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BURSTING PHENOMENA IN EXCITABLE MEMBRANES*

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Abstract. A generalized Hodgkin–Huxley model of excitable membranes is defined, and traveling wave solutions of the model are analyzed using singular perturbation methods in phase space. A complete classification determines whether a system exhibits finite wave train and periodic bursting behavior or only single pulse and regular periodic behavior. Qualitative properties of the bursts are deduced and used to suggest underlying membrane mechanisms. The conclusions shed new light on the mechanisms of bursting in the epileptogenic focus and Aplysia ganglia.

While periodic bursting is shown to be possible in a large class of membranes, a membrane which satisfies a special additional condition is shown to embody an infinite-dimensional temporal code in the form of arbitrary sequences of bursts. Other examples exhibit nonuniqueness and chaos.

1. Introduction. In this paper we show that the mechanisms of ordinary single pulse transmission possess built-in capability for periodic bursting. That is, the membrane permeability to sodium and potassium allows the transmission of bursts of spikes which are separated by quiet spells. The analysis of a generalized Hodgkin–Huxley [11] model which yields this result also gives information about the qualitative properties of each burst. Membranes with one or more additional ionic processes, such as K^+ inactivation or Cl^- activation, transmit bursts with different qualitative properties. Thus, the fine structure of spikes within a burst provides information concerning the underlying membrane processes, regardless of whether the source of stimulus is synaptic or endogenous.

We shall classify bursting phenomena according to the structure of the spike patterns, as follows.

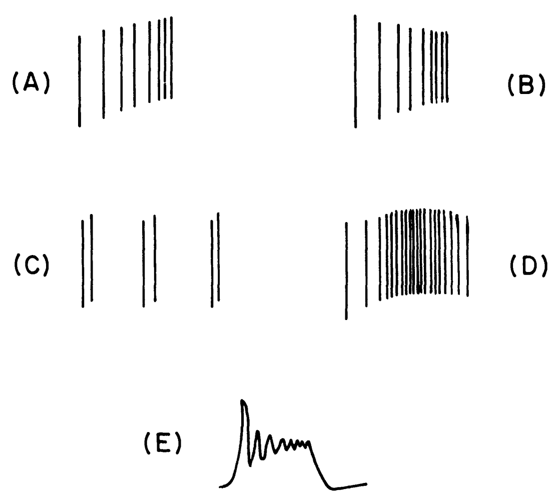

FIG. 1. *Bursting patterns of TYPE I (A, B, C), II (D), and III (E). Only the rising phase of each spike is shown.*

Type I (Fig. 1(A, B, C)) is exemplified by a bursting neuron of the frog optic nerve, as described by Chung, Raymond, and Lettvin. "One type generated bursts of 10–15

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spikes. Each burst had a distinct form wherein the longer pulse intervals occurred at the beginning. Progressively shorter intervals followed the first few spikes, and the burst terminated at a relatively high frequency." [6, p. 76] In the model, too, maximum and minimum values of membrane potential during a given spike often increase during the burst (Fig. 1(A)), but this is not a necessary property of Type I bursting (Fig. 1(B)). The shoulder of the falling phase of each spike may lengthen during the burst, but this is not necessary either. We include as Type I those bursts with so few spikes that the spiking frequency cannot be said to increase or decrease during the burst.

Type II (Fig. 1(D)) is exemplified by the much-studied abdominal ganglia of the sea slug *Aplysia* [9], [14], [17]. During a burst, the spiking frequency first increases, as in Type I, but then decreases. Because of this a plot of spike order vs. interspike interval is parabolic, and the cells are known as parabolic bursters. The maximum and minimum values of membrane potential in a Type II burst first increase and then decrease somewhat. The shoulder of the falling phase becomes elongated during the burst.

Type III (Fig. 1(E)) bursting appears in pyramidal cells of the cat hippocampus, as recorded by Kandel and Spencer [13]. After one normal spike, the spike amplitude decreases until membrane potential fluctuates near a mean excited state before returning near rest.

We shall show that a large class of generalized Hodgkin–Huxley neurons, obeying the classical rules of Na^+ activation and inactivation and K^+ activation, are capable of propagating Type I bursts. Type II bursts appear in models with one or more additional ionic processes, such as a slow K^+ and/or Cl^- current or K^+ accumulation around the membrane or else in a system with some other inhibitory feedback. Type III bursts are not within the scope of the models discussed here and seem to depend upon the interactive properties of the cells in which they appear.

It is important to note that many Hodgkin–Huxley neurons contain within them the capability of Type I bursting. An application of this observation may be seen in the following example, in which a Type I burst was interpreted by an experimenter as anomalous and thus in need of a special theoretical explanation.

Autonomous bursting in the cerebral cortex is a salient characteristic of epileptic seizures. A. Ward [18] describes the epileptogenic focus as a damaged portion of the cortex from which bursts of activity travel to normal cells, disrupting activity. He describes neurons in the focus "which fire in stereotyped bursts where the timing pattern within bursts reveals an *unusually long interval between the first and second spikes of each burst, with the later spikes time-locked to the second spike*, not to the first spike." [18, p. 279]. Ward proceeds to base his theory upon this observation, under the assumption that "the presence of the long first intervals · · · places certain constraints on hypotheses utilized to explain the genesis of such bursts. It is most difficult to see how ordinary synaptic input could account for them either with regenerative [endogenous] firing mechanisms or ones which follow a synaptic depolarization." [18, p. 280]. He suggests, therefore, that the first spike moves away from the focus and excites a distant cell body, which returns a volley of evenly-spaced spikes in return.

Inspection of the original data [1] reveals, however, that the bursts are Type I, with spiking frequency increasing continuously throughout the burst. The spacing of spikes within the burst is *not* as described by Ward. Thus his proposed explanation would require further evidence. Our analysis suggests that the activity observed at the epileptogenic focus is precisely that which would be expected in a normal neuron lacking such inhibitory mechanisms as feedback from other cells or the ability to maintain the proper external K^+ concentration.

The results presented in this paper continue the analysis begin in [2], [3], [4], where we prove the existence of single pulse and periodic solutions; elongated plateau solutions; and finite wave train solutions for the generalized Hodgkin–Huxley system (HH). The notion of singular solution developed in those papers is here applied to prove the existence of burst solutions.

In § 2 we rigorously define the model and prove that the system exhibits finite wave train and periodic bursting solutions if and only if a certain hypothesis is satisfied. This hypothesis is satisfied by "half of the systems" in a sense made precise in Theorem 1.

In § 3 we discuss the predicted qualitative properties of bursts.

Bursting in Aplysia abdominal ganglia is discussed in § 4 and the basic model of § 2 is expanded and analyzed. In particular, we show that the principal features of bursts from Aplysia are present in a model which adds K^+ inactivation to the other membrane processes of § 2. This model is compared with others in which a fast outward potassium current I_A is added to the ionic current.

In § 5 we prove that an excitable membrane which satisfies a very restrictive hypothesis could embody an infinite-dimensional temporal code. That is, if a low-dimensional system, with processes which correspond to Na^+ activation and inactivation and K^+ activation, satisfies the hypothesis, then, given any sequence of positive integers $N_1, N_2, N_3, \cdots$ the system admits solutions with N_i spikes in the ith bursting interval. Moreover, the sequence of bursts is uniquely characterized by wave speed with a lexicographic order: a sequence $N_1, N_2 \cdots$ is transmitted more rapidly than a sequence $M_1, M_2, \cdots$ iff $N_i = M_i$ $(i = 1, \cdots, K-1)$ and $N_K > M_K$, for some K. Thus the system can transmit an arbitrary sequence of signals.

Section 6 contains a nonuniqueness result, showing that a specially-constructed system may admit any number of solutions with precisely N spikes; other systems are constructed to exhibit chaotic solutions. However, a conjecture about local uniqueness may be made.

An explicit example of a system which admits bursting solutions is computed in § 7.

Proofs are contained in § 8.

The model defined in § 2 contains three positive parameters, ε, δ, and θ. ε is the order of magnitude of the rate at which Na^+ inactivation and K^+ activation occur; δ^{-1} is the order of magnitude of the rate at which Na^+ activation occurs; and θ is the speed of wave propagation. Throughout, the existence of solutions is proved for ε and δ near zero. Examples 1 and 2 in § 2 illustrate that the analysis of the model may be carried out for widely varying values of θ. In fact, these examples answer, for special cases, the general question: How is a periodic solution deformed as system parameters vary? An open problem is to analyze the behavior, as ε and δ increase, of the families of solutions described in this paper for small ε and δ.

The existence of single pulse solutions of (HH) has also been proved by Hastings [10], and single pulse and regular periodic solutions of the model have been the subject of extensive numerical analysis. The conditions which imply bursting, however, could not be discovered using numerical examples. Previous mathematical analyses have not included bursting phenomena. At most, the regular periodic subthreshold potassium current is discussed, that is, the endogenous mechanism which underlies bursting in Aplysia when normal sodium activation is blocked by TTX [16].

2. Existence of periodic bursts. The model under consideration here is a generalization of the classical Hodgkin–Huxley [11] model of nerve impulse transmission in the squid axon. Like Hodgkin and Huxley, we postulate only the transmembrane currents of sodium and potassium, but allow the statistics governing their activation and inactivation to vary.

The Hodgkin–Huxley model has the form:

(1)
$$\frac{1}{R}\frac{\partial^2 v}{\partial x^2} = C\frac{\partial v}{\partial t} + g(v, m, h, n)$$
$$\frac{\partial m}{\partial t} = \gamma_m(v)(m_\infty(v) - m)$$
$$\frac{\partial h}{\partial t} = \gamma_h(v)(h_\infty(v) - h)$$
$$\frac{\partial n}{\partial t} = \gamma_n(v)(n_\infty(v) - n),$$

where x is the distance from the stimulus; t is the time since the stimulus; $(1/R)(\partial^2 v/\partial x^2)$ is the total membrane current; $C(\partial v/\partial t)$ is the capacitance current; $g(v, m, h, n)$ is the total ionic current; and m, h, n represent local changes in membrane permeability to Na^+ and K^+ in response to changes in v. In [11]

(2)
$$g(v, m, h, n) = \bar{g}_{Na} m^3 h(v - v_{Na}) + \bar{g}_K n^4 (v - v_K) + \bar{g}_L(v - v_L),$$

the sum of sodium, potassium, and leakage currents. Since $v_K < 0 < v_L < v_{Na}$; $\bar{g}_{Na}, \bar{g}_K, \bar{g}_L > 0$; and $0 < m, h, n, < 1$; the inward Na^+ current and outward K^+ current are represented, respectively, by negative and positive contributions to g when $v_K < v < v_{Na}$.

The fact that Na^+ is turned on much more rapidly than it is turned off and K^+ turned on is represented by:

(3)
$$\gamma_m \gg \gamma_n, \gamma_h.$$

In the original Hodgkin–Huxley model, $\gamma_m \approx 10\gamma_n$, $10\gamma_h$. This rate difference is physiologically reasonable. For example, if K^+ exited as rapidly as Na^+ entered, there would be no net change in voltage and hence no impulse.

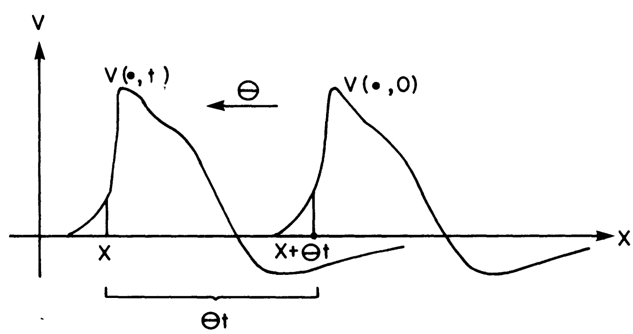


FIG. 2. *A single pulse traveling to the left with speed* θ. $v(x, t) = v(x + \theta t, 0) = v(s)$.

An impulse transmitted at a constant speed, θ, is represented by a traveling wave solution of (1); that is $v(x, t)$, $m(x, t)$, $h(x, t)$, and $n(x, t)$ are functions of a single variable, $s = x + \theta t$, as in Fig. 2. By the chain rule, $\partial/\partial x = d/ds$ and $\partial/\partial t = \theta(d/ds)$, and

(1) becomes:

$$
\begin{aligned}
\dot{v} &= w \\
\dot{w} &= R(C\theta w + g(v, m, h, n)) \\
\theta\dot{m} &= \gamma_m(v)(m_\infty(v) - m) \qquad (4)\\
\theta\dot{h} &= \gamma_h(v)(h_\infty(v) - h) \\
\theta\dot{n} &= \gamma_n(v)(n_\infty(v) - n),
\end{aligned}
$$

where $\cdot = d/ds$. If we set $R = C = 1$, for simplicity, and introduce the small parameters $\varepsilon, \delta > 0$, to emphasize the fast and slow time scales, (4) becomes:

$$
\begin{aligned}
\dot{v} &= w \\
\dot{w} &= \theta w + g(v, m, h, n) \\
\theta\dot{m} &= \delta^{-1}\gamma_m(v)(m_\infty(v) - m) \qquad (5)\\
\theta\dot{h} &= \varepsilon\gamma_h(v)(h_\infty(v) - h) \\
\theta\dot{n} &= \varepsilon\gamma_n(v)(n_\infty(v) - n).
\end{aligned}
$$

We now introduce the fundamental hypothesis, which abstracts the essential properties from the original Hodgkin–Huxley system. When variables other than m, h, n are needed, this hypothesis is modified as appropriate.

Let $m_\infty(0) \equiv m_0$, $h_\infty(0) \equiv h_0$, $n_\infty(0) \equiv n_0$, and $g(v, m_\infty(v), h, n) \equiv G(v, n, h)$.

HYPOTHESIS 1. *There exist* $v_K < 0 < v_{Na}$ *such that* (A)–(G) *hold for every* $m, h, n \in (0, 1)$.

(A) $g, \gamma_m, \gamma_h, \gamma_n, m_\infty, h_\infty, n_\infty$ *are twice continuously differentiable.*

(B) $\theta, \varepsilon, \delta, \gamma_m, \gamma_h, \gamma_n > 0$, *and* $0 < m_\infty, h_\infty, n_\infty < 1$.

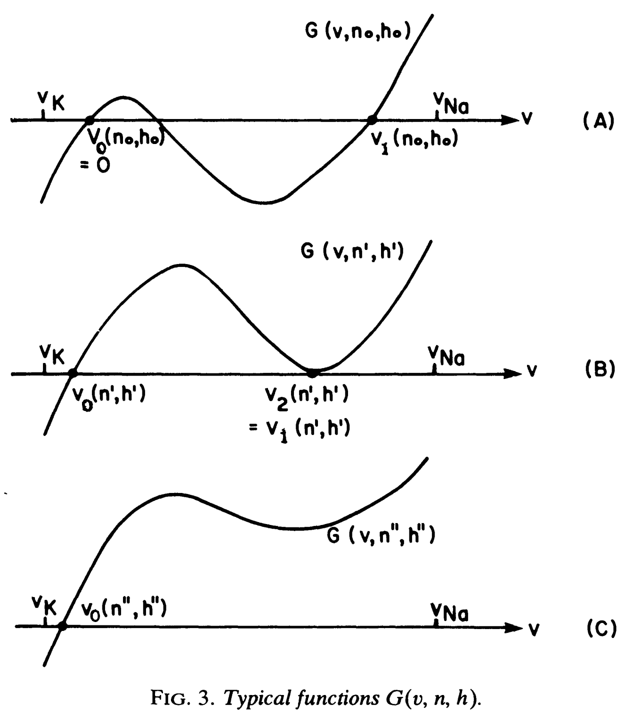


FIG. 3. *Typical functions* $G(v, n, h)$.

(C) (*Unique rest point*) $g(v, m_\infty(v), h_\infty(v), n_\infty(v))=0$ *iff* $v=0$.

(D) (*Maximal and minimal values of* v) $g(v_K, m, h, n)<0<g(v_{Na}, m, h, n)$ (Fig. 3).

(E) (*Cubic-like* G) *For each fixed* n, h *there exist at most three* $v \in (v_K, v_{Na})$ *such that* $G(v, n, h)=0$ (*counting multiplicities*). *Moreover, if* $G(v, n, h)=\partial G/\partial v(v, n, h)=0$, *then* $\partial^2 G/\partial v^2(v, n, h)\neq 0$ (Fig. 3).

(F) $G(v, n_0, h_0)$ *admits three zeros*, $v_0(n_0, h_0)$, $v_1(n_0, h_0)$, *and* $v_2(n_0, h_0)$. *Moreover* $0=v_0(n_0, h_0)<v_2(n_0, h_0)<v_1(n_0, h_0)$; $\partial G/\partial v(0, n_0, h_0)>0$; *and* $\int_0^{v_1(n_0,h_0)} G(v, n_0, h_0)\,dv<0$ (Fig. 3A).

(G) (*Excitatory* m, *inhibitory* n, h) $g_m<0$, $m'_\infty>0$, $g_h<0$, $h'_\infty<0$, $g_n>0$, *and* $n'_\infty>0$.

A system which satisfies Hypothesis 1 has a unique critical point. Since $g_m m'_\infty$ is negative (G), the variable m represents an excitatory process. To see why this inequality represents excitation, consider the space-clamped version of (1), in which $v_{xx}\equiv 0$. Then $Cv_t=-g(v, m, n, h)$, so, as v increases, m increases, g decreases, $-g$ increases, and v increases still further. Similarly, since $g_h h'_\infty$ and $g_n n'_\infty$ are positive, n and h represent inhibitory processes, which tend to drive v down toward the rest state.

In order to analyze (5), we shall rely heavily upon the different time scales involved. Note first that as $\delta\to 0$, m converges rapidly to $m_\infty(v)$. Let us for the moment, set $m\equiv m_\infty(v)$ and examine the resulting system:

$$(6;\theta,\varepsilon)\qquad \begin{aligned} \dot v &= w,\\ \dot w &= \theta w + G(v, n, h),\\ \theta \dot n &= \varepsilon\gamma_n(v)(n_\infty(v)-n),\\ \theta \dot h &= \varepsilon\gamma_h(v)(h_\infty(v)-h). \end{aligned}$$

A regular perturbation argument [2], [4] implies that a bounded solution of (6) corresponds to a nearby bounded solution of (5) for all small $\delta>0$.

Hypothesis 1 (E, F) determines the geometry of the "slow manifold" of (6), the set on which $\dot v=\dot w=0$. Off the slow manifold, when ε is small, solutions of (6) stay near solutions of the system when $\varepsilon=0$. If $\dot v$ and $\dot w$ are near zero, however, $\dot n$ and $\dot h$ are relatively large, even if ε is very small. Hypothesis 1 (E, F) implies that the slow manifold contains a two-dimensional surface with three sheets above each point in an open subset of $\langle n, h\rangle$-space. For each point $\langle n, h\rangle$ in this open set, $G(v, n, h)$ has three zeros. Each $\langle n, h\rangle$ in the boundary of this set corresponds to a fold in the surface, at a point where $G(v, n, h)$ contains a double zero.

In order to distinguish the three sheets of the slow manifold, we next define three functions $v_0(n, h)$, $v_1(n, h)$, $v_2(n, h)$ on connected open domains Π_0, Π_1, $\Pi_2=\Pi_0\cap\Pi_1$ such that $G(v_i(n, h), n, h)=0$ $(i=0, 1, 2)$ and, when $\langle n, h\rangle\in\Pi_0\cap\Pi_1$, $v_0(n, h)< v_2(n, h)<v_1(n, h)$. Intuitively, $v_0(n, h)$, $v_1(n, h)$, and $v_2(n, h)$ represent, respectively, the left, right, and middle zeros of $G(v, n, h)$ (Fig. 3). The slow manifold contains the three sets:

$\{\langle v, w, n, h\rangle : v=v_0(n, h),\ w=0, \text{ and } \langle n, h\rangle\in\Pi_0\}$ (lower sheet);

$\{\langle v, w, n, h\rangle : v=v_1(n, h),\ w=0, \text{ and } \langle n, h\rangle\in\Pi_1\}$ (upper sheet);

$\{\langle v, w, n, h\rangle : v=v_2(n, h),\ w=0, \text{ and } \langle n, h\rangle\in\Pi_2\}$ (middle sheet).

