

TRAVELING PULSES IN A NONLOCAL EQUATION ARISING NEAR A SADDLE-NODE INFINITE CYCLE BIFURCATION*

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Abstract. We formally derive a simple normal form for the dynamics of a nonlocally coupled neural field model when the local dynamics is near a saddle-node infinite cycle (SNIC) bifurcation. The derivation produces a nonlocally coupled scalar model which does not satisfy the comparison principle (ordered initial data produces ordered dynamical solutions). We prove the existence of unique traveling waves for the corresponding nonlocal evolution problem with a new tool that does not use the comparison principle. We obtain sharp estimates for the speed of fast and slow waves and compare these to numerical results.

Key words. traveling waves, nonlocal equations, neural field

AMS subject classifications. 92C20, 45G10, 34B15

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1. Introduction. Traveling pulses occur widely in excitable media such as the action potential in the squid giant axon [17]. In models of the axon and related systems, coupling is through local diffusion and existence of such waves is shown by reducing the partial differential equation to an ordinary differential equation and then using shooting methods to prove existence of homoclinic orbits [15, 3]. Such pulses also occur in cerebral cortex slices [13, 25], and there have been a number of models that describe them [24, 1, 5]. In the models for such cortical pulses, propagation of activity is not via diffusion, but rather through nonlocal spatial convolutions. Ermentrout and McLeod [8] showed the existence of front solutions in a scalar nonlocal equation, and these results have been generalized by Chen [4]. Pinto and Ermentrout used the results in [8] to construct traveling pulses in a slow fast equations where fronts and backs were “glued” together by matching. They also constructed solutions when the nonlinearity was a step-function. Hastings [15] and Faye [10] have also recently constructed pulses in these singular systems with a smooth nonlinearity.

In this paper, we will study the existence of pulses in a very simple model based on the so-called theta neuron that is a scalar representative of an excitable medium. We first derive the equation that we will study from a formal expansion for a spatially coupled system near a saddle-node infinite cycle (SNIC) bifurcation for which the theta model is a normal form. We then turn to the analysis of the resulting nonlocal equations, which turns out to require proving the existence of a front to a particular set of equations. While this may sound like the results of [4], the dynamical system that we obtain here does not obey a comparison principle; e.g., large initial data may not yield large solutions. Thus, many tools for parabolic local and nonlocal equations such as [4] do not apply. A similar paper [23] studied a nonlocally coupled theta model where the interaction was through time-dependent synapses rather than pulse coupling as in this paper. We will highlight differences in the discussion.

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2. Derivation of the model. Neural field models describe populations of excitatory and inhibitory neurons in some spatial region. Each spatial location is typically represented by a pair of variables $(e(x, t), i(x, t))$ that describe the probability that neurons at that location are firing at some given time. The local behavior (in absence of space) is determined by the dynamics of the planar system:

$$(2.1) \quad \begin{aligned} e_t &= -e + f(a_{ee}e - a_{ie}i - b_e), \\ \tau i_t &= -i + f(a_{ei}e - a_{ii}i - b_i). \end{aligned}$$

All parameters are positive with a_{jk} representing the connection strengths between the populations, τ a relative time scale for the inhibition, and $b_{e,i}$ firing thresholds. Waves occur when the local behavior is excitable and the coupling is dominated by connections between the excitatory cells, $e(x, t)$. There are two classes of excitability [26] called Class I and Class II. Most of the analysis of waves in excitable neural media have considered only Class II excitable media [14, 2, 1, 24, 11]. Here, we are interested in Class I excitability which is characterized as being close to a SNIC bifurcation [26, 19]. This bifurcation arises when a dynamical system has an invariant circle formed by a pair of heteroclinic orbits joining two fixed points (Figure 1A). As some parameter varies, the two fixed points merge at a saddle-node, leaving one fixed point and a homoclinic orbit (Figure 1B), and then disappear, leaving a limit cycle (Figure 1C). We now formally derive a simple "normal form" for the propagation of waves in the Class I excitable neural field model by adding weak spatial interactions to (2.1) and assuming that they are near the SNIC bifurcation depicted in Figure 1B.

For simplicity of the derivation, we will assume coupling only between the excitatory variables although we can derive similar equations with full coupling (see remarks below). We first review the singular perturbation argument for (2.1) at the SNIC, $(e, i)^T := U$. The behavior near the equilibrium point is governed by the so-called outer equation,

$$\frac{dz}{ds} = qz^2 + \eta,$$

where $s = \epsilon t$ is the slow time scale. We assume $q > 0$, and when $\eta > 0$, the equation for z blows up periodically. In [6], it was shown that the full orbit around the SNIC consists of the outer equation combined with the so-called inner equation (the actual global homoclinic orbit) and the common part of the expansion. Combining these together, it was found that

$$(2.2) \quad U(s) = U_0 + (U_H(s/\epsilon) - U_0) + \epsilon \left[z(s) - \frac{1}{\pi/2 - \sqrt{|\eta q|}s} - \frac{1}{-\pi/2 - \sqrt{|\eta q|}s} \right] \Phi.$$

The part of the equation involving z does not blow up as the singular parts are subtracted away.

With these preliminaries in mind, we now sketch the derivation of the model that will be the subject of our analysis.

$$(2.3) \quad \begin{aligned} e' &= -e + f \left(a_{ee}e - a_{ie}i - b_{e0} + \epsilon \left[c_e \int_R J(x-y)e(y, t) dy - e(x, t) \right] + \epsilon^2 b_{e1} \right), \\ i' &= [-i + f(a_{ei}e - a_{ii}i - b_i)]/\tau. \end{aligned}$$

We have chosen the threshold parameter for the excitatory population to be the value for which there is a saddle node, b_{e0} , so that b_{e1} represents the perturbation away

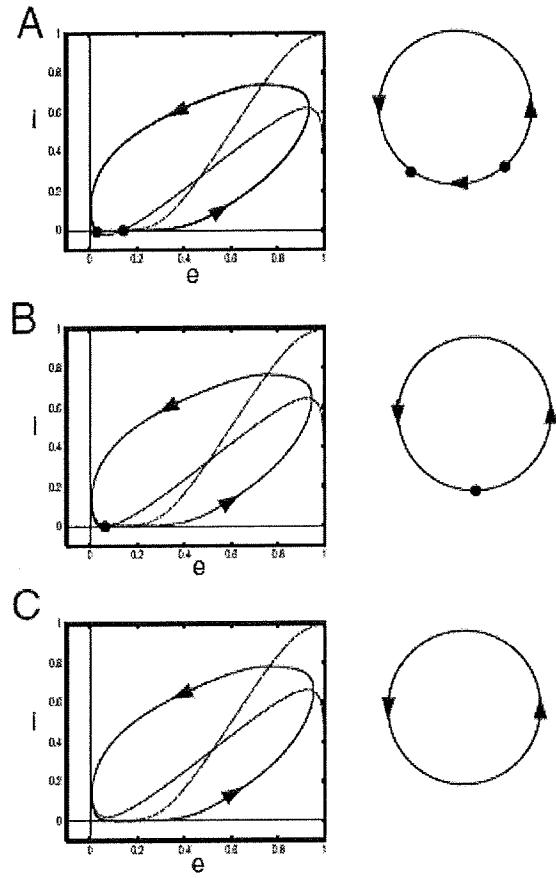


FIG. 1. *Class I excitability in (2.1) as the threshold b_e decreases showing transition from excitable to oscillatory behavior. In each panel, the solid curves show the invariant circle; the dashed curves are the excitatory nullcline ($de/dt = 0$) and the inhibitory nullcline ($di/dt = 0$). (A) Two equilibria lie on an invariant circle formed by a pair of heteroclinic orbits. (B) The two equilibria merge at a saddle-node with a homoclinic orbit. (C) Limit cycle. In (A), $f(u) = 1/(1 + \exp(-u))$, $a_{ee} = 15, a_{ie} = 12, a_{ei} = 25, a_{ii} = 10, b_e = 3.9, b_i = 10, \tau = 3$ for the top panel. In the next two panels, $b_e = 3.6, 3.4$, respectively.*

from this. (In keeping with the fact that there is a local saddle-node bifurcation, the perturbation of the parameter governing the saddle node is order ϵ^2 .) Setting $\epsilon = 0$, we let (e_0, i_0) denote the fixed point and A the linearization at the equilibrium. By assumption, there is a vector Φ such that $A\Phi = 0$, and since 0 is a simple eigenvalue, there is a vector Ψ with $A^T\Psi = 0$ and $\Psi \cdot \Phi = 1$. We can expand the $\epsilon = 0$ right-hand side of (2.3) as $AU + Q(U, U) + \dots$, where $Q(U, U)$ represents the quadratic terms of the Taylor expansion around (e_0, i_0) . Applying the methods in [18], we see that near the equilibrium

$$U(x, t) = U_0 + \epsilon z(x, s)\Phi + O(\epsilon^2).$$

$z(x, s)$ satisfies the outer equation:

$$(2.4) \quad \frac{\partial z(x, s)}{\partial s} = q_2 z^2 + q_0 b_{e1} + \frac{1}{\epsilon} \Psi \cdot [f_e c_e \int_R J(y) e(y, s) dy - e(x, t)],$$

where

$$\begin{aligned} f_e &= f'(a_{ee}e_0 - a_{te}i_0 - b_{e0}), \\ q_2 &= \Psi \cdot Q(\Phi, \Phi), \\ q_0 &= \Psi \cdot [f_e, 0]^T. \end{aligned}$$

We have purposely left the coupling part unsimplified and unexpanded since we have to incorporate the full asymptotic expansion from (2.2). There are two pieces in the coupling term—the outer part, which we will defer for the moment, and the inner part, which consists of the large homoclinic orbit. Let $\zeta(x)$ denote the time (in slow time units) at which the excitatory population at x fires (that is, traverses the homoclinic orbit); there may be multiple times, but let us focus on the first time. The term $\Psi \cdot [e_H((s - \zeta(x))/\epsilon) - e_0]/\epsilon$ is nothing more than a weighted Dirac delta function as $\epsilon \rightarrow 0$, so the fast inner part of the coupling takes the form of a delta function. Now, what about the order ϵ terms? These take the form of

$$f_e c_e d_2 \left[\int_R J(y) z(x - y, s) dy - z(x, s) \right],$$

along with the corrections to account for the matching as in (2.2), so that combining with the inner equation, we obtain the following equation for $z(x, s)$:

$$(2.5) \quad \frac{\partial z(x, s)}{\partial s} = q_2 z^2 + q_0 b_{e1} + c_e f_e \int_R J(x - y) [d_1 \delta(s - s^*(y)) + d_2 (z(y, s) - z(x, s))] dy.$$

