be chosen so that $\theta_\epsilon \to \bar\theta$ as $\epsilon \to 0$.

(2.7) First construct A_1, B_1 as in Theorem 2.5, with $\bar{\bar y} = \bar y \cdot^2 \bar t$.

We next construct a block A_2 for $(2.5)_2$ and, from it, a block B_2 for (2.2). Choose $\tilde y \in \Pi_2$, $0 < t_0 < t_1 < t_2 < t_3$ such that $\bar y = \tilde y \cdot^2 t_0$, $\bar{\bar y} = \tilde y \cdot^2 t_2$, $\theta(\tilde y \cdot^2 t_1) > -\bar\theta$, $\theta(\tilde y \cdot^2 t_3) < -\bar\theta$, and $\tilde y \cdot^2 [t_1, t_3] \subseteq \mathrm{int}(A_1)$. By Lemma 1.2(B) there exists a block A_2 for $(2.5)_2$ and $\alpha \subseteq a_2^+$ such that $\tilde y \in \alpha$, $A_2 \subseteq \alpha \cdot^2 [0, t_3]$, $\alpha \cdot^2 t_1 \subseteq \{\theta(y) > -\bar\theta\}$, $\alpha \cdot^2 t_3 \subseteq \{\theta(y) < -\bar\theta\}$, and $\alpha \cdot^2 [t_1, t_3] \subseteq \mathrm{int}(A_1)$. Construct B_2 from A_2 as in 2.5.

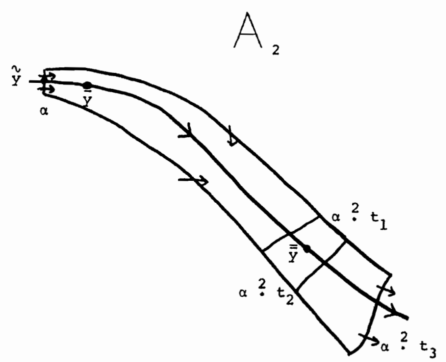

FIG. 25. A_2.

Let $\Delta = \{\langle V, W, y\rangle \in b_2^- : y \in \alpha \cdot^2 (t_1, t_2)$ and $W + (\bar\theta + 1)(V - V_2(y)) = -(\bar\theta + 1)c\}$, $\delta_0 = \mathrm{cl}\Delta \cap (\alpha \cdot^2 t_1)$, and $\delta_1 = \mathrm{cl}\Delta \cap (\alpha \cdot^2 t_2)$ (Fig. 6). If c, $|\theta - \bar\theta|$, ϵ are small, $\Delta \subseteq D_1^+$, $\phi_1^+(\delta_0 \cup \delta_1) \subseteq D_1^-$, and $\phi_1^- \cdot \phi_1^+(\delta_0)$ and $\phi_1^- \cdot \phi_1^+(\delta_1)$ are contained in distinct components of b_1^-. In addition, no positive half solution is contained in B_2 if c is small.

As in Theorem 2.5, now, for small ϵ there exists a path in $U(\langle 0, 0, \bar y\rangle)$, as θ varies, so that hypothesis (1.6, HOM) is satisfied. The result follows from Theorem 1.7.

(2.9) We first construct a family of blocks $\{P_s : s \in (0, 1]\}$ and let $B_1 = P_s$ for some s, chosen after B_2 is constructed.

(A) No positive half solution is contained in B_1 or B_2.

(B) There exist $\Gamma \subseteq b_1^- \cap D_2^+$, $\Delta \subseteq b_2^- \cap D_1^+$ such that $(b_1^- - \Gamma)$ consists of two components, α_0 and α_1; and $(b_2^- - \Delta)$ consists of two components, β_0 and β_1. In addition, if $\gamma_i \equiv \alpha_i \cap \mathrm{cl}(\Gamma)$ and $\delta_i \equiv \beta_i \cap \mathrm{cl}(\Delta)$, then $\phi_2^- \circ \phi_2^+(\gamma_i) \subseteq \mathrm{int}(\beta_i)$ and $\phi_1^- \circ \phi_1^+(\delta_i) \subseteq \mathrm{int}(\alpha_i)$ $(i = 0, 1)$.

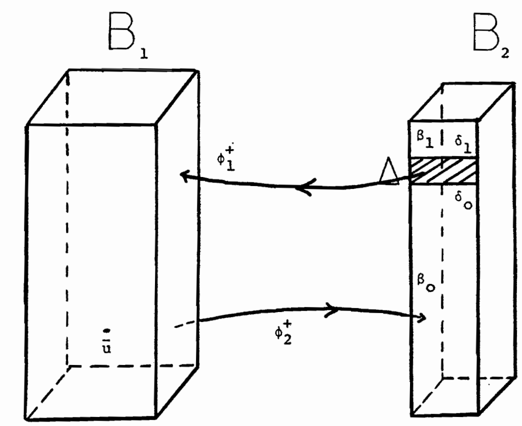

FIG. 6. B_1, B_2 satisfy (1.6, HOM), with b_1^- = front and back; b_2^- = front, back, and top.

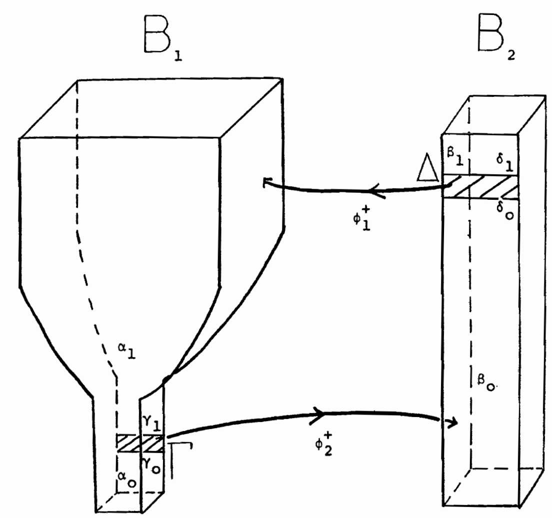

FIG. 7. B_1, B_2 satisfy (1.8, PER), with b_1^- = front, back, and bottom; b_2^- = front, back, and top.

(C) There exist homeomorphisms $h_j : b_j^- \to [0, 1]^{n-2} \times [-1, 2]$ such that

$$h_1(\Gamma) = [0, 1]^{n-2} \times (0, 1),$$
$$h_1(\gamma_i) = [0, 1]^{n-2} \times \{i\},$$
$$h_2(\Delta) = [0, 1]^{n-2} \times (0, 1),$$

and

$$h_2(\delta_i) = [0, 1]^{n-2} \times \{i\}.$$

THEOREM 1.9 (Periodic solutions of (1.3)). *Hypothesis* (1.8, PER) *implies that* (1.3, σ) *admits a periodic solution.*

2. TRAVELING WAVE SOLUTIONS OF A NONLINEAR DIFFUSION EQUATION

In this section we apply the abstract results of Section 1 to find traveling wave solutions of a nonlinear diffusion equation coupled with l "slow" equations

$$\partial^2 \bar{V}/\partial x^2 = (\partial \bar{V}/\partial s) + G(\bar{V}, \bar{y}), \qquad \frac{\partial \bar{y}}{\partial s} = \epsilon H(\bar{V}, \bar{y}), \tag{2.1}$$

where $\bar{V} \in (V_\alpha, V_\beta) \subseteq \mathbb{R}$; $\bar{y} \in \Omega_y \subseteq \mathbb{R}^l$; and $\epsilon > 0$.

A *traveling wave solution* of (2.1) (with speed θ) consists of a solution $\langle \bar{V}(x, s), \bar{y}(x, s)\rangle$ of (2.1) such that $\bar{V}(x, s) = V(t)$, $\bar{y}(x, s) = y(t)$ where $t = (x + \bar{\theta} s)$. An application of the chain rule gives traveling wave solutions of (2.1) as solutions $\langle V, W, y\rangle$ of the $(2 + l)$ equations

$$\dot{V} = W, \qquad \dot{W} = \theta W + G(V, y), \qquad \dot{y} = \epsilon\theta^{-1} H(V, y). \tag{2.2}$$

Hypothesis (2.2, CUBIC) will provide the principal restriction on G, namely, that G be a "cubic" function of V for fixed y (Fig. 10). Hypotheses (2.4, HET′), (2.6, HOM′), and (2.8, PER′) give sufficient conditions for the existence of heteroclinic, homoclinic, and periodic solutions of (2.2) provided that ϵ is small. These hypotheses do not involve blocks; rather, they require the existence of a "singular solution."

