INITIAL BOUNDARY VALUE PROBLEMS FOR COUPLED NERVE FIBRES

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0. Introduction

In this paper we analyse the electrical behaviour within systems of long and short coupled nerve axons by using a geometric approach to obtain a priori bounds on solutions. In [4] we developed a general model for a bundle of *n*-uniform unmylinated nerve fibres. If FitzHugh-Nagumo dynamics, [3] are used to describe the ionic membrane currents, then the model takes the form

$$W_{t} = MW_{xx} + F(W) - Z$$

$$Z_{t} = \sigma W - \gamma Z.$$
(*)

Here $W = (w_1, \ldots, w_n)^T$ denotes the membrane action potentials for each fibre in the bundle and $Z = (z_1, \ldots, z_n)^T$ represents the recovery variables for each fibre, which control the return to the resting equilibrium after any transmission of signals.

 $F: \mathbb{R}^n \to \mathbb{R}^n$ is a continuous nonlinear vector field and σ and γ are non-negative diagonal matrices. The electrical interaction between separate fibres within the bundle is controlled by the matrix M, which is taken to be of the form

$$M = \Lambda I - \alpha B$$

where I is the identity matrix on \mathbb{R}^n , B is the adjacency matrix for a graph on *n*-vertices representing the location and interaction of the fibres in cross-section, and Λ and α are positive constants (see [4]).

We assume that the bundle is semi-infinite, and seek solutions of (*) for $x \ge 0$, $t \ge 0$, when appropriate Dirichlet boundary conditions are applied at x=0. Such conditions may be thought of as modelling a stimulus provided by synaptic transmission between axons further down the bundle.

Numerical and physiological evidence suggests that a strong stimulus of short duration or a weak stimulus of long duration is sub-threshold, i.e. the resultant potentials within the bundle will decay to the inactive rest-state. We show that for zero initial data, and compactly supported boundary data the solution of (*) is bounded for

all time by a constant multiple of the total stimulus, and that if the stimulus is sufficiently small, the solution has exponential decay.

M. Schonbeck [7] considers a similar problem for the FitzHugh-Nagumo equations, and our analysis, like hers, requires the existence of certain contracting blocks for the associated vector fields, (see [6] and [4]).

Finally we show that if the bundle is assumed to be of finite length L, then the resting equilibrium is globally stable when L is small enough.

Although we obtain results concerning the action potentials for each fibre within the bundle, we do not gain much insight into the precise nature of ephaptic stimulation between fibres. An alternative approach using comparison principals and explicit solutions for a simplified twin fibre problem yields more qualitative information for this problem (see [5]).

1. Existence of solvability of solutions

Firstly we consider a general system of coupled non-linear diffusion equations and ordinary differential equations. We state two theorems which are due to Schonbeck [7], which provide a base from which we can go to discuss boundary value problems for coupled nerve fibre models.

Before proceeding we pause to make the following definitions.

Definition 1.1. Let $p: [0, \infty) \to \mathbb{R}$ be a bounded continuous function with support contained in $[0, s_0]$. Then we define the norm $\|\cdot\|_1$ by

$$||p||_1 = \int_0^{s_0} |p(s)| ds.$$

If $P(s) = (p_1(s), \dots, p_m(s))^T$ is such that for $k = 1, \dots, m$, $p_k: [0, \infty) \to \mathbb{R}$ is a bounded continuous function with support in $[0, s_0]$ then we extend the norm $\|\cdot\|_1$ by defining

$$||P||_{1,m} = \sum_{k=1}^{m} ||p_k||_1$$

If the assumption of compact support is dropped we define the norm $\| \cdot \|_{\infty}$ by

$$||p_k||_{\infty} = \sup_{s \ge 0} |p_k(s)|$$

and

$$||P||_{\infty,m} = \sum_{k=1}^m ||p_k||_{\infty}.$$

Finally if $W \in \mathbb{R}^m$, where $W = (w_1, \dots, w_m)^T$, say, then we define the norm $\|\cdot\|_m$ on \mathbb{R}^m by

$$\left\|W\right\|_{m} = \sum_{k=1}^{n} \left|w_{k}\right|$$

We consider a general system of the form

$$V_t = BV_{xx} + G(V)$$
 $x \ge 0, t \ge 0$ (1.1)

where V is a function of two independent variables x and t, and $V(x,t) \in \mathbb{R}^m$; G is a smooth vector field over \mathbb{R}^m satisfying G(0) = 0 and B is a non-negative $m \times m$ diagonal matrix say $B = \text{diag}(b_1, b_2, \dots, b_m)$.

We will assume that the equations have been ordered so that for some integer p we have

$$b_k > 0$$
 for $1 \leq k \leq p$
 $b_k = 0$ for $p < k \leq m$.

If $p \neq 0$, then in order to have a well posed problem, we will impose some boundary conditions at x=0. Firstly we adopt the following conventions. Let $BC(\mathbb{R}^+, \mathbb{R}^m)$ denote the space of continuous bounded functions from \mathbb{R}^+ to \mathbb{R}^m .

Let
$$BC^{k}(\bar{\mathbb{R}}^{+}, \mathbb{R}^{m}) = \left\{ W \middle| \left(\frac{\partial}{dx} \right)^{j} W \in BC(\bar{\mathbb{R}}^{+}, \mathbb{R}^{m}); \text{ for } j = 0, \dots, k \right\}$$

 $BC^{k}_{0}(\bar{\mathbb{R}}^{+}, \mathbb{R}^{m}) = \left\{ W \middle| W \in BC^{k}(\bar{\mathbb{R}}^{+}, \mathbb{R}^{m}) \text{ and } w(x) \to 0 \text{ as } x \to \infty \right\}$
 $W^{p}_{k} = \left\{ W \in L_{p} \middle| \left(\frac{d}{dx} \right)^{j} W \in L_{p} \text{ for } 0 \leq j \leq k \right\}.$

Finally let B denote any one of the Banach spaces above, and define C([0, T]1B) to be the space of continuous functions from the interval [0, T] into B, with norm

$$||U||_{C([0, T]|B)} = \sup_{0 \le t \le T} ||U(t)||_{B}.$$

Returning to (1.1) we write $V(x,t) = (v_1(x,t), \dots, v_m(x,t))^T$ and impose the following initial and boundary conditions

$$v_k(x,0) = g_k(x) \in B \quad \text{for} \quad 1 \le k \le m$$

$$v_k(0,t) = h_k(t) \in BC \quad \text{for} \quad 1 \le k \le p.$$
(1.2)

Notice that the boundary conditions at x=0 are only given on v_1, \ldots, v_p .