Here $s^*(x)$ is the time at which the excitation at spatial point x traverses the homoclinic. Finally, we let $z(x, s) = \tan(\theta(x, s)/2)$, so that z blows up when $\theta \rightarrow \pi$, where it is reset to $-\pi$. Equation (2.5) becomes

$$(2.6) \quad \frac{\partial \theta(x, s)}{\partial s} = q_2 (1 - \cos(\theta)) + (1 + \cos \theta) \left[q_0 b_{e1} + c_e f_e \int_R J(x - y) [d_1 \delta(\theta(y, s) - \pi) + d_2 (R(\theta(y, s)) - R(\theta(x, s)))] dy \right]$$

$$(2.7) \quad R(\theta) = \tan(\theta/2) - \frac{2}{\pi - \theta} + \frac{2}{\pi + \theta}.$$

The term $R(\theta)$ is the correction in terms of θ that appears in (2.2) and keeps the behavior near the saddle node bounded for all θ . We remark that $R(\theta)$ is defined only on $(-\pi, \pi)$, has a finite limit as $\theta \rightarrow \pm\pi$, and can be extended periodically.

Although (2.6) represents a significant reduction of the full model, it is still very hard to prove anything about it. In Figure 2A, we show a plot of $R(\theta)$ along with a smooth delta function $\delta_s(\theta)$. The main roles of R are to provide a small amount of positive input right before the delta function and to prevent the neural population at x from firing again once it has crossed π since R is negative for $\theta \in (0, -\pi)$, the interval after the neurons have fired. Thus, to simplify the reduced model, we include only the smooth delta function, but we shift the peak of it from π to $\theta_T < \pi$ so that the neuron will fire with smaller input and take longer to recover once it has fired. Figure 2B shows the traveling wave for the full version of (2.6) and for the case in which we only include the shifted smooth delta function. The red and black curves represent the full version of the equations (with $R(\theta)$) at locations 100, 150, and the green and blue depict the same for the solution when we only use the shifted smooth

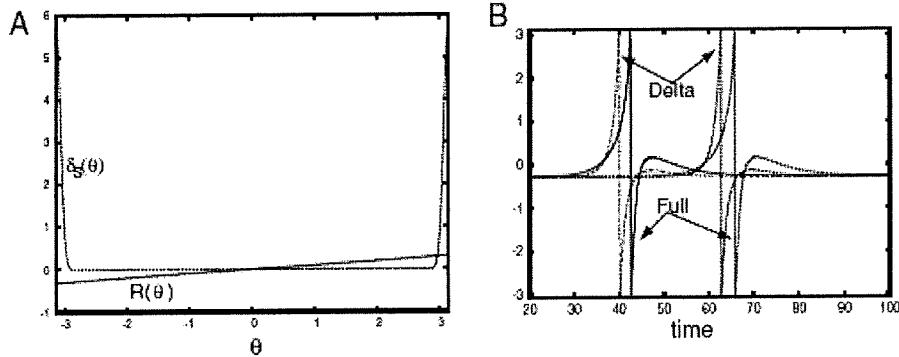


FIG. 2. The reduced model near the SNIC. (A) Plot of the function $R(\theta)$ defined by (2.7) (solid line) and the smooth delta function, $\delta_s(\theta) = \exp(-200(1 + \cos \theta))/\sqrt{(\pi/100)}$. (B) Numerical solutions to the spatially discretized version of (2.6) at location 100 (left) and location 150 (right) with full equation, $q_2 = 1$, $q_{\text{abet}} = -0.02$, $d_1 = d_2 = 1$, $c_{\text{effe}} = 4.2$, and with Dirac delta function, $d_2 = 0$, $c_{\text{effe}} = 8$, $\theta_T = 2.5$.

delta function. Since the shape is similar and the velocity is also similar, we will focus here on the simplified version of (2.6), where we set $d_2 = 0$. For the analysis and theorems that follow, we first look at the case of a Dirac delta function and then look at the smooth version of it.

Remarks. I. As we noted in the formal derivation of the model, we only included excitatory-excitatory connections. A natural question is how (2.6) would change with other types of coupling. Instead of the integral term in (2.4), we would obtain

$$\Psi \cdot \begin{pmatrix} f_e(c_{ee}(J_{ee}(x) * e - e) - c_{et}(J_{et}(x) * i - i)) \\ (f_t/\tau)(c_{te}(J_{te}(x) * e - e) - c_{tt}(J_{tt}(x) * i - i)) \end{pmatrix},$$

where $J(x) * e$ means the convolution over the real line. The part of (2.6) that includes the Dirac delta function would consist of the convolution with a function $J(x)$ that is a weighted sum of the four functions J_{ee} , J_{te} , J_{et} , J_{tt} , and the “outer” portion (terms with the function $R(\theta)$) would have a different weighted sum for the convolution. For example, the effective $J(x)$ could have regions where it is positive and negative which could oppose the formation of traveling waves; or the effective $J(x)$ could, again, be similar to the case with pure excitation. For simplicity, we restrict our attention to the case shown in (2.6).

II. In Figure 2, we have plotted the numerical solutions to (2.6) in such a way that they look like traveling pulses by plotting θ on the interval $[-\pi, \pi]$. We note that the traveling waves here are *fronts*, but since $\theta(x, s)$ lies on a circle, the starting and ending points are physically the same point but are just unwrapped from the circle, similar to the pulses computed in [9].

3. Preliminaries. Henceforth, we will set $d_2 = 0$ in (2.6), rescale time ($q_2 s = t$), let $\theta(x, s) = u(x, t)$, set $\beta = c_{\text{effe}} d_1 / q_2$, and set $-a^2 = q_0 b_{e1} / q_2$ so that we now consider monotonic traveling waves for the evolution problem

$$(3.1) \quad u_t = 1 - \cos u + (1 + \cos u)(\beta J(x) * Q(u(x, t)) - a^2) \quad \text{on } \mathbb{R} \times (0, \infty),$$

where $u = u(x, t)$ is the unknown function, $*$ is convolution as above, and a and β are positive constants. By a *traveling wave*, we search for a solution of the form $u(x, t) =$

$v(x+ct)$, where c is a constant. Thus, we are looking for $(c, v) \in (0, \infty) \times C^1(\mathbb{R})$ such that

$$(3.2) \quad \begin{cases} cv' = f(v) + \beta g(v)J(y) * Q(v(y)), & v' > 0 \quad \text{on } \mathbb{R}, \\ v(-\infty) = -\hat{\theta}_0, \quad v(\infty) = 2\pi - \hat{\theta}_0, \quad v(0) = \theta_1, \end{cases}$$

where θ_1 is a certain constant in $(\hat{\theta}_0, \pi)$ and

$$(3.3) \quad f(s) := 1 - a^2 - (1 + a^2) \cos s, \quad g(s) := 1 + \cos s,$$

and $\hat{\theta}_0$ is a root of

$$f(s) + g(s)\beta Q(s) = 0,$$

where we have assumed that $\int_{-\infty}^{\infty} J(x) dx = 1$. Throughout this paper, we will assume that $Q(s)$ is zero away from a neighborhood of θ_1 , so that $\hat{\theta}_0 = \theta_0$, where

$$\theta_0 := 2 \arctan a.$$

While in some of our numerical examples (such as Figure 2), $Q(\theta) > 0$ everywhere, at θ_0 , it is very small (less than 10^{-25} in Figure 2), so that θ_0 is very close to θ_0 .

We assume the following:

$$(A1) \quad J(z) = \frac{1}{2}e^{-|z|} \text{ for } z \in \mathbb{R}; \quad a \in (0, \infty); \quad \theta_0 := 2 \arctan a \in (0, \pi).$$

$$(A2) \quad Q \text{ is nonnegative, periodic with period } 2\pi, \text{ in } L^1((0, 2\pi)), \text{ and } \int_0^{2\pi} Q(s) ds = 1.$$

Note that since Q is not monotonic, the dynamical system does not obey a comparison principle; e.g., large initial data may not yield large solutions. Thus, the many tools for parabolic local and nonlocal equations do not apply. For this reason, in this paper, we shall consider only two special cases; one is a singular problem, and the other is a singular perturbation:

$$(A2S) \quad Q(\cdot) = \delta(\cdot - \theta_1) \text{ for some } \theta_1 \in (\theta_0, \pi); \text{ here } \delta(\cdot) \text{ is the Dirac mass concentrated at the origin.}$$

$$(A2R) \quad Q(\cdot) = 0 \text{ on } [-\theta_0, \theta_1] \cup [\theta_1 + \varepsilon, 2\pi - \theta_0], \text{ where } \theta_1 \in (\theta_0, \pi) \text{ and } 0 < \varepsilon < 2\pi - \theta_1 - \theta_0.$$

Our main results are the following.

