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THRESHOLD BEHAVIOR AND PROPAGATION FOR NONLINEAR DIFFERENTIAL-DIFFERENCE SYSTEMS MOTIVATED BY MODELING MYELINATED AXONS*

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Abstract. Using a comparison theorem technique, we study the long time behavior of certain classes of nonlinear difference-differential systems. Zero is a solution for these systems. We are concerned in this paper with conditions forcing nonconvergence to zero of solutions as time approaches infinity; that is, we obtain threshold properties of the systems. The results parallel results by Aronson and Weinberger on reaction-diffusion equations somewhat, and the study was motivated by consideration of models for myelinated nerve axons.

1. Introduction. In this paper we study the long time behavior of solutions of nonlinear difference-differential systems of the form

$$du_j/dt = u_{j+1} - 2u_j + u_{j-1} + f(u_j) \qquad (j \in \mathbf{Z}) \tag{1.1}$$

where $f(u)$ will be allowed to have various qualitative behaviors to be specified below.

System (1.1) arises as a model in various contexts and we will consider forms of the function $f(u)$ suggested by some of these applications. For example system (1.1) occurs in the study of population genetics where spatially discrete (i.e. isolated) populations of diploid individuals are considered. One can derive (1.1) from model-derivation arguments given in [1] if the author' continuously distributed habitat assumption is replaced by an appropriate discrete populations assumption. In [1], Aronson and Weinberger consider three possible types of $f(u)$, specified below by (2.1)–(2.3). Our results also apply to these classes of f 's.

Another application from which system (1.1) is derived concerns the propagation of nerve pulses in myelinated axons where the membrane is excitable only at spacially discrete sites. In the Appendix we give a derivation of (1.1) based on modeling myelinated nerve axons which motivated consideration of the particular questions addressed in this paper. Specifically, a question of importance for any nerve model is whether it displays

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threshold behavior. To explain this more fully, let $u_j(t)$ represent the potential at the jth active site at the time t. If we give conditions on the initial voltage distribution, $\{u_j(0)\}_{j\in\mathbf{Z}}$ such that $\lim_{t\to\infty} u_j(t) = q_j \equiv 0$, for all j, then we have established subthreshold conditions. If the limiting sequence q_j is nonzero, then threshold conditions have been obtained. One can loosely interpret subthreshold as decay of a nerve response while interpreting threshold to firing of the nerve.

Such conditions were discussed in [2] for (1.1), as well as a more complicated model, with $f(u)$ having behavior given by (2.3) below. In [2] a subthreshold condition was given for (1.1) using a comparison theorem, and a threshold condition was given using a Lyapunov function. In this paper we concentrate on establishing threshold conditions for (1.1) using comparison theorem techniques. Using the comparison theorem approach the results presented here are stronger than what can be obtained by Lyapunov methods, so that this paper can be considered an extension of [2].

Of course, if time and $f(u)$ are rescaled to have h^2 as multiplicative factor, (1.1) could be considered a spatially discrete approximation to the limiting equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u), \tag{1.2}$$

where the second differential operator is approximated by the central difference operator with $u_j(t) = u(t, x_j)$, with $x_j = jh$. Indeed, the asymptotic behavior we obtain in this paper for (1.1) has its analogue for (1.2). But in the context of our physical motivation explained in the Appendix, it is inappropriate to interpret (1.1) as a spatially discrete approximation to (1.2). Nevertheless, equation (1.2) can be considered a nerve axon model where the nerve membrane is continuously excitable, and one can proceed to address the analogous threshold questions. This is what Aronson and Weinberger do in [1], and so this paper follows their format. The main tool of [1] and this paper is the comparison principle, which both (1.1) and (1.2) have. In some situations we obtain results identical to the analogous ones in [1], while in other situations there are substantial differences. But there is a crucial difference in the analysis of (1.1) versus (1.2). Various steady state solutions for (1.2) can be constructed using phase plane methods and these solutions are used with the comparison theorem in [1] to obtain threshold results. But in considering (1.1), we do not have at our disposal the powerful phase plane technique and other methods of ordinary differential equations to construct our steady state solutions. Thus, to construct steady state solutions of (1.1) for comparison purposes, we must report to more ad hoc approaches.

In the next section we present the appropriate comparison theorem and use it to prove a lemma which is our main tool for developing threshold results. Subthreshold and threshold results are then obtained in section three. Although we develop these results for (1.1) for $j \in \mathbf{Z}$ analogous results could be derived for the initial-boundary value problem (that is, for $j = 0, 1, 2, \cdots$ with $u_0(t)$ specified as well as $u_j(0)$) without introducing any essentially new ideas.

In Sec. four we give results related to the asymptotic speed of propagation of a "wave of excitation" for system (1.1). These results are motivated by similar work on (1.2) in [1] and work on an epidemiological model due to Aronson (personal communication). Again the principal tool in this section is the comparison theorem.

2. Comparison principals. To study (1.1) we impose some restrictions on $f(u)$. We always assume $f(u)$ is piecewise C^1 on $[0, 1]$, and C^1 in a neighborhood of any point where $f(u) = 0$. We also assume without further mention that $f(0) = f(1) = 0$. Thus $u_j \equiv 0$ and $u_j \equiv 1$ are always solutions to (1.1). We will be interested in solutions $u_j(t)$ of (1.1) with $u_j \in [0, 1]$ for all $j \in \mathbf{Z}$, and all $t \geqslant 0$.

Standard results [7] on ordinary differential equations in Banach spaces insure that if $\{u_j(0)\}_{j\in\mathbf{Z}}$ is specified, there exists a local solution to (1.1) in $l^\infty(\mathbf{Z})$. Further, the set $\{(v_j) \in l^\infty\colon 0 \leqslant v_j \leqslant 1,\ j \in \mathbf{Z}\}$ is invariant, so if $0 \leqslant u_j(0) \leqslant 1$ for all j, then the solution is global and $0 \leqslant u_j(t) \leqslant 1$.