A general problem of the form (1.1), (1.2) has been considered by Schonbeck ([7], §2), who obtained the following two theorems.

Theorem 1.1. Suppose g_1, \ldots, g_m , h_1, \ldots, h_p satisfy $h_k \in B$, $g_k \in B$, $g_k(0) = h_k(0)$ for $1 \leq k \leq p$ and $g_k \in B \cap C^{\infty}$ for $p+1 \leq k \leq m$, then there exists a constant $t_0 > 0$, depending only on G, g_j and h_k such that the Dirichlet problem (1.1), (1.2) has a unique solution V in $C([0, t_0]|B)$ and $\|V\|_{C((0, t_0]|B)} \leq 2(2\|h\|_{\infty, p} + \|g\|_B)$.

$$(Here \ h = (h_1, ..., h_p)^T \ and \ g = (g_1, ..., g_m)^T).$$

Theorem 1.2. Suppose that $V \in C([0, t_0]|B)$ is a solution of (1.1), (1.2) and g and h satisfy

- (i) $g_k \in BC^0(\bar{\mathbb{R}}^+)$ k = 1, ..., p
- (ii) $g_k \in C^{\infty}(\mathbb{R}^+)$ $k = p+1, \ldots, n$
- (iii) $h_k \in BC(\mathbb{R}^+)$ $k = 1, \dots, p$.

Then $V \in C^{\infty}(\Omega)$ where $\Omega = \mathbb{R}^+ \times \mathbb{R}^+$.

2. Contracting blocks and global existence

We consider the system (*) that is

$$W_t = MW_{xx} + F(W) - Z$$

$$Z_t = \sigma W - \gamma Z$$
(2.1)

where W(x, t), $Z(x, t) \in \mathbb{R}^n$ and σ , γ , M and F satisfy the following hypotheses.

- (i) $\sigma = \text{diag}(\sigma_1, \dots, \sigma_n), \ \gamma = \text{diag}(\gamma_1, \dots, \gamma_n)$ are diagonal matrices and $\sigma_i, \ \gamma_i > 0$ for $i = 1, \dots, n$.
- (ii) M is a real symmetric matrix with strictly positive eigenvalues d_1, \ldots, d_n
- (iii) There exists a unitary matrix A such that

$$A^T M A = D_1 = \operatorname{diag}(d_1, \ldots, d_n).$$

(iv) $F(W) = (f(w_1), f(w_2), \dots, f(w_n))^T$ where $W = (w_1, w_2, \dots, w_n)^T$ and f(y) = y(1-y)(y-a)for some $a \in (0, \frac{1}{2})$.

In view of (iii) above we may set $U = A^T W$ and obtain the new system

$$U_{t} = D_{1}U_{xx} + A^{T}F(AU) - A^{T}Z$$

$$Z_{t} = \sigma AU - \gamma Z.$$
(2.2)

Setting $V = (U,Z)^T$ we see that (2.2) is of the general form (1.1), so we may apply Theorems 1.1 and 1.2 when considering the quarter plane Dirichlet problem for (2.2).

Definition 2.1. Let H denote a vector field over \mathbb{R}^m and let S denote some bounded convex set in \mathbb{R}^m , with boundary ∂S .

S is contracting for H if for every $W \in \partial S$ and for every outward normal, n, to ∂S at W, we have $H(W) \cdot n < 0$. If S is of the form $\pi_{k=1}^{m} [-\alpha_{k}, \beta_{k}]$ where $-\alpha_{k} < \beta_{k}, (k=1,...,m)$ then it will be called a contracting block.

Also (2.2) is precisely the set of equations discussed in [4] and we state the following Lemmas which concern the existence of contracting rectangles for the non-linear field G,

given by

$$G(U,Z) = \begin{vmatrix} A^{T}(F(AU) - Z) \\ \sigma AU - \gamma Z \end{vmatrix}.$$
(2.3)

Lemma 2.1. There exists a positive constant r, depending only on the matrix A, such that if

$$a > r \max_{1 \leq j \leq n} \frac{\sigma_j}{\gamma_j}$$

then there exists a block $\subset \mathbb{R}^{2n}$, containing the origin, which is contracting for G.

Lemma 2.2. If $a > r \max_{1 \le j \le n} \sigma_j / \gamma_j$, then there exists a block $R_C \subset \mathbb{R}^{2n}$, containing the origin, with the following property.

For any compact set $Q \subset int(R_c)$, there is a block R, containing the origin, and a constant k > 0, such that $Q \subset R \subset R_c$, and for all $\tau \in (0, 1]$ we have, $G(U, Z) \cdot n < -k\tau$ for all $(U, Z) \in \partial(\tau R)$, and any outward normal n to $\partial(\tau R)$ at (U, Z).

Lemma 2.3. If $1 \le n \le 3$, then there exists a block $\mathbb{R}^C \subset \mathbb{R}^{2n}$, containing the origin with the following property.

For any compact set Q in the exterior of R^{C} , there exists a block R such that

- (i) $R^C \subset R$,
- (ii) Q is in the exterior of R and τR is contracting for G(U, Z) for all $\tau \in [1, \infty)$.

We remark that the hypothesis $1 \le n \le 3$ in Lemma 2.3, may be relaxed in certain cases, and we refer to [4] for a fuller discussion of the existence of large contracting blocks for the field G. We use contracting blocks to define nonlinear functionals on the solutions of (2.1)

Definition 2.2. Let R be a block in \mathbb{R}^m . Let $|\cdot|_R$ be the norm on \mathbb{R}^m defined by

$$|U|_R = \inf \{t \ge 0 | U \in t \cdot R\}$$

i.e. $|U|_R$. R is the smallest multiple of R containing the point U.

We define a continuous map, $P_R: BC \to \mathbb{R}$ by

$$P_{R}(W) = \sup_{x \in \mathbb{R}^{+}} |W(x)|_{R}.$$

Lemma 2.4. Let G(W) be a vector field over \mathbb{R}^m and let R be a rectangle in \mathbb{R}^m with $0 \in int(R)$. Suppose $W \in C((T-\delta, T+\delta)|BC_0)$ is a solution of

$$W_t = DW_{xx} + G(W) \qquad x \ge 0$$
$$|T - t| < \delta$$

such that $P_R(W(T)) = S$ and $P_R(W(T,0)) < S$ where D is a non-negative diagonal matrix. If there exists $\eta > 0$ such that for all $W \in \partial(SR)$ and n(W), normal to $\partial(SR)$ at W, we have

$$G(W)n(W) < -\eta$$

then

$$\bar{D}P_{R}(W(T)) \leq \frac{-2\eta}{L}P_{R}(W(T))$$

where L is the length of the largest side of R.