THEOREM 1. *Assume (A1) and (A2S). Let*

$$(3.4) \quad a := \tan \frac{\theta_0}{2}, \quad b := \tan \frac{\theta_1}{2},$$

$$\beta_*(a, b) = \frac{16a(a+b)^2}{1+b^2}, \quad \beta^*(a, b) := \frac{2(a+b)^2(3b+8a)}{1+b^2}.$$

If $0 < \beta \leq \beta_(a, b)$, there does not exist any solution to (3.2).*

If $\beta \geq \beta^(a, b)$, there exists a unique traveling wave solution $(c, v) \in (0, \infty) \times C^1(\mathbb{R})$ of (3.2). In addition, denoting the wave speed by $c = S(\beta)$, we have $S(\cdot) \in C^\infty([\beta^*, \infty))$ and*

$$(3.5) \quad \begin{aligned} \frac{dS(\beta)}{d\beta} &> 0 \quad \forall \beta \geq \beta^*(a, b), \\ S(\beta) &= \frac{1+b^2}{4(a+b)^2} \beta - 2a + O\left(\frac{1}{\beta}\right) \quad \text{as } \beta \rightarrow \infty. \end{aligned}$$

THEOREM 2. *There exists a positive function $\varepsilon^*(\cdot, \cdot, \cdot)$ that does not depend on Q such that for each $\theta_0 \in (0, \pi)$, $\theta_1 \in (\theta_0, \pi)$, $\beta \geq \beta^*(a, b)$, and $\varepsilon \in (0, \varepsilon^*(\theta_0, \theta_1, \beta)]$, under the assumptions (A1), (A2), and (A2R), there exists a unique traveling wave solution $(c, v) \in (0, \infty) \times C^1(\mathbb{R})$ of (3.2). In addition, denoting by (c_s, v_s) the associated solution given by Theorem 1, then*

$$|c - c_s| + \|v - v_s\|_{L^\infty(\mathbb{R})} = O(\varepsilon).$$

Here and in what follows, $O(\varepsilon) = O(1)\varepsilon$, where $O(1)$ is a generic quantity bounded by a constant that does not depend on Q and ε .

Theorem 1 will be proven in section 4. Theorem 2 will be proven in section 5. Concluding remarks and possible extensions will be given in section 6.

4. The singular case. In this section we prove Theorem 1. We introduce an auxiliary function

$$(4.1) \quad w(x) := \beta J(x) * Q(v(x)).$$

Under the assumptions (A1) and (A2S), we can evaluate

$$(4.2) \quad J(x) * Q(v(x)) = \int_{\mathbb{R}} J(x-y) \frac{Q(v(y))}{v'(y)} dv(y) = \frac{J(x)}{v'(0)} = \frac{e^{-|x|}}{2v'(0)}.$$

Upon noting that $w' = w$ in $(-\infty, 0)$ and $w' = -w$ in $(0, \infty)$, we analyze and solve (3.2) as follows.

1. If (c, v) is a solution of (3.2), then (c, v, w) , with w defined by (4.1), satisfies

$$(4.3) \quad \begin{cases} cv' = f(v) + wg(v), & w' = w \quad \text{in } (-\infty, 0), \\ v(-\infty) = -\theta_0, & w(-\infty) = 0, \quad v(0) = \theta_1; \end{cases}$$

$$(4.4) \quad \begin{cases} cv' = f(v) + wg(v), & w' = -w \quad \text{in } (0, \infty), \\ v(0) = \theta_1, & w(0) = h; \end{cases}$$

$$(4.5) \quad h = w(0), \quad \beta = \frac{2w(0)[f(\theta_1) + g(\theta_1)w(0)]}{c}.$$

We solve (4.3), (4.4), and (4.5) as follows.

2. For each $c > 0$, we solve (4.3). Since $(-\theta_0, 0)$ is a saddle point on the v - w phase plane, there is a unique solution satisfying $v' > 0$ and $w' > 0$ on \mathbb{R} . We set $W_-(c) = w(0)$ and denote the trajectory by γ_1 ; see Figure 3.
3. For each $c > 0$ and $h > 0$ we solve (4.4). On the v - w phase plane, $(2\pi - \theta_0, 0)$ is a stable node. The reflection of γ_1 about the vertical line $v = \pi$, denoted by γ_1^* , is a trajectory of (4.4). Every trajectory of (4.4) that is below γ_1^* enters the equilibrium $(2\pi - \theta_0, 0)$ either from the left or from the right; see Figure 3. We denote by γ_2 the trajectory with $h = W_-(c)$. Then γ_2 enters $(2\pi - \theta_0, 0)$, either from the left or right.

When $c \in (2a, \infty)$, there exists $W_+(c) > 0$ such that when $h = W_+(c)$, the corresponding trajectory, denoted by γ_3^* , enters the equilibrium from the left in the eigendirection $[-1, (1+a^2)(c/2-a)]$. Trajectories lying between γ_1^* and

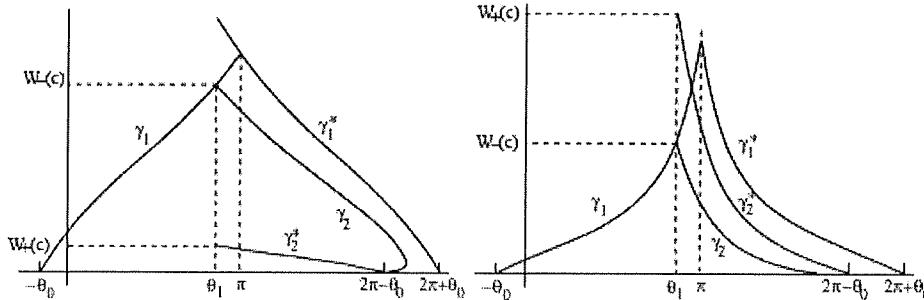


FIG. 3. A cartoon of the trajectory of (3.2) (with the condition $v' > 0$ deleted) which is the union of γ_1 and γ_2 . If $c \leq 2a$ or if $c > 2a$ and $W_-(c) > W_+(c)$, γ_2 lies between γ_1^* and γ_2^* so it enters the equilibrium from the right; see the left figure. If $c > 2a$ and $W_-(c) < W_+(c)$, then γ_2 lies below γ_2^* so it enters the equilibrium from the left; see the right figure.

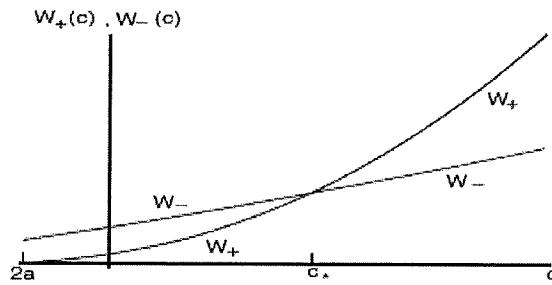


FIG. 4. Numerical evaluation shows that there is a $c_*(a, b) \in (2a, \infty)$ such that when $c \in (0, c_*)$, $W_-(c) > W_+(c)$; when $c \in (c_*, \infty)$, $W_-(c) < W_+(c)$. We have been unable to rigorously verify the uniqueness of the intersection of the curves $h = W_+(c)$ and $h = W_-(c)$.

γ_2^* enter the equilibrium from the right. Trajectories lying above the v -axis and below γ_2^* enter the equilibrium from the left.

Thus, when $h \in (0, W_+(c))$, the solution of (4.4) satisfies

$$(4.6) \quad v' > 0 > w' \text{ on } (0, \infty), \quad v(\infty) = 2\pi - \theta_0, \quad w(\infty) = 0.$$

If $W_-(c) \leq W_+(c)$, γ_2 enters the equilibrium from the left; if $W_-(c) > W_+(c)$, γ_2 enters the equilibrium from the right. The functions $W_{\pm}(c)$ are depicted in Figure 4.

When $c \in (0, 2a]$, γ_2^* is part of the v -axis, so $W_+(c) = 0$, and γ_2 enters the equilibrium from the right.

4. Define $(v(\cdot, c), w(\cdot, c))$ as the unique solution of (4.3) on $(-\infty, 0]$ and the unique solution of (4.4) with $h = W_-(c)$ on $(0, \infty)$. Then $(c, v(\cdot, c))$ is a solution of (3.2) if and only if

$$(4.7) \quad c > 2a, \quad \beta = B(c), \quad W_+(c) \geq W_-(c),$$

where, with $b := \tan \frac{\theta_1}{2}$ and $a = \tan \frac{\theta_0}{2}$,

$$(4.8) \quad B(c) := \frac{2W_-(c)}{c} \left(f(\theta_1) + W_-(c)g(\theta_1) \right) = \frac{4W_-(c)[b^2 - a^2 + W_-(c)]}{(1 + b^2)c}.$$

In summary,

- (a) if c satisfies (4.7), then $(c, v(\cdot, c))$ is a solution of (3.2);
- (b) if (c, v) is a solution of (3.2), then $v = v(\cdot, c)$ and c satisfies (4.7).

In conclusion, under the assumptions (A1) and (A2S),

the traveling wave problem (3.2) is equivalent to the algebraic problem (4.7).

5. To solve (4.7), we prove the following:

- (a) If $c \geq b + a$, then $B'(c) > 0$. In addition, $B \in C^\infty((0, \infty))$, and with β^* as in (3.4),

$$(4.9) \quad \max_{c \in [2a, b+2a]} B(c) < \beta^*(a, b), \quad \lim_{c \rightarrow \infty} \left[c - \frac{1+b^2}{4(a+b)^2} B(c) \right] = -2a.$$

- (b) If $c \geq b + 2a$, then $W_-(c) < W_+(c)$.

As a result, if $\beta \geq \beta^*(a, b)$, then (4.7) for c admits a unique solution, and the solution satisfies $c > b + 2a$; that is, (3.2) admits a unique solution.

In the rest of this section, we supply the missing arguments for the above derivations.

4.1. The left-half branch.

In this subsection, we solve (4.3).

LEMMA 1. *For each $c > 0$, problem (4.3) admits a unique solution. The solution satisfies $v' > 0$ and $w' > 0$ on \mathbb{R} . Denote the solution restricted on $(-\infty, 0]$ by $(v(\cdot, c), w(\cdot, c))$, and set $W_-(c) := w(0, c)$. Then $W_- \in C^\infty((0, \infty))$ and*

$$(4.10) \quad \lim_{c \searrow 0} W_-(c) = a^2; \quad W'_-(c) > 0 \quad \forall c > 0;$$

$$W'_-(c) > \frac{W_-(c)}{c+2a}, \quad \frac{a+b}{c} > \frac{(c+2a)(a+b)}{W_-(c)} - 1 > \frac{a+b}{2a+2c} \quad \forall c \geq 2a.$$

In addition, the function $B(\cdot)$ defined in (4.8) satisfies

$$(4.11) \quad 0 < \frac{B(c)[1+b^2]}{4(a+b)^2} - \left(c + 2a \right) < \frac{b}{1 + \frac{2c}{b+3a}} \quad \forall c \geq 2a;$$

$$(4.12) \quad B'(c) > 0 \quad \forall c \geq a+b.$$

Furthermore, for $\beta^*(a, b)$ defined in (3.4), if $\beta \geq \beta^*(a, b)$, there exists a unique $c \in [2a, \infty)$ that satisfies $\beta = B(c)$; the solution satisfies $c > b + 2a$ and $B'(c) > 0$.