To obtain the results on the asymptotic behavior of solutions of (1.1) we must impose additional conditions on $f(u)$. We consider three cases. The first case is

$$f(u) > 0 \quad \text{for } 0 < u < 1, f'(0) > 0. \tag{2.1}$$

This is the heterozygote intermediate case discussed in [1]. The next case (Aronson and Weinberger's heterozygote superiority case) is

$$\begin{aligned}&\text{for some } \alpha \in (0,1), f(\alpha) = 0, \text{ with } f(u) > 0 \text{ for } 0 < u < \alpha \text{ and } f(u) < 0\\ &\text{for } \alpha < u < 1;\ f'(0), f'(1) > 0.\end{aligned} \tag{2.2}$$

The last case, which corresponds to Aronson and Weinberger's heterogyzote inferiority case, and which is the case most pertinent to the axonal modeling situation, is

$$\begin{aligned}&\text{for some } \alpha \in (0,1), f(\alpha) = 0, \text{ with } f(u) < 0 \text{ for } 0 < u < \alpha \text{ and } f(u) > 0\\ &\text{for } \alpha < u < 1.\end{aligned} \tag{2.3}$$

LEMMA 1. Suppose that $u_j(t)$ and $v_j(t)$ satisfy the following conditions:

For $i < j < k$,

$$\begin{aligned}&\text{(i)} \quad \frac{du_j}{dt} - u_{j+1} + 2u_j - u_{j-1} - f(u_j) \geqslant \frac{dv_j}{dt} - v_{j+1} + 2v_j - v_{j-1} - f(v_j),\\ &\text{(ii)} \quad u_j(t), v_j(t) \in [0, 1],\\ &\text{(iii)} \quad 0 \leqslant v_j(0) \leqslant u_j(0) \leqslant 1.\end{aligned} \tag{2.4}$$

Further, if $i > -\infty$ and/or $k < \infty$,

$$v_i(t) \leqslant u_i(t) \textit{ and/or } v_k(t) \leqslant u_k(t). \tag{2.5}$$

Then for all $t > 0$, $i < j < k$,

$$u_j(t) \geqslant v_j(t). \tag{2.6}$$

Remarks. Lemma 1 is a comparison theorem, analogous to Proposition 2.1 of [1], and can be proved via essentially the same methods. (Since the second derivative is replaced by a second difference there are some slight changes in the proof of the maximum principle, but the changes are minor.) Note that condition (2.4)(ii) need not hold for $j = i$ or $j = k$.

LEMMA 2. Suppose that for $i < j < k$, $\{q_j\}$ satisfies $0 \leqslant q_j \leqslant 1$ and

$$q_{j+1} - 2q_j + q_{j-1} + f(q_j) = 0; \tag{2.7}$$

if $i > -\infty$ assume $q_i \leqslant 0$ and if $k < \infty$ assume $q_k \leqslant 0$. Let $\{u_j(t)\}$ be a solution of (1.1) with $u_j(0) = q_j$ for $i < j < k$ and $u_j(0) = 0$ for all other values of j. Then for each j, $u_j(t)$ is a nondecreasing function of t, with

$$\lim_{t\to\infty} u_j(t) = \tau_j \tag{2.8}$$

where $\{\tau_t\}$ is the smallest nonnegative solution to (2.7) valid for all $j \in \mathbf{Z}$ which satisfies $\tau_j \geqslant q_j$ for $i < j < k$.

Proof. By Lemma 1, $0 \leqslant u_j(t) \leqslant 1$ for all j. Also, for $i < j < k$, $u_j(t) \geqslant q_j$. Thus $u_j(t) \geqslant u_j(0)$ for all j, so that for any $h > 0$, $u_j(h) \geqslant u_j(0)$. Again, lemma 1 applies and yields $u_j(t+h) \geqslant u_j(t)$ for any $t, h > 0$ and any j. Hence for each j, $u_j(t)$ is monotonically increasing in t. Since $u_j(t)$ is monotonically increasing and bounded above, $u_j(t) \uparrow \tau_j$ as $t \to \infty$ for some τ_j. For each j, du_j/dt can be expressed as the right side of (1.1). Since $\lim_{t\to\infty} u_j(t) = \tau_j$ for all j, it follows that as $t \to \infty$, du_j/dt approaches some constant value for each fixed j. Now $u_j(t)$ is nondecreasing so that $\lim_{t\to\infty}(du_j/dt) \geqslant 0$. If $\lim_{t\to\infty}(du_j/dt) = \varepsilon > 0$ then for $t \geqslant t_0$, t_0 sufficiently large, $u_j(t) \geqslant (\varepsilon/2)(t - t_0)$, which contradicts the fact that $u_j \leqslant 1$ for all t. Hence $\{\tau_j\}$ represents a steady state of (1.1), that is $\{\tau_j\}$ satisfies (2.7) with $0 \leqslant \tau_j \leqslant 1$ for $j \in \mathbf{Z}$.

If $\{\sigma_j\}$ represents another global steady state for (1.1) with $\sigma_j \geqslant q_j$ for $i < j < k$ and $\sigma_j \geqslant 0$ elsewhere, then $\sigma_j \geqslant u_j(0)$ for all j. By Lemma 1, $u_j(t) \leqslant \sigma_j$ and hence $\tau_j \leqslant \sigma_j$.

Remarks. If $w_j(0) \geqslant q_j$ but $w_j(0) \not\equiv q_j$ then Lemma 2 does not apply to $w_j(t)$. In particular, $w_j(t)$ need not increase monotonically. However, we may compare $w_j(t)$ with $u_j(t)$ via Lemma 1 to conclude that $w_j(t) \geqslant u_j(t)$, which is how the lemmas will be used in what follows.

3. Threshold results. Using Lemma 2 of the last section we now establish a number of threshold results depending on the particular type f's given by (2.1)–(2.3).

THEOREM 1. Suppose $\{u_j(t)\}$ satisfies (1.1) with $u_j(t) \in [0, 1]$ for all $j \in \mathbf{Z}$, $t > 0$.

(i) If (2.1) holds then either $u_j(t) \equiv 0$ for all j or $\lim_{t\to\infty} u_j(t) = 1$ for all j.

(ii) If (2.2) holds then either $u_j(t) \equiv 0$, $u_j(t) \equiv 1$, or $\lim_{t\to\infty} u_j(t) = \alpha$ for all j.

Proof (i) First we must analyze the steady states of (1.1) under hypothesis (2.1). Suppose that $\{q_j\}$ is a steady state of (1.1) with $0 \leqslant q_j \leqslant 1$ and $q_j \not\equiv 0$. Since (1.1) is invariant under shifts $j \to j + k$ and reflections $j \to -j$ we may assume that $0 < q_0$ and $q_1 \leqslant q_0$ without loss of generality. If $q_1 < q_0$ then $q_0 - q_1 = \varepsilon > 0$. By (1.1) $q_2 - q_1 = q_1 - q_0 - f(q_1) \leqslant q_1 - q_0 = -\varepsilon$ since $f(u) \geqslant 0$. In general, $q_j - q_{j-1} \leqslant q_{j-1} - q_{j-2}$; so by induction $q_j - q_{j-1} \leqslant -\varepsilon$ for $j > 0$. We have $q_n = q_0 + \sum_{j=1}^{n}(q_j - q_{j-1}) \leqslant q_0 - n\varepsilon$. Since $\varepsilon > 0$, $q_0 - n\varepsilon < 0$ for n sufficiently large, so eventually $q_n < 0$. Thus there can exist no global nonconstant steady states for (1.1) under hypothesis (2.1). If $q_j \equiv q_0$ then q_0 must satisfy $f(q_0) = 0$ so $q_0 = 0$ or $q_0 = 1$. Thus the only global steady states for (1.1) under hypothesis (2.1), are $q_j \equiv 0$ and $q_j \equiv 1$. However, it is possible to construct nonglobal steady states which can be used in Lemma 2 as comparison functions. If we choose a value for q_0, we may then set $q_{\pm 1} = q_0 - \frac{1}{2}f(q_0)$. Then the steady state Eq. (2.7) holds for $j = 0$. If $q_{\pm 1} \leqslant 0$ then we can use $\{q_{-1}, q_0, q_1\}$ for comparison with a general solution in Lemma