If ϵ, $|\theta - \bar{\theta}|$ are small, solutions of (2.2, θ, ϵ) stay close to solutions of (2.2, $\bar{\theta}$, 0) provided $\dot{V}$ or $\dot{W}$ is not small. If $\dot{V} \cong 0$ and $\dot{W} \cong 0$ and $\epsilon > 0$, y becomes "fast" relative to $\langle V, W\rangle$. A *singular solution* (*ss*) consists of alternating solutions or solution segments of the two systems (2.2, $\bar{\theta}$, 0) and $\dot{y} = H(V, y)$,

If $\int_{V_1(y)}^{V_2(y)} G(V, y)\, dV \geq 0$, the argument is similar, where $\Lambda(y, \theta(y))$ runs from $\langle V_2(y), 0, y\rangle$ to $\langle V_1(y), 0, y\rangle$ if $\theta(y) \leq 0$. (B) follows from the fact that $\partial G/\partial y_k > 0$.

(B) implies that $\{\theta(y) = \bar{\theta}\}$ is the graph of a function of $\langle y_1 \cdots y_{k-1} y_{k+1} \cdots y_l\rangle$.

(2.5) By Lemma 1.2A there exists a block $\bar{A}$ for $(2.5)_1$ such that $\bar{a}^- = \phi$ and $y \in S(\bar{y})$ if $y \cdot [0, \infty) \subseteq \bar{A}$. Choose $T > 0$ such that $\bar{y} \cdot^1 [T, \infty) \subseteq \text{int}(\bar{A})$. By Lemma 1.2B there exists a block $\bar{\bar{A}}$ for $(2.5)_1$ such that $\bar{y} \cdot^1 [0, T] \subseteq \text{int}(\bar{\bar{A}})$; $\bar{\bar{a}}^- \subseteq \text{int}(\bar{A})$; and no set $y \cdot^1 [0, \infty) \subseteq \bar{\bar{A}}$. Then $A = \bar{A} \cup \bar{\bar{A}}$ is a block for $(2.5)_1$ with $a^- = \phi$; $y \in S(\bar{y})$ if $\bar{y} \cdot^1 [0, \infty) \subseteq A$; and $\bar{y} \cdot^1 [0, \infty) \subseteq \text{int}(A) \cap S(\bar{y})$.

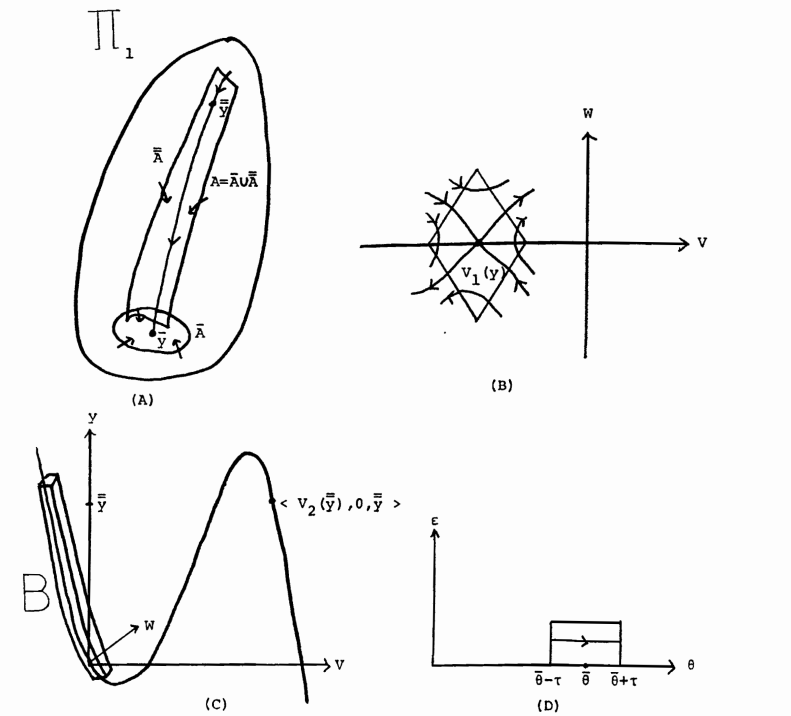

FIG. 24. (A) Π_1 ($l = 2$). (B) B for fixed y. (C) B for (2.3, FN) (see Fig. 11). (D) Parameter range where B is a block.

Let $\bar{\theta} \equiv -\theta(\bar{y}) > 0$. For $c > 0$ let $B \equiv \{\langle V, W, y\rangle : y \in A$ and $|W \pm (\bar{\theta} + 1)(V - V_1(y))| \leq (\bar{\theta} + 1)c\}$ (Fig. 24B).

If c, $|\theta - \bar{\theta}|$, ϵ are small, B is a block for (2.2, θ, ϵ) with $b^- = B \cap \{|W + (\bar{\theta} + 1)(V - V_1(y))| = (\bar{\theta} + 1)c\}$ and $\langle V, W, y\rangle \in S(\langle 0, 0, y\rangle)$ if $\langle V, w, y\rangle \cdot [0, \infty) \subseteq B$ (Fig. 24C).

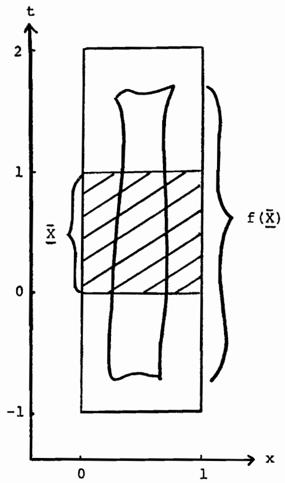

FIG. 22. $n = 3$. Compare Fig. 7.

f_2 is a continuous map from Γ to Δ. Thus $f \equiv h_1 \circ \phi_1^- \circ \phi_1^+ \circ f_2 \circ h_1^{-1}$ satisfies the hypotheses of the lemma and there exists $(\bar{x}, \bar{t})$ such that $f(\bar{x}, \bar{t}) = (\bar{x}, \bar{t})$. If $F_0(u) \notin [0, 1]$, $\phi_1^- \circ \phi_1^+ \circ f_2(u) \notin \Gamma$, so $h_1(u)$ is not a fixed point of f. If $\bar{u} \equiv h_1^{-1}(\bar{x}, \bar{t})$, then $f_2(\bar{u}) = \phi_2^- \circ \phi_2^+(\bar{u})$, $\phi_1^- \circ \phi_1^+ \circ \phi_2^- \circ \phi_2^+(\bar{u}) = \bar{u}$, and $\bar{u}$ is contained in a periodic solution of $(1.3, \sigma)$.

(2.3) (A) Choose $y \in \Pi_1 \cap \Pi_2$ such that $\int_{V_1(y)}^{V_2(y)} G(V, y)\, dV < 0$. $\Lambda(y, 0)$ leaves $\{W > 0\}$ at $\langle V_0, 0\rangle$, where $\int_{V_1(y)}^{V_0} G(V, y)\, dV = 0$ and $V_0 < V_2(y)$. If $0 < \theta \ll 1$, $\Lambda(y, \theta)$ leaves $\{W > 0\}$ near $\langle V_0, 0\rangle$. If $\theta \gg 1$, $\Lambda(y, \theta)$ enters $\{V > V_2(y)\}$; thenceforth $\dot{V}, \dot{W} > 0$. For some intermediate value $(\theta = \theta(y))$ $\Lambda(y, \theta(y))$ joins the two rest points $\langle V_1(y), 0, y\rangle$ and $\langle V_2(y), 0, y\rangle$.

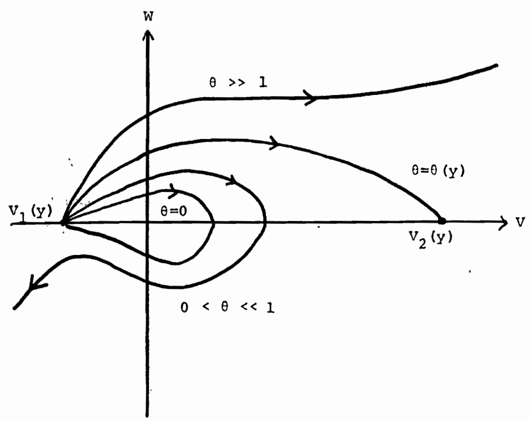

FIG. 23. y fixed, $\epsilon = 0$.

the latter being defined on a component of $\{W = G(V, y) = 0$ and $(\partial G/\partial V)(V, y) \neq 0\}$ (Fig. 8, 9). Theorems 2.5, 2.7, and 2.9 show that the existence of a singular heteroclinic, homoclinic, or periodic solution of $(2.2, \bar{\theta}, 0)$ implies the existence of a solution of $(2.2, \theta, \epsilon)$ of the same type. Moreover solutions of $(2.2, \theta, \epsilon)$ converge to the ss as $\langle \theta, \epsilon\rangle \to \langle \bar{\theta}, 0\rangle$.