Note that (3.5) follows from (4.11) and (4.7). Also, by the lower bound of $B(c)$ in (4.11) and the fact that $c > 2a$, we see that (3.2) does not have any solution when $0 < \beta < \beta^*(a, b)$, where $\beta^*(a, b)$ is as in (3.4). The proof of this lemma is found in the appendix.

4.2. The right-half branch.

Here we study problem (4.4).

LEMMA 2. *There exists a smooth positive function $W_+(\cdot)$ defined on $(2a, \infty)$ such that for each constant $c \in (2a, \infty)$ and $h \in (0, W_+(c)]$, the unique solution of the initial value problem (4.4) satisfies (4.6). On the other hand, if $c \in (0, 2a]$ or if $c > 2a$ and $h > W_+(c)$, then the solution of (4.4) does not satisfy (4.6).*

In addition, $W_+(2a+) = 0$ and

$$(4.13) \quad W'_+(c) > 0, \quad W_+(c) > c \left\{ c - 2a - b + \frac{\pi}{2} \sqrt{c^2 - 2ac} \right\} \quad \forall c > 2a.$$

The proof of this lemma can be found in the appendix.

4.3. Joining the two solutions. We now piece together the solutions of (4.3) and (4.4).

LEMMA 3. *If $c \geq b + 2a$, then $W_-(c) < W_+(c)$.*

The proof of this is given in the appendix.

4.4. Completion of the proof of Theorem 1. Assume that $\beta \geq \beta^*(a, b)$. Then by Lemma 1, there exists a unique $c \geq 2a$ that solves the algebraic problem $B(c) = \beta$. In addition, the solution satisfies $c > b + 2a$ and $B'(c) > 0$. Then by Lemma 3, $W_-(c) < W_+(c)$. Thus, setting $h = W_-(c)$ in (4.4) and piecing together the solutions of (4.3) and (4.4), we obtain a solution of

$$cv' = f(v) + g(v)w, \quad v > 0 \quad \text{in } \mathbb{R}, \quad v(-\infty) = -\theta_0, \quad v(\infty) = 2\pi - \theta_0,$$

where $w = W_-(c)e^{-|x|}$. By (4.2) and (4.7), we find that $w = \beta J * Q(v)$; thus we obtain a solution of (3.2). Since the solution of $\beta = B(\cdot)$ is unique in $[2a, \infty)$, the solution of (3.2) is also unique. The rest of Theorem 1 follows from Lemma 3 and the discussion presented at the beginning of this section. This completes the proof of Theorem 1.

4.5. Nonmonotonic solutions. Notice that trajectories of (7.2) and (7.6) are symmetric about the line $v = \pi$. As shown in Figure 3, since $\theta_1 < \pi$, the trajectory γ_2 of (4.4) lies below γ_1^* . Hence, the solution of (4.4) with $h = W_-(c)$ satisfies

$$\lim_{x \rightarrow \infty} v(x) = 2\pi - \theta_0.$$

In $c > 2a$ and $W_+(c) \leq W_-(c)$, we have $v' > 0$ on \mathbb{R} ; if $c \in (0, 2a]$ or if $c > 2a$ and $W_-(c) > W_+(c)$, we have $v'(x) < 0$ for $x \gg 1$. The union of the solution of (4.3) and (4.4) satisfies

$$cv' = f(v) + g(v)W_-(c)e^{-|x|} \quad \forall x \in \mathbb{R}, \quad v(-\infty) = -\theta_0, \quad v(\infty) = 2\pi - \theta_0.$$

Consequently, we have a traveling wave if and only if $c > 0$ is the solution of the algebraic equation

$$\beta = B(c) := \frac{4}{1+b^2} \frac{W_-(c)}{c} \left(b^2 - a^2 + W_-(c) \right).$$

Since $W_-(c) = a^2 + O(c)$ as $c \searrow 0$, we see that $B(0+) = \infty$ and $B(\infty) = \infty$. Thus, under the assumptions (A1) and (A2S),

there exists $\hat{\beta}(a, b) > 0$ such that the following hold:

1. *If $0 < \beta < \hat{\beta}(a, b)$, then there is no traveling wave solution.*
2. *If $\beta > \hat{\beta}(a, b)$, there exist at least two solutions; the smaller speed c_1 and the large speed c_2 admit the following asymptotic as $\beta \rightarrow \infty$:*

$$(4.14) \quad c_1 = \frac{4a^2b^2}{1+b^2} \frac{1}{\beta} + \frac{O(1)}{\beta^2}, \quad c_2 = \frac{1+b^2}{4(a+b)^2} \beta - 2a + \frac{O(1)}{\beta},$$

where $O(1)$ is bounded by a constant that does not depend on β .

Although we have not been able to prove it, we expect that $B(\cdot)$ is a convex function with a positive minimum attained at $\hat{\beta}(a, b)$ so that there are exactly two solutions when $\beta > \hat{\beta}(a, b)$; see the numerical results in the next subsection.

4.6. Numerical results. In Theorem 1, we treat c as a parameter and show that there is minimum value of β above which there is a unique branch of *monotonic* waves that travel at some velocity c . We solve the same boundary value problem as in the proof of the theorem but reverse the roles and find β as a function of c . We solve

$$\frac{dw}{dv} = \frac{cw}{f(v) + wg(v)}, \quad v \in (-\theta_0 + \mu, \theta_1],$$

with $w(-\theta_0, \mu) = (1 + a^2)(a + c/2)\mu$, where μ is chosen to be small (here we take $\mu = 0.001$). We integrate this until $v = \theta_1$ to get

$$\beta = B(c) := \frac{2w(\theta_1)}{c} [f(\theta_1) + g(\theta_1)w(\theta_1)].$$

Figure 5A shows the function $\beta = B(c)$ with c as the vertical axis. There are two values of c for each value of β corresponding to the fast c and the slow c . The velocity of the upper value of c (fast waves) increases with the strength of coupling as expected, while the lower branch (slow waves) decreases with strength. The two branches come together at β_0 , the minimum coupling strength. We pick $\beta = 3$ and look at the solutions for $\xi > 0$ in panel B. As shown by the theorem, the fast wave approaches $2\pi - \theta_0$ monotonically, while the slow wave is nonmonotonic in its approach. While we have not proven the existence of the slow branch of solutions, we see from the numerical solutions that they are all part of the same branch. Fast and slow branches of waves are known to occur in many other wave problems in excitable media, and generally the fast waves are stable and the slow waves are unstable. In panel A, we have also plotted the lines c_1, c_2 defined in (4.14). In the inset of the figure, we plot the slow branch and c_1 in an expanded view. The match is very good; the velocity is essentially a linear function of β except near the limiting minimal value. Figure 5C shows the dependence of the minimal value of β , β_0 as a function of θ_1 and in panel D as a function of a , where $a = \tan(\theta_0/2)$. The larger a (less excitable the medium) the larger β must be to obtain a wave, an intuitively clear point. The dependence on θ_1 is also monotonic. We also plot the upper and lower bounds $\beta^*(a, b), \beta_*(a, b)$ for $a = 0.2$ in panel C and $\theta_1 = 1.5$ ($b = \tan(0.75)$) in panel D.

Denote by c_0 the wave speed that corresponds to the minimum value of $\beta = \beta_0$, and by c_* the speed at which $W_-(c_*) = W_+(c_*)$ (cf. Figure 3). Numerically we find that $c_* > c_0$. Hence, when $\beta \in (\beta_0, B(c_*))$, both waves are nonmonotonic.

5. The singular perturbation problem.

In this section we prove Theorem 2.

Assume that Q satisfies (A2) and (A2R) where $\theta_0 \in (0, \pi)$, $\theta_1 \in (\theta_0, \pi)$, and $\beta \geq \beta^*(a, b)$. The associated singular problem discussed in the previous section admits a unique solution, which we denote by (c_s, v_s, w_s) . Note that we have $\beta = B(c_s)$, $B'(c_s) > 0$, and $W_-(c_s) < W_+(c_s)$. We now establish the existence for the regular problem. We assume that ε is sufficiently small. As a start, we assume that $0 < \varepsilon \leq \frac{\pi - \theta_1}{2}$.

5.1. Construction of the solution. Note that $w(x) = \beta J(x) * Q(v(x))$ satisfies the differential equation

$$-w'' + w = \beta Q(v(x)).$$

We construct a solution by joining three pieces as follows.

1. Fix $c > 2a$. We define $(v(\cdot, c), w(\cdot, c))$ on $(-\infty, 0]$ as the unique solution of (4.3), as stated in Lemma 1.

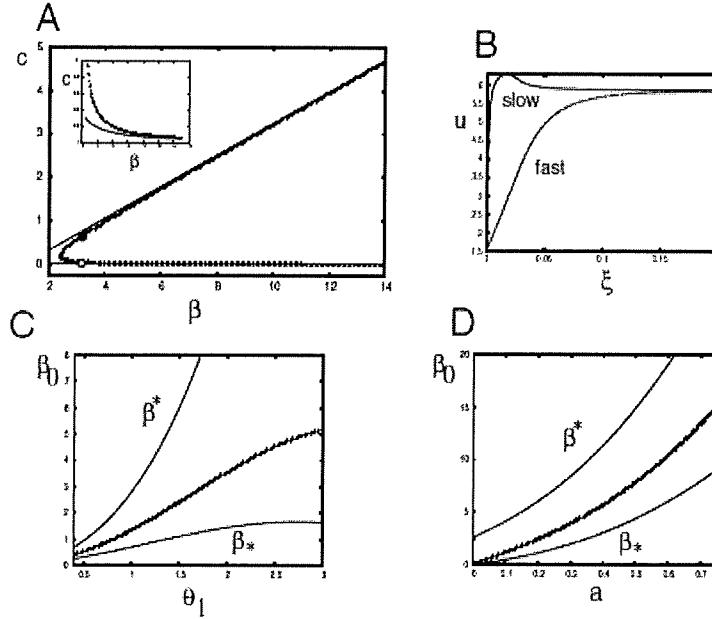


FIG. 5. Numerical solutions to the boundary value problem. (A) Velocity of the wave (stippled curve) as a function of β for $\theta_1 = 1.5, a = 0.2$ ($\theta_0 = 0.395$). The upper line is $c_2(\beta)$ from (4.14), and the lower line is $c_1(\beta)$. The inset shows an expanded view of the slow velocity (stippled) and c_1 (solid). (B) The solution $v(\xi)$ for $\xi > 0$ for the two different values of c indicated by the filled circles in panel A. ($c_{\text{slow}} = 0.3833$ indicated by the white circle and $c_{\text{fast}} = 0.9733$ indicated by the black circle at $\beta = 3$.) (C) The minimum value of β as a function of θ_1 and (D) as a function of a , along with the upper and lower bounds β^*, β_* from (3.4).