2. If $q_{\pm 1} > 0$ then let $q_{\pm 2} = 2q_{\pm 1} - q_0 - f(q_{\pm 1})$ and so on. With such a choice for q_j, $-k \leqslant j \leqslant k$, we see that (2.7) holds for all j with $-k < j < k$. Also, we have the following estimate, derived as before:

$$q_n \leqslant q_0 + \sum_{j=1}^{n} (q_j - q_{j-1}) \leqslant q_0 - nf(q_0)/2 \tag{3.1}$$

and similarly for q_{-n}. Thus for some k we have $q_j > 0$ for $-k < j < k$ and $q_{\pm k} \leqslant 0$.

To see that all nonzero solutions of (1.1) approach $q_j \equiv 1$ if (2.1) holds, we will show that if $1 \geqslant u_j(0) > 0$ for some j, then $\{u_j(t)\}$ is bounded below by a solution that tends to $q_j = 1$. Suppose without loss of generality that $u_0(0) = u_* > 0$, and that $0 \leqslant u_j(0) \leqslant 1$ for all j. By (1.1),

$$du_0/dt = u_1 - 2u_0 + u_{-1} + f(u_0) \geqslant -2u_0$$

so $u_0(t) \geqslant u_* e^{-2t}$. Similarly,

$$du_1/dt = u_2 - 2u_1 + u_0 + f(u_1) \geqslant -2u_1 + u_* e^{-2t};$$

Thus $e^{2t}[du_1/dt + 2u_1] = d(e^{2t}u_1)/dt \geqslant u_*$. Since $u_1(0) \geqslant 0$, we have $u_1(t) \geqslant te^{-2t}u_*$. By the same arguments $u_{-1}(t) \geqslant te^{-2t}u_*$. Suppose that

$$u_j(t) \geqslant e^{-2t}t^j u_*/j!.$$

Then $du_{j+1}/dt = u_{j+2} - 2u_{j+1} + u_j + f(u_j) \geqslant -2u_{j+1} + u_j$ so

$$\frac{d}{dt}\left(e^{2t}u_{j+1}\right) \geqslant e^{2t}u_j \geqslant \frac{t^j}{j!}u_*;$$

since $u_j(0) \geqslant 0$, we have

$$u_{j+1}(t) \geqslant \frac{e^{-2t}t^{j+1}}{(j+1)!}u_*.$$

Thus, by induction,

$$u_j(t) \geqslant \frac{e^{-2t}t^j}{j!}u_* \quad \text{for all } j. \tag{3.2}$$

By (2.1) and the general assumptions on $f(u)$, we have $f'(0) = f_1 > 0$ and $f(0) = 0$ so for some $\rho > 0$, $f'(u) \geqslant f_1/2$ and thus $f(u) \geqslant (f_1/2)u$ for $0 \leqslant u \leqslant \rho$. Applying the last estimate to the inequality (3.1) for the steady state $\{q_j\}$ yields $q_j \leqslant (1 - f_1 j/4)q_0$ as long as $q_0 \leqslant \rho$. Choose $N > 4/f_1$. By (3.1), the steady state $\{q_j\}$ will then satisfy (2.7) for $-k < j < k$, and $q_{\pm k} \leqslant 0$, with $k \leqslant N$. (As q_0 changes, k may also change, but as long as $q_0 < \rho$, $k \leqslant N$.) Let $t = 1$ in (3.2); then $u_j(1) \geqslant e^{-2}u_*/j!$ for all j. Choosing q_0 with $0 < q_0 < \min\{\rho, u_* e^{-2}/N!\}$ we have $u_j(1) \geqslant q_0 \geqslant q_j$ for $|j| \leqslant N$. Let $w_j(t) = u_j(t+1)$ and let $v_j(t)$ be the solution to (1.1) with $v_j(0) = q_j$, $-k < j < k$, and $v_j(0) = 0$, $|j| \geqslant k$. Then $w_j(0) = u_j(1) \geqslant v_j(0)$ for all j, so by Lemma 1, $u_j(t) = w_j(t-1) \geqslant v_j(t)$ for all $t \geqslant 1$. Also, Lemma 2 applies to $v_j(t)$; however, we have established that the only global steady state for (1.1) subject to (2.1) which lies above $\{q_j\}$ is $\tau_j \equiv 1$. Thus by Lemma 2 $v_j(t) \uparrow 1$ and $t \to \infty$. Hence as $t \to \infty$, $u_j(t) \geqslant v_j(t) \uparrow 1$ so the conclusion of (1) holds.

The analysis in case (ii) is very similar to that in case (i). First, we see by the same reasoning as in (i) that there are no nonconstant global steady states. (Any steady state which is nonconstant must eventually leave the interval [0, 1].) Any solution which is not identically zero or one will have $0 < u_j(0) < 1$ for some j, and, as in case (i), the solution will be bounded below by a solution, constructed as in (i), which tends to α as $t \to \infty$. A similar construction (or the same one applied after a change of variables $\tilde{u}_j = 1 - u_j$) shows that $\{u_j(t)\}$ is also bounded above by a solution which tends to α, yielding the desired conclusion.

Remarks. Note that the condition $f'(0) > 0$ and the smoothness of $f(u)$ were only used to obtain the "hair-trigger" effect, and that it is enough to assume that $f(0) = f(1) = 0$, $f(u) > 0$ on $(0, 1)$ if we only wish to exclude the possibility of nontrivial global steady states for (1.1).

As noted above, if (2.1) or (2.2) holds then (1.1) has no nontrivial global steady states. The situation is different under hypothesis (2.3) in that various types of nontrivial steady states may occur. For example, suppose that there exist $a, b \in (0, 1)$ such that $0 < a < \alpha < b < 1$, with $2(b - a) + f(a) = 0$ and $2(a - b) + f(b) = 0$, and let $q_0 = a$, $q_1 = b$, $q_{j+2} = q_j$ for all j. Then $\{q_j\}$ is a nontrivial global steady state for (1.1). Some specific cases occur when

$$f(1/4) = -1, f(3/4) = 1, \quad \text{so } a = 1/4, b = 3/4;$$

or

$$f(1/3) = -2/3, f(2/3) = 2/3, \quad \text{so } a = 1/3, b = 2/3.$$

The existence of such steady states depends only on the value of $f(u)$ at two points, so these steady states cannot be eliminated by any integral condition on $f(u)$, and a given function $f(u)$ may admit many such steady states.