EXAMPLE 2.1 (The FitzHugh–Nagumo equations). Traveling wave solutions of (0.2) are solutions of the system

$$\begin{aligned} \dot{V} &= W, \\ \dot{W} &= \theta W - f(V) + y, \qquad (2.3, \text{FN}) \\ \dot{y} &= \epsilon\theta^{-1}(V - \gamma y), \end{aligned}$$

where $V, W, y \in \mathbb{R}$, $\theta > 0$ and $\epsilon, \gamma \geqslant 0$. f is "cubic," $f(\bar{V}) = 0$, and $\int_0^{\bar{V}} f(V)\, dV > 0$ (Fig. 8).

If γ is small and $\epsilon > 0$, $\langle 0, 0, 0\rangle$ is the unique rest point of (FN). Notice that $\{\langle V, W, y\rangle: -f(V) + y = W = 0$ and $f'(V) < 0\} \subseteq \{\dot{V} = \dot{W} = 0\}$ consists of two components, χ_1 and χ_2, with $\langle 0, 0, 0\rangle \in \chi_1$ and $\langle \bar{V}, 0, 0\rangle \in \chi_2$. For $i = 1, 2$,

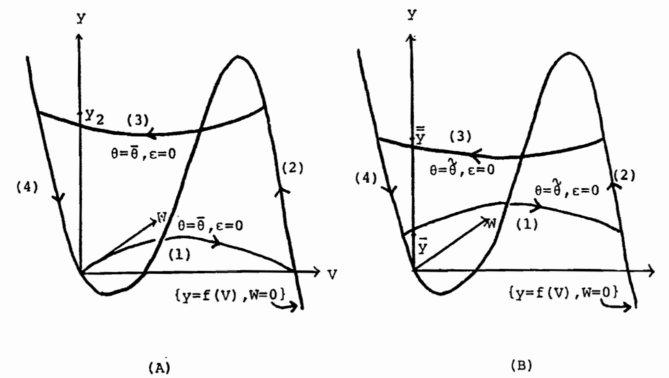

FIG. 8. (A) Homoclinic singular solution of (2.3, FN). (B) Periodic singular solution of (2.3, FN).

if Π_i is the image of χ_i under the map $\langle V, W, y\rangle \to y$, there is a function V_i such that $\chi_i = \{\langle V_i(y), 0, y\rangle : y \in \Pi_i\}$. Let $(\text{FN})_i$ be the system defined on Π_i:

$$\dot{y}^i = (V_i(y) - \gamma y). \qquad (2.4, \text{FN})_i$$

Note that $(V_2(y) - \gamma y) > 0$; and $(V_1(y) - \gamma y) < 0$ when $y > 0$.

A homoclinic singular solution of (FN) (Fig. 8A) consists of

(1) a heteroclinic solution of $(\text{FN}, \bar{\theta}, 0)$ from $\langle 0, 0, 0\rangle$ to $\langle \bar{V}, 0, 0\rangle$ for some $\bar{\theta}$;

(2) a solution segment of $(FN)_2$ from 0 to y_2;

(3) a heteroclinic solution of $(FN, \bar{\theta}, 0)$ from $\langle V_2(y_2), 0, y_2\rangle$ to $\langle V_1(y_2), 0, y_2\rangle$; and

(4) a positive half solution of $(FN)_1$ from y_2 to 0.

Periodic singular solutions are similar; in fact, there exists a periodic singular solution of (FN) for every $\tilde{\theta} \in (0, \bar{\theta})$ (Fig. 8B).

If we allow γ to increase, (FN) acquires rest points $\langle V_2(y_\gamma), 0, y_\gamma\rangle$:

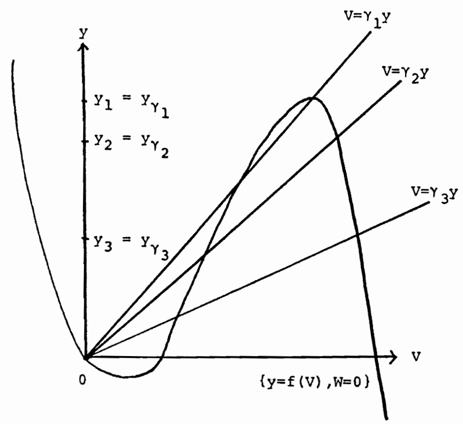

FIG. 9. (2.3, FN) with γ varying.

Define y_1, y_3 by the equations $f'((V_2(y_1)) = 0$; and $\int_{V_1(y_3)}^{V_2(y_3)} (-f(V) + y_3)\, dV = 0$. For $i = 1, 2, 3$ let $\gamma_i = V_2(y_i)/y_i$.

(A) If $\gamma \in [0, \gamma_2)$, (FN) admits a homoclinic ss from and to $\langle 0, 0, 0\rangle$ for $\theta = \bar{\theta}$.

If $\gamma \in (\gamma_2, \gamma_3)$, (FN) admits a homoclinic ss from and to $\langle V_2(y_\gamma), 0, y_\gamma\rangle$ for some $\theta \in (0, \bar{\theta})$.

(B) If $\gamma \in (\gamma_1, \infty)$, (FN) admits a heteroclinic ss from $\langle 0, 0, 0\rangle$ to $\langle V_2(y_\gamma), 0, y_\gamma\rangle$ for $\theta = \bar{\theta}$.

If $\gamma \in (\gamma_1, \gamma_3)$, (FN) admits a heteroclinic ss from $\langle V_2(y_\gamma), 0, y_\gamma\rangle$ to $\langle 0, 0, 0\rangle$ for some $\theta \in (0, \infty)$ (Fig. 11).

(C) If $\gamma \in [0, \gamma_2]$, (FN) admits a periodic ss for *every* $\theta \in (0, \bar{\theta})$.

If $\gamma \in (\gamma_2, \gamma_3)$, (FN) admits a periodic ss for *every* $\theta \in (0, \theta_\gamma)$, for some $\theta_\gamma \in (0, \bar{\theta})$.

We now return to (2.2).

Topological degree [30, Section 10.3; 13]. Let $\bar{\Psi}$ be a bounded open subset of $\mathbb{R}^k$ and F a continuous function from $\bar{\Psi}$ into $\mathbb{R}^k$.

Let F be a simplicial mapping of $\bar{\Psi}$ into $\mathbb{R}^k$. The *degree* of F at a point $u \in \mathbb{R}^k - F(\partial\bar{\Psi})$ $(\deg(F, \bar{\Psi}, u))$ is the algebraic number of times that (almost all) points are covered, in the region U_i containing u [30, p. 80].

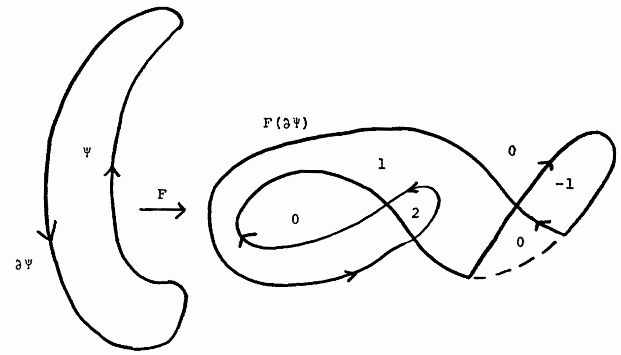

FIG. 21. Degree of F in several regions [30, p. 79].

The degree of a continuous map is defined by simplicial approximation.

(i) If $\deg(F, \bar{\Psi}, u) \neq 0$ then $u \in F(\bar{\Psi})$.

(ii) If $F = f - I$, where I is the identity, and $\deg(F, \bar{\Psi}, 0) \neq 0$, then f admits a fixed point in $\bar{\Psi}$.

(iii) If $u \in F(\bar{\Psi})$ and F is a homeomorphism, then $\deg(F, \bar{\Psi}, u) = \pm 1$.

(iv) (Homotopy) If $\{f_s : s \in [0, 1]\}$ is a continuous family and $f_s(u) - u \neq 0$ for $u \in \partial\bar{\Psi}$, then $\deg(f_0 - I, \bar{\Psi}, 0) = \deg(f_1 - I, \bar{\Psi}, 0)$. ($f_0$ is *fp-homotopic* to f_1.)