First, let Π_2 be the component containing $\langle n_0, h_0\rangle$ of $\{\langle n, h\rangle\in[0, 1]^2$: $G(v, n, h)$ has three zeros$\}$. For $\langle n, h\rangle\in\Pi_2$, let $v_0(n, h)<v_2(n, h)<v_1(n, h)$ be those zeros, and

extend each $v_i(n, h)$ continuously to $\partial\Pi_2$. Let $\partial\Pi_1 \equiv \{\langle n, h\rangle \in \partial\Pi_2 : v_1(n, h) = v_2(n, h)\}$. Hypothesis 1(D, E) implies that for $\langle n, h\rangle \in \partial\Pi_1$, $G_v(v_1(n, h), n, h) = 0$, $G_{vv}(v_1(n, h), n, h) > 0$, $G_v(v_0(n, h), n, h) > 0$, and $G(v, n, h) < 0$ if $v_K < v < v_0(n, h)$. By the implicit function theorem, $v_0(n, h)$ can be extended continuously to a neighborhood of Π_1 in whose closure $G(v_0(n, h), n, h) = 0$ and $G(v, n, h) < 0$ if $v < v_0(n, h)$; let Π_0 be the union of that neighborhood and Π_2. Π_1 is defined similarly. Note that $G_v(v_0(n, h), n, h) > 0$ if $\langle n, h\rangle \in \Pi_0$; $G_v(v_1(n, h), n, h) > 0$ if $\langle n, h\rangle \in \Pi_1$; and $G_v(v_2(n, h), n, h) < 0$ if $\langle n, h\rangle \in \Pi_2 = \Pi_0 \cap \Pi_1$.

The next lemma shows the existence of a function $\theta(n, h)$ from $\Pi_0 \cap \Pi_1$ into $\mathbb{R}$. When $\theta(n, h)$ is positive, the system (6), with $\theta = \theta(n, h)$ and $\varepsilon = 0$, admits a solution which runs from the lower sheet to the upper sheet, i.e., a jump up. When $\theta(n, h)$ is negative, the system (6), with $\theta = -\theta(n, h)$ and $\varepsilon = 0$, admits a solution which runs from the upper sheet to the lower sheet, i.e., a jump down.

LEMMA 1: $\theta(n, h)$. *Assume Hypothesis* 1. *Then there exists a function* $\theta(n, h)$: $\Pi_0 \cap \Pi_1 \to \mathbb{R}$ *such that*:

(i) *if* $\int_{v_0(n,h)}^{v_1(n,h)} G(v, n, h)\, dv \leqq 0$, *then* $\theta(n, h) \geqq 0$ *and* (6; $\theta(n, h)$, 0) *admits a solution from* $\langle v_0(n, h), 0, n, h\rangle$ *to* $\langle v_1(n, h), 0, n, h\rangle$; *and*

(ii) *if* $\int_{v_0(n,h)}^{v_1(n,h)} G(v, n, h)\, dv \geqq 0$, *then* $\theta(n, h) \leqq 0$, *and* (6; $-\theta(n, h)$, 0) *admits a solution from* $\langle v_1(n, h), 0, n, h\rangle$ *to* $\langle v_0(n, h), 0, n, h\rangle$.

Let $\theta(n_0, h_0) \equiv \bar\theta$ and extend $\theta(n, h)$ continuously to cl $(\Pi_0 \cap \Pi_1)$. When $\theta = \bar\theta$ and $\varepsilon = 0$, (6) admits a solution from $\langle v_0(n_0, h_0), 0, n_0, h_0\rangle$ to $\langle v_1(n_0, h_0), 0, n_0, h_0\rangle$. Let UP be the set of all $\langle n, h\rangle$ in cl $(\Pi_0 \cap \Pi_1)$ such that (6; $\bar\theta$, 0) admits a solution from $\langle v_0(n, h), 0, n, h\rangle$ (lower sheet) to $\langle v_1(n, h), 0, n, h\rangle$ (upper sheet). By definition, $\langle n_0, h_0\rangle$ is contained in UP (Fig. 4). Similarly, let DOWN be the set of all $\langle n, h\rangle$ such that (6; $\bar\theta$, 0) admits a solution from $\langle v_1(n, h), 0, n, h\rangle$ (upper sheet) to $\langle v_0(n, h), 0, n, h\rangle$ (lower sheet).

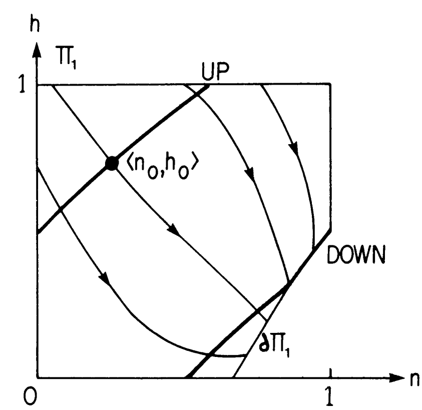


FIG. 4. *A flow on* Π_1: *there is no critical point and all solutions with initial values in* UP *cross* DOWN.

The next lemma characterizes UP and DOWN in terms of the function $\theta(n, h)$. In particular, $\theta(n, h)$ is positive on UP and $\theta(n, h)$ is negative on DOWN. Portions of UP and DOWN may be contained in $\partial\Pi_0$ or $\partial\Pi_1$.

LEMMA 2: UP *and* DOWN. *Assume Hypothesis* 1.

(A) *If* $\langle n, h\rangle \in \partial\Pi_0$, *there is a solution of* (6; θ, 0) *from* $\langle v_0(n, h), 0, n, h\rangle$ *up to* $\langle v_1(n, h), 0, n, h\rangle$ *for all* $\theta \geqq \theta(n, h)$. *If* $\langle n, h\rangle \in \partial\Pi_1$, *there is a solution of* (6; θ, 0) *from* $\langle v_1(n, h), 0, n, h\rangle$ *down to* $\langle v_0(n, h), 0, n, h\rangle$ *for* $\theta \geqq -\theta(n, h)$.

(B) *For* $\langle n, h\rangle \in \Pi_0 \cap \Pi_1$, $\langle n, h\rangle \in$ UP *iff* $\theta(n, h) = \bar{\theta}$ *and* $\langle n, h\rangle \in$ DOWN *iff* $\theta(n, h) = -\bar{\theta}$. *For* $\langle n, h\rangle \in \partial\Pi_0$, $\langle n, h\rangle \in$ UP *iff* $\theta(n, h) \leqq \bar{\theta}$. *For* $\langle n, h\rangle \in \partial\Pi_1$, $\langle n, h\rangle \in$ DOWN *iff* $-\theta(n\ h) \leqq \bar{\theta}$. UP[DOWN] *is the graph of an increasing function of n, for n in a subinterval of* $[0, 1]$. *At the left endpoint of* UP[DOWN], $n = 0$ *or* $h = 0$; *at the right endpoint,* $n = 1$ *or* $h = 1$.

Consider now the systems defined on Π_0 and Π_1:

$$(7; i) \qquad \begin{aligned} \dot{n}^i &= \gamma_n(v_i(n, h))(n_\infty(v_i(n, h)) - n) \\ \dot{h}^i &= \gamma_h(v_i(n, h))(h_\infty(v_i(n, h)) - h), \end{aligned}$$

where $i = 0, 1$. (7; 0) defines a flow on the lower sheet of the slow manifold and (7; 1) defines a flow on the upper sheet. As shown in [2], [4], Lemma 2 and Hypothesis 1 (B, C, G) imply that any solution of (7; 1) with initial value in UP crosses DOWN in finite time (Fig. 4) and any solution of (7; 0) with initial value in DOWN either crosses UP $\cap\, \partial\Pi_0$ in finite time or converges to $\langle n_0, h_0\rangle$ at $+\infty$. Also, $\langle n_0, h_0\rangle$ is a stable node of $\langle 7; 0\rangle$, and exactly one solution, Σ, approaches $\langle n_0, h_0\rangle$ in the set where $n > n_0$ and $h < h_0$ (Fig. 5).

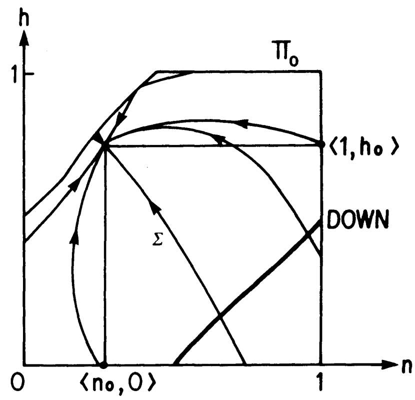


FIG. 5. *A flow on* Π_0. Σ *is a separatrix.*

Hypothesis 1 establishes the fundamental properties of the excitable membrane model, but a system which satisfies this hypothesis needs to satisfy a further condition in order to admit the bursting solutions considered in this paper. Some notation will next be introduced to state this condition.

Notation: Let F_1: UP $\rightarrow$ DOWN be the map which sends a point in UP to the first point in DOWN on its forward trajectory in cl (Π_1) (Fig. 6(A)). Let F_0: DOWN $\rightarrow$ UP be the map which sends a point in DOWN to the first point (if any) in UP on its forward trajectory in cl (Π_0), and let $F_0(n, h)$ be $\langle n_0, h_0\rangle$ if the solution converges to $\langle n_0, h_0\rangle$ without first crossing UP. In Fig. 6(B), $F_0(n, h) = \langle n_0, h_0\rangle$ iff $\langle n, h\rangle$ lies on or below the separating solution Σ.

If $F_0 \circ F_1(n_0, h_0) = \langle n_0, h_0\rangle$, then $(F_0 \circ F_1)^j(n_0, h_0) = \langle n_0, h_0\rangle$ for all $j \geqq 1$. If $F_0 \circ F_1(n_0, h_0) \in \{n_0 < n < 1$ and $h_0 \leqq h < 1\}$, Lemma 2 implies that $(F_0 \circ F_1)^j(n_0, h_0)$ is a monotone sequence of points in UP converging to a point $\langle \bar{n}, \bar{h}\rangle \in \{n_0 < n < 1$ and $h_0 < h < 1\}$ (Fig. 6). Similarly if $F_0 \circ F_1(n_0, h_0) \in \{0 < n < n_0$ and $0 < h < h_0\}$, $(F_0 \circ F_1)^j(n_0, h_0)$ converges to a point $\langle \bar{n}, \bar{h}\rangle$. In any case, $\lim_{j\to\infty} (F_0 \circ F_1)^j(n_0, h_0) \equiv \langle \bar{n}, \bar{h}\rangle$ exists and is a fixed point of $F_0 \circ F_1$.

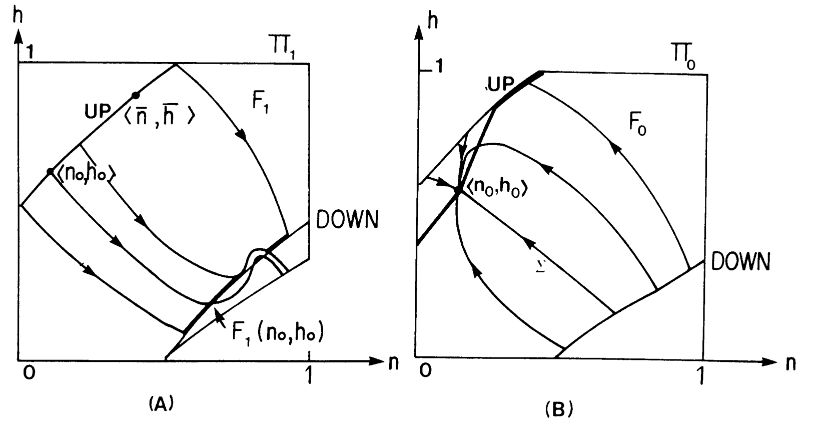


FIG. 6. (A) F_1(UP) *has two components.* (B) *Points below* Σ *are mapped to* $\langle n_0, h_0 \rangle$ *by* F_0.

The system (5) will be said to be *admissible* if, for each $j = 0, 1, 2, \cdots$, the flow (7; 0) is not tangent to UP at $(F_0 \circ F_1)^j(n_0, h_0)$ and the flow (7; 1) is not tangent to DOWN at $F_1 \circ (F_0 \circ F_1)^j(n_0, h_0)$. Assume also that solutions of (7; 0) cross DOWN transversally (Fig. 5); and solutions of (7; 1) cross UP transversally (Fig. 4). Although

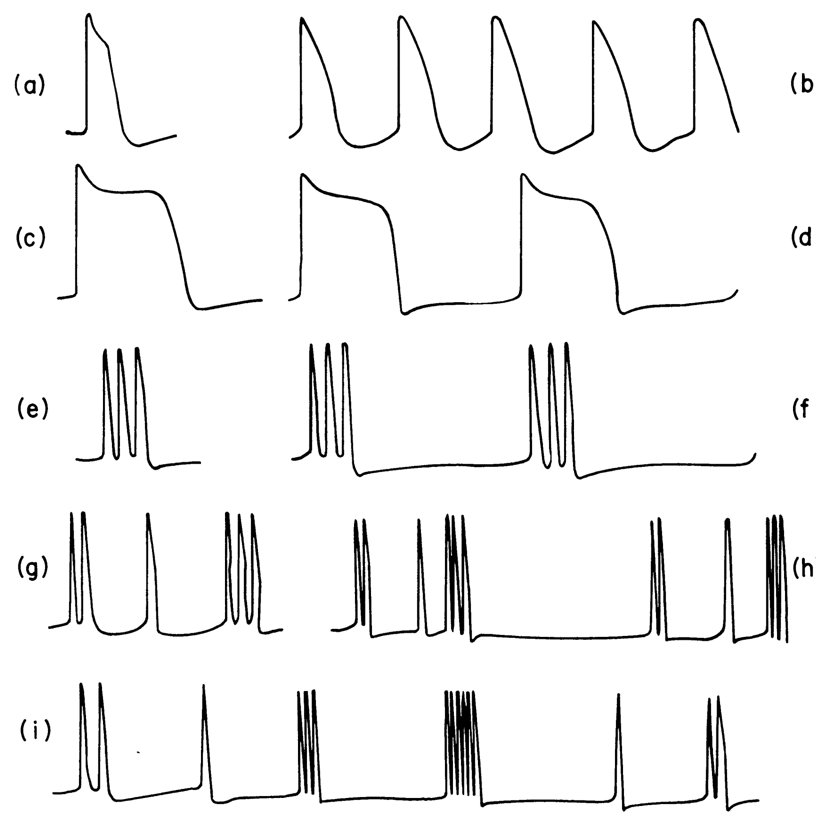


FIG. 7. a, c, e, *and* g *go to rest at* $\pm\infty$; b, d, f, *and* h *are periodic solutions which converge to* a, c, e *and* g *as the period becomes infinite.* i *goes to rest at* $-\infty$. a *is a single pulse*; c *is a pulse plateau*; e *is a finite wave train of length* 3; g *is a finite sequence of wave trains of length* 2, 1, 3; i *is an infinite sequence of wave trains with* N_i *bursts in the i-th bursting interval, where* $\{N_1, N_2, \cdots\} = \{2, 1, 3, 6, 1, 2, \cdots\}$.

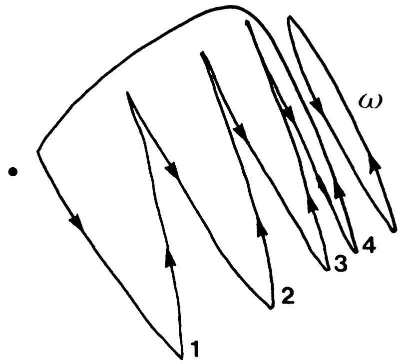


FIG. 8. *Projected phase portrait of a burst solution with four spikes and a periodic solution $\omega \in \Omega$. The spike train approaches ω during a burst and returns to near the critical point during the quiet spell.*

these transversality conditions are not always necessary (compare Example 3 in § 6), they are included to simplify the arguments.

Condition α: $\langle \bar{n}, \bar{h} \rangle \neq \langle n_0, h_0 \rangle$.

Condition β: In Π_0, the solution with initial value $\langle \bar{n}, \bar{h} \rangle$ converges to $\langle n_0, h_0 \rangle$ at $+\infty$. That is, this solution does not run to $\partial\Pi_0$.

Condition α is satisfied by half of all systems (5) in the sense that Σ separates DOWN into two components, and any solution in Π_0 with initial value in one of the two crosses UP. In Fig. 6(B) for example, Condition α is satisfied iff $F_1(n_0, h_0)$ lies above Σ, since a point below Σ is mapped to $(n_0, h_0\rangle$ by F_0. Condition β is trivially satisfied if all points on the boundary of DOWN run to $\langle n_0, h_0 \rangle$ in Π_0 (Fig. 5).

Theorem 1 states that the solution types admitted by (5) are classified according to whether Condition α and/or Condition β holds. Since β must hold if α fails, there are only three cases.

THEOREM 1: *Single pulse and bursting solutions. Assume that an admissible flow* (5) *satisfies Hypothesis* 1. *Then for sufficiently small* ε *and* δ, *the generalized Hodgkin–Huxley model* (5) *admits single pulse, finite wave train, and periodic bursting solutions according to the following rules.*

Case (A). *Assume that Conditions* α *and* β *both hold. Then* (5) *admits bursting solutions with any number of spikes. That is, for each* $N \geqq 1$, (5) *admits a finite wave train*

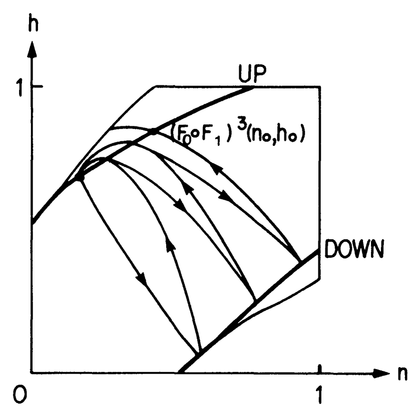


FIG. 9. *Case* (*B*) *of Theorem* 1, *with* $M = 3$.

with N spikes (Fig. 7a, e) *and a family of periodic solutions which alternate between N spikes and a quiet spell (Fig.* 7b, f). *The periodic bursting solutions converge to a finite wave train as the quiet spell becomes infinite. Conditions α and β also imply the existence of a family, Ω, of periodic solutions, each solution having evenly spaced spikes.*

If N is large, spikes within a burst approach one of the regular periodic solutions in Ω, but the trajectory returns to near the critical point during the quiet spell. A burst with four spikes is illustrated schematically in Fig. 8. *The last spike is close to a periodic solution in Ω.*

Case (B). *Assume Condition α holds but Condition β fails. Let $M \geqq 1$ be the smallest integer such that $(F_0 \circ F_1)^M(n_0, h_0)$ does not converge to $\langle n_0, h_0\rangle$ at $+\infty$ (Fig.* 9). *Then for each $N < M$* (5) *admits a finite wave train with N spikes and a family of periodic bursting solutions with N spikes, as in Case* (A). *Moreover,* (5) *also admits a family, Ω, of periodic solutions with evenly spaced spikes for the parameter values shown in the shaded region of Fig.* 10(B).

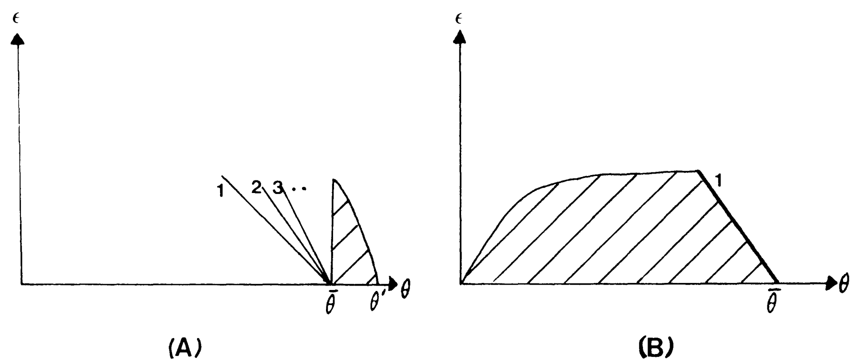


FIG. 10. (A) *Parameter values which yield finite wave trains with* $1, 2, 3, \cdots$ *spikes. Periodic bursting solutions occur for parameter values in a region to the right of the respective wave train curves. Each region extends to include a set such as the shaded area in which $\bar{\theta} \leqq \theta \leqq \theta'$. In addition, when $\langle \theta, \varepsilon \rangle$ is in a region which includes the shaded area and which extends down to* $\langle 0, 0\rangle$, *as in* (B), *the system admits a regular periodic solution in Ω.*

(B) *Parameter values which yield single pulse solutions* (*Case* (*C*)) *and regular periodic* (*shaded*) *solutions. The period becomes small in the left of the shaded region.*

Case (C). *Assume Condition β holds but Condition α fails* (e.g., Fig. 6(B), if $F_1(n_0, h_0)$ lies below Σ). *Then* (5) *admits a single pulse solution and a family of periodic solutions which converge to the single pulse solution as the period becomes infinite* (*Fig.* 7a, b). *If γ_n/γ_h is large or small, the solutions contain an elongated plateau* (*Fig.* 7c, d).