Similarly, it is possible to give criteria for existence of global steady states of the form $q_0 = a$, $q_1 = a$, $q_2 = b$, $q_{j+3} = q_j$ for all j; other forms can also occur. Another type of steady state may occur. Suppose that $f(u)$ satisfies (2.3) with $\alpha = \frac{1}{2}$ and is symmetric in the sense $-f(\frac{1}{2} + v) = f(\frac{1}{2} - v)$ for $0 \leqslant v \leqslant \frac{1}{2}$. Consider the equation

$$u_{j+1} - 2u_j + u_{j-1} + \varepsilon f(u_j) = 0, \tag{3.3}$$

where $\varepsilon > 0$. Let $u_0 = u_* \in (\frac{1}{2}, 1)$, let $u^\varepsilon_{\pm 1} = \mathrm{u}_* - (\varepsilon/2)f(u_*)$ and define u^ε_j for other value of j via (3.3). We have

$$u^\varepsilon_2 = 2u^\varepsilon_1 - u_* - \varepsilon f(u^\varepsilon_1) = u_* - \varepsilon\Big[f(u_*) - f(u^\varepsilon_1)\Big];$$

$$u^\varepsilon_3 = u_* - \varepsilon\Big[\tfrac{3}{2}f(u_*) - 2f(u^\varepsilon_1) - f(u^\varepsilon_2)\Big],$$

and in general it follows by induction that

$$u^\varepsilon_{\pm n} = u_* - \varepsilon\left[\frac{n}{2}f(u_*) + \sum_{k=1}^{n-1}(n-k)f(u^\varepsilon_k)\right]. \tag{3.4}$$

Thus if $u^\varepsilon_j > \alpha$ for $j < N$, $u^\varepsilon_N \leqslant u_* - N\varepsilon f(u_*)/2$. Also, if $\sup_{0 \leqslant u \leqslant 1}|f(u)| = f_0$, $u^\varepsilon_N \leqslant u_* - \varepsilon C_N f_0$ where C_N is independent of ε or u_*. It follows that if we choose $u_* > \alpha$, then we can extend $\{u_j^\varepsilon\}$ outward until for some N, $u_{\pm N}^\varepsilon \leqslant \alpha$. If $u_{\pm N}^\varepsilon = \alpha$ then $u_{N+1}^\varepsilon = 2u_N^\varepsilon - u_{N-1}^\varepsilon - f(u_N^\varepsilon) = 2\alpha - u_{N-1}^\varepsilon$ so $u_{N+1}^\varepsilon - \alpha = -(u_{N-1}^\varepsilon - \alpha)$. Since $f(u)$ was assumed to be symmetric in the odd sense about $u = \alpha$, the steady state $\{u_j^\varepsilon\}$ can be extended from $-N < j < N$ to $-3N < j < 3N$ by symmetry and so on repeatedly to obtain a global steady state. If $u_N^\varepsilon < \alpha$ then as $\varepsilon > 0$, u_N will increase toward u_* and eventually pass through α. The point is that by varying u_* and ε appropriately, a wide variety of periodic steady states can be obtained. If u_* is taken near one and ε is small, such steady states may have long periods with respect to j. Since any such steady state only involves finitely many values of u_j, once a steady state has been found, adding "spikes" to $\varepsilon f(u)$ at points not on the original steady state will not destroy that steady state, although it may produce others such as the two point type discussed previously.

The point of the above discussion is that under hypothesis (2.3) Eq. (1.1) may have a wide variety of steady states. Since there may be various steady states, there are more possibilities for the asymptotic behavior of solutions to (1.1) under hypothesis (2.3) than under (2.1) or (2.2). Three possible behaviors are decay to zero, growth to one, and evolution to some other nontrivial solution, possibly a steady state. The next lemma gives a condition for the decay of a response. This lemma was proved in [2] but is included for completeness.

LEMMA 3. Suppose (2.3) holds, $\{u_j(t)\}$ is a solution of (1.1) and $0 \leqslant u_j(0) \leqslant \alpha - \varepsilon$ for some $\varepsilon > 0$. Then $u_j(t) \to 0$ as $t \to \infty$ for all j.

If (1.1) admits steady state solutions of the form $\{q_j\}$ with q_i, $q_k \leqslant 0$ and $q_j > 0$ for $i < j < k$, then any solution $u_j(t)$ with $u_j(0) > q_j$ for $i < j < k$ and $u_j(0) \geqslant 0$ for other values of j will satisfy $u_j(t) \geqslant q_j$ for $i < j < k$ and all t by Lemma 1. Thus if such steady states exist, Eq. (1.1) displays a form of threshold (or at least non-decay) behavior. The following result gives conditions for the existence of such steady states.

THEOREM 2. Suppose $f(u)$ satisfies (2.3). Let $m = -\inf_{0 \leqslant u \leqslant 1} f(u) > 0$. Suppose that for some $q_* > \alpha$,

$$f(q_*)^2 - 2mf(q_*) - 8m\alpha \geqslant 0. \tag{3.5}$$

Then (1.1) admits steady state solutions of the form $\{q_j\}$, $i < j < l$ with q_i, $q_l \leqslant 0$, and hence displays threshold behavior. In particular if $\{u_j(t)\}$ satisfies (1.1) with $u_j(0) \geqslant 0$ for all j and $u_j(0) \geqslant q_j$ for $i < j < l$, then for some fixed k between i and l, $u_k(t) \geqslant q_*$ for all t. Finally

$$l - i \leqslant \frac{4(q_* - \alpha)}{f(q_*)} + \frac{2f(q_*)}{m}.$$

Proof. The steady state we construct will be symmetric about a central point. Without loss of generality we may assume that the point is $j = 0$. Given $q_* > \alpha$ satisfying (3.5), let $q_0 = q_*$, and let $q_{\pm 1} = q_* - \frac{1}{2}f(q_*)$. Extend $\{q_j\}$ via (2.7). As long as $q_j \geqslant \alpha$ we have $q_{j+1} - q_j = q_j - q_{j-1} - f(q_j) \leqslant q_j - q_{j-1}$; also, $q_1 - q_0 = -(\frac{1}{2})f(q_*)$ so $q_{j+1} - q_j \leqslant -(\frac{1}{2})f(q_*)$ as long as $q_j \geqslant \alpha$. Suppose that q_{k+1} is the first term less than α in $\{q_j\}$. Since