2. We define $(x_1, v(\cdot, c), w(\cdot, c)) \in (0, \infty) \times C^1([0, x_1]) \times C^1([0, x_1])$ as the solution of the initial value problem

$$(5.1) \quad \begin{cases} cv' = f(v) + g(v) \max\{w, 0\}, & -w'' + w = \beta Q(v) \text{ on } [0, x_1], \\ v(0, c) = \theta_1, & w(0, c) = W_-(c), \quad w'(0, c) = W_-(c), \\ v' > 0 \text{ on } [0, x_1], & v(x_1, c) = \theta_1 + \varepsilon. \end{cases}$$

The system of differential equations with initial value (v, w, w') at $x = 0$ admits a unique solution, and the solution can be extended to the interval $[0, \infty)$. The point x_1 is defined as follows. Note that when $v \in [\theta_1, \theta_1 + \varepsilon]$, we have

$$cv' = f(v) + g(v) \max\{w, 0\} \geq f(v) \geq f(\theta_1) = \frac{2(b^2 - a^2)}{1 + b^2}.$$

Thus,

$$(5.2) \quad v'(x, c) \geq \frac{f(\theta_1)}{c} \quad \text{as long as } v(x, c) \in [\theta_1, \theta_1 + \varepsilon].$$

Consequently, there exists $x_1 > 0$ such that $v(x_1, c) = \theta_1 + \varepsilon$ and $v' > 0$ in $[0, x_1]$. By the mean value theorem, $\varepsilon = v(x_1, c) - v(0, c) = v'(\xi, c)x_1$ for some

$\xi \in [0, x_1]$, so

$$(5.3) \quad 0 < x_1 \leq \frac{c\varepsilon}{f(\theta_1)}.$$

We show that $w > 0$ in $[0, x_1]$. Indeed, integrating $[e^x(w - w')]' = \beta e^x Q(v)$ over $[0, x]$ for $x \in [0, x_1]$ and using $w(0, c) = w'(0, c)$, we obtain

$$\begin{aligned} w - w' &= \beta \int_0^x e^{y-x} Q(v(y, c)) dy = \beta \int_0^x e^{y-x} \frac{Q(v) dv}{v'} \\ &= \frac{\beta e^{\xi-x}}{v'(\xi, c)} \int_{\theta_1}^{v(x, c)} Q(s) ds \leq \frac{c\beta}{f(\theta_1)} \int_{\theta_1}^{\theta_1+\varepsilon} Q(v) dv = \frac{c\beta}{f(\theta_1)}. \end{aligned}$$

Integrating $(e^{-x}w)' = e^{-x}(w' - w)$, we obtain (from the mean value theorem)

$$\begin{aligned} e^{-x}w(x, c) &= w(0, c) - \int_0^x e^{-z} \beta \int_0^z e^{y-z} Q(v(y, c)) dy dz \\ (5.4) \quad &\geq W_-(c) - \int_0^x \frac{c\beta e^{-z}}{f(\theta_1)} dz \geq W_-(c) - \frac{c\beta x_1}{f(\theta_1)}. \end{aligned}$$

In view of (5.3), we find that when ε is small enough, we have $w > \frac{1}{2}W_-(c)$. We now improve the estimates (5.2) and (5.3) as follows: In $[0, x_1]$, using $v \in [\theta_1, \theta_1 + \varepsilon]$, and $w > \frac{1}{2}W_-(c)$, we have

$$v' > \frac{g(\theta_1 + \varepsilon)w}{c} \geq \frac{g(\theta_1 + \varepsilon)W_-(c)}{2c} \geq \frac{2\cos^2 \frac{\theta_1 + \varepsilon}{2}(c + 2a)(a + b)}{2[c + a + b]}.$$

Thus

$$(5.5) \quad v' \geq a \cos^2 \frac{\theta_1 + \pi}{4} \quad \text{on } [0, x_1], \quad x_1 < \frac{\varepsilon}{a \cos^2 \frac{\theta_1 + \pi}{4}}.$$

Notice that these estimates do not depend on c . Revising the estimate (5.4), we conclude that there exists a positive constant $\varepsilon_1(a, b, \beta)$ that depends only on a , b , and β such that when $\varepsilon \in (0, \varepsilon_1(a, b, \beta))$, problem (5.1) admits a unique solution, and the solution satisfies (5.5). We record the basic L^∞ estimate as follows: for $x \in (0, x_1]$,

$$(5.6) \quad \frac{W_-(c)}{2} < w \leq W_-(c)e^x, \quad w - \frac{\beta}{a \cos^2 \frac{\theta_1 + \pi}{4}} \leq w' \leq w, \quad 0 < v' \leq O(1).$$

Here $O(1)$ does not depend on $c \geq 2a$ or on $\varepsilon \in (0, \varepsilon_1(a, b, \beta))$.

Finally, we integrate $[e^{-x}(w + w')]' = -e^{-x}Q(v)$ over $[0, x_1]$ to obtain

$$\begin{aligned} e^{-x_1}[w(x_1, c) + w'(x_1, c)] &= [w(0, c) + w'(0, c)] - \beta \int_0^{x_1} e^{-y} Q(v(y)) dy \\ &= 2W_+(c) - \beta \int_0^{\theta_1+\varepsilon} \frac{e^{-y} Q(v) dv}{v'(y, c)}. \end{aligned}$$

Define

$$\begin{aligned} (5.7) \quad j(c) &:= v'(0, c)e^{-x_1}[w(x_1, c) + w'(x_1, c)] \\ &= B(c) - \beta \int_0^{\theta_1+\varepsilon} \frac{e^{-y} v'(0, c)}{v'(y, c)} Q(v) dv \\ &= B(c) - \beta - \beta\eta(c), \end{aligned}$$

where

$$(5.8) \quad \eta(c) = \int_{\theta}^{\theta+\varepsilon} \frac{e^{-y} v'(0, c) - v'(y, c)}{v'(y, c)} Q(v) dv.$$

We search for c such that

$$(5.9) \quad c > 2a, \quad j(c) = 0, \quad w_-(c) := w(x_1, c) < W_*(\theta_1 + \varepsilon, c).$$

3. Assume that (5.9) holds. We define $(v(\cdot, c), w(\cdot, c))$ on (x_1, ∞) as the solution of

$$(5.10) \quad \begin{cases} cv' = f(v) + wg(v), & w' = -w \quad \text{in } (x_1, -\infty), \\ v(x_1, c) = \theta_1 + \varepsilon, & w(x_1+, c) = w_-(c). \end{cases}$$

First, since $0 < w_-(c) < W_*(\theta_1 + \varepsilon, c)$, following the proof of Lemma 2, we can show that the solution of (5.10) satisfies $v' > 0 > w'$ on $[x_1, \infty)$ and $\lim_{x \rightarrow \infty} (v, w) = (2\pi - \theta_0, 0)$.

Next, note that $w'(0\pm, c) = w(0, c)$. Also, as $j(c) = 0$, $w'(x_1\pm, c) = -w(x_1, c)$, so $w \in C^1(\mathbb{R})$. Since $v < \theta_1$ in $(-\infty, 0)$ and $v > \theta_1 + \varepsilon$ in (x_1, ∞) , we see that $Q(v) = 0$ on $(-\infty, 0) \cup (x_1, \infty)$. Thus, w is the solution of

$$-w'' + w = \beta Q(v) \quad \text{on } \mathbb{R}, \quad w(\pm\infty) = 0.$$

This implies that $w = \beta J \star Q(v)$. In conclusion, $(c, v(\cdot, c)) \in (0, \infty) \times C^1(\mathbb{R})$ is a solution of the traveling wave problem (3.2).

4. On the other hand, if (c, v) is a solution of (3.2), one can show that $v = v(\cdot, c)$ is the function described as above and c is a solution of (5.9). Thus, solving the traveling wave problem (3.2) is equivalent to solving the algebraic problem (5.9).

In the next subsection, we solve (5.9).

5.2. The algebraic equation (5.9). To solve (5.9), we first show that $\eta = O(\varepsilon)$. Note that for $x \in [0, x_1]$,

$$e^{-x} v'(0, c) - v'(x, c) = \int_0^x [-e^y v'(0, c) - v''(y, 0)] dy.$$

Differentiating $cv' = f + gw$, we find that, in view of (5.6) and (4.10) for $W_-(c)$,

$$v'' = \frac{1}{c} ([f_v + g_v w] v' + gw') = \frac{[f_v + g_v w][f + gw]}{c^2} + \frac{gw'}{c} = O(1).$$

Here $O(1)$ is bounded by a constant depending only on a, b , and β , but not on c and ε . It then follows that

$$|e^{-x} v'(0, c) - v'(x, c)| \leq O(1)x_1.$$

Consequently, by the definition of η , we find that

$$|\eta(c)| \leq \frac{O(1)x_1}{\min_{[0, x_1]} v'(\cdot)} \int_{\theta_1}^{\theta_1 + \varepsilon} Q(v) dv \leq O(1)\varepsilon.$$

Now let (c_s, v_s, w_s) be the solution of the associated singular problem discussed in the previous section. Assume that $c \in [c_s - \sqrt{\varepsilon}, c_s + \sqrt{\varepsilon}]$. Then we have

$$j(c) = B(c) - \beta - \beta\eta(c) = B(c) - B(c_s) + O(\varepsilon) = B'(c_s)(c - c_s) + O(\varepsilon).$$

Thus, when ε is sufficiently small, $j(c_s - \sqrt{\varepsilon}) < 0 < j(c_s + \sqrt{\varepsilon})$. By the mean value theorem, there exists $c_\varepsilon \in [c_s - \sqrt{\varepsilon}, c_s + \sqrt{\varepsilon}]$ such that $j(c_\varepsilon) = 0$. As $B'(c_s) > 0$ and $\eta = O(\varepsilon)$, we find that $c_\varepsilon = c_s + O(\varepsilon)$. Thus, $c = c_\varepsilon$ is a solution of (5.9), from which we obtain a traveling wave solution of (3.2). Denoting the corresponding solution by $(v_\varepsilon, w_\varepsilon)$, one can show that

$$(5.11) \quad |c_\varepsilon - c_s| + \|v_\varepsilon - v_s\|_{L^\infty(\mathbb{R})} + \|w_\varepsilon - w_s\|_{L^\infty(\mathbb{R})} = O(1)\varepsilon.$$

5.3. Uniqueness of the solution. The equation $j(c) = 0$ can be written as

$$B(c) = \{1 + O(1)\varepsilon\}\beta,$$

where $O(1)$ is a quantity bounded by a constant depending only on a, b , and β , but not on c and ε . Thus, the equation $j(c) = 0$ implies that $c = c_s + O(\varepsilon)$.