LEMMA. *Let f be a continuous map from $[0, 1]^{n-2} \times [0, 1]$ to $(0, 1)^{n-2} \times [-1, 2]$ such that $f(x, 0) \in (0, 1)^{n-2} \times [-1, 0)$ and $f(x, 1) \in (0, 1)^{n-2} \times (1, 2]$ for all $x \in [0, 1]^{n-2}$. Then there exists $(\bar{x}, \bar{t})$ such that $f(\bar{x}, \bar{t}) = (\bar{x}, \bar{t})$.*

Proof of Lemma. Let $f_1(x, t) = \langle \frac{1}{2} \cdots \frac{1}{2}, 2t - \frac{1}{2}\rangle$ and $\bar{\Psi} = (0, 1)^{n-2} \times (0, 1)$. Then f is *fp*-homotopic to f_1 with $f_s = (1 - s) f + s f_1$. Since $f_1 - I$ is a homeomorphism, $\deg(f - I, \bar{\Psi}, 0) = \deg(f_1 - I, \bar{\Psi}, 0) = \pm 1$. Thus f has a fixed point in $\bar{\Psi}$ (Leray–Schauder).

Proof of Theorem. Let $h_2 \circ \phi_2^- \circ \phi_2^+ \equiv \langle F_1 \cdots F_{n-2} F_0\rangle$ and

$$\begin{aligned} f_2(u) &\equiv \phi_2^- \circ \phi_2^+(u) && \text{if } 0 \leqslant F_0(u) \leqslant 1, \\ &\equiv h_2^{-1}(\langle F_1(u) \cdots F_{n-2}(u), 0\rangle) && \text{if } F_0(u) \leqslant 0, \\ &\equiv h_2^{-1}(\langle F_1(u) \cdots F_{n-2}(u), 1\rangle) && \text{if } F_1(u) \geqslant 1. \end{aligned}$$

and is unbounded; let Γ be the other branch. Then there exist $\theta_{\max}$, $\theta_{\min}$, $E, D > 0$ such that Γ is unbounded if one of the following holds:

(i) $\theta \geqslant \theta_{\max}$,

(ii) $\theta \leqslant \epsilon\theta_{\min}$,

(iii) $\epsilon \geqslant E$, *or*

(iv) $\delta \geqslant D/\epsilon$.

6. Proofs

(1.2) (A) The proof is standard [11].

(B) [32]. If $f(u) \equiv (u - \tilde{u})$: $G(\tilde{u})$ and $| u - \tilde{u} |$ is small, $\dot{f}(u) = G(u)$: $G(\tilde{u}) > 0$. If $\overline{\Psi}(\eta) \equiv \{u: f(u) = 0$ and $| u - \tilde{u} | \leqslant \eta\}$ and $\bar{\eta}$ is small, let

$$B_1 \equiv \bigcup_{t \in [0,T]} \Psi((2 - (t/T))\bar{\eta}) \cdot t$$

and

$$B_2 \equiv \bigcup_{t \in [0,T]} \Psi((1 + (t/T))\bar{\eta}) \cdot t.$$

(1.3) (See [11] for a similar proof.) Let $u_n \to u$ in D^+. For some $\epsilon > 0$, $u \cdot [T^+(u), T^+(u) + \epsilon] \subseteq \operatorname{int}(B)$ and $u \cdot [T^+(u) - \epsilon, T^+(u)] \cap B = \phi$. Thus for large n, $u_n \cdot (T^+(u) + \epsilon) \in \operatorname{int}(B)$ and $u_n \cdot (T^+(u) - \epsilon) \notin B$, so $\overline{\lim}\, T^+(u_n) \leqslant T^+(u) + \epsilon$. Since ϵ was arbitrary, T^+ is usc.

If ϵ is small, the distance from b^+ to $u \cdot [\epsilon, T^+(u) - \epsilon]$ is positive. Thus for large n the distance from b^+ to $u_n \cdot [\epsilon, T^+(u) - \epsilon]$ is positive. Thus $\underline{\lim}\, T^+(u_n) \geqslant T^+(u) - \epsilon$ and T^+ is lsc.

The proof that T^- is continuous on D^- is similar, and $\phi^\pm$ is then the composition of continuous functions.

(1.5) Since ϕ^+ is continuous, it maps a path Π in D^+ to a path in B^+. If $\phi^+(\Pi)$ is contained in D^-, $\phi^- \circ \phi^+(\Pi)$ is a path in b^-. Thus $\phi^+(\Pi)$ is *not* contained in D^- if the endpoints of $\phi^+(\Pi)$ are mapped by ϕ^- to distinct components of b^-. In this case, one positive half solution beginning at a point in $\phi^+(\Pi)$ is contained in B. This is the case if we assume Hypothesis (1.4, HET), so u_s is contained in a heteroclinic solution of (1.3, σ_s) for some $s \in (0, 1)$.

(1.7) If Π is a path in D_2^+ and no positive half solution is contained in B_2, Lemma 1.3 implies that $\phi_2^- \circ \phi_2^+(\Pi)$ is a path in b_2^-. If the endpoints of this path are contained in β_0, β_1 respectively, there exists a path $\tilde{\Pi} \subseteq \operatorname{cl}(\Delta) \cap \phi_2^- \circ \phi_2^+(\Pi)$ whose endpoints are contained in δ_0, δ_1, respectively. Thus, Hypothesis (1.6, HOM) and the previous remark imply the existence of a homoclinic solution of (1.3).

(1.9) The proof applies the notion of topological degree.

Hypothesis (2.2, CUBIC). (A) $V_\alpha < 0 < V_\beta$, and $G(V_\alpha, y) < 0 < G(V_\beta, y)$ for every y.

(B) For every y there exist at most *three* V such that $G(V, y) = 0$; for some y, there exist exactly three. Moreover, $(\partial^2 G/\partial V^2)(V, y) \neq 0$ if $G(V, y) = (\partial G/\partial V)(V, y) = 0$.

(C) $\partial G/\partial y_k > 0$ for some k.

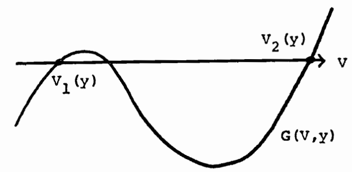

Fig. 10. "Cubic" G.

Definitions (χ, χ_i, Π_i, V_i, $y \cdot^i t$, $\Lambda(y, \theta)$).

Let $\chi \equiv \{\langle V, W, y\rangle: W = G(V, y) = 0$ and $(\partial G/\partial V)(V, y) > 0\}$. (2.2, CUBIC) then implies that χ has two components, χ_1 and χ_2, with $V < V'$ when $\langle V, 0, y\rangle \in \chi_1$ and $\langle V', 0, y\rangle \in \chi_2$. For $i = 1, 2$, let Π_i be the image of χ_i under the map $\langle V, W, y\rangle \to y$. By the implicit function theorem, there exists V_i: $\Pi_i \to (V_\alpha, V_\beta)$ such that $\langle V, 0, y\rangle \in \chi_i$ iff $y \in \Pi_i$ and $V = V_i(y)$. Note that $V_1(y) < V_2(y)$ when $y \in \Pi_1 \cap \Pi_2$;

$$\frac{\partial V_i}{\partial y_j} = \frac{-\partial G/\partial y_j}{\partial G/\partial V}; \quad \text{and} \quad \operatorname{sgn}\left(\frac{\partial V_i}{\partial y_j}\right) = -\operatorname{sgn}\left(\frac{\partial G}{\partial y_j}\right).$$

For $y \in \Pi_i$, (2.2) defines a system on Π_i:

$$\dot{y}^i = H(V_i(y), y) \tag{2.5$_i$}$$

(see Fig. 14, where $l = 2$).

Let $y \cdot^i t$ denote a solution of $(2.5)_i$.

For every $y \in \Pi_1 \cap \Pi_2$ and $\theta \in \mathbb{R}$, $\langle V_i(y), 0, y\rangle$ is a rest point of (2.2, $|\theta|$, 0) with one positive and one negative eigenvalue. If $\theta \geqslant 0$ let $\Lambda(y, \theta)$ be that branch of $U(\langle V_1(y), 0, y\rangle)$ with negative half solution contained in $\{W > 0\}$; if $\theta \leqslant 0$, let $\Lambda(y, \theta)$ be that branch of $U(\langle V_2(y), 0, y\rangle)$ with negative half solution contained in $\{W < 0\}$. (In Fig. 8A, (1) is $\Lambda(0, \bar{\theta})$ and (2) is $\Lambda(y_2, -\bar{\theta})$.)