$q_{j+1} - q_j \leq -(\frac{1}{2})f(q_*)$ for $0 \leq j \leq k$, $q_j \leq q_* - (j/2)f(q_*)$ so $q_j < \alpha$ when $j > 2(q_* - \alpha)/f(q_*)$ and thus $k \leq 2(q_* - \alpha)/f(q_*)$. To estimate q_j for $j > k$ observe that $q_{k+1} - q_k \leq -(\frac{1}{2})f(q_*)$, $q_{k+2} - q_{k+1} = q_{k+1} - q_k - f(q_{k+1}) \leq -(\frac{1}{2})f(q_*) + m$, and in general $q_{k+n} - q_{k+n-1} \leq -(\frac{1}{2})f(q_*) + m(n-1)$ by induction. Hence

$$q_{k+n} - q_{k+1} = \sum_{l=1}^{n-1} q_{k+l+1} - q_{k+l} \leq \sum_{l=1}^{n-1} \left[-(1/2)f(q_*) + ml\right]$$
$$\leq -\frac{(n-1)}{2}f(q_*) + \frac{n(n-1)m}{2}.$$

Since $q_{k+1} \leq \alpha$, we have

$$q_{k+n} \leq -\frac{(n-1)}{2}f(q_*) + \frac{n(n-1)m}{2} + \alpha$$
$$= \left(\frac{m}{2}\right)n^2 - \left(\frac{f(q_*) + m}{2}\right)n + \alpha + \left(\frac{1}{2}\right)f(q_*). \tag{3.6}$$

If the quadratic in n on the right side of (3.6) is nonpositive on an interval containing a positive integer, then we have $q_{k+n} \leq 0$ for some n. The quadratic will be nonpositive on such an interval provided it has real roots at a distance at least one unit apart, which is true when

$$\left\{\left[\left(f(q_*) + m\right)/2\right]^2 - 4\left(\frac{m}{2}\right)\left(\alpha + \frac{1}{2}f(q_*)\right)\right\} / \left(\frac{m}{2}\right)^2 \geq 1. \tag{3.7}$$

Simplifying (3.7) yields (3.5). The larger of the two roots of the quadratic in (3.6) is

$$n_1 = \frac{1}{m}\left[\left(\frac{f(q_*) + m}{2}\right) + \left\{\left(\frac{f(q_*) + m}{2}\right)^2 - f(q_*)m - 2m\alpha\right\}^{1/2}\right]$$
$$\leq \frac{1}{m}\left[\frac{f(q_*) + m}{2} + \frac{f(q_*) - m}{2}\right] = f(q_*)/m.$$

Hence, (3.5) implies there is an $n \leq f(q_*)/m$ such that $q_{k+n} \leq 0$. By (3.6), however, $q_{k+n} \leq \alpha$ as long as

$$-\frac{(n-1)}{2}f(q_*) + \frac{n(n-1)m}{2} \leq 0,$$

that is, for $n \leq f(q_*)/m$; so we have $q_{k+n} \leq \alpha < q_*$ until n is large enough that $q_{k+n} \leq 0$. By the way $\{q_j\}$ was constructed, $q_{-j} = q_j$, so the same estimates hold for negative values of j. The estimate (3.6) combined with (3.5) implies that for some $n < f(q_*)/m$, $q_{k+n} \leq 0$; therefore $q_{-(k+n)} \leq 0$, establishing the existence of the desired steady state. Furthermore, for all j such that $-(n+k) \leq j \leq (n+k)$, $q_j \leq q_*$, and $n + k \leq 2(q_* - \alpha)/f(q_*) + f(q_*)/m$. Thus if $u_j(0) \geq q_*$ for an interval of j values larger than $4(q_* - \alpha)/f(q_*) + 2f(q_*)/m$, then a translate of $\{q_j\}$ lies below $\{u_j(0)\}$ so $\{u_j(t)\}$ is bounded below by that translate of $\{q_j\}$ for all t, by Lemma 1. In $\{q_j\}$ there is always the center point with value q_*, so for some j, $u_j(t) \geq q_*$.

Remarks. It is easy to find examples where the hypotheses of Theorem 2 are satisfied. Suppose that $\sup_{0<u\leqslant 1} f(u) = 2 = f(2/3)$, $\inf_{0\leqslant u\leqslant 1} f(u) = -\frac{1}{2}$, and $\alpha = 1/2$. Choose $q_* = 2/3$; then $f(q_*)^2 - 2mf(q_*) - 8m\alpha = 0$ so Theorem 2 applies and a steady state exists. Also, the last inequality in the statement of Theorem 2 yields $l - i \leqslant 25/3$; so if $u_j(0) \geqslant 2/3$ for $i \leqslant j \leqslant i + 25/3$, then for some j, $u_j(t) \geqslant 2/3$ for all t.

We can carry through the same type steady state construction in the theorem's proof without the symmetry assumption by specifying that q_{-1} is some multiple of q_1, but no new ideas are introduced by that generalization.

In general solutions to (1.1) under hypothesis (2.3) which are bounded below by a steady state as in Theorem 2 need not have $\lim_{t\to\infty} u_j(t) = 1$. Thus there are cases where solutions may be bounded away from both $u_j \equiv 0$ and $u_j \equiv 1$.

Example. Suppose that in (2.3) we have $\alpha = 1/2$, $f(1/3) = -4/3$ and $f(2/3) = 4/3$. Suppose that $0 \leqslant u_0(0) < 1/3$, $2/3 < u_1(0) \leqslant 1$, and $0 \leqslant u_j(0) \leqslant 1$ for all j. The values $q_{-1} = 1$, $q_0 = 1/3$, $q_1 = 1$ satisfy (2.7) for $j = 0$; since $u_{\pm 1}(t) \leqslant 1$, we may apply Lemma 1 and conclude that $u_0(t) \leqslant 1/3$ for all t. Similarly $q_0 = 0$, $q_1 = 2/3$ and $q_2 = 0$ satisfy (2.7) at $j = 1$, and $u_0(t)$, $u_2(t) \geqslant 0$, so $u_1(t) \geqslant 2/3$. Since $u_0(t) \leqslant 1/3$ and $u_1(t) \geqslant 2/3$, the solution $u_j(t)$ to (1.1) can neither go to zero nor to one. (This example also shows that data with $u_j(0) = 0$ for some values of j and $u_j(0) = 1$ for the remaining values of j cannot evolve to a travelling wave front which goes from zero to one). Theorem 2 can also be used to give a criterion for guaranteeing that a solution $\{u_j(t)\}$ of (1.1) cannot converge to one. If $\{q_j\}$ is a solution to (2.7), then $p_j = 1 - q_j$ is a solution to $p_{j+1} - 2p_j + p_{j-1} + F(p_j) = 0$, where $F(p) = -f(1 - p)$ also satisfies (2.3). Then one can give analogous arguments as in Theorem 2 if some $p_* = 1 - q_* > 1 - \alpha$ is considered such that $f(q_*)^2 + 2Mf(q_*) - 8M(1 - \alpha) \geqslant 0$, where

$$M = \sup_{0\leqslant q\leqslant 1} f(q) = \inf_{0\leqslant p\leqslant 1} F(p).$$

In fact, the same sort of reasoning used in Theorem 2 can also be used to provide criteria for the existence of steady states which start at or above one, dip below α, then come back above one over a finite range of values of j. If such steady states exist, such as in the last example, solutions may be bounded away from either zero or one or both, and hence certain types of initial data, for example $u_j(0) = 0$ for $j < 0$ and $u_j(0) = 1$ for $j \geqslant 0$ may not be able to evolve to wave fronts going between zero and one. However, conditions can also be given which exclude the possibility of certain steady states and allow the solution $\{u_j(t)\}$ of (1.1) to converge to one.