The proof of Lemma 2.4 is almost identical to that of Lemma 3.8, [6]. The extra condition $P_R(W(T,0)) < S$ is needed to ensure that $W(T,0) \notin \partial(SR)$.

Theorem 2.5. Suppose $n \leq 3$. Consider the system (2.2) together with initial and boundary data given by

$$(U(0, x), Z(0, x)) = (g_1(x), \dots, g_{2n}(x))^T = g(x)$$

$$U(t,0) = (h_1(t), \ldots, h_n(t))^T = h(t),$$

where the functions g_k , h_k satisfy $h_k \in BC$, $g_j \in B \cap BC_0$, and $h_k(0) = g_k(0)$ for k = 1, ..., n; and $g_k \in C^{\infty} \cap B$ for k = n + 1, ..., 2n.

Then there is a unique solution (U, Z) in $C([0, \infty)|B \cap BC_0)$.

Proof. By Lemma 2.3 we may choose a sufficiently large rectangle $R \subset \mathbb{R}^{2n}$ such that R is contracting for the vector field G(U, Z) given by (2.3), and

$$P_R(g(x)) < 1$$
 for all $x \ge 0$.

and

$$P_{R}(h(t)) < 1 \quad \text{for all} \quad t \ge 0. \tag{2.4}$$

Now, Theorem 1.1 implies the existence of a solution $(U, Z) \in C([0, t_0]|B)$ of (2.2) with the initial and boundary conditions given above.

We claim that $P_R(U(t), Z(t)) < 1$ for $0 < t < t_0$.

If this were not so then we may set

$$\tilde{t} = \inf \{ t \in (0, t_0) : P_R(U(t), Z(t)) = 1 \}.$$

By the continuity of P_R and (2.4) we have $\tilde{t} > 0$.

By Lemma 2.4 we have

$$\bar{D}P_{R}(U(\tilde{t}),Z(\tilde{t}))<0.$$

Thus for any $t \in (\tilde{t} - \varepsilon, \tilde{t})$ we have $P_R(U(t), Z(t)) > 1$, where $\varepsilon > 0$ is chosen small enough. But this contradicts the definition of \tilde{t} . The estimate $P_R(U(t), Z(t)) < 1$ for $t \in [0, t_0]$ is the sup norm estimate needed to extend the local solution to a global solution with $P_R(U(t)) < 1$ for all $t \ge 0$. Uniqueness follows directly from the uniqueness of local solutions.

Theorem 2.6. (sup norm estimate theorem). Let $1 \le n < 3$. If $(U, Z) \in C([0, \infty) | BC_0)$ is a solution of (2.2) together with Dirichlet boundary data

$$U(t, 0) = (h_1(t), \dots, h_n(t)) = h(t)$$

satisfying $h_k \in BC$ for k = 1, ..., n and h(t) = 0 for $t \ge T$, then we have

$$\left\| (U(t), Z(t)) \right\|_{\infty, 2n} \leq \text{constant} \left\| (U(T), Z(T)) \right\|_{\infty, 2n} \quad \text{for all} \quad t \geq T.$$

Proof. Since h(t) = 0 for $t \ge T$, there exists a rectangle R which is contracting for G, such that (U(T, x), Z(T, x)) lies in R for all $x \ge 0$ and for $t \ge T \ge 0$

$$Z(t,0) = Z(T,0)e^{\gamma(T-t)} \in R$$
$$U(t,0) = 0 \in R.$$

Thus the rectangle R contains the solution for all time $t \ge T$ and provides the required sup-norm estimate.

We remark that the hypothesis $n \leq 3$ in Theorems 2.5 and 2.6 is required to guarantee the existence of large contracting rectangles for the field. If the coupling matrix M in (2.1) is such that large rectangles exist for G, then Theorems 2.5 and 2.6 will apply.

3. The threshold problem

We consider the system (2.2) and seek solutions on the domain $\mathbb{R}^+ \times \mathbb{R}^+$ together with initial and boundary data given by

$$(U(x,0), Z(x,0)) = g(x,0) = 0$$
 for all $x \in \mathbb{R}^+$ (3.1)

$$U(0,t) = h(t) = (h_1(t), \dots, h_n(t))^T \quad \text{for all} \quad t \in \mathbb{R}^+$$
(3.2)

where each h_k is a bounded continuous function satisfying

$$h_k(0) = 0$$

$$h_k(t) = 0 \quad \text{for all} \quad t \ge t_0$$
(3.3)

for some constant $t_0 \ge 0$.

Through this section we will assume the following conditions hold on the field G given by (2.3):

H1: There exists a rectangle $R_C \subset \mathbb{R}^{2n}$, containing the origin with the following property:

For any compact set $Q \subset int(R_c)$, there is a rectangle R, containing the origin and a constant k>0 such that $Q \subset R \subset R_c$ and for all $\tau \in (0,1]$ we have $G(U,Z)n < -k\tau$ for all $(U,Z) \in \partial(\tau R)$ and any outward normal, n, to $\partial(\tau R)$ at (U,Z).

H2: There exists a rectangle $R^{C} \subset \mathbb{R}^{2n}$, containing the origin with the following property:

For any compact set Q in the exterior of R^c there is a rectangle R such that $R^c \subset R, Q$ is in the exterior of R and τR is contracting for G for all $\tau \in [1, \infty)$.

Remark. H1 is precisely the consequence of Lemma 2.2 and, by Lemma 2.3, H2 certainly holds if n=2 or 3. We make these hypotheses so that the Global Existence and Sup Norm Estimate Theorems of §2 apply to the Dirichlet problem (2.2), (3.1), (3.2).

Returning to (3.2), since h_k is a bounded continuous function, for each k, there is a positive constant M_0 such that

$$\|h\|_{\infty,n} \le M_0. \tag{3.4}$$

(Conversely $||h||_{\infty,n} \leq M_0$ implies $||h_k||_{\infty} \leq M_0$ for all k = 1, ..., n.)