To establish the uniqueness of the solution, we need only establish the smallness of the variation of η with respect to c . For this, we use the phase plane, taking v as the independent variable. Since $dv/dx \neq 0$ at $x = 0, v = \theta_1$, we can invert dv/dx and express x as a function of v , say $X(v, c)$, and by the chain rule, express, w, p as functions of (v, c) , say $W(v, c), P(v, c)$. Hence, we write the system

$$\frac{dv}{dx} = \frac{f(v) + g(v)w}{c}, \quad \frac{dw}{dx} = p, \quad \frac{dp}{dx} = w - \beta Q(v) \quad \text{for } x \in [0, x_1]$$

as

$$\begin{aligned} \frac{d}{dv} \begin{bmatrix} X(v, c) \\ W(v, c) \\ P(v, c) \end{bmatrix} &= \frac{c}{f(v) + g(v)W} \begin{bmatrix} 1 \\ P \\ W - \beta Q(v) \end{bmatrix} \quad \text{for } v \in [\theta_1, \theta_1 + \varepsilon], \\ \begin{bmatrix} X(\theta_1, c) \\ W(\theta_1, c) \\ P(\theta_1, c) \end{bmatrix} &= \begin{bmatrix} 0 \\ W_-(c) \\ W_-(c) \end{bmatrix}. \end{aligned}$$

Differentiating with respect to c and denoting (X_c, P_c, Q_c) as the partial derivative of (X, Q, P) with respect to c , we find that

$$\begin{aligned} \frac{d}{dv} \begin{bmatrix} X_c(v, c) \\ W_c(v, c) \\ P_c(v, c) \end{bmatrix} &= \frac{f(v) + g(v)W - cg(v)W_c}{[f(v) + g(v)W]^2} \begin{bmatrix} 1 \\ P \\ W - \beta Q(v) \end{bmatrix} + \frac{c}{f(v) + g(v)W} \begin{bmatrix} 0 \\ P_c \\ W_c \end{bmatrix}, \\ \begin{bmatrix} X_c(\theta_1, c) \\ W_c(\theta_1, c) \\ P_c(\theta_1, c) \end{bmatrix} &= \begin{bmatrix} 0 \\ W'_-(c) \\ W'_-(c) \end{bmatrix}. \end{aligned}$$

Since $\int_{\theta_1}^{\theta_1 + \varepsilon} |Q(v)|dv = 1$, we can solve the linear system to obtain

$$X_c, W_c, P_c = O(1).$$

Since $X_c(\theta_1, c) = 0$ and $X'_c = O(1)$, we find that $X_c(x, c) = O(1)x$. In addition, we can differentiate the first equation with respect to c to obtain

$$\frac{d^2 X_c(v, c)}{dv^2} = O(1) + O(|P|) = O(1).$$

Now we calculate the variation of $\eta(c)$ with respect to ε :

$$\begin{aligned}\eta(c) &= \int_{\theta_1}^{\theta_1+\varepsilon} \frac{e^{-X(v,c)} \frac{1}{X'(\theta_1,c)} - \frac{1}{X'(v,c)}}{\frac{1}{X'(v,c)}} Q(v) dv = \int_{\theta_1}^{\theta_1+\varepsilon} \frac{e^{-X(v,c)} X'(\theta_1,c)}{X'(\theta_1,c)} Q(v) dv - 1, \\ \frac{d\eta(c)}{dc} &= \int_{\theta_1}^{\theta_1+\varepsilon} \frac{X_c(v,c) X_v(\theta_1,c) X_{vv}(v,c) - [X_v(\theta_1,c) X_{vc}(v,c) - X_v(v,c) X_{vc}(\theta_1,c)]}{X_v^2(\theta_1,c) e^{X(v,c)}} Q(v) dv \\ &= O(\varepsilon) \int_{\theta_1}^{\theta_1+\varepsilon} Q(v) dv = O(1)\varepsilon.\end{aligned}$$

Hence, $j'(c) = B'(c) + O(\varepsilon) > 0$ when $c = c_s + o(1)$. This implies that the solution is unique. This completes the proof of Theorem 2.

5.4. Numerical results. We numerically compute the solution to the equation

$$(5.12) \quad \begin{cases} c\theta' = f(\theta) + g(\theta)w, \\ w'' = w - \beta Q(\theta - \theta_1), \end{cases}$$

where

$$Q(\theta) = \frac{(1 + \cos(\pi\theta/\varepsilon))^2}{3\varepsilon}, \quad |\theta| < \varepsilon,$$

and is zero outside of this region. Note that we center Q around θ_1 rather than choosing θ_1 as the left endpoint of its support. As $\varepsilon \rightarrow 0^+$, $Q(\theta)$ approaches the Dirac delta function. $Q(\theta)$ is also C^2 , which is useful for the numerical solution. To solve (5.12), we compute the heteroclinic orbit via shooting and then continue with AUTO. With $a = \tan(0.25)$, $\theta_1 = 1.5$, $\varepsilon = 0.2$, we show how the velocity varies with β in Figure 6. The picture is quite similar to Figure 5A.

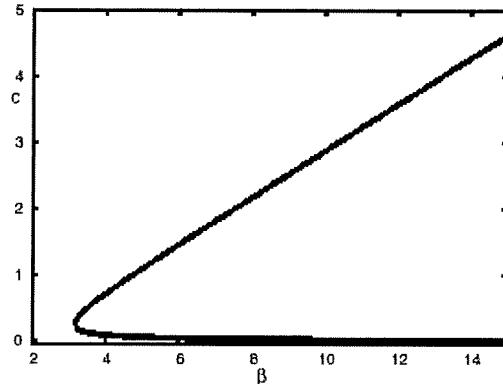


FIG. 6. Numerical computation of the velocity of the traveling wave solution to (5.12) where $\theta_0 = 0.5$, $\theta_1 = 1.5$, $\varepsilon = 0.2$, and β varies.

6. Extensions. After formally deriving (2.6), we considered three simplifications of the model: we assumed that the convolution kernel was $J(x) = \exp(-|x|)/2$; we assumed that $Q(u)$ was either a Dirac function or that it had compact support in a very small neighborhood around $\theta = \theta_1$; and we ignored the “subthreshold” part of the equation, $R(u)$. A natural question is whether or not we can still construct solutions (either rigorously, or numerically) for traveling waves to the more general nonlocal

equations. If the kernel is exponential, then we reduce the existence of the traveling waves to finding a heteroclinic orbit to (5.12). For general kernels, we consider the case of $Q(u) = \delta(u - \theta_1)$ as before, but now we allow $J(x)$ to be any symmetric kernel that is integrable on $[0, \infty)$. The traveling wave equation is

$$(6.1) \quad c \frac{du}{dx} = f(u(x)) + BJ(x)g(u(x)),$$

with

$$\lim_{x \rightarrow \infty} u(x) = 2\pi - \theta_0 \quad (\text{i}),$$

$$\lim_{x \rightarrow -\infty} u(x) = -\theta_0 \quad (\text{ii}),$$

and $u(0) = \theta_1$. The parameter $B = \beta/u'(0)$. So for given B , if we can find a solution to (6.1), then we evaluate $u'(0)$ and use this to get the appropriate value of β . Equation (6.1) is a scalar nonautonomous equation, so it may be possible to use phase-plane methods again on this equation. Since $J(x) \rightarrow 0$ as $x \rightarrow \infty$ and $2\pi - \theta_0$ is a stable equilibrium for $cu' = f(u)$, then as long as $u(x)$ integrated forward in time does not increase too quickly (e.g., $J(x)$ decreases quickly), then $u(x)$ will land in the basin of attraction of $2\pi - \theta_0$. Thus, the forward x integration will not be a problem for this generalization. However, the backward integration for $x < 0$ does present a problem since for large negative x , we have $cu' = f(u)$ and the equilibrium $-u_0$ is a repellor as $x \rightarrow -\infty$. We would like to show that there is a value of c so that condition (ii) holds. We have not been able to prove this rigorously; however, we can solve the problem using a numerical method as follows. Let $x = Py$ be a scaling of x . We solve

$$\frac{du}{dy} = -P[f(u) + BJ(Py)g(u)]/c$$

with $u(0) = \theta_1$ on $0 < y \leq 1$, and we vary c until $u(1) = -\theta_0$. Once we have solved this boundary value problem, we numerically continue it (using e.g., XPPAUT [7]) by increasing P (equivalent to letting $x \rightarrow P$) and then continue the large P solution as we vary, say, B . Then, we use the relationship between B and β to get the corresponding β . As examples, we have chosen $J(x) = e^{-x^2}/\sqrt{\pi}$ (Gaussian) and $J(x) = \sqrt{2}/\pi^2/(1+x^4)$ (Power) along with our default kernel, $J(x) = \exp(-|x|)/2$. The results of these calculations are shown in Figure 7. There are several clear differences. First, both the power law and Gaussian kernels produce waves at lower values of β . We expect that the reason for this is that they are concentrated close to $x = 0$ so that the impact of the active part of the wave is larger and can push the unexcited tissue past the threshold θ_0 . On the other hand, the fact that the exponential is more “spread out” allows it to effectively excite more distant areas once β is large enough, leading to a faster velocity for a given value of β . Interestingly, the power law kernel combines a lower minimum value of β for propagation with fast velocity.