THEOREM 3. Suppose $f(u)$ satisfies (2.3). Let $m \equiv -\inf_{0\leqslant u\leqslant 1} f(u) > 0$, $M \equiv \sup_{0\leqslant u\leqslant 1} f(u) > 0$ and suppose there exists constants β, γ with $\alpha < \beta < \gamma < 1$ such that $2u - f(u) < 0$ for $u \in (\beta, \gamma)$ with $2u - f(u) = 0$ at $u = \beta, \gamma$. Suppose one of the following holds:

$$2\beta + m \leqslant \gamma; \tag{3.8}$$

$$\beta + 1 + M \leqslant 2\gamma. \tag{3.9}$$

If $\{u_j(t)\}$ is a solution to (1.1) with $u_j(0) \geqslant 0$ for all j and $u_j(0) \geqslant \beta$ for some i, then

$$\lim_{t \to \infty} u_j(t) = 1, \quad \textit{for all } j.$$

Proof. First we will show how the hypothesis (3.8) of the theorem excludes certain steady state solutions to (1.1). Suppose $\{q_j\}$ is a steady state for (1.1) and that for some j, $\beta \leqslant q_j \leqslant \gamma$. Then $q_{j+1} + q_{j-1} = 2q_j - f(q_j) \leqslant 0$ so $q_{j+1} \leqslant 0$ or $q_{j-1} \leqslant 0$. If either q_{j+1} or q_{j-1} is less than zero, $\{q_j\}$ is not a global nonnegative steady state for (1.1). If, say, $q_{j+1} = 0$, then $q_{j+2} = 2q_{j+1} - q_j - f(q_{j+1}) = -q_j < 0$ so again, $\{q_j\}$ is not global. Thus (1.1) cannot have a global nonnegative steady state with any points in $[\beta, \gamma]$. Suppose now that a steady state has a point, say q_0, with $q_0 < \beta$. Then by (3.8),

$$q_1 + q_{-1} = 2q_0 - f(q_0) \leqslant 2\beta + m \leqslant \gamma.$$

If $\{q_j\}$ represents a global nonnegative steady state then $q_1 \leqslant \gamma$ and $q_{-1} \leqslant \gamma$; but we have already seen that for any such global steady state, no value of q_j may lie in $[\beta, \gamma]$, so $q_{\pm 1} < \beta$. Thus if $q_0 < \beta$, then $q_1 < \beta$ and $q_{-1} < \beta$. It follows by induction that $q_j < \beta$ for all j. We have proved that under the hypotheses of Theorem 3, any nonnegative global steady state for (1.1) that has any value below β must have all its values below β. Finally, suppose that $q_0 \in (\beta, 1)$ for some steady state. (Actually, since we have excluded the possibility that $q_0 \in [\beta, \gamma]$, we need only consider $q_0 \in (\gamma, 1)$.) Then, since $\beta > \alpha$, $q_1 + q_{-1} = 2q_0 - f(q_0) < 2q_0$, so either $q_1 < q_0$ or $q_{-1} < q_0$. Since the equation is symmetric there is no loss of generality in assuming $q_1 < q_0$. As long as $q_j \geqslant \alpha$ we have $q_{j+1} - q_j = q_j - q_{j-1} - f(q_j) \leqslant q_j - q_{j-1}$, so $q_{j+1} - q_j \leqslant q_1 - q_0 = -\varepsilon < 0$, and thus $q_{j+1} \leqslant q_0 - \varepsilon(j + 1)$. It follows that for j sufficiently large, $q_{j+1} \leqslant \alpha < \beta$. By the previous argument, $q_j < \beta$ for all j, which is a contradiction to our assumption that $q_0 \in (\beta, 1)$. Thus, the only possiblity for a global nonnegative steady state with any points above β is the case when $q_0 = 1$, which implies that $q_j \equiv 1$.

Suppose that $u_j(0) \geqslant 0$ and that $u_0(0) \geqslant \beta$. (If $u_j(0) \geqslant \beta$ for some other j, then simply make a translation in j.) Let $\{v_j(t)\}$ be the solution of (1.1) with initial data $v_j(0) = 0$ for $j \neq 0$, $v_0(0) = \beta$. Then since the three points $q_{-1} = 0$, $q_0 = \beta$, $q_1 = 0$ yield a solution of (2.7) at $j = 0$, we may apply Lemma 2 and conclude that for each j, $v_j(t)$ is a monotone increasing function in t, with $\lim_{t\to\infty} v_j(t) = \tau_j$, where $\{\tau_j\}$ is the smallest global steady state for (1.1) with points lying above β. However, the only such steady state is $\tau_j \equiv 1$, so $\lim_{t\to\infty} v_j(t) = 1$. Since $u_j(0) \geqslant v_j(0)$, Lemma 1 implies $u_j(t) \geqslant v_j(t)$ for all t, j so $\lim_{t\to\infty} u_j(t) = 1$ for all j.

Condition (3.8) in the proof was used to show that if a global steady state for (1.1) has any value below β, then all its values are below β. Similarly, condition (3.9) can be used in the same way to show if a global steady state has any value above γ, then all its values must lie above γ, so the steady state must be constant and hence identically 1. Then the rest of the arguments go through to complete the theorem's proof.

Remark. It is interesting to compare this result with a similar result for the continuous membrane case (1.2). Theorem 3.3 in [1] gives a condition for the solution $u(x, t)$ to (1.2) to satisfy $\lim_{t\to\infty} u(x, t) = 1$, uniformly in x. The condition can be interpreted to say that the initial condition $u(x, 0)$ must be large enough, that is above the threshold level, over a long enough x interval. Very few conditions on $f(u)$ are needed. In contrast, for Theorem 3 we needed to restrict our class of f's, but we only needed $u_j(0)$ to be big enough at one node.