For k = 1, ..., n define the following functions:

$$\widetilde{K}_{k}(t, y, x) = \frac{1}{\sqrt{4d_{k}t\pi}} \left\{ \exp\left(-(y-x)^{2}/4d_{k}t\right) - \exp\left(-(y+x)^{2}/4d_{k}t\right) \right\}$$
(3.5)

$$H_{k}(t,x) = -2 \int_{0}^{t} h_{k}(s) \frac{\partial K_{k}(t-s, y, x)}{\partial y} \bigg|_{y=0} ds$$

= $-\frac{1}{\sqrt{\pi}} \int_{0}^{t} \frac{h_{k}(s)x \exp(-x^{2}/4d_{k}(t-s))}{(d_{k}(t-s))^{3/2}} ds.$ (3.6)

Then if (U(x,t), Z(x,t)) is a solution of (2.2) subject to (3.1) and (3.2) then the components $u_k(x,t)$, $z_j(x,t)$ satisfy

$$u_{k}(x,t) = H_{k}(t,x) + \int_{0}^{t} \int_{0}^{\infty} \tilde{K}_{k}(t-s,y,x) G_{k}(U(y,s),Z(y,s)) \, dy \, ds \tag{3.7}$$

$$z_j(x,t) = \int_0^t G_{n+j}(U(x,s), Z(x,s)) \, ds, \tag{3.8}$$

where G_m is the *m*th component of the field G, given by (2.3).

Also from (2.2) we have

$$z_{jt} = \sigma_j (AU)_j - \gamma_j z_j$$
 for $j = 1, \dots, n$

using $z_i(x,0) = 0$, we may rearrange and integrate between 0 and t, to obtain

$$z_j(x,t) = \sigma_j \int_0^t e^{\gamma_j(s-t)} (AU(x,s))_j ds, \text{ for } j=1,...,n$$

which we write as the vector equation

$$Z(x,t) = \sigma \int_{0}^{t} e^{\gamma(s-t)} A U(x,s) \, ds.$$
(3.9)

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The following Theorem is the main result of this section, and is a generalization of a theorem due to M. Schonbeck, who proves the same result for the FitzHugh-Nagumo equations ([7], Theorem 5.1).

Theorem 3.1. Suppose H1 and H2 hold. For all $T > t_0$, there exists a constant $k^* = k^*(T, t_0, M_0, G, D)$, growing at most like max $\{1/(T - t_0), \exp(T)\}$ such that, if (U, Z) is the solution of (2.2) subject to (3.1), (3.2), then

$$\left\| (U(\cdot,t), Z(\cdot,t)) \right\|_{\infty, 2n} \leq k^* \|h\|_{1,n} \quad \text{for all} \quad t \geq T.$$

Proof. By the Global Existence Theorem 2.5, there is a unique solution (U, Z) to (2.2), (3.1) and (3.2) and a constant \tilde{k} such that

$$\|(U(t,x),Z(t,x))\|_{2n} \leq \tilde{k}$$
 for all $x \geq 0, t \geq 0$.

The non-linearity G is smooth and G(0) = 0. Since (U, Z) ranges over a bounded set, there is a constant $\bar{k} > 0$, such that

$$\|G(U(x,t),Z(x,t))\|_{2n} \le \bar{k} \|(U(x,t),Z(x,t))\|_{2n} \quad \text{for all} \quad x \ge 0, \ t \ge 0.$$
(3.10)

We also note that for each k = 1, ..., 2n we have

$$0 \le |G_k(U(x,t), Z(x,t))| \le ||G(U(x,t), Z(x,t))||_{2n}.$$
(3.11)

Now

$$\left\| (U(x,t), Z(x,t)) \right\|_{2n} = \sum_{k=1}^{n} \left\{ \left| u_k(x,t) \right| + \left| z_k(x,t) \right| \right\}$$
(3.12)

(from the definition of $\|\cdot\|_m$ in §2). So we will prove the following two inequalities

$$|u_{k}(T, x)| \leq \text{constant}(T, t_{0}, M_{0}, G, D) \cdot ||h||_{1, n}$$

for all $k = 1, ..., n$ for $T > t_{0}$, and (3.13)
all $x \geq 0$
 $|z_{k}(T, x)| \leq \text{constant}(T, t_{0}, M_{0}, G, D) \cdot ||h||_{1, n}$ for
all $k = 1, ..., n$ for $T > t_{0}$ and (3.14)
all $x \geq 0$.

Then the "sup-norm estimate" Theorem 2.6 in §2 implies the desired result.

Proof of (3.13). Let $t \ge T > t_0$. Using (3.7) and (3.8) we obtain

$$|u_{k}(x,t)| \leq |H_{k}(t,x)| + \int_{0}^{t} \int_{0}^{\infty} \tilde{K}_{k}(t-s,y,x) |G_{k}(U(y,s),Z(y,s))| dy \, ds$$
(3.15)

and

$$|z_k(x,t)| \leq \int_0^t |G_{n+k}(U(x,s),Z(x,s))| ds$$
 (3.16)

Consider (3.6), $h_k(t) = 0$ for $t \ge t_0$, so

$$|H_k(t,x)| \leq \text{constant} \int_0^{t_0} \frac{|h_k(s)|x \exp[-x^2/4d_k(t-s)]}{(4d_k(t-s))^{1/2}d_k(t-s)} ds$$

but

$$\frac{x}{\sqrt{4d_k(t-s)}} \exp\left[-\frac{x^2}{4d_k(t-s)}\right] \leq \text{constant}(d_k)$$

for all $x \geq 0$ and $s \in [0, t_0]$.

Thus

$$|H_k(t,x)| \leq \text{constant } \int_0^{t_0} \frac{|h_k(s)|}{(t-s)} ds$$
$$\leq \frac{\text{constant }}{(T-t_0)} \int_0^{t_0} |h_k(s)| ds = \frac{\text{constant }}{(T-t_0)} ||h_k||_1.$$

Thus

$$|H_k(t,x)| \le \text{constant} \quad (T,t_0) ||h_k||_1.$$
 (3.17)

This provides the estimate for the first term on the right hand side of (3.15). Notice $||h_k||_1 \leq ||h||_{1,n}$. To estimate the second term in (3.15) we use (3.11) and (3.10) to bound $|G_k(U,Z)|$, again choosing $t \geq T > t_0$.

$$\int_{0}^{T} \int_{0}^{\infty} \tilde{K}_{k}(T-s, y, x) |G_{k}(U(y, s), Z(y, s))| dy ds$$

$$\leq k \int_{0}^{T} \int_{0}^{\infty} \tilde{K}_{k}(T-s, y, x) ||U(y, s), Z(y, s)||_{2n} dy ds.$$
(3.18)