Lemma 2.3 shows that for fixed $y \in \Pi_1 \cap \Pi_2$, $\Lambda(y, \theta)$ or $\Lambda(y, -\theta)$ runs between χ_1 and χ_2 in (2.2, θ, 0) for some $\theta \geqslant 0$.

Lemma 2.3 (Jump sets exist). *Assume Hypothesis* (2.2, CUBIC).

(A) [25] *There exists a continuous function* $\theta(y): \Pi_1 \cap \Pi_2 \to \mathbb{R}$ *such that* $\Lambda(y, \theta(y))$ *is a solution of* (2.2, $|\theta(y)|$, 0) *from* $\langle V_1(y), 0, y\rangle$ *to* $\langle V_2(y), 0, y\rangle$ *if* $\int_{V_1(y)}^{V_2(y)} G(V, y)\, dV \leqslant 0$; *and* $\Lambda(y, \theta(y))$ *is a solution of* (2.2, $|\theta(y)|$, 0) *from* $\langle V_2(y), 0, y\rangle$ *to* $\langle V_1(y), 0, y\rangle$ *if* $\int_{V_2(y)}^{V_1(y)} G(V, y)\, dV \geqslant 0$ (*Fig.* 8). $\theta(y)$ *acquires a half-line of values on* $\{y \in \partial(\Pi_1 \cap \Pi_2): \partial G/\partial V(V_i(y), y) = 0,\ i = 1, 2\}$. *For* y *in this set,* $\theta(y) > [<, =]C$ *means that at least one value of* $\theta(y)$ *is greater than* [*less than, equal to*] C.

(B) $\theta(y)$ *decreases as* y_k *increases.*

(C) $\{y \in \bar{\Pi}_1 \cap \bar{\Pi}_2 : \theta(y) = \tilde{\theta}\}$ *is an* $(l-1)$*-manifold. If* $\tilde{\theta} \geqslant 0$,

$\{\theta(y) = \tilde{\theta}\}$ *is the jump set from* $\bar{\Pi}_1$ *to* $\bar{\Pi}_2$; *if* $\tilde{\theta} \leqslant 0$ *it is the jump set from* $\bar{\Pi}_2$ *to* $\bar{\Pi}_1$ (*Fig.* 12).

HYPOTHESIS (2.4, HET′). (A) Let $\bar{y} \in \Pi_1$ be a rest point of $(2.5)_i$ whose eigenvalues have negative real part. (For simplicity, assume $V_1(y) = 0$.)

Let $\bar{\bar{y}} \in \Pi_1 \cap \Pi_2$ be a rest point of $(2.5)_2$.

(B) $\int_{V_1(\bar{\bar{y}})}^{V_2(\bar{\bar{y}})} G(V, \bar{y})\, dV > 0$.

(C) $\bar{y} \in S(y)$ in $(2.5)_1$.

This hypothesis is satisfied by (2.3, FN) if $\gamma \in (\gamma_1, \gamma_3)$ with $\bar{y} = 0$ and $\bar{\bar{y}} = y_\gamma$.

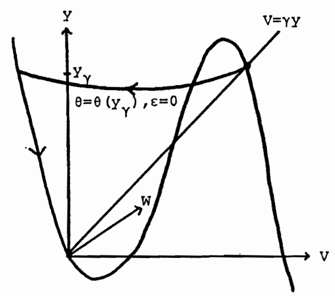

FIG. 11. Heteroclinic singular solution of (2.3, FN), where $y_\gamma = y$ and $\bar{y} = 0$.

THEOREM 2.5 (Heteroclinic solutions of (2.2)). *Hypotheses* (2.2, CUBIC) *and* (2.4, HET′) *imply that for all small* $\epsilon > 0$ (2.2, θ_ϵ, ϵ) *admits a heteroclinic solution from* $\langle V_2(\bar{y}), 0, \bar{y}\rangle$ *to* $\langle 0, 0, \bar{y}\rangle$ *for some* $\theta_\epsilon > 0$. *Moreover* $\theta_\epsilon \to |\theta(\bar{y})|$ *as* $\epsilon \to 0$.

HYPOTHESIS (2.6, HOM′). (A) Let $\bar{y} \in \Pi_1$ be a rest point of (2.2) whose eigenvalues have negative real part. (For simplicity, assume $V_1(\bar{y}) = 0$.)

(B) $\int_{V_1(\bar{y})}^{V_2(\bar{y})} G(V, \bar{y})\, dV < 0$. (Let $\bar{\theta} \equiv \theta(\bar{y})$.)

If (4.1, FAST) holds and δ is small, we would expect solutions of (4.1) to be close to solutions of (2.2) with $G(V, y) \equiv g(V, y, z(V, y))$ and $H(V, y) \equiv h(V, y, z(V, y))$. This is the content of Theorem 4.2. In particular, results of Section 3 hold for (HH) with δ small whenever (3.1, H) or (3.3, H) satisfies the appropriate hypotheses.

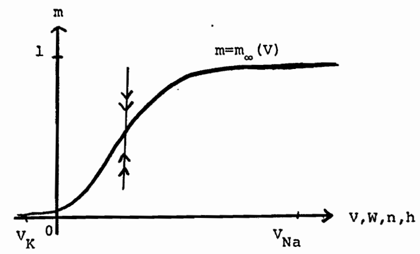

FIG. 20. (HH) with δ small.

THEOREM 4.2. *Assume Hypothesis* (4.1, FAST), *and assume that* (2.2) *satisfies Hypothesis* (2.4, HET′) (*or* (2.6, HOM′) *or* (2.8, PER′)). *Then* (4.1, δ) *admits a heteroclinic* (*or homoclinic or periodic*) *solution for all small* $\delta > 0$. *Moreover, the solutions of* (4.1, δ) *correspond to solutions of* (2.2) *as* $\delta \to 0$.

5. BOUNDED SOLUTIONS AND PARAMETER ESTIMATES OF NERVE IMPULSE EQUATIONS

In Theorem 5.1(A) we construct a compact set which contains all bounded solutions of (HH) independent of ϵ, δ and depending on θ only in the W-coordinate. (B) states that both branches of $U(\langle 0, 0, m_0, n_0, h_0\rangle)$ are unbounded if θ, ϵ, or δ is too large or if θ is too small. In particular, (HH) admits no homoclinic solutions in this case. An analogous theorem holds for (2.3, FN) if $\gamma > 0$.

THEOREM 5.1. (A) *Suppose* (HH) *is defined for* $\langle V, W, m, n, h\rangle \in \mathbb{R}^5$. *Assume that* $g \in C^2$; $0 < m_\infty, n_\infty, h_\infty < 1$; $g(V, m, n, h) < 0$ *if* $V \leqslant V_K$; *and* $g(V, m, n, h) > 0$ *if* $V \geqslant V_{Na}$. *Then any bounded solution of* (HH) *is contained in* $[V_K, V_{Na}] \times [-\theta^{-1}M, \theta^{-1}M] \times [\alpha, 1-\alpha]^3$, *where* $0 < \alpha < \min\{m_\infty(V), n_\infty(V), h_\infty(V), 1 - m_\infty(V), 1 - n_\infty(V), 1 - h_\infty(V) : V \in [V_K, V_{Na}]\}$; *and* $M \geqslant \max\{|g(V, m, n, h)| : V \in [V_K, V_{Na}]$ *and* $m, n, h \in [0, 1]\}$.

(B) *Assume* (CUBIC, H) *and suppose that* $m_\infty' > 0$; $\partial g/\partial V > 0$; *and* $\partial g/\partial m < 0$. *Then one branch of* $U(\langle 0, 0, m_0, n_0, h_0\rangle)$ *is contained in* $\{W < 0\}$

Remarks. $\bar{h} = h_a(n_0)$ and $h_0 = h_b(n_0)$. Let $f(n) \equiv \theta(n, h_b(n)) + \theta(n, h_a(n))$. Then $f(n_0) > 0$; $f(n)$ decreases as n increases; and $f(n_1) = 0$ for some $n_1 > n_0$. Let $\bar{\theta} \equiv \theta(n_0, h_0)$ and $\theta_1 \equiv \theta(n_1, h_b(n_1)) > 0$.

THEOREM 3.8 (Plateau solutions of the Hodgkin–Huxley Equations). *Assume Hypotheses* (3.1, CUBIC, H) and (3.7, PLATEAU).