4. Propagation. Let $\{u_j\}$ be a solution to (1.1) where f satisfies (2.3). Throughout this section, assume

$$\lim_{t\to\infty} u_j(t) = 1 \quad \text{for all } j \in \mathbf{Z}. \tag{4.1}$$

In what follows we will consider the behavior of $u_{j\pm[ct]}(t)$ as $t \to \infty$, where the square brackets denote "integer part".

Theorem 4 shows that if $u_j(0)$ is nonzero for only finitely many values of j, then for c sufficiently large, $u_{j\pm[ct]}(t) \to 0$ as $t \to \infty$, so that if we move rapidly enough we outdistance the "wave of excitation" and see only an unexcited state. Theorem 5 shows that if $u_j(0)$ is sufficiently large for some values of j, then for c sufficiently small, $u_{j\pm[ct]}(t) \geqslant u_j(0)$ for all t. Together, the results give bounds on the speed of propagation of a wave of excitation.

THEOREM 4. Suppose that $u_j(t)$ satisfies (1.1), (1.4), and

$$u_j(0) = u_j^0 \in [0,1] \quad \text{for all } j,\ u_j^0 = 0 \text{ for } |j| > J. \tag{4.2}$$

Suppose that $f(u)$ satisfies (2.3). Then there exists a $\bar{c} > 0$ such that for each $j \in \mathbf{Z}$, $\lim_{t\to\infty} u_{j\pm[ct]}(t) = 0$, if $c > \bar{c}$.

Proof. Let $\sigma \equiv \sup_{0<u<1}\{f(u)/u\}$ and define the operator $\mathscr{Q}_\sigma$ on $l^\infty(Z)$ componentwise by $(\mathscr{Q}_\sigma u)_j = u_{j+1} + u_{j-1} - (2-\sigma)u_j$. We will abuse notation by writing $\mathscr{Q}_\sigma u_j$ for $(\mathscr{Q}_\sigma u)_j$. Then (1.1) may be rewritten as

$$du_j/dt - \mathscr{Q}_\sigma u_j = f(u_j) - \sigma u_j \leqslant 0,$$

The inequality follows from the definition of σ and the comparison theorem since $u_j^0 \in [0,1]$ implies $u_j(t) \in [0,1]$. Define $w_i(t) = Ap(t)e^{-\mu(|i|-ct)}$, where μ, c, A are positive constants to be determined. A simple calculation shows that $\mathscr{Q}_\sigma w_i = Ae^{-\mu(|i|-ct)}p(t)\Gamma_i$, where

$$\Gamma_i = \Gamma_i(\mu) \equiv \begin{cases} e^{\mu} + e^{-\mu} - 2 + \sigma, & i \neq 0 \\ 2e^{-\mu} - 2 + \sigma, & i = 0. \end{cases}$$

Thus

$$\begin{aligned} \frac{dw_i}{dt} - \mathscr{Q}_\sigma w_i &= Ae^{-\mu(|i|-ct)}\left\{\frac{dp}{dt} + (\mu c - \Gamma_i)p\right\} \\ &\geqslant Ae^{-\mu(|i|-ct)}\left\{\frac{dp}{dt} + (\mu c - \Gamma)p\right\} \end{aligned}$$

if $p(t) \geqslant 0$ and $\Gamma = \Gamma(\mu) \equiv \max_i \Gamma_i(\mu) = e^{-\mu} + e^{\mu} - 2 + \sigma$. Let $p(t) \equiv e^{-\mu(c-\Gamma/\mu)t}$, then

$$\frac{dw_i}{dt} - \mathscr{Q}_\sigma w_i \geqslant 0 \geqslant \frac{du_i}{dt} - \mathscr{Q}_\sigma u_i.$$

Now $w_i(0) = Ae^{-\mu|i|} \geqslant u_i^0$ if we define $A \equiv \sup_i \{e^{\mu|i|}u_i^0\}$, which is finite because of the compact support assumption (4.2). Therefore, by the comparison theorem, $w_i(t) \geqslant u_i(t)$ for all i, all $t \geqslant 0$; that is

$$Ae^{-\mu(|i|-ct)}e^{-\mu(c-\Gamma/\mu)t} \geqslant u_i(t).$$

If $y = m\mu + b$ represents the tangent line to $\Gamma(\mu)$, $\mu > 0$ at $\mu = \mu_0$, then $m = 2\sinh\mu_0$ and $b = \Gamma(\mu_0) - 2\mu_0\sinh(\mu_0)$. Let $\bar{\mu}$ be the value of μ_0 such that the tangent line at $(\bar{\mu}, \Gamma(\bar{\mu}))$ passes through the origin. Then

$$\Gamma(\bar{\mu}) = 2\bar{\mu}\sinh(\bar{\mu})$$

or

$$\cosh(\bar{\mu}) - 1 + \sigma/2 = \bar{\mu}\sinh(\bar{\mu}), \text{ and } m = \bar{c} = 2\sinh(\bar{\mu}).$$

If $c > \bar{c}$, there are $\mu_{\pm} = \mu_{\pm}(c) > 0$ such that for $\bar{\mu} < \mu < \mu_+$, $c > \Gamma(\mu)/\mu$. Let $i = j \pm [ct]$, then $|i| - ct \geqslant \pm j - 1$ for t sufficiently large, and thus

$$Ae^{\mu(1 \mp j)}e^{-\mu(c-\Gamma/\mu)t} \geqslant u_{j\pm[ct]}(t).$$

For $c > \bar{c}$ and μ in the appropriate interval mentioned above, taking the limit as $t \to \infty$ of this expression yields the desired result.

THEOREM 5. Suppose that (1.1) admits a steady state $\{q_j\}$, $|j| \leqslant J < \infty$ with $q_j > 0$ for $|j| < J$ and $q_{\pm J} \leqslant 0$. Suppose further that the only nonnegative global steady state $\{\tau_j\}$ for (1.1) with $\tau_j \geqslant q_j$ for $|j| < J$ is $\tau_j \equiv 1$. If $\{u_i(t)\}$ satisfies (1.1) with $u_{i+j}(0) \geqslant q_j$ for $|j| < j$, then there is a constant $\underline{c} > 0$ such that for any $c < \underline{c}$ and $\varepsilon > 0$ there exists $T(\varepsilon, c) < \infty$ so that $u_{i\pm[ct]}(t) \geqslant 1 - \varepsilon$ for all $t > T(\varepsilon, c)$.