More precisely, for each small $\delta > 0$, there are values of θ, ε, as shown in Fig. 10, *for which* (5) *admits the solutions of Cases* (A), (B), *and* (C).

Remarks. The system of equations (5) admits a single pulse solution in each case except (B) when $M = 1$, where $F_0 \circ F_1(n_0, h_0) \in \partial\Pi_0$.

The proof of Theorem 1 depends upon the notion of a singular solution. A *singular solution of length N* consists of a sequence $\{\sigma_1 \cdots \sigma_{2N}\}$ which satisfies (i)–(iv) below (Fig. 11).

(i) σ_{2j} is a solution segment in Π_0 and σ_{2j-1} is a solution segment in Π_1 $(j = 1, \cdots, N)$.

(ii) σ_1 begins at $\langle n_0, h_0\rangle$ and σ_{2N} converges to $\langle n_0, h_0\rangle$ at $+\infty$.

(iii) For $j = 1, \cdots, N$, the end point of σ_{2j-1} is contained in DOWN and is equal to the initial point of σ_{2j}.

(iv) For $j = 1, \cdots, N-1$, the end point of σ_{2j} is contained in UP and is equal to the initial point of σ_{2j+1}.

When k is odd, σ_k is a solution in Π_1 from UP to DOWN. When k is even, σ_k is a solution in Π_0 from DOWN to UP. If the solution segments $\sigma_1 \cdots \sigma_{2N}$ are projected into $\Pi_0 \cap \Pi_1$, the resulting curve looks like the projection of a homoclinic orbit approaching $\langle n_0, h_0 \rangle$ at $\pm\infty$ (Fig. 11).

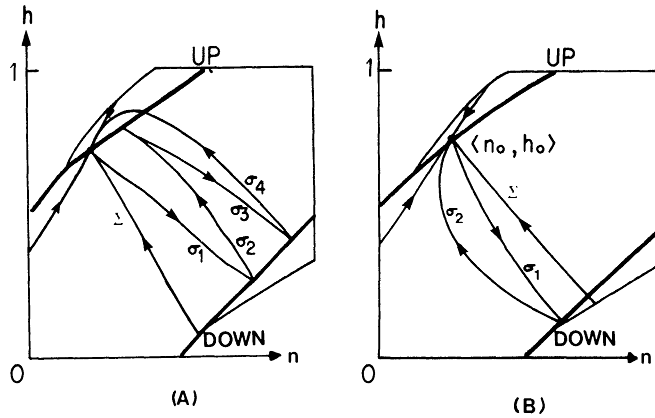


FIG. 11. *Singular solutions of length* 2(A) *and* 1(B).

The conditions of Theorem 1 establish criteria for the existence of singular solutions of any length (Case (A)); of length $1, \cdots, M-1$ (Case (B)); or of length 1 only (Case (C)). The proof, then, need only show that the existence of a singular solution of length N implies the existence of finite wave train and bursting solutions with N spikes. For each singular solution of length N, the set of parameter values for which $(5; \theta, \varepsilon, \delta)$ admits a wave train with N spikes contains a continuum in the following sense. For fixed small $\delta > 0$, if $\{\langle \theta(s), \varepsilon(s) \rangle : 0 \leqq s \leqq 1\}$ is *any arc* such that $\theta(0) < \bar{\theta} < \theta(1)$ and $\varepsilon(s)$ is small, then there is some s such that $(5; \theta(s), \varepsilon(s), \delta)$ admits a wave train solution with N spikes.

A singular solution should be thought of as the singular limit of a solution of (6), where solution segments in the slow manifold are connected by fast jumps of v up at UP and back down at DOWN. During the interval between the jth and $(j+1)$st spikes, in the time scale of $\tau = \varepsilon s$, the finite wave train solution is near $\{\langle v, w, n, h \rangle : \langle n, h \rangle \in \sigma_{2j}, v = v_0(n, h)$, and $w = 0\}$, a solution segment in the lower sheet of the slow manifold. After N spikes, the solution approaches the rest point $\langle 0, 0, n_0, h_0 \rangle$.

A periodic solution, on the other hand, is determined by a fixed point of a return map, where a point in phase space is mapped back to itself in finite time. Like a finite wave train solution, a periodic bursting solution with N spikes corresponds to N solution segments in the lower sheet of the slow manifold connected by fast jumps to N solution segments in the upper sheet. After N spikes, the burst solution, instead of returning to the rest point, returns to the point at which it began and N more spikes follow. In general, the jumps up and down for a periodic bursting solution occur for $\theta \neq \bar{\theta}$. Thus, in order to determine the location of the periodic solutions of (5), the definitions of F_0 and F_1 must be extended, as follows.

If $\theta(n, h) > 0$, let

$$\tau(n, h) \equiv \sup \{\tau > 0 : \langle n, h \rangle \cdot^1 \tau \in \Pi_1 \text{ and } \theta(\langle n, h \rangle \cdot^1 \tau) > -\theta(n, h)\}$$

and

$$F_1(n, h) \equiv \langle n, h\rangle \overset{1}{\cdot} \tau(n, h).$$

To understand the definitions of τ and F_1, fix $\langle n', h'\rangle$ such that $\theta(n', h') > 0$ and let $\langle n'', h''\rangle \equiv F_1(n', h')$. Then $\tau(n', h')$ is the time a solution segment in Π_1 takes to go from $\langle n', h'\rangle$ to $\langle n'', h''\rangle$. By Lemmas 1 and 2, there is a solution of (6) from the upper sheet to the lower sheet of the slow manifold when $\theta = \theta(n', h')$, $\varepsilon = 0$, and $\langle n, h\rangle = \langle n'', h''\rangle$. The jump occurs at the boundary of Π_1 if $-\theta(n'', h'') < \theta(n', h')$. The jump occurs in the interior of Π_1 if $-\theta(n'', h'') = \theta(n', h')$.

Similarly, if $\theta(n, h) < 0$, let

$$\tau(n, h) \equiv \sup\{\tau > 0 : \langle n, h\rangle \overset{0}{\cdot} \tau \in \Pi_0 \text{ and } \theta(\langle n, h\rangle \overset{0}{\cdot} \tau) < -\theta(n, h)\},$$

and

$$F_0(n, h) \equiv \begin{cases} \langle n, h\rangle \overset{0}{\cdot} \tau(n, h) & \text{if } \tau(n, h) < \infty, \\ \langle n_0, h_0\rangle & \text{if } \tau(n, h) = \infty. \end{cases}$$

If we fix $\langle n', h'\rangle$ such that $\theta(n', h') < 0$ and let $\langle n'', h''\rangle \equiv F_0(n', h')$, then, if $\tau(n', h')$ is finite, there is a solution of (6) from the lower sheet to the upper sheet of the slow manifold when $\theta = -\theta(n', h')$, $\varepsilon = 0$, and $\langle n, h\rangle = \langle n'', h''\rangle$. The jump occurs at the boundary of Π_0 if $\theta(n'', h'') < -\theta(n', h')$. The jump occurs in the interior of Π_0 if $\theta(n'', h'') = -\theta(n', h')$. If $\tau(n', h') = \infty$, then $\langle n', h'\rangle \overset{0}{\cdot} [0, \infty)$ converges to $\langle n_0, h_0\rangle$ in Π_0.

Finally, if $\theta(n, h) > 0$, let

$$T(n, h) \equiv \max\{\tau \geqq 0 : \langle n, h\rangle \overset{0}{\cdot} \tau \in \Pi_0 \text{ and } \theta(\langle n, h\rangle \overset{0}{\cdot} \tau) = \theta(n, h)\};$$

and, if $T(n, h)$ is positive, let

$$\phi(n, h) \equiv \langle n, h\rangle \overset{0}{\cdot} T(n, h).$$

That is, $\phi(n, h)$ is the last point on $\langle n, h\rangle \overset{0}{\cdot} [0, \infty)$ for which there is a jump up when $\theta = \theta(n, h)$ and $\varepsilon = 0$. If there is no such point on $\langle n, h\rangle \overset{0}{\cdot} (0, \infty)$, then $T(n, h) = 0$ and $\phi(n, h)$ is not defined.

In a sense made precise below, a regular periodic solution in the family Ω corresponds to a fixed point of $F_0 \circ F_1$. A burst solution with N spikes corresponds to a fixed point of $\phi \circ (F_0 \circ F_1)^N$. To illustrate, consider Fig. 8 as a projection into $\Pi_0 \cap \Pi_1$. On the solution ω, the uppermost point is a fixed point of $F_0 \circ F_1$. On the burst solution with four spikes, the left-most corner is a fixed point of $\phi \circ (F_0 \circ F_1)^4$, and $(F_0 \circ F_1)^4$ evaluated at that point is near the upper right corner of the solution.

The proof of the existence of periodic bursting solutions depends upon the notion of an l-dimensional singular solution, as developed in [3]. l is the number of "slow" variables, so, for (5), $l = 2$. The singular solution defined for finite wave trains is constructed by following the single point $\langle n_0, h_0\rangle$ along trajectories in Π_0 and Π_1. The union of these trajectories is a one-dimensional singular solution. A two-dimensional singular solution is constructed by following an entire interval along trajectories in Π_0 and Π_1.

Given any $\theta' > 0$, a *two-dimensional singular solution of length N* is a closed connected set $I \subseteq \{\langle n, h\rangle : \theta(n, h) = \theta'\}$ such that $\phi \circ (F_0 \circ F_1)^N(I)$ is contained in the interior of I. The results of [3] imply that if I is a two-dimensional singular solution of length N then $(5; \theta', \varepsilon, \delta)$ admits periodic bursting solutions with N spikes for all small $\varepsilon, \delta > 0$.

A *regular two-dimensional singular solution* is a closed connected set $I \subseteq (UP)' \equiv \{\langle n, h\rangle \in \Pi_0 : \theta(n, h) = \theta'\} \cup \{\langle n, h\rangle \in \partial\Pi_0 : \theta(n, h) \leqq \theta'\}$ such that $F_0 \circ F_1(I)$ is contained in the interior of I. For example, if $0<\theta'<\bar{\theta}$, (UP)$'$ is itself a regular two-dimensional singular solution. The existence of I implies that (5; θ', ε, δ) admits a regular periodic solution in the class Ω for all small ε, $\delta>0$. If Condition α is satisfied, (5) admits regular two-dimensional singular solutions for all θ' in some interval $[\bar{\theta}, \theta_1)$. For example, in Fig. 11(A) if $\theta'=\bar{\theta}$, then $I\equiv\{\langle n, h\rangle \in \mathrm{UP}: n \geqq n_0\}$ is a regular two-dimensional singular solution. These regular solutions are the ones studied in [3]. If I is a two-dimensional singular solution, I contains a fixed point of $\phi\circ(F_0\circ F_1)^N$ (or of $F_0\circ F_1$). These are the fixed points illustrated in Fig. 12(D) and 14(D) below. In those examples, the fixed point sets summarize the qualitative behavior of families of solutions as the parameter θ varies.

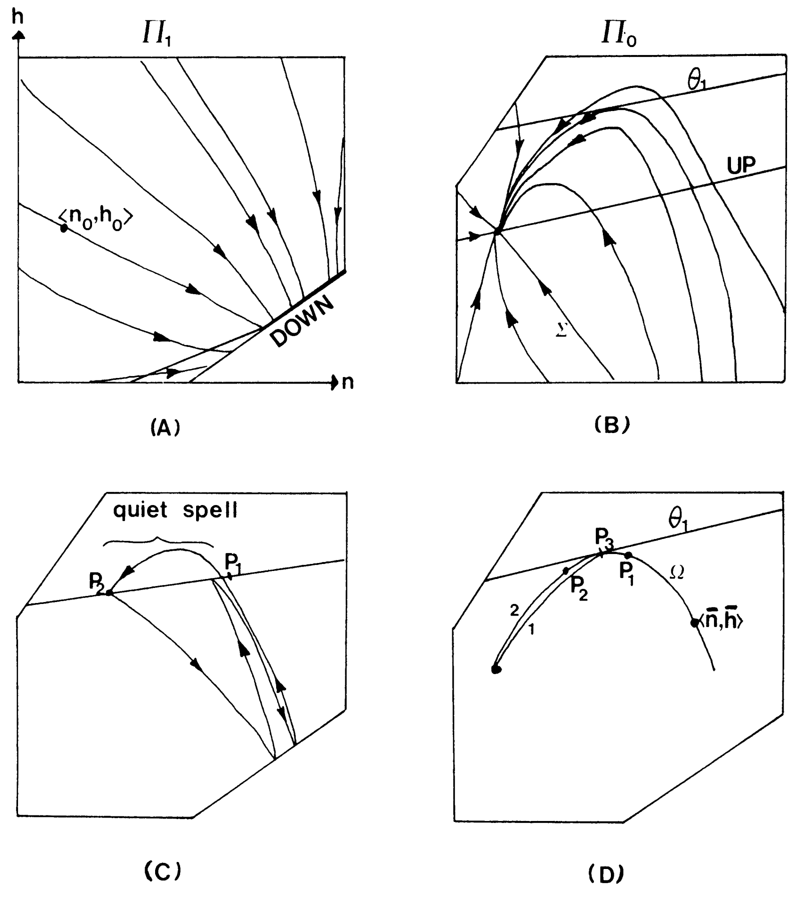


FIG 12. (A), (B) *Phase portrait of a flow which satisfies Conditions α and β.*

(C) *P_1 is a fixed point of $F_0\circ F_1$ and corresponds to a solution in Ω. P_2 is a fixed point of $\phi\circ(F_0\circ F_1)^2$ and corresponds to a burst solution with two spikes.*

(D) *The set of fixed points of $F_0\circ F_1$ extends to the right of P_3 and is labeled "Ω". For each N the set of fixed points of $\phi\circ(F_0\circ F_1)^N$ extends from $\langle n_0, h_0\rangle$ to P_3. The fixed points are shown for $N=1, 2$.*

Example 1.

Consider the system depicted in Fig. 12(A, B) (Case (A) of Theorem 1). For each N, the set of fixed points of $\phi\circ(F_0\circ F_1)^N$ meets the set of fixed points of $F_0\circ F_1$ at a point P_3, where $\theta(n, h)=\theta_1$. In Fig. 12(D), the fixed point sets of $\phi\circ(F_0\circ F_1)^1$ and $\phi\circ(F_0\circ F_1)^2$ are shown and are labeled "1" and "2", respectively. The fixed point set of

$F_0 \circ F_1$ is labeled "Ω". The point P_2 (Fig. 12(C)) is a fixed point of $\phi \circ (F_0 \circ F_1)^2$. If $\langle n, h\rangle = P_2$ then $\tau(n, h)$ is the time the solution segment in Π_1 (upper sheet) takes to go from $\langle n, h\rangle$ to $F_1(n, n)$; $\tau(F_1(n, h))$ is the time the solution segment in Π_0 (lower sheet) takes to go from $F_1(n, h)$ to $F_0 \circ F_1(n, h)$; $\tau(F_0 \circ F_1(n, h))$ is the time the solution segment in Π_1 takes to go from $F_0 \circ F_1(n, h)$ to $F_1 \circ (F_0 \circ F_1)(n, h)$; and $\tau(F_1 \circ (F_0 \circ F_1)(n, h))$ is the time the solution segment in Π_0 takes to go from $F_1 \circ (F_0 \circ F_1)(n, h)$ to $(F_0 \circ F_1)^2(n, h)$. Finally, the "quiet spell" $T((F_0 \circ F_1)^2(n, h))$ is the time the solution segment in Π_0 takes to go from $(F_0 \circ F_1)^2(n, h)$ back to the starting point $\langle n, h\rangle = \phi \circ (F_0 \circ F_1)^2(n, h)$. Since the time a solution spends jumping between the upper and lower sheets of the slow manifold is small compared to the time spent on the slow manifold, it is reasonable to define the period of the singular solution of length 2 through P_2 to be the sum of the times spent on the slow manifold, i.e., $\tau(n, h) + \tau(F_1(n, h)) + \tau(F_0 \circ F_1(n, h)) + \tau(F_1 \circ (F_0 \circ F_1)(n, h)) + T((F_0 \circ F_1)^2(n, h))$. When $\theta = \theta(P_2)$ and ε and δ are small, there is a periodic bursting solution with two spikes near this singular solution and, in the time scale of $\tau = \varepsilon s$, its period is close to the period of the singular solution and the length of its quiet spell is close to $T((F_0 \circ F_1)^2(n, h))$.

More generally, if $\langle n, h\rangle$ is a fixed point of $\phi \circ (F_0 \circ F_1)^N$, define the *period of the singular solution through* $\langle n, h\rangle$ to be $\tau(n, h) + \tau(F_1(n, h)) + \tau((F_0 \circ F_1)(n, h)) + \cdots + \tau(F_1 \circ (F_0 \circ F_1)^{N-1}(n, h)) + T((F_0 \circ F_1)^N(n, h))$. If $\langle n, h\rangle$ is a fixed point of $(F_0 \circ F_1)$, define the period of the singular solution through $\langle n, h\rangle$ to be $\tau(n, h) + \tau(F_1(n, h))$. The relationship between the period of the singular solution through $\langle n, h\rangle$ and $\theta(n, h)$ is shown in Fig. 13(A).

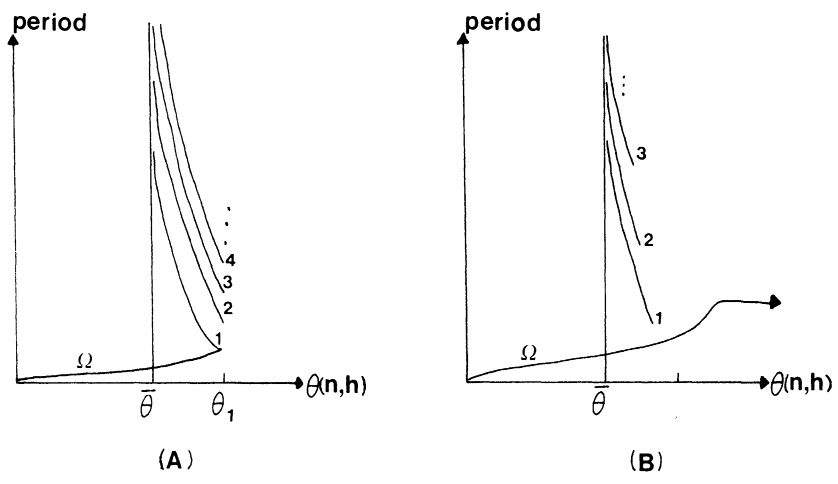


FIG. 13. (A) *Example* 1: *period of a singular solution vs.* $\theta(n, h)$. *As* $\theta \downarrow \bar{\theta}$, *the solutions with N bursts converge to the singular solutions of length N.*

(B) *Period vs.* $\theta(n, h)$ *for other examples which satisfy Conditions* α *and* β. *The curve* Ω *either extends to* $+\infty$ *or is finite.*

Figure 12(D) and 13(A) summarize the qualitative properties of a family of periodic bursting solutions with N spikes. The family begins at a finite wave train solution with N spikes, that is, a solution whose quiet spell is infinite. As the wave speed θ increases, the length of the quiet spell decreases from infinity ($\theta \simeq \bar{\theta}$) to zero ($\theta \simeq \theta_1$). Where the quiet spell goes to zero, the family of bursting solutions merges with the family Ω of regular periodic solutions. At that point, the period of the regular periodic solution is relatively large (low frequency); as θ then decreases (along the curves labeled

Ω in Figs. 12(D) and 13(A)), the period decreases to near zero. Note, in particular, that for $\bar{\theta} < \theta < \theta_1$, the curve labeled "1" in Figure 13(A) corresponds to a family of periodic solutions with evenly-spaced spikes of low frequency. Following that curve from $\theta = \bar{\theta}$ to $\theta = \theta_1$ and then following the curve Ω, the period of the singular solution decreases from infinity to zero (Fig. 13(A)).