Now from (3.5) we see that

$$\widetilde{K}_{k}(T-s, y, x) \leq \frac{\text{constant}}{(T-s)^{1/2}} \quad \text{for all} \quad x, y \geq 0.$$
(3.19)

Since the numerator of \tilde{K}_k is bounded above by $\exp[-(y-x)^2/4d_k(T-s)] \leq 1$ then using (3.19) in (3.18) we obtain

$$\int_{0}^{T} \int_{0}^{\infty} \widetilde{K}_{k}(T-s, y, x) |G_{k}(U(y, s), Z(y, s))| dy ds$$

$$\leq \text{constant} \int_{0}^{T} \int_{0}^{\infty} \frac{||U(y, s), Z(y, s)||_{2n}}{(Y-s)^{1/2}} dy ds.$$

Thus we need to show that

$$\int_{0}^{T} \int_{0}^{\infty} \frac{\|U(y,s), Z(y,s)\|_{2n}}{(T-S)^{1/2}} dy \, ds \leq \operatorname{constant}(T, M_0, G, T_0) \cdot \|h\|_{1,n}.$$
(3.20)

This, together with (3.18), (3.17) and (3.15) will imply (3.13) as required.

In order to establish (3.20), we will prove the preliminary result

$$\int_{0}^{T} \int_{0}^{\infty} \|U(x,s), Z(x,s)\|_{2n} \, dx \, ds \leq \text{constant} \left(T, M_0, G, t_0, D\right) \cdot \|h\|_{1,n}.$$
(3.21)

Using (3.12), (3.15), (3.16) and (3.10) we obtain for $0 \le t \le T$

$$\int_{0}^{t} \int_{0}^{\infty} \|U(x,s), Z(x,s)\|_{2n} dx ds$$

$$\leq \sum_{k=1}^{n} \left\{ \frac{1}{\sqrt{\pi}} \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \frac{|h_{k}(q)|x}{d_{k}^{3/2}(s-q)^{3/2}} \exp\left(-x^{2}/4d_{k}(s-q)\right) dq dx dy$$

$$+ k \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \int_{0}^{\infty} \tilde{K}_{k}(s-q, y, x) \|(U(y,q), Z(y,q))\|_{2n} dy dq dx ds$$

$$+ k \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \|(U(x,q), Z(x,q))\|_{2n} dq dx ds \right\}.$$
(3.22)

Rewrite the right hand side of (3.22) as

$$\sum_{k=1}^{n} \{I_k + \overline{k}II_k + \overline{k}III_k\}.$$

Changing the order of integration in II_k we have

$$II_{k} = \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \int_{0}^{\infty} \widetilde{K}_{k}(s-q, y, x) ||(U(y, q), Z(y, q))||_{2n} dx dq dy ds$$
$$= \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} ||(U(y, q), Z(y, q))||_{2n} \int_{0}^{\infty} \widetilde{K}_{k}(s-q, y, x) dx dq dy ds.$$

Using (3.5) and deleting the term in $\exp(-(x+y)^2/4d_k(s-q))$ we can bound II_k above by

$$II_{k} = \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \left\| (U(y,q), Z(y,q)) \right\|_{2n} \int_{0}^{\infty} \frac{\exp\left(-(y-x)^{2}/4d_{k}(s-q)\right)}{\sqrt{4d_{k}(s-q)}} \, dx \, dq \, dy \, ds.$$

Now

$$\int_{0}^{\infty} \frac{\exp\left(-(y-x)^{2}/4d_{k}(s-q)\right)}{(4d_{k}(s-q))^{1/2}} dx$$

$$\leq 2 \int_{0}^{\infty} \frac{\exp\left(-x^{2}/4d_{k}(s-q)\right)}{(4d_{k}(s-q))^{1/2}} dx \quad \text{for all} \quad y \ge 0.$$

for all $y \ge 0$, $s > q \ge 0$.

Thus

$$II_k \leq \text{constant} \int_0^t \int_0^\infty \int_0^s \left\| (U(y,q), Z(y,q)) \right\|_{2n} dq \, dy \, ds.$$

Comparing the right hand side with III_k , we see that (3.23) implies

$$II_{k} + III_{k} \leq \text{constant} \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} ||U(x,q), Z(x,q)||_{2n} dq \, dx \, ds.$$
(3.24)

Now returning to (3.22), we have

$$I_{k} \leq \text{constant} \int_{0}^{t} \int_{0}^{\infty} \int_{0}^{s} \frac{|h_{k}(q)|x \exp(-x^{2}/4d_{k}(s-q))}{(s-q)^{3/2}d_{k}^{3/2}} dq \, dx \, ds$$

and on rearranging the order of integration

$$I_{k} \leq \text{constant} \int_{0}^{t} |h_{k}(q)| \int_{q}^{t} \frac{1}{d^{1/2}(s-q)^{1/2}} \int_{0}^{\infty} \frac{2x \exp(-x^{2}/4d_{k}(s-q))}{4d_{k}(s-q)} dx \, ds \, dq.$$

Now

$$\int_{0}^{\infty} \frac{2x}{4d_{k}(s-q)} \exp(-x^{2}/4d_{k}(s-q)) \, dx = 1$$

so

$$I_k \leq \text{constant}(d_k) \int_0^t |h_k(q)| \int_q^t \frac{1}{(s-q)^{1/2}} ds dq$$

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Now

$$\int_{q}^{t} \frac{ds}{(s-q)^{1/2}} \leq 2t^{1/2} \quad \text{for all} \quad t \geq q \geq 0.$$

Thus

$$I_{k} \leq \text{constant} \int_{0}^{t} t^{1/2} |h_{k}(q)| dq$$

$$\leq \text{constant} T^{1/2} \int_{0}^{t} |h_{k}(q)| dq$$

$$\leq \text{constant} T^{1/2} ||h_{k}||_{1} ds. \qquad (3.25)$$

Now using (3.24) and (3.25) in (3.22) we obtain

$$\int_{0}^{t} \int_{0}^{\infty} \|(U(x,s), Z(x,s))\|_{2n} dx ds$$

$$\leq \text{constant} (T^{1/2}) \|h\|_{1} + \text{constant} \int_{0}^{t} \int_{0}^{s} \int_{0}^{\infty} \|(U(x,q), Z(x,q))\|_{2n} dx dq ds.$$
(3.26)

Now applying Gronwall's inequality to (3.26) we obtain the estimate (3.21) as required.