Proof. We may assume without loss of generality that $i = 0$ and recover the original result via a translation in j. Let $\{w_l(t)\}$ be the solution to (1.1) with $w_l(0) = q_l$ for $|l| < J$ and $w_l(0) = 0$ for all other values of l. By Lemma 2, $w_l(t) \to 1$ monotonically for each l as $t \to \infty$. Thus, for each $\varepsilon > 0$ there is a $t_1(\varepsilon)$ such that for $t \geqslant t_1(\varepsilon)$, $w_0(t) \geqslant 1 - \varepsilon$. Also, since there are only finitely many values of l with $|l| < J$, there exists $t_2 < \infty$ such that for $t \geqslant t_2$ and $|l| < J$, $w_{l+1}(t) \geqslant w_l(0)$. Since $w_l(0) = 0$ for $|l| \geqslant J$, $w_{l+1}(t) \geqslant w_l(0)$ for all l as long as $t \geqslant t_2$. In particular, $w_{l+1}(t_2) \geqslant w_l(0)$ so by Lemma 1, $w_{l+1}(t + t_2) \geqslant w_l(t)$ for all $t \geqslant 0$. By induction it follows that $w_k(t + kt_2) \geqslant w_0(t)$ for $t > 0$, $k \in \mathbf{Z}^+$, which implies that $w_k(t) \geqslant w_0(t - kt_2)$ for $t \geqslant kt_2$. By a similar analysis, $w_{l-1}(t_3) \geqslant w_l(0)$ for some $t_3 < \infty$ so $w_{-k}(t) \geqslant w_0(t - kt_3)$ for $t \geqslant kt_3$. Let $t_4 = \max\{t_2, t_3\}$; then $w_{\pm k}(t) \geqslant w_0(t - kt_4)$ since $w_0(t)$ increases monotonically.

Consider $w_{\pm[ct]}(t)$ where $c \leqslant \underline{c} = 1/t_4$. For some $\delta > 0$ depending on c, $c = (1 - \delta)/t_4$. Let $T(\varepsilon, c) = t_1(\varepsilon)/\delta$. When $t \geqslant T(\varepsilon, c)$ we have (using the fact that $w_0(t)$ is monotone increasing)

$$\begin{aligned} w_{\pm[ct]}(t) &\geqslant w_0(t - [ct]t_4) \geqslant w_0(t(1 - ct_4)) \\ &\geqslant w_0(\delta t) \geqslant w_0(t_1(\varepsilon)) \geqslant 1 - \varepsilon. \end{aligned}$$

(When $t > T(\varepsilon, c)$, we have $t - [ct]t_4 > 0$.)

To obtain the conclusion of the theorem we observe that $u_l(0) \geqslant q_l = w_l(0)$ so by Lemma 1, $u_l(t) \geqslant w_l(t)$ for $t \geqslant 0$. Thus $u_{\pm[ct]}(t) \geqslant w_{\pm[ct]}(t) \geqslant 1 - \varepsilon$ for $t \geqslant T(\varepsilon, c)$.

Remarks. The hypotheses of Theorem 5 will be satisfied if $f(u)$ satisfies (2.1) or if $f(u)$ satisfies (2.3) and the hypotheses of Theorems 2 and 3 hold.

Appendix. Modeling myelinated nerves. A large precentage of nerve processes in man are mylinated. That is, the axonal membrane of the nerve cell is wrapped in a layered, fatty myelin tissue which is periodically spaced so that small, excitable membrane sites called nodes of Ranvier are exposed. The nodes have conduction properties similar to unmyelinated nerve membrane, while the myelin has a much higher resistence and lower capacitance than the axonal membrane [4]. We assume the myelin is a perfect insulator, the nodes are resularly spaced and identical electrically, the axon is infinite in extent, and use the circuit model of Fig. 1. This is, of course, an idealized viewpoint of myelinated fiber. In the central nervous system nodes tend to have a relatively large surface area and synapses often arise at the nodes. Hence, the model more appropriately represents the morphology of peripheral myelinated nerve.

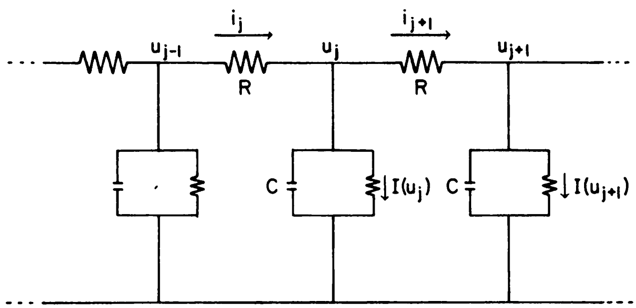

FIGURE 1

The R and C in Fig. 1 represent lumped resistance and capacitance, and i_j, u_j, $I(u_j)$ represent internodal current, membrane potential and ionic current at the jth node respectively (j running over the intergers). Applying Kirchoff's laws to the circuit yields

$$u_{j-1} - u_j = Ri_j, \qquad i_j - i_{j+1} = C\,du_j/dt + I(u_j).$$

This circuit has been used by other authors, e.g. Scott[6], but different nodal dynamics, $I(u)$, were considered than in this article and other authors were not concerned with threshold questions. At each node we adopt FitzHugh-Nagumo dynamics which have been studied extensively in modeling unmyelinated axons. For some background on the spatially continuous FitzHugh-Nagumo model, see [5]. Thus, the model becomes

$$\begin{aligned} u_{j-1} - u_j &= Ri_j, \\ i_j - i_{j+1} &= C\frac{du_j}{dt} - f(u_j) + w_j, \\ \sigma u_j - \gamma w_j &= \frac{dw_j}{dt}, \end{aligned} \tag{A.1}$$

where w_j represents a recovery variable at node j, σ and γ are nonnegative constants, and $f(u)$ has the bistable behavior given by (2.3).

In this paper we consider the case of no recovery at the nodes, that is $w_j \equiv 0$ for all j, so that the last equation in (A.1) can be ignored. Cohen [3] suggests this might model the treatment of the nodal membranes by certain toxins. By eliminating the variables i_j from the first two equations in (A.1) and scaling $R = C = 1$, we obtain system (1.1). In Bell [2], subthreshold and threshold conditions were given for the full model (A.1) using Lyapunov techniques.

References

[1] D. G. Aronson and H. F. Weinberger: *Nonlinear diffusion in population genetics, combustion, and nerve propagation*, Proceedings of the Tulane Program in Partial Differential Equations and Related Topics, Lecture Notes in Math., vol. 446, Springer-Verlag, New York, 1975

[2] J. Bell, *Some threshold results for models of myelinated nerves*, Math. Biosciences **54** (1981), 181–190

[3] H. Cohen, *Nonlinear diffusion models*, Studies in Applied Mathematics, ed. A. Taub, Math. Assoc. Amer., 1971

[4] P. Morell and W. T. Norton, *Myelin*, Sci. Amer. **242** (1980), 88–118

[5] J. Rinzel, *Integration and propagation of neuroelectric signals*, Studies in Mathematical Biology, ed. S. A. Levin, Math. Assoc. Amer., 1977

[6] A. C. Scott, *Analysis of a myelinated nerve model*, Bull. Math. Biophys. **26** (1964), 247–254

[7] W. Walter, *Differential and integral inequalities*, Springer-Verlag, New York, 1970