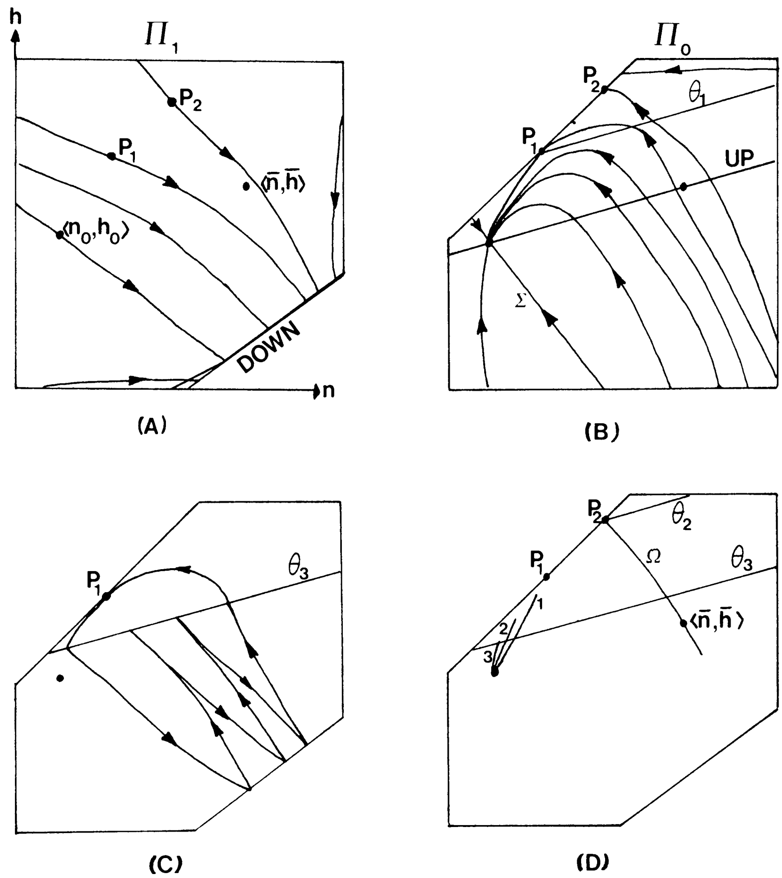


FIG. 14. (A), (B) *Phase portrait of an example of Case* (*B*) *of Theorem* 1, $M = 4$.
(C) *When* $\theta(n, h) = \theta_3$, *the singular solution of length* 3 *touches* $\partial\Pi_0$ *at* P_1.
(D) *Singular solutions of length* 3 *persist for* $\bar{\theta} < \theta < \theta_3$. *The curves of fixed points of* $\phi \circ (F_0 \circ F_1)^N$ ($N = 1, 2, 3$) *all end at the trajectory in* Π_0 *through* P_1. *There is some* θ_2 *such that* P_2 *is a fixed point of* $F_0 \circ F_1$ *for* $\theta \geqq \theta_2$.

Example 2.

The system depicted in Fig. 14(A), (B) is an example of Theorem 1(B) with $M = 4$. The system admits wave train and burst solutions with 1, 2, or 3 spikes. The curves of $\theta(n, h)$ vs. period of a singular solution are similar to those of Fig. 13(B) for $N = 1, 2$, or 3. The value of $\theta(n, h)$ for the family Ω extends from 0 to $+\infty$.

Examples 1 and 2 indicate the wealth of information to be derived from a singular phase plane analysis. One might conjecture that any system which satisfies Conditions α and β has a fixed point set like that of Fig. 12(D), but this is false. Even if the solution in Π_0 with initial value $\langle \bar{n}, \bar{h} \rangle$ goes to $\langle n_0, h_0 \rangle$ at $+\infty$, a solution beginning at another fixed point of $F_0 \circ F_1$ may go to $\partial\Pi_0$. Suppose $\langle \bar{\bar{n}}, \bar{\bar{h}} \rangle$ is such a point. In that case, the curve (Ω) of fixed points of $F_0 \circ F_1$ extends to $\partial\Pi_0$ and each of the curves of fixed points of $\phi \circ (F_0 \circ F_1)^N$ $(N = 1, 2, 3, \cdots)$ ends at a point on the trajectory in Π_0 through $\langle \bar{\bar{n}}, \bar{\bar{h}} \rangle$. The curves $\theta(n, h)$ vs. period of the singular solution have the properties shown in Fig. 13(B).

3. Properties of bursts. The proof of Theorem 1 (§ 8) implies that a singular solution, along with its connecting jumps between UP and DOWN, is close to the corresponding solutions of the full system (5). Thus, qualitative information about the true solutions may be obtained by analysis of the singular phase portraits.

PROPOSITION 1: *Properties of Type I bursts. The finite wave train and bursting solutions of* § 2 *have properties* (i)–(vi) *below. These properties are characteristic of the Type I bursts described in* § 1.

(i) *If the rate of onset* K^+ *activation* (n) *is about the same as the rate of onset of* Na^+ *inactivation* (h), *either the membrane does not sustain bursts* (*Case* (C) *of Theorem* 1) *or the interval between the first and second spike of the burst is so long that the burst looks like a single spike. Thus some skewing of the n-h rates is the principal membrane property to cause bursting. In terms of the system* (5), *n-h rates are skewed if* γ_n/γ_h *is not too near* 1. *This also implies that the shoulder of the falling phase is longer than it is in single spikes.*

(ii) *During each burst, the interspike interval decreases*; *i.e., the spiking frequency increases. After a few spikes, the frequency becomes nearly constant* (*Fig.* 1(A), (B)).

(iii) *The maximum and the minimum values of v tend to increase or decrease during a burst* (*Fig.* 1(A), (B), (C)).

(iv) *Spikes are separated by intervals of hyperpolarization* $(v < 0)$ *which end abruptly when the membrane jumps, almost instantly, into the excited state at the onset of the spike.*

(v) *Sometimes the length of the shoulder of the falling phase increases or decreases during the burst.*

(vi) *Bursts are separated by quiet spells. The length of the quiet spell increases with the number of spikes in the previous burst. For a given membrane, the length of the quiet spell approaches an upper bound as the number of spikes in the previous burst becomes large.*

The important point of Proposition 1 is that properties (i)–(vi) are to be expected in a single membrane with fast Na^+ activation and slow Na^+ inactivation and K^+ activation. Deviations from these properties imply the presence of additional membrane processes.

4. Aplysia. The most carefully studied examples of bursting pacemaker cells are the abdominal ganglia of Aplysia, which appear to be activated by an endogenous depolarizing substance [17]. Several qualitative properties of these Type II bursts indicate that more membrane processes are active than was the case for the bursts of § 2 and § 3. These include:

(i) the increase and subsequent decrease of spiking frequency during the bursts;

(ii) the increase and subsequent decrease of the maximum and minimum values of v during most of the bursts (Fig. 1(D));

(iii) the elongated shoulder of the falling phase;

(iv) the presence of a fast subthreshold outward current near the beginning of each burst [9]; and

(v) the elongated N-shape of the graph of v between bursts (post-burst hyperpolarization), as shown in Fig. 15.

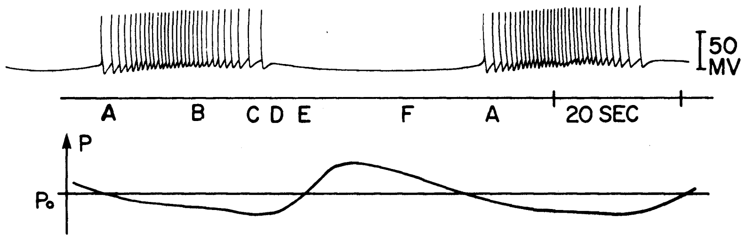


FIG. 15. *Intracellular recording from Aplysia spikes, redrawn from* [17, p. 295]. *The time course of p is traced during the burst and quiet spell.*

It is important to note that microelectrode measurements in Aplysia ganglia are taken at the cell body, whereas the models discussed in this paper are of the propagated action potential. An interesting theoretical and experimental question is: What is the relationship between spikes measured at the cell body and the signals transmitted along the axon to other cells?

The principal feature of recent models of bursting cells in Aplysia is the addition of a term, I_A, to the total ionic current [9], [16]:

$$g = I_{Na} + I_K + I_A + I_K.$$

Faber and Klee [9] also state that K^+ inactivation and anaomalous rectification (the decrease of resistance with hyperpolarization) are likely to account for certain properties of the burst which I_A alone does not explain. They conclude with the remark that experiments indicate that I_A, anomalous rectification, and K^+ inactivation may be linked processes.

A singular perturbation analysis such as that of § 2 and § 3 reveals that properties of bursting in Aplysia may be explained in terms of K^+ inactivation alone. I_A was added to the models because the fast outward current was observed, not because of the discovery of a new membrane process; but the outward current would be an expected result of K^+ inactivation.

An example of a model which includes K^+ inactivation is (5) with:

$$\begin{aligned} g(v, m, n, h, p) &= \overline{g_{Na}} m^3 h(v - v_{Na}) + \overline{g_K}(np)^4 (v - v_K) + \overline{g_L}(v - v_L), \\ \dot{p} &= \varepsilon \kappa \gamma_p(v)(p_\infty(v) - p), \end{aligned} \tag{8}$$

where $\kappa > 0$ is small and $p'_\infty < 0$. (See Fig. 16.)

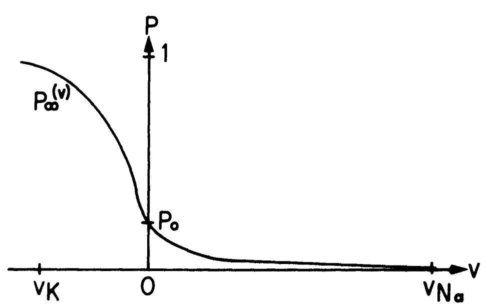


FIG. 16. *A typical $p_\infty(v)$ must increase sharply for $v < 0$ since the extra outward current is seen only if the membrane has been hyperpolarized before depolarization* [9].

An example of a model with I_A is:

$$
(9)\quad \begin{aligned} &g(v, m, n, h, p)=\overline{g_{Na}}m^3h(v-v_{Na})+\overline{g_K}n^4(v-v_K)+g_Ap(v-v_K)+g_L(v-v_L),\\ &\dot{p}=\varepsilon\kappa\gamma_p(v)(p_\infty(v)-p). \end{aligned}
$$

As (8) and (9) illustrate, the main difference between the two theories is that in (8) p^4 multiplies the potassium permeability, g_Kn^4, of (5) and in (9) g_Ap is added to g_Kn^4.

Steps (A)–(F) below (see Figs. 15, 17) outline the qualitative analysis of (8), where slow K^+ inactivation multiplies the potassium current in (5); in other respects the model remains the same as in § 2. Hypothesis 1 and Conditions α and β are assumed in the appropriate modified form.

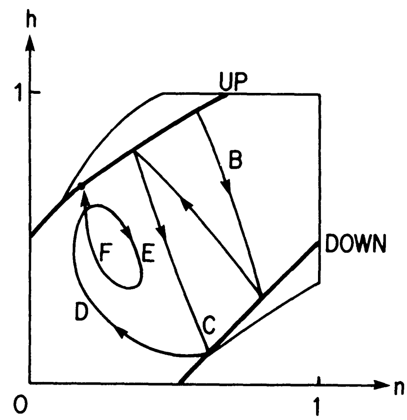


FIG. 17. *Singular phase portrait of a burst with K^+ inactivation.*

(A) Near the beginning of a burst, p is near p_0 and the spiking frequency decreases as in the model of § 2 (Figs. 1(A) and (D), 15(A)). Repeated depolarization makes p begin to decrease.

(B) As p decreases (less K^+ inactivation) the phase portrait of Fig. 15(A) is altered, so that the solutions in Π_0 and Π_1 begin to be dragged back down (Fig. 17). The maximum and minimum values of v level out and then decrease.

(C) Singular solutions in Π_0 slow down as they get closer to the critical point, increasing the interspike interval, during which the cell is hyperpolarized. p thus begins to increase again.

(D) The singular solution is now in the component of Π_0 where UP is never reached. The system is hyperpolarized and is slowly approaching the critical point, with v increasing. p has enough time to begin to increase.

(E) p approaches $p_\infty(v) > p_0$, while $n \simeq n_\infty(v)$ and $h \simeq h_\infty(v)$ and v decreases.

(F) When $p \simeq p_\infty(v)$, the entire system slowly moves back toward the critical level. v increases slowly until the point where step (A) is begun again.

5. An infinite dimensional temporal code. In this section we introduce Condition γ, which is much more difficult to satisfy than Condition α or Condition β of § 2. The result of imposing Condition γ upon the model (5) is the existence of solutions with arbitrary burst sequences. The significance of this result lies in the fact that the model is deterministic and still relies upon the usual mechanisms of Na^+ and K^+ activation and Na^+ inactivation. In a more general context, Theorem 2 says that a simple system which relies only upon local, statistically-defined on-off mechanisms (here, m, n, h) can process inputs to yield arbitrarily complex signals.

Condition γ: In Π_0, the solution with initial value $F_1(n_0, h_0)$ crosses UP at least twice.

Compare Fig. 18 with Fig. 11. In Fig. 18, any $F_1(n_0, h_0)$ above Δ satisfies γ, and any $F_1(n_0, h_0)$ either above Δ or below Σ satisfies β. The system in Fig. 11 could not satisfy γ no matter where $F_1(n_0, h_0)$ is in DOWN. Condition γ is seen to require much more nonlinearity in the phase portrait Π_0 or the set UP than is needed to imply the repetitive bursting of Theorem 1. Clearly, Condition γ implies Condition α.

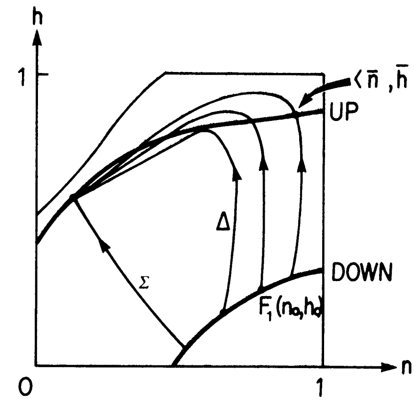


FIG. 18. *A system which satisfies Condition* γ.

THEOREM 2: *Arbitrary sequences of bursts. Assume Hypothesis* 1 *and Conditions* β *and* γ. *Then, give any infinite sequence* $\{N_i : i = 1, 2, \cdots\}$ *of positive integers, for all small* ε, $\delta > 0$ *there exists a solution of* (5) *which begins at rest* (*at* $-\infty$); *exhibits* N_1 *rapid spikes followed by an interval of quiet; then* N_2 *spikes followed by an interval of quiet; and so on,* (*Fig.* 7(i)). *Within each burst, spiking frequency increases.*

Given any finite sequence, $N_1, \cdots, N_K$, *there exists a solution which begins and ends at rest and which exhibits* N_i *bursts in the i-th bursting interval* (*Fig.* 7(g)). *Moreover, there is a family of periodic solutions with sequences of* $N_1, \cdots, N_K$ *bursts separated by longer intervals of quiet which become infinite as the period goes to infinity* (*Fig.* 7(h)).

For fixed ε, $\delta > 0$ *each sequence* $\{N_i\}$ *has a characteristic wave speed. In fact, if* $\theta_N \sim \{N_i\}$ *and* $\theta_M \sim \{M_i\}$; $N_i = M_i$, $i = 1, \cdots, K-1$; *and* $N_K > M_K$, *then* $\theta_N > \theta_M$. *That is, the sequences have a lexicographic order which is reflected in their wave speeds. The first bursting interval reflects the principal component of the wave speed.*

6. Nonuniqueness and chaos. In this section we give two examples to illustrate the types of complexities which arise in a system (5). Like the system which satisfies Condition γ of § 5, these systems must be more nonlinear than those of § 3.

Example 3 generalizes to the following nonuniqueness result.

For any $K \geqq 1$ there is a class of systems (5) with K singular solutions of length N ($N = 1, 2, 3, \cdots$). Thus, given such a system, for all small ε, $\delta > 0$ and $N = 1, 2, \cdots$ there is a continuum of values of θ for which (5; θ, ε, δ) admits K distinct burst solutions with N spikes each.

Example 4 combines the idea of § 5 and the nonuniqueness result to show that a system (5) may exhibit chaotic behavior. That is, given any $L \geqq 1$, there is a class of systems (5), each of which admits L disjoint classes $\Omega_1, \cdots, \Omega_L$ of regular periodic solutions. Moreover, given any sequence of pairs $\{\langle N_i, M_i\rangle : i = 1, 2, 3, \cdots\}$ with $N_i \geqq 1$ and $1 \leqq M_i \leqq L$, for all small ε, $\delta > 0$ there is a solution of (5) with N_i spikes in the ith bursting interval, and these N_i spikes are close to a solution in the class Ω_{M_i}. In addition, given any finite sequence $\{\langle N_i, M_i\rangle\}$ there is a family of periodic bursting solutions which repeat the pattern of N_i spikes near Ω_{M_i}.

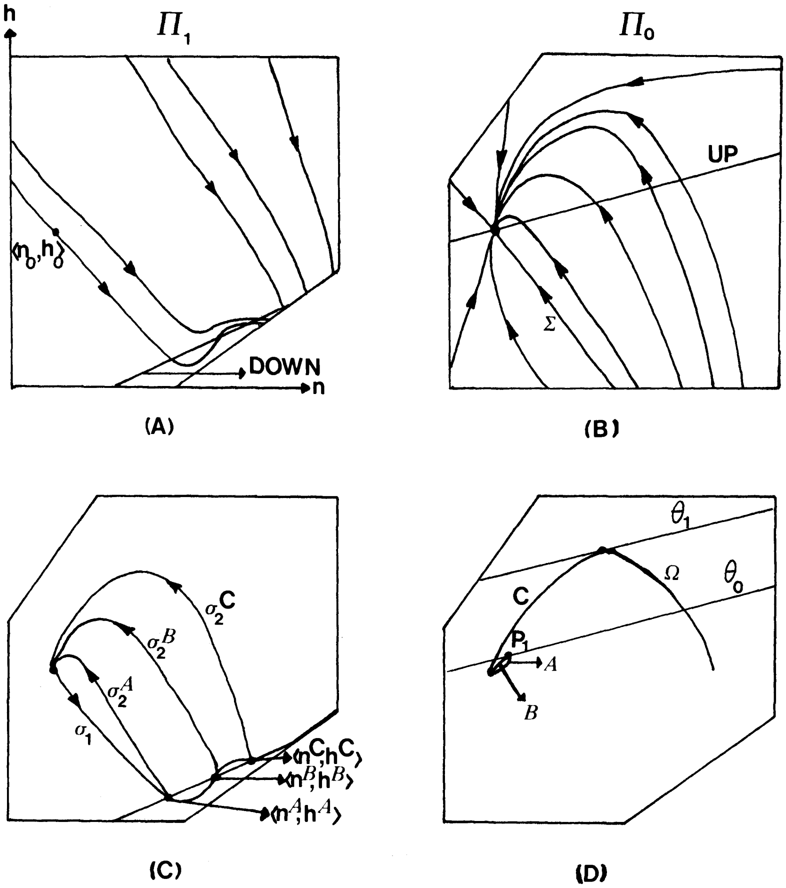


FIG. 19. (A), (B) *A flow which satisfies Conditions α and β.*
(C) *Three singular solutions of length* 1.
(D) *Let* $F_1^A(n, h)$ *be the first point on* $\langle n, h\rangle \cdot \tau$ *where* $\theta = -\theta(n, h)$; *if they exist, let* $F_1^B(n, h)$ *and* $F_1^C(n, h)$ *be the second and third such points for* $\bar{\theta} < \theta(n, h) < \theta_0$. *The sets A, B, and C are fixed points of* $\phi \circ (F_0 \circ F_1^A)$, $\phi \circ (F_0 \circ F_1^B)$, *and* $\phi \circ (F_0 \circ F_1^C)$. *The solution in* Π_1 *through* P_1 *is tangent to* $\{\theta(n, h) = -\theta_0\}$. *For* $\theta_0 < \theta < \theta_1$, $F_1 = F_1^C$, *and C joins the fixed point set of* $F_0 \circ F_1$ *at* $\theta = \theta_1$.