(A) *If* ϵ *is small and* ϵ/τ *is large,* (3.3, H, $\theta_{\tau\epsilon}$, τ, ϵ) *admits a homoclinic solution with a plateau for some* $\theta_{\tau\epsilon} > 0$. *Moreover* $\theta_{\epsilon\tau} \to \theta(n_0, h_0)$ *as* $\epsilon \to 0$ *and* $\epsilon/\tau \to \infty$.

(B) *For fixed* $\theta \in (\theta_1, \bar{\theta})$, *if* ϵ *is small and* ϵ/τ *is large,* (3.3, H, θ, τ, ϵ) *admits a periodic solution oscillating between two plateaux.*

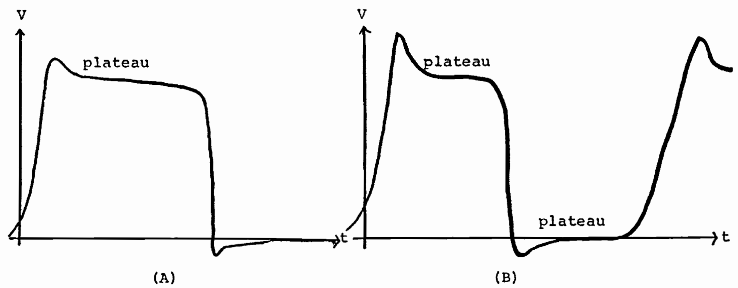

FIG. 19. (A) Plateau homoclinic solutions. (B) Plateau periodic solution.

4. FAST VARIABLES

In this section we add fast variables to the system (2.2):

$$\begin{aligned} \dot{V} &= W, \\ \dot{W} &= \theta W + g(V, y, z), \\ \dot{y} &= \epsilon\theta^{-1}h(V, y, z), \\ \dot{z} &= \delta^{-1}\theta^{-1}q(V, y, z), \end{aligned} \tag{4.1}$$

where $z \in \Omega_z \subseteq \mathbb{R}^m$ and $\delta > 0$ is small.

HYPOTHESIS (4.1, FAST). (A) There exists a C^1 function $z(V, y)$: $(V_\alpha, V_\beta) \times \Omega_y \to \Omega_z$ such that $q(V, y, z) = 0$ iff $z = z(V, y)$.

(B) The eigenvalues of $D_z q(V, y, z(V, y))$ have negative real part.

(C) There exist $\bar{t}$, $\eta > 0$ such that $\theta(\bar{y} \cdot^2 t) > -\bar{\theta}$ if $\bar{t} - \eta < t < \bar{t}$ and $\theta(\bar{y} \cdot^2 t) < -\bar{\theta}$ if $\bar{t} < t < \bar{t} + \eta$.

(D) $\bar{y} \cdot^2 \bar{t} \subseteq S(\bar{y})$ in $(2.5)_1$.

Remarks. In Fig. 8A, $\bar{y} = 0$; $\bar{y} \cdot^2 \bar{t} = y_2$; and (4) is contained in $S(\bar{y})$. The case $l = 2$ (HH) is illustrated in Fig. 12.

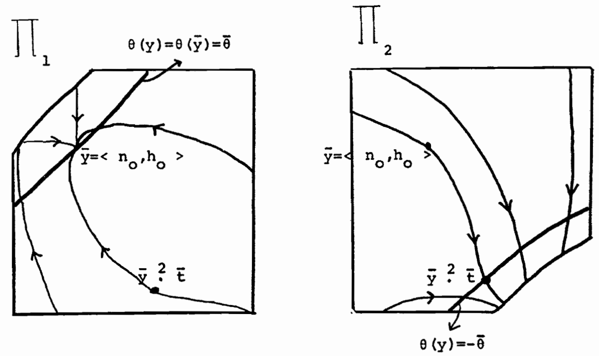

FIG. 12. A homoclinic singular solution of (2.2) with $l = 2$.

(C) is satisfied if all functions are real analytic. Henceforth we shall assume that this is the case.

(D) holds if $\bar{y}$ is globally asymptotically stable in Π_1.

THEOREM 2.7 (Homoclinic solutions of (2.2)). *Hypotheses* (2.2, CUBIC) *and* (2.6, HOM′) *imply that for all small* $\epsilon > 0$ (2.2, θ_ϵ, ϵ) *admits a homoclinic solution from and to* $\langle 0, 0, \bar{y}\rangle$ *for some* $\theta_\epsilon > 0$. *Moreover* $\theta_\epsilon \to \theta(\bar{y})$ *as* $\epsilon \to 0$.

Next we show the existence of periodic solutions of (2.2, θ, ϵ) for fixed $\theta \in (0, \bar{\theta})$ and small $\epsilon > 0$. The proof of Theorem 2.9 requires that there be only one slow variable in (2.2).

HYPOTHESIS (2.8, PER′). (A) $l = 1$.

(B) There exist $\bar{y}, \bar{\bar{y}} \in \Pi_1 \cap \Pi_2$ such that $0 < \theta(\bar{y}) = -\theta(\bar{\bar{y}})$. (Let $\tilde{\theta} \equiv \theta(\bar{y})$.)

(C) $H(V_1(y), y) < 0 < H(V_2(y), y)$ for every $y \in [\bar{y}, \bar{\bar{y}}]$ (see Fig. 8B).

THEOREM 2.9 (Periodic solutions of (2.2)). *Hypotheses* (2.2, CUBIC) *and* (2.8, PER′) *imply that* (2.2, θ, ϵ) *admits a periodic solution if* $0 < \theta < \theta(\bar{y})$ *and* $0 < \epsilon < \epsilon_\theta$.

3. Nerve Impulse Equations

We now apply the results of Section 2 to the Hodgkin–Huxley equations (with $m = m_\infty(V)$). Hypothesis (3.1, CUBIC, H) is analogous to (2.2, CUBIC). Assuming (3.1) and the weak hypothesis (3.3, HOM, H), (3.1, H) admits a homoclinic solution. The more restrictive hypotheses (3.5, WAVE TRAIN) and (3.7, PLATEAU) give conditions for the existence of finite wave train and plateau solutions. Homoclinic wave train solutions of any length exist if the singular solutions in Π_1 cross $\{\theta(n, h) = \theta(n_0, h_0)\}$ before returning to rest. Homoclinic and periodic plateau solutions exist if $\gamma_n/\gamma_h \gg 1$ or $\gamma_h/\gamma_n \gg 1$.

Results in Section 4 imply that all solutions in Section 3 correspond to traveling wave solutions of (0.1) provided δ is small.

If $R = C = 1$ (for simplicity), traveling wave solutions of the Hodgkin–Huxley equations (0.1) with $m = m_\infty(V)$ are solutions of

$$\begin{aligned} \dot V &= W, \\ \dot W &= \theta W + G(V, n, h), \\ \dot n &= \epsilon\theta^{-1}\gamma_n(V)(n_\infty(V) - n), \\ \dot h &= \epsilon\theta^{-1}\gamma_h(V)(h_\infty(V) - h), \end{aligned} \qquad (3.1,\ \text{H})$$

where $G(V, n, h) \equiv g(V, m_\infty(V), n, h)$. Note that $\langle V, W, n, h\rangle$ is a rest point of (H) if $W = G(V, n, h) = n_\infty(V) - n = h_\infty(V) - h = 0$. If $V = 0$ is to represent the unique rest state of the nerve, we would expect that $G(V, n_\infty(V), h_\infty(V)) = 0$ iff $V = 0$. If $m_\infty(0) \equiv m_0$, $n_\infty(0) \equiv n_0$, and $h_\infty(0) \equiv h_0$, $\langle 0, 0, m_0, n_0, h_0\rangle$ is the unique rest point of (HH).

Hypothesis (3.1, CUBIC, H). There exist $V_K < 0 < V_{Na}$ such that for every $n, h \in [0, 1]$:

(A) $G(V_K, n, h) < 0 < G(V_{Na}, n, h)$ and $G \in C^2$.

(B) There exist at most three $V \in (V_K, V_{Na})$ such that $G(V, n, h) = 0$. Moreover, if $G(V, n, h) = (\partial G/\partial V)(V, n, h) = 0$, $(\partial^2 G/\partial V^2)(V, n, h) \neq 0$ and $V > 0$ if $(\partial^2 G/\partial V^2)(V, n, h) > 0$.

(C) $(\partial G/\partial V)(0, n_0, h_0) > 0$, and there exists $V_2 > 0$ such that $G(V_2, n_0, h_0) = 0$ and $\int_0^{V_2} G(V, n_0, h_0)\, dV < 0$.