Now we must establish (3.20), which in turn establishes (3.12). In a similar manner to that by which we obtained (3.22) we have

$$\int_{0}^{T} \int_{0}^{\infty} \frac{\|(U(y,s), Z(y,s))\|_{2n}}{(T-s)^{1/2}} dy ds$$

$$\leq \text{constant} \sum_{k=1}^{n} \left\{ \int_{0}^{T} \int_{0}^{\infty} \int_{0}^{s} \frac{|h_{k}(q)|}{(T-s)^{1/2}} \frac{x}{(s-q)^{3/2}} \exp\left|\frac{-x^{2}}{4(s-q)d_{k}}\right| dq dx ds$$

$$+ k \int_{0}^{T} \int_{0}^{\infty} \int_{0}^{s} \int_{0}^{\infty} \frac{1}{(T-s)^{1/2}} \tilde{K}_{k}(s-q, y, x) \|U(y, q), Z(y, q)\|_{2n} dy dq dx ds$$

$$+ k \int_{0}^{T} \int_{0}^{\infty} \int_{0}^{s} \frac{\|(U(x, q), Z(x, q))\|_{2n}}{(T-s)^{1/2}} dq dx ds \right\}.$$
(3.27)

Say

$$\leq \operatorname{constant} \sum_{k=1}^{n} \{ IV_k + V_k + VI_k \}.$$

Now $V_k \leq \text{constant } VI_k$, by the same argument used to obtain (3.23). Thus we have

$$V_{k} + VI_{k} \leq \text{constant} \int_{0}^{T} \int_{0}^{\infty} \int_{0}^{s} \frac{\|(U(x,q), Z(x,q))\|_{2n}}{(T-s)^{1/2}} dq \, dx \, ds$$

$$\leq \text{constant} \int_{0}^{T} \frac{1}{(T-s)^{1/2}} \int_{0}^{\infty} \int_{0}^{s} \|(U(x,q), Z(x,q))\|_{2n} dq \, dx \, ds$$

$$\leq \text{constant} \|h\|_{1,n} \int_{0}^{T} \frac{ds}{(T-s)^{1/2}}$$
(3.28)

using (3.21).

Now rearranging the order of integration in IV_k we obtain

$$IV_{k} = \text{constant} \int_{0}^{T} \left| h_{k}(q) \right| \int_{q}^{T} \frac{1}{(T-s)^{1/2}} \frac{1}{(s-q)^{1/2}} \int_{0}^{\infty} \frac{2x}{(s-q)4d_{k}} \exp\left(-\frac{x^{2}}{4d_{k}}(s-q)\right) dx \, ds \, dq.$$

Continuing as we did to obtain (3.25) we have

$$IV_{k} = \text{constant} \int_{0}^{T} |h_{k}(q)| \int_{q}^{T} \frac{1}{(T-s)^{1/2}} \frac{1}{(s-q)^{1/2}} \, ds \, dq.$$

But

$$\int_{q}^{T} \frac{1}{(T-s)^{1/2}} \frac{1}{(s-q)^{1/2}} ds = \pi.$$

Thus

$$IV_{k} \leq \text{constant} \int_{0}^{T} |h_{k}(q)| dq$$
$$\leq \text{constant} ||h||_{1,n}. \tag{3.29}$$

Now using (3.28) and (3.29) in (3.27) we have (3.20) as required. This proves (3.13).

Proof of (3.14). From (3.9) we have

$$Z(x,t) = \sigma \int_{0}^{t} e^{\gamma(s-t)} A U(x,t) \, ds$$

so

$$|Z(x,t)| \leq ||Z(x,t)||_{n} \leq \bar{\sigma} \int_{0}^{T} e^{\gamma(s-t)} ||A|| \cdot ||U(x,s)||_{n} ds$$
$$\leq \bar{\sigma} ||A|| \int_{0}^{T} \sum_{k=1}^{n} |u_{k}(x,s)| ds$$

where

$$\bar{\sigma} = \max_{j} \{\sigma_{j}\}$$
 and $\gamma = \min_{j} \{\gamma_{j}\}.$ (3.30)

Now using (3.5), (3.6) and (3.15) we have for k = 1, ..., n;

$$\int_{0}^{T} |u_{k}(x,s)| ds \leq \text{constant} \left\{ \int_{0}^{T} \int_{0}^{s} \frac{|h_{k}(q)| x \exp(-x^{2}/4d_{k}(s-q))}{(s-q)^{3/2}} dq \, ds + k \int_{0}^{T} \int_{0}^{s} \int_{0}^{\infty} \tilde{K}_{k}(s-q,y,x) || (U(y,q), Z(y,q)) ||_{2n} dy \, dq \, ds \right\}$$

$$\leq \text{constant} \int_{0}^{T} |h_{k}(q)| \int_{q}^{T} \frac{x}{(s-q)^{3/2}} \exp(-x^{2}/4d_{k}(s-q)) \, ds \, dq$$

$$+ \text{constant} \int_{0}^{T} \int_{0}^{s} \int_{0}^{\infty} \frac{||(U(y,q), Z(y,q))||_{2n}}{(s-q)^{1/2}} \, dy \, dq \, ds \qquad (3.31)$$

where we have used (3.19) to bound \tilde{K}_k .

Now consider

$$\int_{q}^{T} \frac{x}{(s-q)^{3/2}} \exp(-x^2/4d_k(s-q)) \, ds = J.$$

.

Set $z = x/(\sqrt{s-q})$, then

$$J \leq \int_{0}^{\infty} \exp\left(-z^2/4d_k\right) dz = \text{constant}.$$

Thus the first term on the right of (3.31) is bounded by a constant multiplied by $||h||_{1,n}$. Consider the second term in (3.31)

$$\int_{0}^{T} \int_{0}^{s} \int_{0}^{\infty} \frac{\|U(y,q), Z(y,q)\|_{2n}}{(s-q)^{1/2}} dy dq ds$$

=
$$\int_{0}^{T} \int_{0}^{\infty} \int_{q}^{T} \frac{\|U(y,q), Z(y,q)\|_{2n}}{(s-q)^{1/2}} ds dy dq$$

=
$$\int_{0}^{T} \int_{0}^{\infty} \|U(y,q), Z(y,q)\|_{2n} \int_{q}^{T} \frac{1}{(s-q)^{1/2}} ds dy dq.$$

But

$$\int_{q}^{T} \frac{1}{(s-q)^{1/2}} ds = [2(s-q)^{1/2}]_{q}^{T} \leq 2T^{1/2}.$$

Thus the right hand side of (3.31) is bounded above by

constant
$$||h||_{1,n}$$
 + constant $\int_{0}^{T} \int_{0}^{\infty} ||(U(y,q), Z(y,q))||_{2n} dy dq$
 $\leq \text{constant } ||h||_{1,n}, \text{ using (3.21).}$

Thus (3.30) is bounded above by a constant multiple of $||h||_{1,n}$, which establishes (3.14), and proves the theorem.