Example 3: Nonuniqueness.

The example shown in Figure 19(A), (B) has three distinct singular solutions of length 1: $\{\sigma_1^A, \sigma_2^A\}$, $\{\sigma_1^B, \sigma_2^B\}$ and $\{\sigma_1^C, \sigma_2^C\}$. σ_1^A is the solution in Π_1 from $\langle n_0, h_0\rangle$ to $\langle n^A, h^A\rangle$ and σ_2^A is the solution in Π_0 from $\langle n^A, h^A\rangle$ to $\langle n_0, h_0\rangle$. Similarly, σ_1^B is the solution in Π_1 from $\langle n_0, h_0\rangle$ to $\langle n^B, h^B\rangle$, etc. The proof of Theorem 1 implies that the wave speeds of the three distinct single pulse speeds increase from A to B to C. All nearby flows admit three distinct singular solutions of length one. Each of the three singular solutions can be continued to at least one singular solution of length N. The sets of fixed points of appropriately-defined return maps, analogous to $\phi \circ (F_0 \circ F_1)$, are shown in Fig. 19(D). For $\bar{\theta} < \theta < \theta_0$, there are three burst solutions with 1 spike. At $\theta = \theta_0$, solutions A and B merge. For $\theta_0 < \theta < \theta_1$, there is just one burst solution with 1 spike.

Analogously, for any $L \geqq 1$ the system (5) exhibits at least L singular solutions of length N if the solution in Π_1 beginning at $\langle n_0, h_0 \rangle$ crosses DOWN at least L times.

CONJECTURE: *Local uniqueness. Assume that* (5) *admits exactly M singular solutions of length N and that no solution segment σ_k of a singular solution is tangent to* UP *or* DOWN. *Then for each small* $\varepsilon, \delta > 0$ *there are exactly M values of θ for which* (5) *admits a finite wave train solution of length N.*

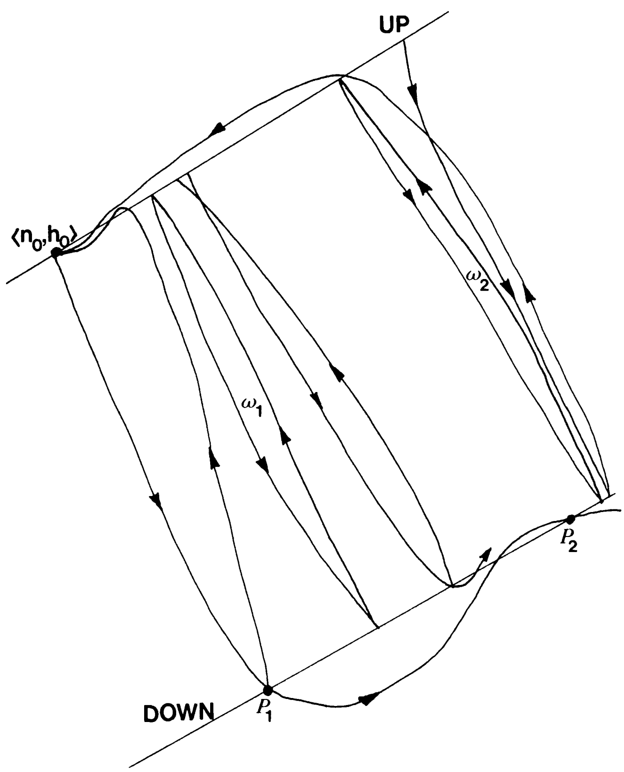


FIG. 20. *A system with chaotic solutions.*

Example 4: Chaos.

In the example illustrated in Fig. 20, there are two classes Ω_1, Ω_2 of regular periodic solutions.

Let $\{\langle N_i, M_i \rangle\}$ be a sequence with $N_i \geqq 1$ and $M_i = 1$ or 2. Suppose, for example, that $M_1 = 2$ and $M_2 = 1$. The singular solution starts at $\langle n_0, h_0 \rangle$ and goes to the point P_2. The singular solutions then jump up and down near ω_2 until there are N_1 spikes. The solution segment σ_{2N_1} runs to a point in UP near $\langle n_0, h_0 \rangle$, where another jump up occurs. The next singular solution segment jumps down near P_1 and continues to jump near ω_1 until there are N_2 spikes in this burst interval. The solution $\sigma_{2(N_1+N_2)}$ crosses UP near ω_1 and jumps up near $\langle n_0, h_0 \rangle$, and so on.

7. An example computed. In general, it is difficult to compute the flow on Π_0, Π_1 and to determine the location of UP and DOWN. Certain simplifications greatly reduce the complexity of computations.

First, n_∞ and h_∞ are nonlinear, but each is nearly linear in the range of values taken on by $v_0(n, h)$ and $v_1(n, h)$. Thus, one may assume that $n_\infty(v) = av + n_0$ for v small and $n_\infty(v) = bv + c$ for v large (Fig. 21). A similar approximation may be made to $h_\infty(v)$.

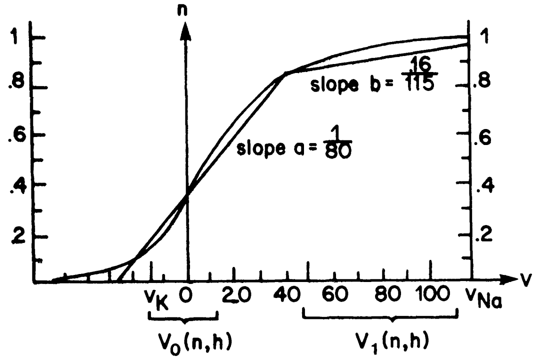


FIG. 21. *$n_\infty(v)$ redrawn from* [11] *and a piecewise-linear approximation.*

For most functions $G(v, n, h)$, $\theta(n, h)$ needs to be approximated using a computer. Hunter, McNaughton and Noble [12] give explicit expressions for $\theta(n, h)$ for certain functions $G(v, n, h)$. They consider the cubic-shaped function

$$G(v, n, h) = C^2(v - v_0)((v_1 - v_0)^k - (v - v_0)^k)((v_2 - v_0)^k - (v - v_0)^k),$$

where $C(n, h)$, $v_0(n, h)$, $v_1(n, h)$, $v_2(n, h)$ are defined on $[0, 1]^2$, cl (Π_0), cl (Π_1), and cl $(\Pi_0 \cap \Pi_1)$, respectively; $C(n, h) \geqq 0$; and $v_0(n, h) \leqq v_2(n, h) \leqq v_1(n, h)$ (Fig. 3). Let

$$\theta(n, h) \equiv \sqrt{k+1}\, C\left(\frac{(v_1 - v_0)^k}{k+1} - (v_2 - v_0)^k\right)$$

and

$$(10; \theta, n, h) \qquad \begin{aligned} \dot{v} &= w \\ \dot{w} &= \theta w + G(v, n, h). \end{aligned}$$

Then there is a solution of $(10; \theta, n, h)$ from $\langle v_0(n, h), 0\rangle$ to $\langle v_1(n, h), 0\rangle$ iff $v_0(n, h) < v_2(n, h)$ and $\theta = \theta(n, h) \geqq 0$ or $v_0(n, h) = v_2(n, h)$ and $\theta \geqq \theta(n, h)$. There is a solution of $(10; \theta, n, h)$ from $\langle v_1(n, h), 0\rangle$ to $\langle v_0(n, h), 0\rangle$ iff $v_1(n, h) > v_2(n, h)$ and $\theta = -\theta(n, h) \geqq 0$ or $v_1(n, h) = v_2(n, h)$ and $\theta \geqq -\theta(n, h)$.

For example, if $k = 1$,

$$G(v, n, h) = C^2(v - v_0)(v - v_1)(v - v_2)$$

is truly cubic. In this case,

$$\theta(n, h) = \sqrt{2}\, C\left(\frac{(v_1 - v_0)}{2} - (v_2 - v_0)\right)$$

$$= \sqrt{2}\, C\left(\frac{v_0 + v_1}{2} - v_2\right),$$

as computed in [5].

If

$$\frac{v_0+v_1}{2} \geqq v_2, \qquad \theta(n, h) \geqq 0$$

and

$$w = w(v) = \frac{-C}{\sqrt{2}}(v-v_0)(v-v_1)$$

is a solution of $(10; \theta(n, h), n, h)$ from v_0 to v_1. To check this, first note that

$$\frac{dw}{dv} = \frac{-C}{\sqrt{2}}(2v-(v_0+v_1)).$$

For $(10; \theta, n, h)$,

$$\begin{aligned}\frac{\dot{w}}{\dot{v}} &= \theta + \frac{G(v, n, h)}{w}\\ &= \theta + \sqrt{2}\,\frac{C^2(v-v_0)(v-v_1)(v-v_2)}{-C(v-v_0)(v-v_1)}\\ &= \theta - \sqrt{2}\,C(v-v_2).\end{aligned}$$

Thus $w = w(v)$ is a solution of $(10; \theta, n, h)$ iff $-C\sqrt{2}\,(v-(v_0+v_1)/2) = \theta - \sqrt{2}\,C(v-v_2)$ iff $\theta = \sqrt{2}\,C((v_0+v_1)/2 - v_2) = \theta(n, h)$.

If $v_0(n, h) = v_2(n, h)$ and $\theta \geqq \theta(n, h)$, the existence of the solution $w = w(v)$ follows from Lemma 2.

In the following example, n_∞, h_∞ are piecewise linear; $G(v, n, h)$ is a cubic function of v; and $v_0(n, h)$, $v_1(n, h)$, $v_2(n, h)$ are linear in n, h. The parameters have been chosen to satisfy inequalities which imply Hypothesis 1.

Example 5. Assume that:

$$\begin{aligned}&G(v, n, h) = C^2(v-v_0)(v-v_1)(v-v_2),\\ &v_0(n, h) = -7(n-n_0)+6(h-h_0),\\ &v_1(n, h) = 95-23(n-n_0)+23(h-h_0),\\ &v_2(n, h) = 10+50(n-n_0)-50(h-h_0),\\ &n_0 = .3, \quad h_0 = .6, \quad v_K = -10, \quad v_{Na} = 115,\\ &\gamma_n(v) = \gamma_h(v) = \text{constant},\end{aligned}$$

$$n_\infty(v) = \begin{cases} \dfrac{v}{80} + n_0 & \text{if } v_K < v < 40,\\[2ex] \dfrac{.16}{115}v + .8 & \text{if } 40 < v < v_{Na},\end{cases}$$

$$h_\infty(v) = \begin{cases} -\dfrac{v}{40} + h_0 & \text{if } v_K < v < 20,\\[2ex] -\dfrac{v}{12{,}000} + .01 & \text{if } 20 < v < v_{Na}.\end{cases}$$

Then:

$$\theta = \frac{C}{\sqrt{2}}(95-20) = \frac{75C}{\sqrt{2}},$$

$$\text{UP} = \{\langle n, h\rangle : 129(h-h_0) = 130(n-n_0)\},$$

$$\text{DOWN} = \{\langle n, h\rangle : 129(h-h_0) = 130(n-n_0) - 150\},$$

$$\partial\Pi_0 = \{\langle n, h\rangle : 56(h-h_0) = 57(n-n_0) + 10\},$$

$$\partial\Pi_1 = \{\langle n, h\rangle : 73(h-h_0) = 73(n-n_0) - 85\}.$$

Inspection of Fig. 22 reveals that any point of DOWN crosses UP in Π_0 and then returns toward $\langle n_0, h_0\rangle$. Thus Conditions α and β of § 2 are satisfied, so this system exhibits finite wave train and bursting solutions with any number of spikes. Condition γ of § 5 could never be satisfied by a system such as this, where the flows on Π_0, Π_1 and UP, DOWN are linear.

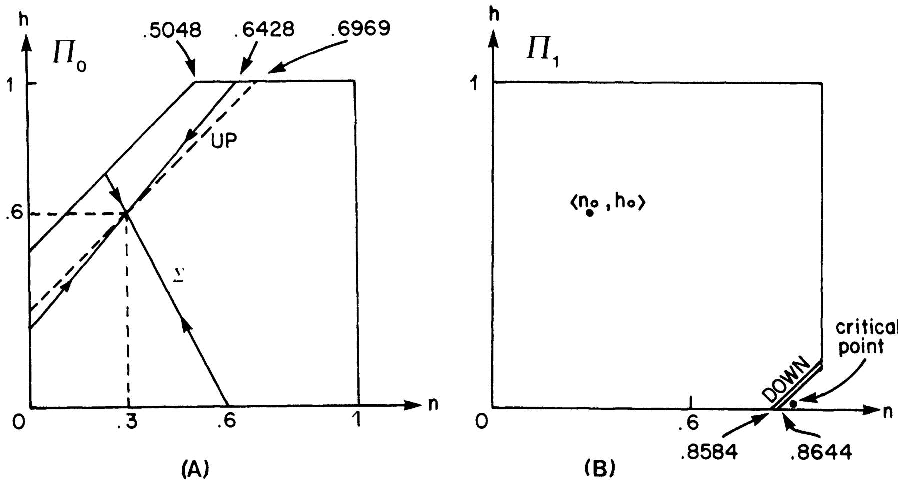


FIG. 22. (A) *Slopes of*: $\partial\Pi_0 = 1.018$; UP $= 1.10078$; *and the eigenvectors* $= 1.167$ *and* -2.
(B) *Slopes of*: $\partial\Pi_1 = 1$ *and* DOWN $= 1.0078$. *The critical point* $\langle .8991, .0044\rangle$ *of the linear flow* (7; 1) *lies outside* Π_1.

8. Proofs.

Proof of Lemma 1. McKean proves this result in [15]. To verify it, note that

$$F(v, w, n, h) \equiv \tfrac{1}{2}w^2 - \int_{v_0(n,h)}^{v} G(v, n, h)\, dv$$

is a Lyapunov function for (6; θ, 0), since

$$\dot{F} = w(\theta w + G(v, n, h)) - G(v, n, h)w$$
$$= \theta w^2 \geqq 0.$$

Thus if $\theta > 0$, any nontrivial bounded solution of (6; θ, 0) connects two distinct points $\langle v, w, n, h\rangle$ where $w = G(v, n, h) = 0$. That is, the solution runs from $\langle v_i(n, h), 0, n, h\rangle$ to $\langle v_j(n, h), 0, n, h\rangle$, where $i, j = 0, 1$, or 2.

(i) Assume first that $\int_{v_0(n,h)}^{v_1(n,h)} G(v, n, h)\,dv < 0$ and fix $\varepsilon = 0$. Let $\mathcal{U}(\theta)$ be that branch of the unstable manifold of $\langle v_0(n, h), 0, n, h\rangle$ with negative half solution in $\Psi \equiv \{w \geqq 0, v \leqq v_1(n, h)\}$. Since $\int_{v_0(n,h)}^{v_1(n,h)} G(v, n, h) < 0$, $\mathcal{U}(\theta)$ leaves Ψ in $\{w = 0\}$ if θ is small. Since $\dot{w} = \theta w + G(v, n, h)$ and G is bounded in $[v_0(n, h), v_1(n, h)]$, $\mathcal{U}(\theta)$ leaves Ψ in $\{v = v_1(n, h)\}$ if θ is large. Thus there exists some $\theta > 0$ such that $\mathcal{U}(\theta)$ never leaves Ψ, and $\mathcal{U}(\theta)$ runs from $\langle v_0(n, h), 0, n, h\rangle$ to $\langle v_1(n, h), 0, n, h\rangle$. An argument similar to that in the proof of Lemma 2(A) below shows that this value of $\theta \equiv \theta(n, h)$ is unique.

If $\theta = 0$ and $\int_{v_0(n,h)}^{v_1(n,h)} G(v, n, h)\,dv = 0$, then $\dot{F} = 0$ and $F(v_0(n, h), 0, n, h) = F(v_1(n, h), 0, n, h) = 0$. Thus, if $v_0(n, h) < v < v_1(n, h)$,

$$w = \pm\left[2\int_{v_0(n,h)}^{v} G(v, n, h)\,dv\right]^{1/2}$$

along two solutions of (6; 0, 0) connecting $\langle v_0(n, h), 0, n, h\rangle$ and $\langle v_1(n, h), 0, n, h\rangle$.

(ii) The second part is verified similarly.

Proof of Lemma 2.

(A) Fix $\langle n, h\rangle \in \partial\Pi_0$ and assume that $\{\langle n_i, h_i\rangle\} \subseteq \Pi_0 \cap \Pi_1 \cap \{\theta(n, h) > 0\}$ is a sequence which converges to $\langle n, h\rangle$. Then the sequence of solutions from $\langle v_0(n_i, h_i), 0, n_i, h_i\rangle$ to $\langle v_1(n_i, h_i), 0, n_i, h_i\rangle$ converges to a solution from $\langle v_0(n, h), 0, n, h\rangle$ to $\langle v_1(n, h), 0, n, h\rangle$ for $\theta = \theta(n, h)$.

Next fix $\theta > \theta(n, h)$ and let $w \equiv w(v)$ along the solution of (6; $\theta(n, h)$, 0) from $\langle v_0(n, h), 0, n, h\rangle$ to $\langle v_1(n, h), 0, n, h\rangle$ and let $B \equiv \{\langle v, w, n, h\rangle : v_0(n, h) \leqq v \leqq v_1(n, h)$ and $0 \leqq w \leqq w(v)\}$. B is *negatively invariant*, that is, no solution of (6; θ, 0) leaves B in backward time. To check this, note that if $v_0(n, h) < v < v_1(n, h)$ and $w = 0$, then

$$\begin{aligned} \dot{w} &= \theta w + G(v, n, h) \\ &= G(v, n, h) < 0. \end{aligned}$$

If $w - w(v) = 0$, then

$$\begin{aligned} (w - w(v))^{\bullet} &= \theta w + G(v, n, h) - \frac{dw}{dv}(v)w \\ &= \theta w + G(v, n, h) - w\left(\theta(n, h) + \frac{G(v, n, h)}{w}\right) \\ &= (\theta - \theta(n, h))w > 0. \end{aligned}$$

Thus the existence of the Lyapunov function F (Lemma 1) implies that any point in B converges to $\langle v_0(n, h), 0, n, h\rangle$ at $-\infty$.

In the v-w plane, the slope of the eigenvector at $\langle v_1(n, h), 0, n, h\rangle$ with negative eigenvalue is

$$S(\theta) = \tfrac{1}{2}(\theta - (\theta^2 + 4G_v)^{1/2}).$$

$S(\theta) < 0$ since $G_v > 0$, and

$$\frac{dS}{d\theta} = \tfrac{1}{2}(1 - \theta(\theta^2 + 4G_v)^{-1/2}) > 0.$$

Since $S(\theta(n, h)) = (dw/dv)(v_1(n, h))$, one branch of the stable manifold of $\langle v_1(n, h), 0, n, h\rangle$ intersects B whenever $\theta \geqq \theta(n, h)$. Thus the entire branch of the stable manifold is contained in B and runs from $\langle v_0(n, h), 0, n, h\rangle$ to $\langle v_1(n, h), 0, n, h\rangle$, and (iii) is proved. The proof of (iv) is similar.

(B) Since $\partial G/\partial n > 0$ and $\partial G/\partial h < 0$ (Hypothesis 1(G)), $(\partial\theta/\partial n)(n, h) < 0$ and $(\partial\theta/\partial h)(n, h) > 0$. Thus for each $\tilde{\theta} \in \mathbb{R}$, $\{\langle n, h\rangle : \theta(n, h) = \tilde{\theta}\}$ is the graph of an increasing function of n, defined on some (possibly empty) subset of $[0, 1]$.