(D) $\partial G/\partial n > 0$ and $\partial G/\partial h < 0$.

(E) $G(V, n_\infty(V), h_\infty(V)) = 0$ iff $V = 0$.

(F) $0 < n_\infty, h_\infty < 1$; $n_\infty' > 0$; and $h_\infty' < 0$.

(G) $\gamma_n, \gamma_h > 0$.

Note that hypotheses on m_∞ are implicit.

admits a homoclinic wave train solution of length k. Moreover, $\theta_{\epsilon,1} < \theta_{\epsilon,2} < \cdots < \theta_{\epsilon,k}$ *if* $0 < \epsilon < \epsilon_k$.

(B) *Assume* (3.5, WAVE TRAIN) (A), (B). *Assume also that after J jumps the singular solution runs to* $\partial\Pi_1$. *Then* (3.1, H, θ_ϵ, ϵ) *admits wave train solutions as in* (A) *for* $k \leqslant J - 1$. ($J = 1$ *is the case where* (3.3, HOM, H) *fails*.)

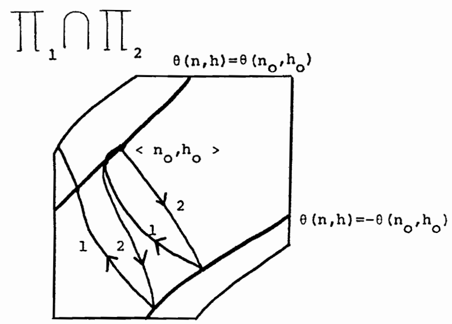

Fig. 18. (HH) with a single pulse homoclinic solution.

Our choice of the parameter ϵ in (3.1, H) indicates that $0(\dot n) = 0(\dot h)$. For the rest of Section 3 we shall examine the case where n and h vary at different rates.

$$\begin{aligned} \dot V &= W, \\ \dot W &= \theta W + G(V, n, h), \\ \dot n &= \tau\theta^{-1}\gamma_n(V)(n_\infty(V) - n), \\ \dot h &= \epsilon\theta^{-1}\gamma_h(V)(h_\infty(V) - h). \end{aligned} \qquad (3.3,\ \text{H})$$

If $\epsilon/\tau \gg 1$, for example, h will vary more rapidly than n (unless $h_\infty(V) - h \simeq 0$) although both vary slowly compared to V, W. (3.1, H) is (3.3, H) with $\tau = \epsilon$.

Theorem 3.8(A) states that if $\epsilon/\tau \gg 1$ and ϵ is small (3.3, H) admits a homoclinic solution which remains at a plateau before returning to rest. (B) states that (3.3, H) admits periodic solutions which oscillate between two plateaux connected by rapid transitions. Analogous results hold when $\tau/\epsilon \gg 1$.

(3.1, CUBIC, H) implies that (3.3, H) with $\tau = 0$ is analogous to (2.3, FN). $\langle V, 0, n, h\rangle$ is a rest point of this system if $h = h_\infty(V)$ and $V = V_1(n, h)$ or $V = V_2(n, h)$. Heteroclinic solutions of (3.3, H) with $\tau = 0$, found as in Example 2.1(B), form the singular solutions. In the periodic case, $l = 1$ of Hypothesis (2.8, PER′) refers only to the slowest variable, n.

Hypothesis (3.7, PLATEAU). (A) For some $\bar h$, $\bar h = h_\infty(V_2(n_0, \bar h))$ and $\theta(n_0, \bar h) > -\theta(n_0, h_0)$ (Fig. 14B).

(B) $\theta(n, h_b(n))$ and $\theta(n, h_d(n))$ decrease as n increases.

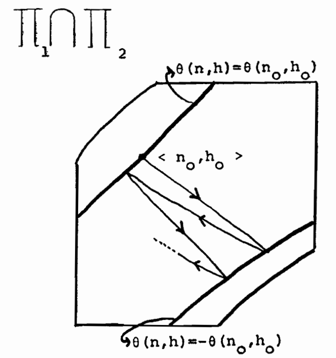

FIG. 16. Singular wave train solution of (HH).

$\{\theta(n, h) = \bar\theta\}$ in one direction. Since $\dot\theta^i = \theta_n \dot n^i + \theta_h \dot h^i$, (A) is satisfied if $\dot n^1 < 0$ and $\dot h^1 > 0$ on $\{\theta(n, h) = -\bar\theta\}$; and $\dot n^2 > 0$ and $\dot h^2 < 0$ on $\{\theta(n, h) = \bar\theta\}$, independent of γ_n, γ_h.

(B) says that if $\langle n, h\rangle = \langle n_0, h_0\rangle \cdot^2 \bar t$ then $\langle n, h\rangle \cdot^1 [0, \infty)$ crosses $\{\theta(n, h) = \bar\theta\}$ before returning to $\langle n_0, h_0\rangle$. If this is the case, (A) implies that all successive "jumps" cross $\{\theta(n, h) = \bar\theta\}$.

(C) implies that $U(\langle 0, 0, n_0, h_0\rangle)$ may return to the rest point after any finite number of jumps. The case in which (C) fails in considered in (3.6)(B).

It is reasonable to expect that a collection of wave train solutions of length $k = 1, 2,\ldots$ converge to a periodic solution. This is in fact the case in a sense discussed in [1].

THEOREM 3.6 (Wave train solutions of the Hodgkin–Huxley equations). *Assume Hypothesis* (3.1, CUBIC, H).

(A) *If* (3.1, H) *satisfies Hypothesis* (3.5, WAVE TRAIN), *there exist* $\{\epsilon_k : \epsilon_1 \geqslant \epsilon_2 \geqslant \cdots\}$, $\{\theta_{\epsilon,k} : k = 1, 2,\ldots, 0 < \epsilon < \epsilon_k\}$ *such that* $(3.1, \mathrm{H}, \theta_\epsilon, \epsilon)$

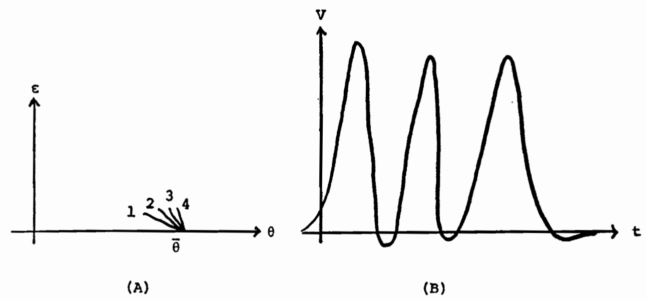

FIG. 17. (A) Parameter values for the existence of wave train solutions of length 1, 2, 3,... . (B) A wave train of length three.

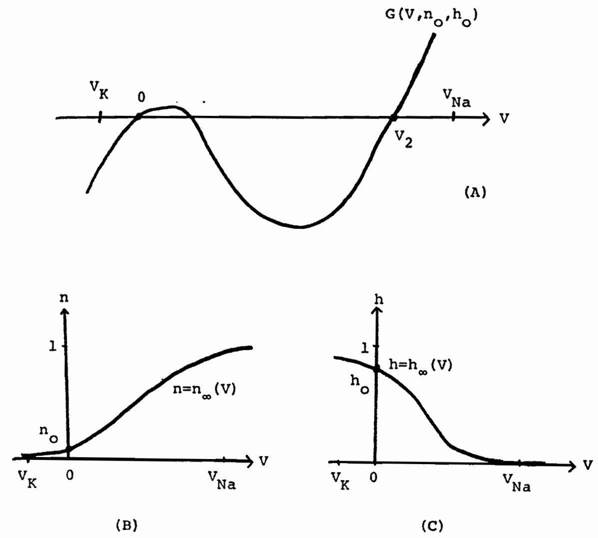

FIG. 13. (A) "Cubic" $G(V, n_0, h_0)$. (B) $n = n_\infty(V)$. (C) $h = h_\infty(V)$.