If we include the subthreshold part of (2.6), $R(u)$, then with an exponential kernel, we can still numerically construct the traveling waves by shooting. If we eliminate the delta function part in (2.6) (that is, $d_1 = 0$), then all we have coupling the neurons is $R(u)$, which is a monotone function, so we expect that the results of [4] may be applied. Numerically, we have found that there are traveling waves to (2.6) with $d_1 = 0$ and c_e very large, but they are not simple translation-invariant waves; rather, they have a spatial periodicity reminiscent of the breathing waves seen in [12]. The remaining question then is by what means could we numerically find a solution to the

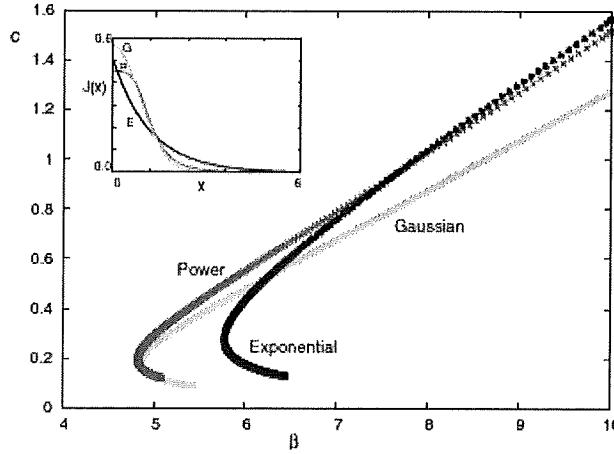


FIG. 7. The speed of the wave for (6.1) for three different kernels (shown in the inset, and defined in the text) as β varies with $\theta_0 = 0.5, \theta_1 = 2.5$.

general kernel, $J(x)$, a general pulse function, $Q(u)$, and including $R(u)$. As above, we write

$$W(x) = J(x) * q(x),$$

where $q(x)$ is some function that has a Fourier transform (e.g., $Q(\theta(x))$). Using the convolution theorem for Fourier transforms, we get

$$\hat{W}(k) = \hat{J}(k)\hat{q}(k),$$

and inverting this, we find

$$\hat{W}(k)/\hat{J}(k) = \hat{q}(k).$$

If we approximate $\hat{J}(k)$ as a rational function of k^2 , say $N(k)/D(k)$, where $N(k), D(k)$ are even degree polynomials in k , then we find

$$D(k)\hat{W}(k) = N(k)\hat{q}(k).$$

Inverting the transform leads to

$$L_D W(x) = L_N Q(\theta(x)),$$

where L_D, L_N are linear constant coefficient differential operators. For example, for the exponential kernel, $L_D W(x) = W'' - W$ and $L_N = 1$. Thus, with such an approximation, we could conceivably compute the numerical speed of the waves using shooting. This transform trick was used in [21] to solve some nonlocal neural equations in two space dimensions.

7. Discussion and conclusions. In this paper, we studied a nonlocally coupled model for pulse waves that was motivated by a reduction of a neural network near a critical bifurcation. For sufficiently strong coupling, we showed that there were two different wave speeds: a fast wave and a slow wave. We have not proven this, but, presumably, the fast wave is stable, and the slow wave is unstable. The numerical solution of the spatially discretized nonlocal equation shown in Figure 2B indicates

that it is the fast wave that is stable. This paper is not the first to examine traveling waves in the theta model. Osan, Rubin, and Ermentrout [23] studied the following equation:

$$(7.1) \quad c \frac{d\theta}{d\xi} = f(\theta) + g(\theta)\beta \int_{-\infty}^{\infty} J(\xi - y)\alpha(y/c) dy,$$

where $\alpha(t)$ satisfies

$$\alpha'' + (a + b)\alpha' + ab\alpha = 0$$

along with $\alpha(0) = 0$, $\alpha'(0) = 1$ with $\alpha(y) = 0$ for $y < 0$. They showed that there were solutions to this equation for β large enough such that (i) $\theta(-\infty) = -\theta_0$ and (ii) $\theta(0) = \pi$. In addition, they proved that there were no solutions that satisfied (i), (ii) such that $\theta(+\infty) = 2\pi - \theta_0$. We have shown in this paper that by letting $\theta(0) = \theta_1 < \pi$, there are such solutions which [23] called single pulse solutions. Furthermore, by relaxing the requirement in [23] that $\theta(0) = \pi$, in this paper we were able to get very good bounds on the regions in parameter space where there are solutions and also good estimates of how the velocity of both the slow and fast waves depends on parameters. Wen et al. [28] avoided the issue of the overshoot of the waves in (7.1) by considering only one-directional coupling that lasts a finite amount of time.

As is well known with pulses in reaction-diffusion systems such as the Hodgkin–Huxley model [22], in addition to a solitary pulse wave, there is a family of traveling periodic waves that travel with a speed that depends on their wavelength forming the so-called dispersion curve. Thus, a natural question to ask about the theta model is whether such waves also exist. Specifically, is there a solution to

$$c\theta' = f(\theta) + \beta g(\theta)J * Q(\theta)$$

such that $\theta(-L/2) = \theta(L/2) + 2\pi$ for each L ? Katriel [20] considered (7.1) on a ring and showed the existence of traveling periodic wave trains. In a follow-up paper, we will prove that such waves exist, thus completing the analogy between nonlocally coupled excitable systems and their reaction-diffusion analogies.

Appendix. The following algebraic relations will be useful in the proofs of the lemmas:

$$\begin{aligned} g(s) &= 1 + \cos s = 2 \cos^2 \frac{s}{2}, & \int \frac{ds}{g(s)} &= \tan \frac{s}{2} + C, \\ f(s) &= (1 - a^2) - (1 + a^2) \cos s = g(s) \left(\tan^2 \frac{s}{2} - a^2 \right), \\ f < 0 &\text{ in } (-\theta_0, \theta_0), \quad f > 0 \text{ in } (\theta_0, 2\pi - \theta_0), & f'(-\theta_0) &= -2a. \end{aligned}$$

Proof of Lemma 1.

Proof. We divide the proof into several steps.

1. First we establish the well-posedness of problem (4.3). For this, on the v - w phase plane, we consider the dynamical system, for fixed positive constant c ,

$$(7.2) \quad cv' = f(v) + wg(v), \quad w' = w.$$

It is easy to check that $(-\theta_0, 0)$ is a saddle point, so there is a unique trajectory, γ , that leaves the saddle point in the $[1, (1 + a^2)(a + \frac{\theta_0}{2})]$ direction of the unstable manifold.

Checking the velocity field on the boundary of the domain

$$\Omega := \left\{ (v, w) \mid v > -\theta_0, w > a^2 - \tan^2 \frac{\min\{v, 0\}}{2} \right\},$$

one sees that Ω is positively invariant. Hence, $\gamma \in \Omega$. This implies that $f(v) + wg(v) > 0$, so $v' > 0$ and $w' > 0$ on \mathbb{R} . It is easy to check that $(w(x), v(x)) \rightarrow (\infty, \infty)$ as $x \rightarrow \infty$. Hence, we can fix the translation by setting $v(0) = \theta_1$. In conclusion, (4.3) admits a unique solution, which satisfies $v' > 0$ and $w' > 0$ on $(-\infty, 0]$. We denote the solution restricted on $(-\infty, 0]$ by $(v(\cdot, c), w(\cdot, c))$.

2. Next we study a monotonic dependence of $(v(\cdot, c), w(\cdot, c))$ with respect to c . Since both v and w are strictly increasing, γ is a graph, so we can express γ as $w = W(v, c)$. Since f and g are analytic and $(-\theta_0, 0)$ is a saddle, it is known that in two-dimensional systems, the unstable manifold W is analytic in both v and c [16]. Denote $F(s, Z) = f(s) + Zg(s)$. Then we have

$$\begin{aligned} \frac{dW(s, c)}{ds} &= \frac{cW(s, c)}{F(s, W(s, c))} > 0 \quad \forall s > -\theta_0, \\ \lim_{s \searrow -\theta_0} \frac{W(s, c)}{s + \theta_0} &= \lim_{s \searrow -\theta_0} \frac{dW(s, c)}{ds} = \left(1 + a^2\right) \left(a + \frac{c}{2}\right). \end{aligned}$$

By continuous dependence of solutions with respect to parameters, we have

$$\begin{aligned} \frac{d}{ds} \left(\frac{\partial W(s, c)}{\partial c} \right) &= \frac{cf}{F^2} \frac{\partial W}{\partial c} + \frac{W}{F}, \\ \lim_{s \searrow -\theta_0} \frac{1}{s + \theta_0} \frac{\partial W(s, c)}{\partial c} &= \frac{1 + a^2}{2}. \end{aligned}$$

It then follows that $\partial W(s, c)/\partial c > 0$ for every $c > 0$ and $s > -\theta_0$.

3. We study the asymptotic behavior of W as $c \searrow 0$. Since $(s, W(s, c)) \in \Omega$, we have

$$W(s, c) > a^2 - \tan^2 \frac{s^-}{2}, \quad s^- := \min\{s, 0\}.$$

Also, for each fixed $\varepsilon > 0$, one can verify that $W(s) = a^2 - \tan^2 \frac{s^-}{2} + \varepsilon e^s$ is a supersolution when c is sufficiently small. (See [27, sect. 1.5] for definitions of super- and subsolutions.) Thus, for each $s > -\theta_0$,

$$a^2 - \tan^2 \frac{s^-}{2} \leq \lim_{c \searrow 0} W(s, c) \leq \lim_{\varepsilon \searrow 0} \left(a^2 - \tan^2 \frac{s^-}{2} + \varepsilon e^s \right) = a^2 - \tan^2 \frac{s^-}{2}.$$

This in particular implies that $W(\theta_1, 0+) = a^2$.