Remark. The growth of k^* follows from the constant in (3.17) which is $O((T-t_0)^{-1})$ and the constant in (3.21) which is obtained via Gronwall's inequality.

4. Stability via contracting rectangles

In this section we study the stability of the zero solution of (2.2), (3.1) and (3.2). We show that if $||h||_{1,n}$ is sufficiently small, then we have exponential decay.

Theorem 4.1. Suppose that H1 of §3 holds. Then there exist positive constants c, k and λ such that if

$$\|h\|_{1,n} \leq \lambda$$

then the solution (U(x,t), Z(x,t)) of the Dirichlet problem (2.2), (3.1), (3.2) satisfies

$$\|U(\cdot,t),Z(\cdot,t)\|_{\infty,2n} \leq k \exp(-ct) \qquad t \geq 0$$

where k and λ depend on T, t₀, M₀ and G and c depends on G.

Proof. It suffices to show that for $t \ge t_0$ and x > 0 there exists a rectangle $R \subset R_c$, contracting for G(U, Z), with the property

$$\bar{D}P_{R}((U(t), Z(t)) \leq -cP_{R}(U(t), Z(t)).$$
(4.1)

To construct R, recall that by Theorem 3.1,

$$\|(U(\cdot, t), Z(\cdot, t))\|_{\infty, 2n} \leq k \|h\|_{1, n}$$
 $t > t_0$

Thus if $||h_1||_{1,n}$ is sufficiently small, there is a compact set $Q \subset \operatorname{int} R_C$ (see H1, §3) such that $(U(t, x), Z(t, x)) \in Q$ for all $x \ge 0$. Hence there is a contracting rectangle for G such that

$$P_{R}((U(\cdot, t), Z(\cdot, t))) < 1 \text{ for } t > t_{0}.$$

We divide the proof that R has the property (4.1) into two cases. Suppose $t > t_0$:

(a) If t is such that

$$P_R((U(\cdot, t), Z(\cdot, t))) > P_R((U(0, t), Z(0, t)))$$

then Lemma 2.4 immediately implies (4.1).(b) If t is such that

 $P_{R}((U(\cdot, t), Z(\cdot, t))) = P_{R}((U(0, t), Z(0, t)))$

let

$$P_{R}((U(\cdot,t),Z(\cdot,t))) = s \text{ and set}$$
$$X = \{x : (U(x,t),Z(x,t)) \in \partial(sR)\}.$$

Then X is not empty, since $0 \in X$ and X is compact since

$$\lim_{x \to \infty} (U(x, t), Z(x, t)) = (0, 0).$$

Let $\Theta = \Theta_1 \cup \{0\}$, be such that Θ is a bounded neighbourhood of X and $0 \notin \Theta_1$. For $t \ge t_0$ we have

$$U(0,t) = 0$$
 and $Z_t(0,t) = -\gamma Z(0,t)$

by hypothesis on h.

Thus $Z(0, t+\eta) = e^{-\gamma \eta} Z(0, t)$, which implies

$$\bar{D}P_{R}((U(0,t+\eta),Z(0,t+\eta))) = -P_{R}((U(0,t+\eta),Z(0,t+\eta)))\gamma < -\frac{\gamma s}{2}$$

So for $|\eta|$ small, $\eta \neq 0$,

$$P_{R}((U(0, t+\eta), Z(0, t+\eta))) \leq s\left(1-\frac{\gamma\eta}{2}\right).$$
 (4.2)

Note by the proof of the Basic Lemma, §3.2, [6], there is a constant $k_1 > 0$ depending on R such that

(i) If $|\eta|$ is small and $\theta \in \Theta_1$

$$P_{R}((U(\theta, t+\eta), Z(\theta, t+\eta))) \leq s(1-k_{1}\eta).$$

$$(4.3)$$

(ii) If $|\eta|$ is small and $x \in R_+ - \Theta$

$$P_{R}((U(x,t+\eta),Z(x,t+\eta))) \leq s(1-k_{1}\eta).$$
(4.4)

Now by (4.2), (4.3) and (4.4) we have for $t > t_0$, $x \ge 0$

$$P_R((U(x,t+\eta),Z(x,t+\eta))) \leq s(1-k_2\eta)$$

where $k_2 = \min(k_1, \gamma/2)$.

Thus $\overline{D}P_{R}((U(\cdot, t), Z(\cdot, t))) \leq -k_{2}s$ which implies (4.1).

Putting parts (a) and (b) together we see that (4.1) is satisfied for all $t > t_0$. Therefore there exist positive constants k and c such that

$$P_R((U(\cdot,t),Z(\cdot,t))) \leq k \exp(-ct)$$

for all $t \ge 0$. This proves the theorem.

5. Global stability of zero for short nerve bundles

Consider the following model for a nerve bundle of length L > 0

$$W_{t} = MW_{xx} + F(W) - Z$$

$$0 \le x \le L$$

$$Z_{t} = \sigma W - \gamma Z$$
(5.1)

Here $W(x,t), Z(x,t): [0,L] \times \mathbb{R}^+ \to \mathbb{R}^n$, and σ, γ and F are as in (*), which is described in the Introduction, §0. In particular, M is a real symmetric matrix with eigenvalues d_1, \ldots, d_n satisfying

$$0 < d_1 \leq d_2 \leq \cdots \leq d_n$$

We impose the following initial and boundary conditions on W and Z

$$W(x,0) = W_0(x); Z(x,0) = Z_0(x), \qquad 0 \le x \le L$$
(5.2)

$$W(0,t) = h(t), \quad t \ge 0$$
 (5.3)

and either;

$$W(L,t) = 0, \qquad t \ge 0 \tag{5.4}$$

or

$$W_x(t,L) + PW(t,L) = 0, \quad t \ge 0.$$
 (5.5)

Here W_0 , Z_0 and h are prescribed functions and P is a real $(n \times n)$ matrix, such that the product MP is positive definite.