Hypothesis 1(G) implies, in addition, that $\partial\Pi_0$ is the graph of an increasing function of n defined on a subinterval of $(0, 1)$ (Fig. 6(B)). $\partial\Pi_1$ is, similarly, the graph of an increasing function of n (Fig. 6(A)). (Hypothesis 1(C) implies that $\partial\Pi_1 \neq \phi$.) UP[DOWN] is, therefore, the graph of the minimum of two increasing functions of n.

Proof of Theorem 1. Assume that $\{\sigma_1 \cdots \sigma_{2N}\}$ is a singular solution of length N. We must show that (6) admits a finite wave train solution with N spikes and a family of periodic bursting solutions which converge to the wave train solution as the length of the quiet spell becomes infinite.

The proof of the existence of a finite wave train solution [2], [4] relies upon the construction of "blocks" [7] $B_1, B_2, \cdots, B_{2N} \subseteq \mathbb{R}^4$. The *exit set* of any block B is the set of points $P \in \partial B$ such that $P \cdot (0, \eta) \cap B = \phi$ for some $\eta > 0$. B has the property that the map which sends a point $P \in B$ to the first point $P \cdot t$ in the exit set of B is continuous where defined. For each $k = 1, 2, \cdots, 2N$, the exit set of B_k contains a set Δ_k and δ_k^0, $\delta_k^1 \subseteq \partial\Delta_k$. If q_1 is any arc in Δ_1 from δ_1^0 to δ_1^1, q_1 contains a subarc which is carried continuously by the flow (6) into Δ_2. Moreover, the image, q_2, of the subarc is an arc from δ_2^0 to δ_2^1. By induction, then, q_2 contains a subarc carried by the flow into Δ_3 and running from δ_3^0 to δ_3^1, etc. (Fig. 23). Finally, if k is even, the subarc of q_{k-1} between δ_{k-1}^0 and the inverse image of q_k contains a point in the stable manifold of $\langle 0, 0, n_0, h_0\rangle$.

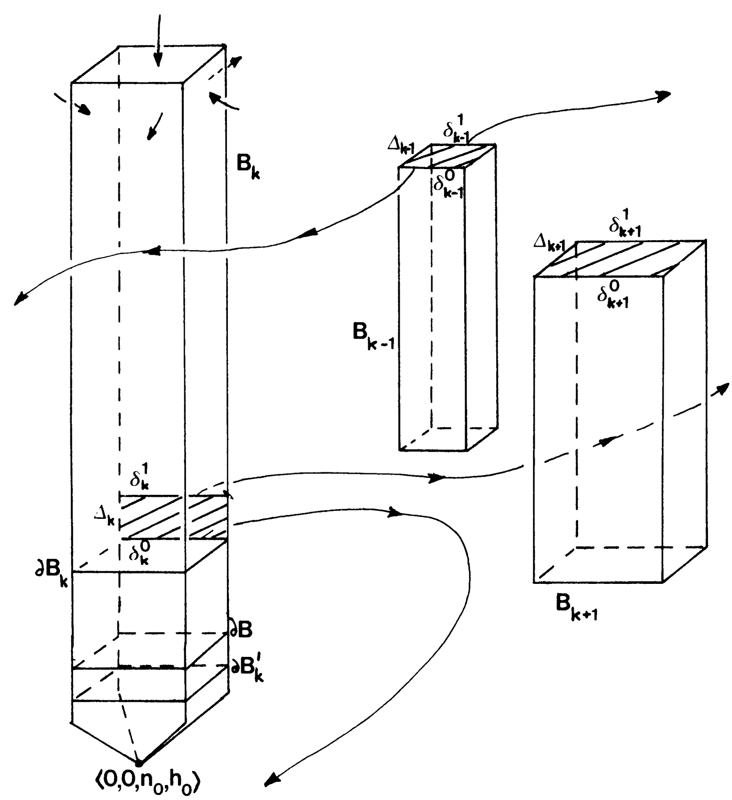


FIG. 23. *Typical B_{k-1}, B_k, and B_{k+1} (k even) projected into $\mathbb{R}^3$. The endpoints of σ_{k-1} and σ_{k+1} are contained in $\partial\Pi_1$.*

Details of the construction of $B_1, B_2, \cdots$ are given at the end of the proof.

Once $B_1, \cdots, B_{2N}$ have been constructed, the proof is straightforward. Let $\{\langle\theta(s), \varepsilon(s)\rangle : 0 \leqq s \leqq 1\}$ be any arc such that $\theta(s), \varepsilon(s) > 0$; $\varepsilon(s)$ and $|\bar{\theta} - \theta(s)|$ are small; and $\theta(0) < \bar{\theta} < \theta(1)$. Then there is an arc $\{q_0(s) : 0 \leqq s \leqq 1\}$ in $\mathbb{R}^4$ near $\langle 0, 0, n_0, h_0\rangle$ such that $q_0(s)$ is in the unstable manifold of $\langle 0, 0, n_0, h_0\rangle$ in the system $(6; \theta(s), \varepsilon(s))$. If $\varepsilon(s)$ and $|\bar{\theta} - \theta(s)|$ are small, $q_0(s)$ is carried continuously by the flow into B_1. Moreover there exist $0 < s_0^1 < s_1^1 < 1$ such that $\{q_0(s) : s_1^0 \leqq s \leqq s_1^1\}$ is mapped into an arc $\{q_1(s) : s_1^0 \leqq s \leqq s_1^1\} \subseteq \Delta_1$ with $q_1(s_1^0) \in \delta_1^0$ and $q_1(s_1^1) \in \delta_1^1$. By induction, then, there is a sequence $s_1^0 < s_2^0 < \cdots < s_{2N}^0 < s_{2N}^1 < \cdots < s_1^1$ such that $\{q_0(s) : s_k^0 \leqq s \leqq s_k^1\}$ is mapped continuously by the flow through $B_1 \cdots B_k$ into $\{q_k(s) : s_k^0 \leqq s \leqq s_k^1\}$, an arc in Δ_k with $q_k(s_k^0) \in \delta_k^0$ and $q_k(s_k^1) \in \delta_k^1$. Finally, if k is even there is $s_k \in (s_{k-1}^0, s_k^0)$ such that $q_{k-1}(s_k)$ is contained in the stable manifold of $\langle 0, 0, n_0, h_0\rangle$. Thus the solution through $q_0(s_k)$ passes through $B_1, \cdots, B_k$ and is contained in the intersection of the stable and unstable manifolds of $\langle 0, 0, n_0, h_0\rangle$. That is, $(6; \theta(s_k), \varepsilon(s_k))$ admits a finite wave train solution with $k/2$ spikes. Note that $s_2 < s_4 < s_6 < \cdots$.

The proof of the existence of a periodic bursting solution with N spikes again relies upon the construction of blocks $B_1, \cdots, B_{2N}$ A certain three-dimensional subset, Δ^*, of the exit set of B_{2N} is mapped by the flow through $B_1, B_2, \cdots, B_{2N}$ and back to the exit set of B_{2N} by a return map f. The map f minus the identity has nonzero degree, and hence has a zero, P. Since, then, $f(P) = P$, P lies on a periodic solution which travels through the blocks $B_1, \cdots, B_{2N}$ and back through Δ^*, which is near the critical point. The proof of the existence of a regular periodic solution is similar, with the solution passing, alternatively, through blocks B_1 and B_2. Details of this construction are given in [3].

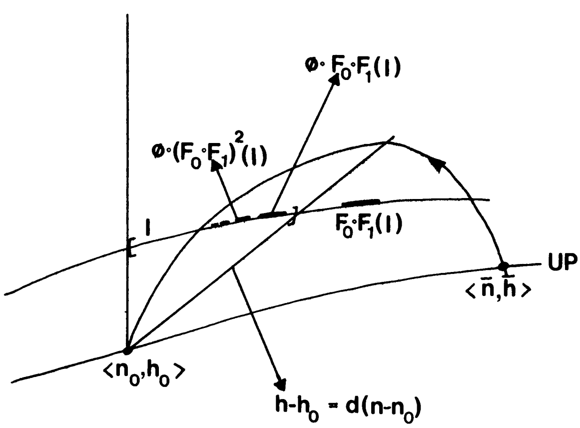


FIG. 24. *In Case* (A), *I is a two-dimensional singular solution of length N for* $N = 1, 2, \cdots$.

We now show that, if (5) admits a singular solution of length N, then (5) admits a nearby family of two-dimensional singular solutions of length N and hence a family of periodic burst solutions with N spikes. For definiteness, assume that σ_{2N} approaches $\langle n_0, h_0\rangle$ in $\{\langle n, h\rangle : \theta(n, h) > \bar{\theta}$ and $n > n_0\}$ (Figs. 9, 11, 12, 14, 19, 22). Choose $d > 0$ such that d is larger than the slope of UP at $\langle n_0, h_0\rangle$ and d is less than the slope of σ_{2N} at $\langle n_0, h_0\rangle$. For $\theta' > \bar{\theta}$, let $I \equiv \{\langle n, h\rangle : \theta(n, h) = \theta'$ and $n_0 \leqq n \leqq n_0 + (h - h_0)/d\}$. I is the set of points in (UP)$'$ between the line $n = n_0$ and the line through $\langle n_0, h_0\rangle$ with slope d (Fig. 24).

If $(\theta' - \theta)$ is small, $\phi \circ (F_0 \circ F_1)^N$ maps I interior to itself. This fact follows from Hypothesis 1, which implies that $\langle n_0, h_0\rangle$ is a stable node and all solutions in Π_0 above Σ either go to $\partial\Pi_0$ or approach $\langle n_0, h_0\rangle$ with slope greater than d.

Construction of $B_1, \cdots, B_{2N}$. Let $\{\sigma_1 \cdots \sigma_{2N}\}$ be a singular solution. Without loss of generality, assume that σ_{2N} approaches $\langle n_0, h_0\rangle$ in $\{\langle n, h\rangle : \theta(n, h) > \bar{\theta}$ and $n > n_0\}$. Other cases are treated similarly.

The constants $d_1 \cdots d_5$, $D_1 \cdots D_3$, $e_1 \cdots e_5$, λ_1, λ_2 below are all positive. The constants d_i are small; D_i are large; and e_i and λ_i are not necessarily either large or small.

Let Φ be a compact neighborhood of $\{\langle v, w, n, h\rangle : \langle n, h\rangle \in \sigma_{2N}$, $v = v_0(n, h)$, and $w = 0\}$ in which $G_v > 0$.

Choose D_1, $d_1 > 0$ such that in Φ,

$$D_1 \geqq G_v, G_n, -G_h, n'_\infty, -h'_\infty, 1,$$

$$(\bar{\theta}+2)\gamma_n/G_v, (\bar{\theta}+2)\gamma_h/G_v, \left.\frac{n'_\infty G_n + G_v}{-n'_\infty G_v}\right|_{\langle 0,0,n_0,h_0\rangle};$$

and

$$d_1 \leqq G_v, G_n, -G_h, n'_\infty, -h'_\infty, (\bar{\theta}+2).$$

Henceforth let $|_0$ denote $|_{\langle 0,0,n_0,h_0\rangle}$.

Let $-\lambda_2 < -\lambda_1 < 0$ be the eigenvalues of (7; 0) at $\langle n_0, h_0\rangle$. λ_1, λ_2 satisfy the equation:

$$\det\left.\begin{pmatrix} \gamma_n(n'_\infty(-G_n/G_v)-1)+\lambda_i & \gamma_n n'_\infty(-G_h/G_v) \\ \gamma_h h'_\infty(-G_n/G_v) & \gamma_h(h'_\infty(-G_h/G_v)-1)+\lambda_i \end{pmatrix}\right|_0 = 0.$$

We have here used $\partial v_0/\partial n = -G_n/G_v$ and $\partial v_0/\partial h = -G_h/G_v$.

Define e_1, e_2, e_3 by:

$$e_1 \equiv \left.\frac{n'_\infty G_n + G_v - G_v\lambda_1/\gamma_n}{-n'_\infty G_h}\right|_0$$

$$= \left.\frac{-h'_\infty G_n}{h'_\infty G_h + G_v - G_v\lambda_1/\gamma_h}\right|_0;$$

$$e_2 \equiv \left.\frac{-h'_\infty G_v}{h'_\infty G_h + G_v}\right|_0; \quad \text{and} \quad e_3 \equiv \left.\frac{n'_\infty G_n + G_v}{-n'_\infty G_h}\right|_0.$$

e_1 is the slope of the eigenvector associated with $-\lambda_1$. It is, therefore, the slope of σ_{2N} at $\langle n_0, h_0\rangle$. Implicit differentiation of $h_\infty(v_0(n, h)) - h = 0$ implies that e_2 is the slope of $\{\langle n, h\rangle : \dot{h}^0 = 0\}$ at $\langle n_0, h_0\rangle$. Implicit differentiation of $n_\infty(v_0(n, h)) - n = 0$ implies that e_3 is the slope of $\{\langle n, h\rangle : \dot{n}^0 = 0\}$ at $\langle n_0, h_0\rangle$.

Choose d_2, e_4, e_5 such that:

$$e_2 + d_2 < e_4 < e_1 - d_2 < e_1 + d_2 < e_5 < e_3 - d_2.$$

Let d_3, $d_4 < 1$ be small positive constants, to be specified in Steps 1–5 below. Define the function $C(n)$ and the sets $A \subseteq \Pi_0$ and $B \subseteq \Phi$ as follows (Fig. 25).

$$C(n) \equiv \begin{cases} d_4(n-n_0) & \text{if } 0 \leqq n - n_0 \leqq d_3/2, \\ d_3 d_4/2 & \text{if } d_3/2 \leqq n - n_0 \leqq d_3; \end{cases}$$

$$A \equiv \{\langle n, h\rangle : e_4(n-n_0) \leqq h - h_0 \leqq e_5(n-n_0) \text{ and } 0 < n - n_0 \leqq d_3\}; \quad \text{and}$$

$$B \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in A \text{ and } |w \pm (\bar{\theta}+2)(v - v_0(n, h))| < (\bar{\theta}+2)C(n)\}.$$

Step 1. $\dot{n} < 0$ and $\dot{h} < 0$ in B.

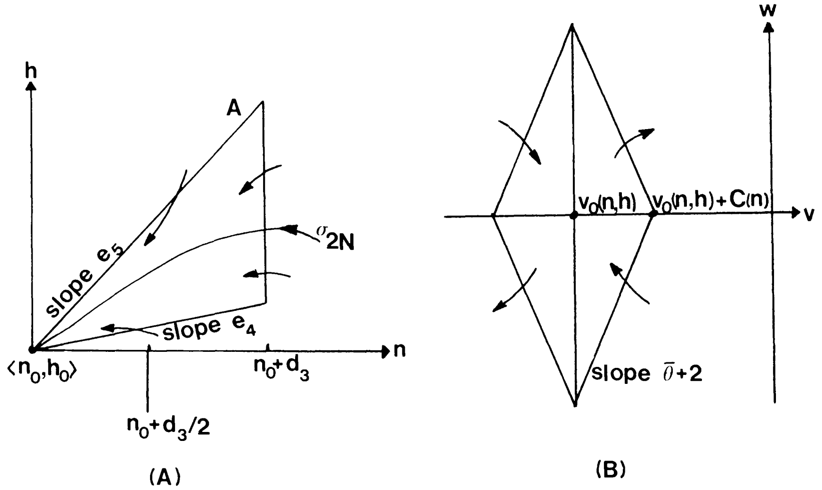


FIG. 25. (A) *The set* $A \subseteq \Pi_0$.
(B) *Projection of B in the* $(v\text{-}w)$*-plane.*

To verify that $\dot{n} < 0$ if d_3 and d_4 are small, note that if $\langle n, h\rangle \in A$, then, for some $D_2 > 0$,

$$\begin{aligned}
n_\infty(v_0(n, h)) - n &\leqq n_\infty(v_0(n, h_0 + e_5(n - n_0))) - n \\
&= (n_0 - n) + [n'_\infty(0)(-G_n/G_v - e_5 G_h/G_v)|_0](n - n_0) + O(n - n_0)^2 \\
&< (n - n_0)\left[-1 + \frac{n'_\infty}{G_v}\left(-G_n - G_h\left(\frac{n'_\infty G_n + G_v}{-n'_\infty G_h} - d_2\right)\right)\Big|_0 + D_2(n - n_0)\right] \\
&= (n - n_0)\left[\frac{n'_\infty G_h}{G_v}\Big|_0 d_2 + D_2(n - n_0)\right] \\
&\leqq (n - n_0)\left[\frac{-d_1^2 d_2}{D_1} + D_2 d_3\right] \\
&\leqq (n - n_0)\left[\frac{-d_1^2 d_2}{2D_1}\right] \quad \text{if} \quad d_3 \leqq \frac{d_1^2 d_2}{2D_1 D_2}.
\end{aligned}$$

(D_2 will be used throughout as a large positive constant multiplying $O(n - n_0)^2$ terms.) Let $d_5 \equiv d_1^2 d_2/(4D_1)$.

Next, $\dot{n} < 0$ iff $n_\infty(v) - n < 0$. In B,

$$\begin{aligned}
n_\infty(v) - n &\leqq n_\infty(v_0(n, h) + C(n)) - n \\
&= (n_\infty(v_0(n, h)) - n) + n'_\infty(v_0(n, h))C(n) + O(C(n)^2) \\
&< (n - n_0)[-2d_5 + D_1 d_4 + D_2 d_3] \\
&\leqq (n - n_0)(-d_5) \quad \text{if } d_4 \leqq d_5/(2D_1) \text{ and } d_3 \leqq d_5/(2D_2).
\end{aligned}$$

The proof that $\dot{h} < 0$ if d_3 and d_4 are small is similar. In fact,

$$h_\infty(v) - h \leqq -d_5(n - n_0)$$

if $d_4 \leqq d_5/(2D_1)$ and $d_3 \leqq d_5/(2D_2)$. Similarly, there is a large constant $D_3 > 0$ such that, in B,

$$n_\infty(v)-n \geqq -D_3(n-n_0) \quad \text{and} \quad h_\infty(v)-h \geqq -D_3(n-n_0).$$

d_3 is also chosen so that the solution segments whose initial portions are σ_k (k even) enter A in $\{\langle n, h\rangle : n-n_0=d_3\}$.

Step 2. The exit set of B. If d_3, d_4, and ε are small and if $\theta<\bar\theta+1$, the exit set of B is $\{\langle v, w, n, h\rangle \in B : w=-(\bar\theta+2)(v-v_0(n, h)\pm C(n))\}$.

To prove this, we must check all points on ∂B and show that solutions enter B on all sides except where $w=-(\bar\theta+2)(v-v_0(n, h)\pm C(n))$. It suffices to show that, in B, inequalities (A)–(G) hold.

(A) If $H_1(v, w, n, h)\equiv w-(\bar\theta+2)(v-v_0(n, h)+C(n))=0$, then $\dot H_1<0$.
(B) If $H_2(v, w, n, h)\equiv w+(\bar\theta+2)(v-v_0(n, h)-C(n))=0$, then $\dot H_2>0$.
(C) If $H_3(v, w, n, h)\equiv w+(\bar\theta+2)(v-v_0(n, h)+C(n))=0$, then $\dot H_3<0$.
(D) If $H_4(v, w, n, h)\equiv w-(\bar\theta+2)(v-v_0(n, h)-C(n))=0$, then $\dot H_4>0$.
(E) If $H_5(v, w, n, h)\equiv (n-n_0)-d_3=0$, then $\dot H_5<0$.
(F) If $H_6(v, w, n, h)\equiv (h-h_0)-e_4(n-n_0)=0$, then $\dot H_6>0$.
(G) If $H_7(v, w, n, h)\equiv (h-h_0)-e_5(n-n_0)=0$, then $\dot H_7<0$.
(A) In B, when $H_1=0$, $v_0(n, h)-C(n)\leqq v\leqq v_0(n, h)$ and $w\geqq 0$.

$$\begin{aligned}
\dot H_1 &= \theta w+G(v, n, h)-(\bar\theta+2)\left(w-\left(\frac{-G_n}{G_v}\dot n-\frac{G_h}{G_v}\dot h\right)+C'(n)\dot n\right)\\
&<(\theta-(\bar\theta+2))w+G_v(v_0(n, h), n, h)(v-v_0(n, h))+O(v-v_0(n, h))^2\\
&\quad -\frac{(\bar\theta+2)}{G_v}G_n\varepsilon\gamma_n(v)(n_\infty(v)-n)-(\bar\theta+2)d_4\varepsilon\gamma_n(v)(n_\infty(v)-n)\\
&<-(\bar\theta+2)(v-v_0(n, h)+C(n))+d_1(v-v_0(n, h))+D_2d_4^2(n-n_0)^2\\
&\quad +\varepsilon D_1(D_1D_3+d_4D_3)\\
&\leqq (n-n_0)(-d_4+D_2d_4^2+\varepsilon D_1D_3(D_1+1))\\
&\leqq (n-n_0)((-d_4/2)+\varepsilon D_1D_3(D_1+1)) \qquad \text{if } d_4\leqq 1/(2D_2)\\
&\leqq 0 \qquad \text{if } \varepsilon\leqq d_4/(2D_1D_3(D_1+1)).
\end{aligned}$$

Parts (B)–(G) are verified similarly.