Clearly (3.1, CUBIC, H) implies (2.2, CUBIC). As in Section 2, let $\chi \equiv \{\langle V, W, n, h\rangle : W = G(V, n, h) = 0 \text{ and } (\partial G/\partial V)(V, n, h) > 0\}$. χ has two connected components, χ_1 and χ_2, with $\langle 0, 0, n_0, h_0\rangle \in \chi_1$ and $\langle V_2, 0, n_0, h_0\rangle \in \chi_2$. For $i = 1, 2$, let Π_i be the image of χ_i under the map $\langle V, W, n, h\rangle \to \langle n, h\rangle$, and define $V_i : \Pi_i \to (V_K, V_{Na})$ by $G(V_i(n, h), n, h) = 0$. Then $\Pi_1 \cup \Pi_2 = (0, 1)^2$ and $\langle n_0, h_0\rangle \in \Pi_1 \cap \Pi_2$. If we extend V_i to $\mathrm{cl}(\Pi_i)$, $(\partial^2 G/\partial V^2)(V_1(n, h), n, h) < 0$ if $\langle n, h\rangle \in \partial\Pi_1 - \partial[0, 1]^2$; and $(\partial^2 G/\partial V^2)(V_2(n, h), n, h) > 0$ if $\langle n, h\rangle \in \partial\Pi_2 - \partial[0, 1]^2$. Also, if $\langle n, h\rangle \in \Pi_i$

$$\frac{\partial V_i}{\partial n} = \frac{-\partial G/\partial n}{\partial G/\partial V} < 0 \quad \text{and} \quad \frac{\partial V_i}{\partial h} = -\frac{\partial G/\partial h}{\partial G/\partial V} > 0.$$

Let $(\mathrm{H})_i$ be the system

$$\begin{aligned} \dot n^i &= \gamma_n(V_i(n, h))(n_\infty(V_i(n, h)) - n), \\ \dot h^i &= \gamma_h(V_i(n, h))(h_\infty(V_i(n, h)) - h), \end{aligned} \qquad (3.2, \mathrm{H})_i$$

where $\langle n, h\rangle \in \mathrm{cl}(\Pi_i)$.

By the Jump Set Lemma (2.3) there exists a function $\theta(n, h) : \mathrm{cl}(\Pi_1 \cap \Pi_2) \to (-\infty, \infty)$ such that $(3.1, \mathrm{H}, |\theta(n, h)|, 0)$ admits a solution from $\langle V_1(n, h), 0, n, h\rangle$ to $\langle V_2(n, h), 0, n, h\rangle$ if $0 \leqslant \theta(n, h)$; or from $\langle V_2(n, h), 0, n, h\rangle$ to $\langle V_1(n, h), 0, n, h\rangle$ if $\theta(n, h) \leqslant 0$. Moreover $\partial\theta/\partial n < 0$ and $\partial\theta/\partial h > 0$ (Fig. 12).

LEMMA 3.2 (Analysis of $(\mathrm{H})_1$ and $(\mathrm{H})_2$). *Assume Hypothesis* (3.1, CUBIC, H).

(H)$_1$: (A) $\langle n_0, h_0\rangle$ *is the unique rest point of* (H)$_1$. *Both its eigenvalues are negative.*

(B) *There exist increasing* C^1 *functions* h_a, h_b *such that in* cl(Π_1),

$$n_\infty(V_1(n, h)) = n \quad \textit{iff} \quad h = h_a(n),$$

and

$$h_\infty(V_1(n, h)) = h \quad \textit{iff} \quad h = h_b(n).$$

Moreover, dom(h_a) $\subseteq (0, 1)$; $h_a(n) = 0$ *for some* n; *range* (h_b) $\subseteq (0, 1)$; *and* $1 \in$ dom(h_b).

(C) $\langle n, h\rangle \in S(\langle n_0, h_0\rangle)$ *if* $\langle n, h\rangle \cdot^1 t$ *is defined for all* $t \geqslant 0$. *All but two solutions approach* $\langle n_0, h_0\rangle$ *in* $\{\dot n^1 > 0, \dot h^1 > 0\} \cup \{\dot n^1 < 0, \dot h^1 < 0\}$.

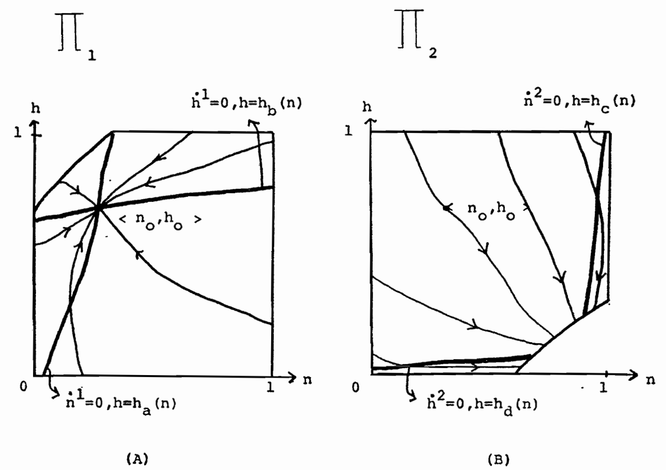

Fig. 14. (A) (3.2, H)$_1$ on Π_1. (B) (3.2, H)$_2$ on Π_2

(H)$_2$: (D) $V_2(n, h) > 0$ *for* $\langle n, h\rangle \in \Pi_2$.

(E) Π_2 *contains no rest points of* (H)$_2$.

(F) *There exist increasing* C^1 *functions* h_c, h_d *such that in* cl(Π_2),

$$n_\infty(V_2(n, h)) = n \quad \textit{iff} \quad h = h_c(n),$$

and

$$h(V_2(n, h)) = h \quad \textit{iff} \quad h = h_d(n).$$

In addition there exist $0 < n_d < n_c < n_c' < 1$, *with* $n_c > n_0$, *such that* dom(h_d) $= [0, n_d]$; dom(h_c) $= [n_c, n_c']$; $h_d(n_d) < h_0$; *and* $h_c(n_c') = 1$.

(G) *For every* $\langle n, h\rangle \in \Pi_2$ *there exists* $t > 0$ *such that* $\langle n, h\rangle \cdot^2 t \in \{\langle n, h\rangle$: $\partial G/\partial V(V_2(n, h), n, h) = 0\}$.

Lemma 3.2 is independent of γ_n, γ_h. Let $\bar\theta \equiv \theta(n_0, h_0)$.

Hypothesis (3.3, HOM, H). There exists $\bar t > 0$ such that, if $\langle n, h\rangle \equiv \langle n_0, h_0\rangle \cdot^2 \bar t$, $\theta(n, h) = -\bar\theta$ and $\langle n, h\rangle \cdot^1 t$ is defined for all $t \geqslant 0$.

Theorem 3.4 (Existence of a homoclinic solution of the Hodgkin–Huxley equations, $m = m_\infty(V)$). *Hypotheses* (3.1, CUBIC, H) *and* (3.3, HOM, H) *imply that for small* $\epsilon > 0$ (3.1, H, θ_ϵ, ϵ) *admits a homoclinic solution for some* $\theta_\epsilon > 0$. *Moreover* $\theta_\epsilon \to \theta(n_0, h_0)$ *as* $\epsilon \to 0$.

When $l = 1$ (FN) the singular homoclinic solution is unique. When $l \geqslant 2$ this may no longer be the case, as illustrated in Fig. 15. The proof of (2.7) implies

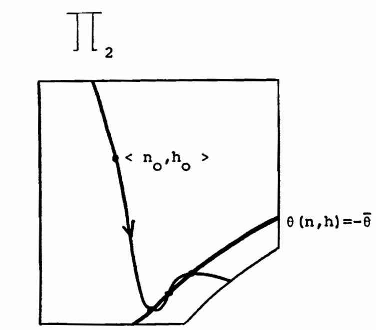

Fig. 15. Homoclinic singular solution crossing $\{\theta(n, h) = -\bar\theta\}$ in three points.

that each crossing yields a homoclinic solution of (3.1, H). In addition, for fixed ϵ the wave speed, θ, increases with the order of the crossings.

The case where (3.3, HOM, H) does not hold is treated in (3.6) (B).

Hypothesis (3.5, WAVE TRAIN). *Let* $\bar\theta \equiv \theta(n_0, h_0)$.

(A) $\dot\theta^1 > 0$ on $\{\theta(n, h) = -\bar\theta\}$ and $\dot\theta^2 < 0$ on $\{\theta(n, h) = \bar\theta\}$.

(B) If $\langle n, h\rangle = \langle n_0, h_0\rangle \cdot^2 \bar t$ and $\theta(n, h) = -\bar\theta$, then $\theta(\langle n, h\rangle \cdot^1 t) = \bar\theta$ for some $t > 0$.

(C) $\langle n, h\rangle \cdot^1 [0, \infty)$ is defined whenever $\theta(n, h) = -\bar\theta$.

Remarks. (3.5) (A) says that all solutions of (H)$_1$, (H)$_2$ cross $\{\theta(n, h) = -\bar\theta\}$,