We suppose that the stimulus h(t) is non-zero only over a finite time interval [0, t] say. Then for $t \ge T$, (W, Z) satisfies a mixed problem with homogeneous boundary data.

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Theorem 5.1. Suppose (W, Z) is a classical solution of (5.1)–(5.3) and one of (5.4) or (5.5) and h(t)=0 for $t \ge T$.

Set

$$s = \max_{k=1,\ldots,n} \left\{ \sup_{y \in \mathbf{R}} f_k(y) / y \right\}.$$

Then

$$L < \frac{\pi}{2} \left(\frac{d_1}{s} \right)^{1/2}$$

implies

$$\|(W,Z)\|_{L_2([0,L])} \leq Ke^{-\alpha t}$$

for some constants K, $\alpha > 0$.

Proof. Suppose (W, Z) is a solution of (5.1)–(5.3) and one of (5.4) to (5.5). Using (5.1) to express $W^T W_t + Z^T \sigma^{-1} Z_t$ we obtain

$$\frac{1}{2}\frac{\partial}{\partial t}\left\{Z^{T}\sigma^{-1}Z+W^{T}W\right\}=W^{T}F(W)-Z^{T}\sigma^{-1}\gamma Z+W^{T}MW_{xx}.$$

Integrating with respect to x over [0, L], we obtain

$$\frac{1}{2} \frac{\partial}{\partial t} \int_{0}^{L} (Z^{T} \sigma^{-1} Z + W^{T} W) dx = \int_{0}^{L} (W^{T} F(W) - Z^{T} \sigma^{-1} \gamma Z + W^{T} M W_{xx}) dx.$$
(5.6)

Now

$$\int_{0}^{L} W^{T} \cdot MW_{xx} = -\int_{0}^{L} W_{x}^{T} MW_{x} dx + [W^{T} MW_{x}]_{0}^{L}.$$

Now

$$W(0,t)^T M W_x(0,t) = 0 \quad \text{for} \quad t \ge T$$

by (5.3) and hypothesis on h. Either

$$W(L,t)^{T}$$
. $MW_{x}(L,t) = 0$ by (5.4)

or

$$W(L,t)^{T} \cdot MW_{x}(L,t) = -W(L,t)^{T} \cdot MPW(L,t)$$

 ≤ 0 by hypothesis on M and P.

Thus

$$\int_{0}^{L} W^{T} \cdot M W_{xx} dx \leq -\int_{0}^{L} W_{x}^{T} M W_{x} dx$$
$$\leq -d_{1} \int_{0}^{L} W_{x}^{T} W_{x} dx$$
$$\leq -\mu d_{1} \int_{0}^{L} W^{T} \cdot W dx$$
(5.7)

where $\mu = (\pi/2L)^2$ is the smallest eigenvalue of the operator $\partial^2/\partial x^2$ with Dirichlet boundary conditions at x=0, and Neumann boundary conditions at x=L (see[2], Chapter 6).

Now, for k = 1, ..., n, set $s_k = \sup_{y \in \mathbb{R}} \{f_k(y)/y\}$ (see Figure 1 below).

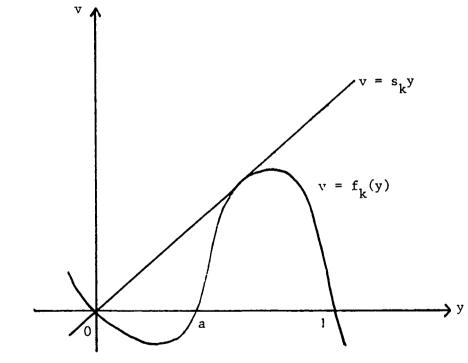


Figure 1

Then

 $s_k y^2 \ge f_k(y) y$ for all $y \in \mathbb{R}$.

Let $s = \max_k \{s_k\}$. Then

$$sW^T \cdot W \ge W^T \cdot F(W)$$
 for all $W \in \mathbb{R}^n$. (5.8)

Using the estimates (5.7) and (5.8) in (5.6), we obtain

$$\frac{1}{2} \frac{\partial}{\partial t} \int_{0}^{L} (W^{T} \cdot W + Z^{T} \sigma^{-1} Z) \leq \int_{0}^{L} ((s - \mu d_{1}) W^{T} \cdot W - Z^{T} \cdot \gamma \sigma^{-1} Z) dx.$$
(5.9)

If $s < \mu d_1$ in(5.9), then

$$\frac{1}{2}C_1 \frac{d}{dt} \| (W, Z) \|_{L_2([0, L])} \leq -C_2 \| (W, Z) \|_{L_2([0, L])} \quad \text{for} \quad t \geq T,$$

where $C_1 = \min\{1, \sigma_i^{-1}\} > 0$

and $C_2 = \min \{\gamma_i / \sigma_i, (\mu d_1 - s)\} > 0.$

It follows that $||(W,Z)||_{L_2([0,L])}$ decays exponentially for $t \ge T$. Since $||(W,Z)||_{L_2([0,L])}$ is bounded for $t \in [0, t)$, the result follows by noticing that $\mu d_1 > s$ is equivalent to

$$L^2 < \pi^2 d_1/4s.$$

REFERENCES

1. J. BELL, Modelling parallel unmyelinated axons: Pulse trapping and ephaptic transmission, SIAM Journal of Appl. Math. 41 (1981).

2. R. COURANT and D. HILBERT, Methods of mathematical physics, Vol. 1 (Interscience, N.Y., 1966).

3. R. FitzHugh, Mathematical models of excitation and propagation in nerve fibres, *Biological Engineering*, Ed. H. P. Schwan (McGraw-Hill, N.Y., 1969).

4. P. GRINDROD and B. D. SLEEMAN, Qualitative analysis of reaction-diffusion systems modelling coupled unmyelinated nerve axons, IMA J. Math. Appl. in Med. and Biol. 1 (1984).

5. P. GRINDROD and B. D. SLEEMAN, Comparison Principles in the Analysis of Reaction-Diffusion Systems Modelling Unmyelinated Nerve Fibres (Dundee University Applied Analysis Report AA843, 1984).

6. J. RAUCH and J. A. SMOLLER, Qualitative theory of the FitzHugh-Nagumo equations, Adv. in Math. 27 (1978).

7. M. E. SCHONBECK, Boundary value problems for the FitzHugh-Nagumo equations, J. Diff. Eqns. 30 (1978).

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