Henceforth, d_3 is fixed.

Step 3. $A_1, A_2, \cdots, A_{2N}$ and $A'_1, A'_2, \cdots, A'_{2N}$.

First, let $L_{2N}\equiv\{P_{r,2N} : |r|\leqq 1\}$ be a line segment in Π_0 and $c_{2N}>b_{2N}>a_{2N}>0$ such that:

(i) $L_{2N} \overset{0}{\cdot} [0, \infty)\subseteq \Pi_0$;
(ii) $P_{0,2N} \overset{0}{\cdot} (0, \infty)$ contains σ_{2N};
(iii) the flow on Π_0 is transverse to L_{2N};
(iv) $L_{2N} \overset{0}{\cdot} a_{2N}\subseteq \{\langle n, h\rangle : 0<\theta(n, h)<\bar\theta\}$;
(v) $L_{2N} \overset{0}{\cdot} b_{2N}\subseteq \{\langle n, h\rangle : \theta(n, h)>\bar\theta\}$; and
(vi) $L_{2N} \overset{0}{\cdot} c_{2N}\subseteq \{\langle n, h\rangle \in \operatorname{int}(A) : d_3/2\leqq n-n_0\leqq d_3\}$.

Let $A_{2N}\equiv\bigcup_{\tau\in[0,b_{2N}]}\{P_{r,2N} \overset{0}{\cdot} \tau : |r|\leqq \tau/c_{2N}\}$. Let $A'_{2N}\equiv\bigcup_{\tau\in[0,c_{2N}]}\{P_{r,2N} \overset{0}{\cdot} \tau ;\ |r|\leqq \tau/c_{2N}\}$ (Fig. 26(A)).

$A_{2N-1}, \cdots, A_1$ and $A'_{2N-1}, \cdots, A'_1$ are now defined inductively. Because the endpoint of σ_k may be contained in $\partial\Pi_1$ if k is odd, the definition of A_k depends upon whether k is odd or even. If the endpoint of σ_k is contained in Π_1 when k is odd, the constriction of A_k is similar to that when k is even.

Assume that $A_{2N}, \cdots, A_{2N-j+1}$ have been defined.

If j is odd and if the endpoint of σ_{2N-j} is contained in $\partial\Pi_1$, let $L_{2N-j} \equiv \{P_{r,2N-j} : |r| \leqq 1\}$ be a line segment in Π_1 and choose $b_{2N-j} > a_{2N-j} > 0$ such that:

(i) $L_{2N-j} \overset{1}{\cdot} [0, a_{2N-j}] \subseteq \Pi_1$;

(ii) $P_{0,2N-j} \overset{1}{\cdot} (0, b_{2N-j})$ contains σ_{2N-j};

(iii) the flow on Π_1 is transverse to L_{2N-j}; and

(iv) $L_{2N-j} \overset{1}{\cdot} a_{2N-j} \subseteq \{\langle n, h\rangle \in \operatorname{int}(A_{2N-j+1}) : 0 > \theta(n, h) > -\bar{\theta}\}$.

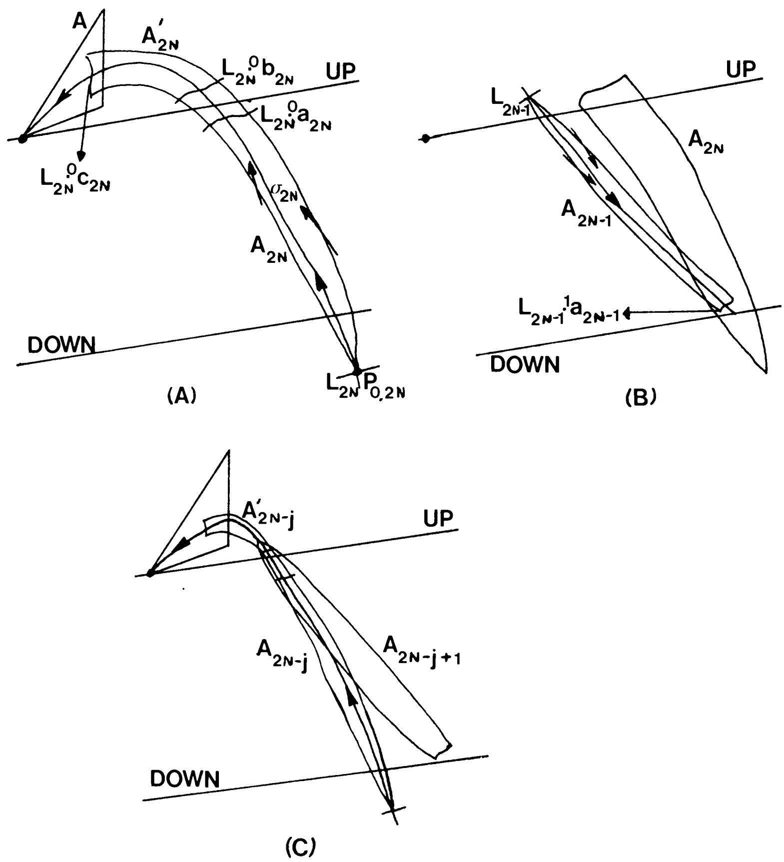


FIG. 26. (A) *A, A_{2N}, and A'_{2N}.* (B) A_{2N-1}. (C) *A_{2N-j} and A'_{2N-j} when j is even.*

Let $A_{2N-j} \equiv \bigcup_{\tau \in [0, a_{2N-j}]} \{P_{r,2N-j} \overset{1}{\cdot} \tau : |r| \leqq \tau / a_{2N-j}\}$. The exit set of A_{2N-j} is $L_{2N-j} \overset{1}{\cdot} a_{2N-j}$ (Fig. 26(B)). Let $A'_{2N-j} \equiv A_{2N-j}$. (For technical reasons, we shall also require, for Step 5(C) below, that $L_{2N-j} \overset{1}{\cdot} a_{2N-j}$ be contained in a certain neighborhood of the endpoint of σ_{2N-j}. For clarity, that neighborhood is left unspecified until (C).)

If j is even, let $L_{2N-j} \equiv \{P_{r,2N-j} : |r| < 1\}$ be a line segment in Π_0 and choose $0 < a_{2N-j} < b_{2N-j} < c_{2N-j}$ such that:

(i) $L_{2N-j} \overset{0}{\cdot} [0, c_{2N-j}] \subseteq \Pi_0$;

(ii) $P_{0,2N-j} \overset{0}{\cdot} (0, b_{2N-j})$ contains σ_{2N-j};

(iii) the flow on Π_0 is transverse to L_{2N-j};

(iv) $L_{2N-j} \overset{0}{\cdot} [a_{2N-j}, b_{2N-j}] \subseteq \operatorname{int}(A_{2N-j+1})$;

(v) $L_{2N-j} \overset{0}{\cdot} a_{2N-j} \subseteq \{\langle n, h\rangle : 0 < \theta(n, h) < \bar{\theta}\}$;

(vi) $L_{2N-j} \overset{0}{\cdot} b_{2N-j} \subseteq \{\langle n, h\rangle : \theta(n, h) > \bar{\theta}\}$; and

(vii) $L_{2N-j} \overset{0}{\cdot} c_{2N-j} \subseteq \{\langle n, h\rangle \in \operatorname{int}(A) : d_3/2 \leqq n - n_0 \leqq d_3\}$.

Let $A_{2N-j} \equiv \bigcup_{\tau\in[0, b_{2N-j}]} \{P_{r,2N-j} \overset{0}{\cdot} \tau : |r| \leqq \tau/c_{2N-j}\}$. Let $A'_{2N-j} \equiv \bigcup_{\tau\in[0, c_{2N-j}]} \{P_{r,2N-j} \overset{0}{\cdot} \tau : |r| \leqq \tau/c_{2N-j}\}$. Then A_{2N-j} is contained in A'_{2N-j}. The exit set of A_{2N-j} is contained in $L_{2N-j} \overset{0}{\cdot} b_{2N-j}$, which is contained in the interior of A_{2N-j+1}. The exit set of $A'_{2N-j} = L_{2N-j} \overset{0}{\cdot} c_{2N-j}$, which is contained in the interior of A (Fig. 26(C)).

Finally, if j is odd and the endpoint of σ_{2N-j} is not contained in $\partial\Pi_1$, then A_{2N-j} is defined with properties analogous to the previous properties (i)–(vi), and $A'_{2N-j} \equiv A_{2N-j}$.

Step 4. $B_1, B_2, \cdots, B_{2N}$ and $B'_1, B'_2, \cdots, B'_{2N}$.

If k is even, let $B_k \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in A_k$ and $|w \pm (\bar{\theta}+2)(v - v_0(n, h))| \leqq (\bar{\theta}+2)d_3d_4/2\}$ and let $B'_k \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in A'_k$ and $|w \pm (\bar{\theta}+2)(v - v_0(n, h))| \leqq (\bar{\theta}+2)d_3d_4/2\}$. If k is odd, let

$$B_k \equiv B'_k \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in A_k \text{ and } |w \pm (\bar{\theta}+2)(v - v_1(n, h))| \leqq (\bar{\theta}+2)d_3d_4/2\}.$$

An analysis similar to that of Step 2 and carried out in [2], [4] implies that if d_4, ε, and $|\theta - \bar{\theta}|$ are small, the exit set of B_k is $\{\langle v, w, n, h\rangle : |w + (\bar{\theta}+2)(v - v_i(n, h))| = (\bar{\theta}+2)d_3d_4/2$ or $\langle n, h\rangle$ is contained in the exit set of $A_k\}$; and the exit set of B'_k is $\{\langle v, w, n, h\rangle : |w + (\bar{\theta}+2)(v - v_i(n, h))| = (\bar{\theta}+2)d_3d_4/2$ or $\langle n, h\rangle$ is contained in the exit set of $A'_k\}$, where $i = 0$ if k is even; $i = 1$ if k is odd. In addition, any solution with initial value in B_k or B'_k leaves that block in finite time.

Step 5. Δ_k, δ_k^0, and δ_k^1.

If k is odd and the endpoint of σ_k is contained in $\partial\Pi_1$, let

$$\Delta_k \equiv \{\langle v, w, n, h\rangle \in B_k : \langle n, h\rangle \text{ is contained in the exit set of } A_k\};$$

$$\delta_k^0 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : w = -(\bar{\theta}+2)(v - (v_1(n, h) - d_3d_4/2))\}; \text{ and}$$

$$\delta_k^1 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : w = -(\bar{\theta}+2)(v - (v_1(n, h) + d_3d_4/2))\}.$$

(See Fig. 23.) In Fig. 25(B), if $\langle n, h\rangle$ is contained in the exit set of A_k, the entire diamond is contained in Δ_k; the lower left edge is contained in δ_k^0; and the upper right edge is contained in δ_k^1.

If k is odd and the endpoint of σ_k is not contained in $\partial\Pi_1$, let

$$\Delta_k \equiv \{\langle v, w, n, h\rangle \in B_k : \langle n, h\rangle \in L_k \overset{1}{\cdot} [a_k, b_k] \text{ and}$$
$$w = -(\bar{\theta}+2)(v - (v_1(n, h) - d_3d_4/2))\};$$

$$\delta_k^0 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : \langle n, h\rangle \in L_k \overset{1}{\cdot} a_k\};$$

and

$$\delta_k^1 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : \langle n, h\rangle \in L_k \overset{1}{\cdot} b_k\}.$$

Note that if $\langle v, w, n, h\rangle \in \delta_k^0$, then $0 < -\theta(n, h) < \bar{\theta}$; if $\langle v, w, n, h\rangle \in \delta_k^1$, then $-\theta(n, h) > \bar{\theta}$.

If k is even, let

$$\Delta_k \equiv \{\langle v, w, n, h\rangle \in B_k : \langle n, h\rangle \in L_k \overset{0}{\cdot} [a_k, b_k] \text{ and}$$
$$w = -(\bar{\theta}+2)(v - (v_0(n, h) + d_3d_4/2))\};$$

$$\delta_k^0 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : \langle n, h\rangle \in L_k \overset{0}{\cdot} b_k\};$$

and

$$\delta_k^1 \equiv \{\langle v, w, n, h\rangle \in \Delta_k : \langle n, h\rangle \in L_k \overset{0}{\cdot} a_k\}.$$

Note that if $\langle v, w, n, h\rangle \in \delta_k^0$, then $\theta(n, h) > \bar{\theta}$; if $\langle v, w, n, h\rangle \in \delta_k^1$, then $\theta(n, h) < \bar{\theta}$.

Finally, (A)–(D) below show that Δ_k, δ_k^0, and δ_k^1 have the required properties if ε, $|\theta - \bar{\theta}|$, and d_4 are small.

First, let

$$E_k^+ \equiv \{\langle v, w, n, h\rangle \in \text{the exit set of } B_k':\ w = -(\bar{\theta}+2)(v-(v_i(n, h)+d_3d_4/2))\}$$

and

$$E_k^- \equiv \{\langle v, w, n, h\rangle \in \text{the exit set of } B_k':\ w = -(\bar{\theta}+2)(v-(v_i(n, h)-d_3d_4/2))\},$$

where $i = 0$ if k is even, $i = 1$ if k is odd.

(A) If k is even and q is an arc in B_k from E_k^- to E_k^+ then q contains a point which never leaves $B_k' \cup B$ and which is contained in the stable manifold of $\langle 0, 0, n_0, h_0\rangle$.

(B) If k is even and q is an arc in B_k from E_k^- to E_k^+, then there is a point $P \in q$ such that P is mapped by the flow to δ_k^0 and all points in q beyond P leave B_k in E_k^+.

(C) If q is an arc in Δ_k from δ_k^0 to δ_k^1, then q contains a subarc mapped by the flow into an arc in B_{k+1} from E_{k+1}^- to E_{k+1}^+. Moreover, if k is odd, $\theta(n, h) < 0$ in the image of q in B_{k+1} (or else $\langle n, h\rangle \in \Pi_0 - \Pi_1$). If k is even, $\theta(n, h) > 0$ in the image of q in B_{k+1}.

(D) Δ_k, δ_k^0, and δ_k^1 have the properties used in the proof of Theorem 1.

Proof of (A)–(D).

(A) q is contained in B_k', and all points in B_k' leave in finite time. Thus q is mapped by the flow to an arc in the exit set of B_k'. The endpoints of q, already in the exit set, remain fixed. Since the image of q joins E_k^- and E_k^+, it must contain a subarc Q from E_k^- to E_k^+ such that Q is contained in $\{\langle v, w, n, h\rangle \in B_k' : \langle n, h\rangle \in \text{the exit set of } A_k'\}$, which is contained in B. Q connects the two components of the exit set of B. If all points of Q left B in finite time, Q would be mapped to an arc in the exit set of B joining the two components, which is impossible. Thus one point in Q never leaves B. Since $\dot{n} < 0$ and $\dot{h} < 0$ in B, this point must converge to $\langle 0, 0, n_0, h_0\rangle$ at $+\infty$.

(B) Suppose the arc q is parameterized by $\eta : q = \{q(\eta): 0 \leqq \eta \leqq 1\}$, so $q(0) \in E_k^-$ and $q(1) \in E_k^+$. Let $\bar{\eta} \equiv \min\{\eta' \in [0, 1]: q(\eta) \text{ leaves } B_k \text{ in } E_k^+ \text{ for all } \eta \in [\eta', 1]\}$ and let $P \equiv q(\bar{\eta})$. Since $q(0) \in E_k^-$, $q(\bar{\eta})$ must be in ∂E_k^+, which is δ_k^0.

(C) First suppose that k is even. In δ_k^0, $\theta(n, h) > \bar{\theta}$. Thus if $\theta = \bar{\theta}$ and $\varepsilon = 0$, and if d_4 is small, a point in δ_k^0 leaves $\{w \geqq 0\}$ in a point where $v < v_1(n, h) - d_3d_4/2$ (see Lemmas 1 and 2). The same is true if ε and $|\theta - \bar{\theta}|$ are small. Also, in δ_k^1, $0 < \theta(n, h) < \bar{\theta}$. Thus if $\theta = \bar{\theta}$ and $\varepsilon = 0$, and if d_4 is small, a point in δ_k^1 leaves $\{v \leqq v_1(n, h)\}$ in a point where $v = v_1(n, h)$ and $w > (\bar{\theta}+2)d_3d_4/2$. The same is true if ε and $|\theta - \bar{\theta}|$ are small. Also, Δ_k is contained in the set where $\langle n, h\rangle \in \operatorname{int}(A_{k+1})$ and $\theta(n, h) > 0$. Thus if d_4, ε, and $|\theta - \bar{\theta}|$ are small, a point in Δ_k leaves $\{\langle v, w, n, h\rangle : w \geqq 0,\ v \leqq v_1(n, h), \text{ and } w \geqq (\bar{\theta}+2)(v-(v_1(n, h)-d_3d_4/2))\}$ in finite time and in the set where $\langle n, h\rangle \in \operatorname{int}(A_{k+1})$ and $\theta(n, h) > 0$. Therefore q is mapped by the flow to an arc Q in $\{\theta(n, h) > 0$ and $\langle n, h\rangle \in \operatorname{int}(A_{k+1})\}$ from $\{w = 0\}$ to $\{v = v_1(n, h)$ and $w \geqq (\bar{\theta}+2)d_3d_4/2\}$. Q contains a subarc in B_{k+1} from $E_{k+1}^- \cap \{w = 0\}$ to $E_{k+1}^+ \cap \{v = v_1(n, h)\}$.

Similarly, if k is odd and the endpoint of σ_k is not contained in $\partial\Pi_1$, q is mapped by the flow to an arc Q in $\{\theta(n, h) < 0$ and $\langle n, h\rangle \in \operatorname{int}(A_{k+1})\}$ from $\{v = v_0(n, h)$ and $w \leqq -(\bar{\theta}+2)d_3d_4/2\}$ to $\{w = 0\}$. Q contains a subarc in B_{k+1} from $E_k^- \cap \{v = v_0(n, h)\}$ to $E_k^+ \cap \{w = 0\}$.

Finally, suppose that k is odd and the endpoint of σ_k is contained in $\partial\Pi_1$. In Δ_k, $0 > \theta(n, h) > -\bar{\theta}$. Thus if $\theta = \bar{\theta}$ and $\varepsilon = 0$, and if d_4 is small, a point in δ_k^0 leaves

$\{v \geqq v_0(n, h)\}$ in a point where $w < -(\bar{\theta}+2)d_3d_4/2$. The same is true if $|\theta - \bar{\theta}|$ and ε are small. Also, if $\theta = \bar{\theta}$ and $\varepsilon = 0$ a point in δ_k^1 leaves $\{v \leqq v_{Na}\}$ in a point where $\{w > 0\}$. The same is true if $|\theta - \bar{\theta}|$ and ε are small.

Now let $q \equiv \{P(\mu): 0 \leqq \mu \leqq 1\}$ be an arc in Δ_k from δ_k^0 to δ_k^1. Let

$$e \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in \text{int}(A_{k+1}), \text{ and } \theta(n, h) < 0 \text{ if } \langle n, h\rangle \in \Pi_0 \cap \Pi_1\};$$

and

$$\begin{aligned} E \equiv \{\langle v, w, n, h\rangle : &\langle n, h\rangle \in \Pi_0 \text{ and} \\ &\text{either } v = v_0(n, h) \text{ and } w \leqq -(\bar{\theta}+2)d_3d_4/2 \\ &\text{or } w = (\theta+2)(v - (v_0(n, h) + d_3d_4/2)) \text{ and } v_0(n, \dot{h}) \leqq v \leqq v_0(n, h) + d_3d_4/2\}. \end{aligned}$$

To complete the proof of (C) it suffices to show that, if $\varepsilon > 0$ and $|\theta - \bar{\theta}|$ are small, there is some $\mu_1 \in (0, 1)$ such that $\{P(\mu): 0 \leqq \mu \leqq \mu_1\}$ is mapped by the flow to an arc $Q \equiv \{Q(\mu): 0 \leqq \mu \leqq \mu_1\} \subseteq E \cap e$ such that $Q(0) \in \{v = v_0(n, h)\}$ and $Q(\mu_1) \in \{w = 0\}$. For, if such a μ_1 exists, then Q contains a subarc $\{Q(\mu): \mu_0 \leqq \mu \leqq \mu_1\} \subseteq B_{k+1}$ with $Q(\mu_0) \in E_{k+1}^- \cap \{v = v_0(n, h)$ and $w = -(\bar{\theta}+2)d_3d_4/2\}$ and $Q(\mu_1) \in E_{k+1}^+ \cap \{v = v_0(n, h) + d_3d_4/2$ and $w = 0\}$.

To see that μ_1 exists, we shall construct a block D with properties (C1)–(C4) below.

(C1) $\Delta_k \subseteq D$.

(C2) If $\langle \bar{n}, \bar{h}\rangle$ is the endpoint of σ_k and $\bar{v} \equiv v_1(\bar{n}, \bar{h})$, then $\bar{P} \equiv \langle \bar{v}, 0, \bar{n}, \bar{h}\rangle \in D$.

(C3) The flow carries all points in D to the exit set of D.

(C4) Any point in ∂D crosses, in finite time, either $E \cap e$ or $\{v = v_{Na}\} \cap e$.

To see that (C1)–(C4) complete the proof, for $0 \leqq \mu \leqq 1$, let $S(\mu) = \sup\{s : P(\mu) \cdot [0, s) \cap (E \cup \{v = v_{Na}\}) = \phi\}$. (C1), (C3), and (C4) imply that each $S(\mu)$ is finite and $Q(\mu) \equiv P(\mu) \cdot S(\mu) \in e \cap (E \cup \{v = v_{Na}\})$. (For comparison, note that if ε were equal to 0 then $S(\mu)$ would be infinite if $P(\mu)$ were contained in the stable manifold of some point $\langle v_1(n, h), 0, n, h\rangle$.) Let $\mu_1 \equiv \sup\{\mu' \in [0, 1]: Q(\mu) \in E$ for each $\mu \in [0, \mu')\}$. Since $Q(\mu) \in E \cap \{v = v_0(n, h)\}$ for μ near 0 and $Q(\mu) \in \{v = v_{Na}\}$ for μ near 1, $0 < \mu_1 < 1$. Since each $Q(\mu)$ crosses E (or $\{v = v_{Na}\}$) transversally and since E is closed, $Q(\mu_1) \in \partial E$, which is contained in $\{w = 0\}$, and $\{Q(\mu): 0 \leqq \mu \leqq \mu_1\}$ is an arc in E.

Construction of D. Since $\langle 0, 0, n_0, h_0\rangle$ is the only rest point of (6) when $\varepsilon > 0$, at the point $\bar{P}$ either $\dot{n} > 0$ or $\dot{h} < 0$. For definiteness, say $\dot{n} > 0$ at $\bar{P}$.

Let:

$$\Pi \equiv \{\langle v, n, h\rangle : |v - \bar{v}| \leqq 1 \text{ and } 0 \leqq n, h \leqq 1\};$$

$$z_1 \equiv \max\{|G_\alpha(v, n, h)|, |G_{\alpha\beta}(v, n, h)|, |G_{vv\alpha}(v, n, h)| : \langle v, n, h\rangle \in \Pi \text{ and } \alpha, \beta = v, n, h\};$$

$$z_2 \equiv G_{vv}(\bar{v}, \bar{n}, \bar{h});$$

$$z_3 \equiv \varepsilon^{-1}\dot{n}|_{P=\bar{P}}; \text{ and}$$

$$z_4 \equiv \left.\frac{\dot{h}}{\dot{n}}\right|_{P=\bar{P}}.$$

Note that $z_1, z_2, z_3 > 0$, and z_4 is the slope of σ_k at $\langle \bar{n}, \bar{h}\rangle$.

Next, construct a triangle $\tilde{\Delta} \subseteq \Pi_0$ as shown in Fig. 27(A), with the properties that, for some $z_5 > 0$:

(C5) the triangle $\tilde{P}\tilde{Q}\tilde{R} \cap \text{cl}(\Pi_1) = \{\tilde{P}\}$, so that $G(v, n, h) > 0$ if $v > v_0(n, h)$ and

$\langle n, h\rangle \in \tilde{\Delta} - \{\langle \bar{n}, \bar{h}\rangle\}$;

(C6) the slope of $\tilde{P}\tilde{S}$ is z_4;

(C7) the slope of $\tilde{Q}\tilde{R}$ is $-1/z_4$;

(C8) the slope of $\tilde{S}\tilde{Q}$ is $z_4 + z_5$; and

(C9) the slope of $\tilde{S}\tilde{R}$ is $z_4 - z_5$.

The existence of $\tilde{\Delta}$ follows from the hypothesis that (5) is admissible, so that z_4 is not equal to the slope of $\partial\Pi_1$ at $\langle \bar{n}, \bar{h}\rangle$.

Using continuity, there exists $z_6 \in (0, 1)$ such that if $|v - \bar{v}|$, $|n - \bar{n}|$, $|h - \bar{h}| \leqq z_6$, then:

(C10) $\dot{n} > \frac{1}{2}\varepsilon z_3$;

(C11) $z_4 \dot{h} \geqq \frac{1}{2}\varepsilon z_3 z_4^2$;

(C12) $-\frac{1}{2}\varepsilon z_3 z_5 \leqq \dot{h} - z_4 \dot{n} \leqq \frac{1}{2}\varepsilon z_3 z_5$;

(C13) $\theta(n, h) < 0$, if $\langle n, h\rangle \in \mathrm{cl}\,(\Pi_0 \cap \Pi_1)$;

(C14) $\langle n, h\rangle \in \mathrm{int}\,(A_{k+1})$; and

(C15) $v - v_0(n, h) > 0$.

Let

$$z_7 \equiv \min\{z_6, \tfrac{2}{3}\bar{\theta} z_6, 2\bar{\theta}^3(z_1(32\bar{\theta}^2 + 24\bar{\theta} + 9))^{-1},$$
$$z_2\bar{\theta}(z_1(32\bar{\theta}^3 + 48\bar{\theta}^2 + 36\bar{\theta} + 9))^{-1}\}.$$

Next, choose constants z_8, z_9, z_{10} so that if Δ is the triangle $\{\langle n, h\rangle : n + z_4 h \leqq z_8;\ -(z_4 + z_5)n + h \leqq z_9;$ and $-(z_4 - z_5)n + h \geqq z_{10}\}$, then $\langle \bar{n}, \bar{h}\rangle \in \Delta$; $\Delta \subseteq \tilde{\Delta} \cap \{\langle n, h\rangle : |n - \bar{n}|, |h - \bar{h}| \leqq z_7^2 \min\{1, z_2(32\bar{\theta}^2 z_1)^{-1}\}\}$; and $G(v, n, h) > 0$ when $\langle n, h\rangle \in \Delta$, $n + z_4 h = z_8$, and $|v - \bar{v}| \leqq z_6$. (See Fig. 27(A).)

Let:

$$z_{11} \equiv \min\{G(v, n, h) : \langle n, h\rangle \in \Delta \text{ and } z_7(2\bar{\theta})^{-1} \leqq |v - \bar{v}| \leqq 3z_7(2\bar{\theta})^{-1}\};$$

and

$$D \equiv \{\langle v, w, n, h\rangle : \langle n, h\rangle \in \Delta;\ |w - \bar{\theta}(v - \bar{v})| \leqq z_7; \text{ and } |w| \leqq \tfrac{1}{2} z_7\} \quad \text{(Fig. 27(B))}.$$

If a_k, L_k, and d_4 are now chosen so that $\Delta_k \subseteq D$, Lemma 3 completes the proof of (C).

LEMMA 3. *Properties of D.*

(C16) *In D,* $|G(v, n, h)| \leqq \frac{1}{4}\bar{\theta} z_7$.

(C17) *In D, if* $z_7(2\bar{\theta})^{-1} \leqq |v - \bar{v}| \leqq 3z_7(2\bar{\theta})^{-1}$, *then* $G(v, n, h) > 0$, *so that* $z_{11} > 0$.

(C18) *In D,* $|v - \bar{v}|$, $|n - \bar{n}|$, $|h - \bar{h}| \leqq z_6$, *so that properties* (C10)–(C15) *hold.*

(C19) *If* $\varepsilon > 0$, $\theta > \frac{1}{2}\bar{\theta}$, *and* $|\theta - \bar{\theta}| < 2z_{11} z_7^{-1}$, *then D is a block for* (6) *with exit set* $\{\langle v, w, n, h\rangle \in \partial D : n + z_4 h = z_8;$ *or* $w = \bar{\theta}(v - \bar{v}) + z_7$; *or* $|w| = \frac{1}{2} z_7\}$.

(C20) *If* $P \in D$ *then* $P \cdot s \in \partial D$ *for some* $s \in [0, \infty)$.

(C21) *If* $|\theta - \bar{\theta}|$ *and* $\varepsilon \geqq 0$ *are small, any point in* ∂D *crosses, in finite time, either* $E \cap e$ *or* $\{v = v_{Na}\} \cap e$.

Proof of Lemma 3.

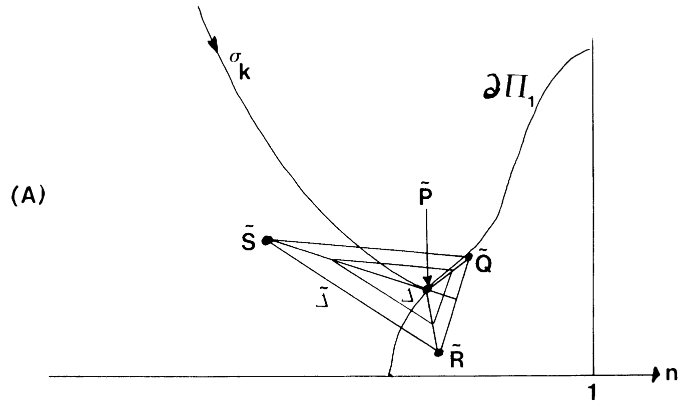
(C16) The proof of (C16) uses the facts that, in D:

$$G(\bar{v}, \bar{n}, \bar{h}) = G_v(\bar{v}, \bar{n}, \bar{h}) = 0;$$

$$|n - \bar{n}|, |h - \bar{h}| \leqq z_7^2;$$

$$|v - \bar{v}| \leqq 3z_7(2\bar{\theta})^{-1};$$

$$z_7 \leqq 1; \quad \text{and} \quad z_7 \leqq 2\bar{\theta}^3(z_1(32\bar{\theta}^2 + 24\bar{\theta} + 9))^{-1}.$$



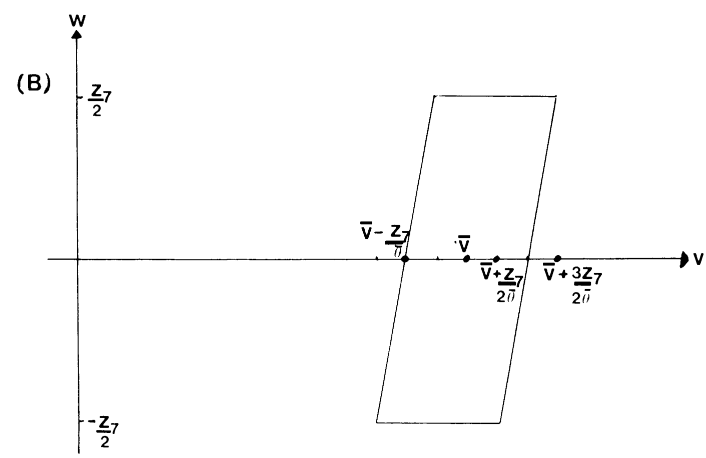


FIG. 27. (A) $\tilde{\Delta}$ *is the triangle* $\tilde{Q}\tilde{R}\tilde{S}$. Δ *is the projection of D into the n-h plane.* (B) *The projection of D into the v-w plane.*

Taking the Taylor series expansion of $G(v, n, h)$ about $\langle \bar{v}, \bar{n}, \bar{h} \rangle$, we see that, in D:

$$\begin{aligned}|G(v, n, h)| \leqq\, & |G(\bar{v}, \bar{n}, \bar{h})| + |G_v(\bar{v}, \bar{n}, \bar{h})(v-\bar{v})| \\ & + |G_n(\bar{v}, \bar{n}, \bar{h})(n-\bar{n})| + |G_h(\bar{v}, \bar{n}, \bar{h})(h-\bar{h})| \\ & + \tfrac{1}{2}z_1[(v-\bar{v})^2 + (n-\bar{n})^2 + (h-\bar{h})^2 \\ & \quad + 2|(n-\bar{n})(h-\bar{h})| + 2|(v-\bar{v})(n-\bar{n})| \\ & \quad + 2|(v-\bar{v})(h-\bar{h})|] \\ \leqq\, & 2z_1z_7^2 + \tfrac{1}{2}z_1[9z_7^2(4\bar{\theta}^2)^{-1} + 4z_7^4 + 6z_7^4\bar{\theta}^{-1}] \\ =\, & z_1z_7^2[2 + 9(8\bar{\theta}^2)^{-1} + 2z_7^2 + 3z_7\bar{\theta}^{-1}] \\ \leqq\, & z_1z_7^2[4 + 3\bar{\theta}^{-1} + 9(8\bar{\theta}^2)^{-1}] \\ =\, & z_1z_7^2(8\bar{\theta}^2)^{-1}(32\bar{\theta}^2 + 24\bar{\theta} + 9) \\ \leqq\, & \tfrac{1}{4}\bar{\theta}z_7.\end{aligned}$$

(C17) The proof of (C17) is similar to that of (C16).

(C18) In D, $|n-\bar{n}|, |h-\bar{h}| \leqq z_7^2 \leqq z_6^2 < z_6$, since $z_6 < 1$. Because $|w - \bar{\theta}(v-\bar{v})| \leqq z_7$; $|w| \leqq \frac{1}{2}z_7$; and $z_7 \leqq \frac{2}{3}\bar{\theta}z_7$, $|v-\bar{v}| \leqq \bar{\theta}^{-1}(z_7+\frac{1}{2}z_7) \leqq 3(2\bar{\theta})^{-1}(\frac{2}{3}\bar{\theta}z_6) = z_6$.

(C19) The proof of (C19) is similar to the verification carried out in Step 2 above.

(C20) follows from the fact that $\dot{n} \geqq \frac{1}{2}\varepsilon z_3 > 0$ in D. ((C10))

(C21) (C15) implies that, if $n + z_4 h = z_8$ in D, then $G(v, n, h) > 0$. (C17) implies that if $w = \bar{\theta}(v-\bar{v}) + z_7$ in D, then $G(v, n, h) > 0$. Thus (C19) implies that, at any point P in the exit set of D, either $\dot{v} = w \neq 0$ or $\dot{w} = \theta w + G(v, n, h) \neq 0$. Therefore (C13) and (C14) imply that when $\theta = \bar{\theta}$ and $\varepsilon = 0$, $P \cdot [0, \infty)$ crosses, transversally and in finite time, either $E \cap e$ or $\{v = v_{Na}\} \cap e$; and the same is true if $|\theta - \bar{\theta}|$ and $\varepsilon > 0$ are small.

(D) Let q_1 be an arc in Δ_1. (C) implies that q_1 contains a subarc mapped into an arc $\{q(\eta): 0 \leqq \eta \leqq 1\}$ in $B_2 \cap \{\theta(n, h) < 0$ if $\langle n, h\rangle \in \Pi_0 \cap \Pi_1\}$ from E_2^- to E_2^+. (B) implies that there is some $\bar{\eta} \in (0, 1)$ such that $q(\bar{\eta})$ is mapped to δ_2^0 and $q(\eta)$ is mapped to E_2^+ if $\eta \geqq \bar{\eta}$. Since $q(1) \in E_2^+ \cap \{\dot{\theta}(n, h) < 0$ if $\langle n, h\rangle \in \Pi_0 \cap \Pi_1\}$ and $\theta(n, h) > 0$ in Δ_2, $\{q(\eta): \bar{\eta} \leqq \eta \leqq 1\}$ contains a subarc mapped to an arc q_2 in Δ_2 from δ_2^0 to q_2^1. (A) implies that $\{q(\eta): 0 \leqq \eta < \bar{\eta}\}$ contains a point in the stable manifold of $\langle 0, 0, n_0, h_0\rangle$. (C) then implies that q_2 contains a subarc carried by the flow into Δ_3 and running from δ_3^0 to δ_3^1, etc.

Proof of Proposition 1. (i) A trajectory in Π_0 slows down as it approaches the critical point $\langle n_0, h_0\rangle$. Thus, the interval between the first and second spikes of a burst is long if σ_2 crosses UP near $\langle n_0, h_0\rangle$. Skewing of n-h tends to make σ_2 cross UP away from $\langle n_0, h_0\rangle$.

(ii) In the singular solution, the duration of σ_{2j} decreases as j increases, since σ_{2j} moves farther away from the slow area near $\langle n_0, h_0\rangle$. σ_{2j} soon approaches the limiting trajectory through $\langle \bar{n}, \bar{h}\rangle$ and so its duration settles down toward a fixed value. The interspike interval in the true solution is near the singular connection σ_{2j} ($j = 1, \cdots, N$).

(iii) In the singular solution, the maximum value of v is equal to $v_1(n, h)$ at the point in UP where the jump from Π_0 to Π_1 occurs, since this jump corresponds to the rising phase of the spike. Thus, if the singular solution is as depicted in Fig. 9 or 11(A), the maximum value of v increases during the burst if $v_1(n, h)$ increases along UP and it decreases during the burst if $v_1(n, h)$ decreases along UP. Similarly, the minimum value of v is equal to $v_0(n, h)$ at the point in DOWN where the jump from Π_1 to Π_0 occurs.

In practice, computation of this property from membrane data is difficult. The point here is that one of the properties (iii) tends to occur and so rising or falling maximum or minimum values of v should cause no surprise.

(iv) Along DOWN $v_0(n, h)$ is several mv. negative, corresponding to hyperpolarization in the true solution. As $\langle n, h\rangle$ approaches UP in Π_0, $v_0(n, h)$ returns near zero.

(v) An elongated shoulder in the falling phase of the jth spike corresponds to a long σ_{2j-1} in the Π_1 phase portrait. This could occur if, for example, there would be a critical point just off $\partial\Pi_1$ if the phase portrait were extended to $(0, 1)^2$.

(vi) The quiet spell increases with the distance, in the phase portrait, between $\text{UP} \cap \sigma_{2N}$ and $\langle n_0, h_0\rangle$. This distance increases as N increases, but is never larger than the distance between $\langle \bar{n}, \bar{h}\rangle$ and $\langle n_0, h_0\rangle$, which determines the upper bound on the length of the quiet spell for fixed θ, $\varepsilon > 0$.

Proof of Theorem 2. As in Theorem 1, the proof depends upon the existence of a singular solution with N_i jumps in the ith bursting interval. In Fig. 18, the singular solution may jump up N_1 times and then return toward rest at $\langle n_0, h_0\rangle$. However, before reaching $\langle n_0, h_0\rangle$ the singular solution recrosses UP, and is thus able to jump again, N_1 times. After N_2 jumps the solution returns toward rest, but the geometry of the phase plane forces this solution also to cross UP, and the jumps begin again.

The correspondence between θ_N and $\{N_i\}$ follows from the construction of the actual solutions, as in Theorem 1. This result generalizes the relationship between θ and the number of spikes depicted in Fig. 10(A).

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