4. We investigate the function $W(\cdot, c)$. Assume that $c \geq 2a$.

Let $\psi(s) = \tan \frac{s}{2} + a$, where $s \in (-\theta_0, \pi)$ and $\psi \in [0, \infty)$. Then

$$\frac{dW(s, c)}{d\psi(s)} = \frac{dW}{ds} \frac{ds}{d\psi} = \frac{cW}{W + \psi^2 - 2a\psi}, \quad W|_{\psi=0} = 0.$$

Introduce a change of variable from $W(s, c)$ to $k(\psi, c)$ by

$$(7.3) \quad W(s, c) = \frac{(c + 2a)\psi}{1 + \frac{\psi}{k(\psi, c)}}, \quad \psi = \tan \frac{s}{2} + a.$$

One can verify that the equation for $W(s, c)$ with $s \in [-\theta_0, \pi)$ becomes

$$\begin{aligned}\frac{dk(\psi, c)}{d\psi} &= \frac{(c-k)\psi + k(2a+2c-k)}{\psi[\frac{\psi^2}{k} + (1 - \frac{2a}{k})\psi + c]} \quad \forall \psi > 0, \\ k(0, c) &= 2a + 2c.\end{aligned}$$

It is easy to see that $\bar{k} = 2a + 2c$ is a supersolution and $\underline{k} = c$ is a subsolution so $c < k(\psi) < 2a + 2c$ for all $\psi > 0$. Substituting this estimate of k into (7.3) and evaluating it at $W(\theta_1, c) = W_-(c)$ and $\psi(\theta_1) = a + b$, we then obtain the second estimate in (4.10).

Next, find a better lower bound of k . Consider the function

$$k_0(\psi, c) = c + \sqrt{(a - \frac{1}{2}\psi)^2 + c^2 + ac - (\frac{1}{2}\psi - a)}.$$

It is the larger of the two roots of the quadratic equation

$$(7.4) \quad (c - k_0)\psi + k_0(2a + 2c - k_0) = 0.$$

We find that $k_0(0, c) = 2a + 2c$; $k_0'(\psi, c) < 0$ for all $\psi > 0$; and $k_0(\infty, c) = c$. Since $k_0' < 0$, it is easy to see that k_0 is a subsolution, so we have

$$(7.5) \quad k_0(\psi, c) < k(\psi, c) < 2a + 2c \quad \forall \psi > 0.$$

5. We find a lower bound for W'_- . For this consider $\zeta := \frac{\partial W(s, c)}{\partial c} - \frac{W(s, c)}{c+2a}$. Note that

$$\begin{aligned}\frac{d\zeta(s, c)}{ds} &= \frac{cf}{F^2} \frac{\partial W}{\partial c} + \frac{W}{F} - \frac{cW}{(c+2a)F} \\ &= \frac{cf\zeta}{F^2} + \frac{gW}{F^2} \left(\psi^2 - 2a\psi + \frac{2aW}{c+2a} \right).\end{aligned}$$

Using (7.3) with $k \geq c$, we obtain

$$\psi^2 - 2a\psi + \frac{2aW}{c+2a} \geq \psi^2 - 2a\psi + \frac{2a\psi}{1 + \frac{\psi}{c}} = \frac{\psi^2(c - 2a + \psi)}{c + \psi} > 0.$$

One can derive that $\zeta(s, c) = O(\psi^2)$ as $\psi \searrow 0$. Thus, by an integrating factor, we find that $\zeta > 0$. The assertion of the lemma for $W_-(c) := W(\theta_1, c)$ thus follows.

6. Finally, we study $B(c)$ defined in (4.8) for $c \geq 2a$. Using $\frac{\partial W}{\partial c} > \frac{W}{c+2a}$ and $W > \frac{(c+2a)\psi}{1+\psi/c}$, we have

$$\begin{aligned}\frac{(1+b^2)c^2}{4} \frac{dB(c)}{dc} &= (b^2 - a^2 + W_-)c \frac{dW_-}{dc} - (b^2 - a^2 + 2W_-)W_- \\ &> \frac{(b^2 - a^2 + 2W_-)cW_-}{c+2a} - (b^2 - a^2 + W_-)W_- \\ &= \frac{W_-}{c+2a} \left[(c-2a)W_- - 2a(b^2 - a^2) \right] \\ &> \frac{W_-}{c+2a} \left[(c-2a) \frac{(c+2a)(b+a)}{1 + \frac{b+a}{c}} - 2a(b^2 - a^2) \right] \\ &= \frac{W_- [b+a][c(c^2 - 2ab - 2a^2) - 2a(b^2 - a^2)]}{(c+2a)(c+b+a)}.\end{aligned}$$

Thus, if $c \geq b + a$, then $B'(c) > 0$.

Next we estimate B . For $c \geq 2a$, using

$$W_-(c) = W(\theta_1, c) = \frac{(c+2a)\psi}{1 + \frac{\psi}{k}} = (c+2a)\psi \left(1 - \frac{\psi}{k(\psi) + \psi}\right) \Big|_{\psi=a+b},$$

we obtain from (4.8) that

$$\begin{aligned} \frac{(1+b^2)B(c)}{4(a+b)^2} &= \frac{(c+2a)}{c} \left(1 - \frac{\psi}{k+\psi}\right) \left(c + \psi - \frac{(c+2a)\psi}{k+\psi}\right) \\ &= \frac{(c+2a)}{c} \left(c + \frac{\psi}{(k+\psi)^2} [(k-c)\psi + k(k-2c-2a)]\right). \end{aligned}$$

First we replace k by its subsolution k_0 defined by (7.4). We find that

$$\frac{(1+b^2)B(c)}{4(a+b)^2} \geq c+2a.$$

Next we replace k by its supersolution $k = 2a + 2c$. We obtain

$$\begin{aligned} \frac{(1+b^2)B(c)}{4(a+b)^2} &\leq \frac{c+2a}{c} \left(c + \frac{(a+b)^2(c+2a)}{(2c+3a+b)^2}\right) \\ &= c+2a + \frac{b(b+3a)+a(a-b)}{2c+3a+b} \frac{(c+2a)^2}{(c+2a)^2 + (c^2 - 4a^2) + c(b-a)} \\ &\leq c+2a + \frac{b(b+3a)}{2c+3a+b} = c+2a + \frac{b}{1 + \frac{2c}{b+3a}}. \end{aligned}$$

This proves (4.11).

Finally, suppose $\beta \geq \beta^*(\theta_0, \theta_1)$ and $\beta = B(c)$ with $c \geq 2a$. Then we have

$$\frac{3}{2}b + 4a = \frac{(1+b^2)\beta^*}{4(a+b)^2} \leq \frac{(1+b^2)\beta}{4(a+b)^2} = \frac{(1+b^2)B(c)}{4(a+b)^2} < c+2a + \frac{b}{1 + \frac{2c}{b+3a}}.$$

This implies that

$$\begin{aligned} c &> \frac{3}{2}b + 2a - \frac{b}{1 + \frac{2c}{b+3a}} > \frac{3}{2}b + 2a - b = \frac{b}{2} + 2a; \\ c &> \frac{3}{2}b + 2a - \frac{b}{1 + \frac{2c}{b+3a}} > \frac{3}{2}b + 2a - \frac{b}{1 + \frac{b+4a}{b+3a}} > b + 2a. \end{aligned}$$

Finally, since $B'(\cdot) > 0$ on $[a+b, \infty)$, we see that the solution c of $\beta = B(c)$ on $[2a, \infty)$ is unique. This completes the proof of Lemma 1. \square

Proof of Lemma 2.

Proof. We divide the proof into several steps.

1. We consider the dynamical system

$$(7.6) \quad cv' = f(v) + wg(v), \quad w' = -w.$$

One can check that $(2\pi - \theta_0, 0)$ is a stable node. The linearized system around the equilibrium can be written as $X' = AX$, where A has eigenpairs

$$\lambda_1 = -\frac{2a}{c}, \quad \mathbf{e}_1 = \begin{bmatrix} -1 \\ 0 \end{bmatrix}; \quad \lambda_2 = -1, \quad \mathbf{e}_2 = \begin{bmatrix} -1 \\ (1+a^2)(\frac{c}{2} - a) \end{bmatrix}.$$

We consider three cases:

1. $0 < c < 2a$. In this case, all trajectories, except those with $w \equiv 0$, can only enter the equilibrium in the $\pm \mathbf{e}_2$ direction; this implies that if the solution of (4.4) with $h > 0$ enters the equilibrium, then v' is eventually negative.
2. $c = 2a$. In this case, $\mathbf{e}_2 = \mathbf{e}_1$. All trajectories with $w > 0$ can only enter the equilibrium in the $\pm \mathbf{e}_1$ direction. If $\lim_{x \rightarrow \infty} v(x) = 2\pi - \theta_0$, then using $w(x) = w(0)e^{-x}$, $v(x) = [2\pi - \theta_0] + O(xe^{-x})$, and an integrating factor, we can derive that

$$v(x) = [2\pi - \theta_0] + e^{-x} \left(O(1) + \frac{w(0)x}{a(1+a^2)} \right) \quad \text{as } x \rightarrow \infty;$$

that is, the solution of (4.4) with $h > 0$ does not satisfy (4.6).

3. $c > 2a$. In this case, there exists exactly one trajectory that enters the equilibrium in the $\pm \mathbf{e}_2$ direction; all other trajectories enter the equilibrium in the $\pm \mathbf{e}_1$ direction. We denote by γ_* the unique trajectory of (7.6) that approaches the equilibrium in the \mathbf{e}_2 direction. Note that the region

$$D := \{(v, w) \mid w > 0, v < 2\pi - \theta_0\}$$

is negatively invariant. Thus, $\gamma_* \in D$. As $f(v) + wg(v) > 0$ when $v \in [\theta_0, 2\pi - \theta_0]$ and $w > 0$, γ_* crosses the vertical line $v = \theta_1$ exactly once. We denote the intersection point by $(\theta_1, W_+(c))$. Then $\bar{\gamma}_* \cap \{(v, w) \mid \theta_1 \leq v \leq 2\pi - \theta_0\}$ is a strictly decreasing smooth curve with endpoints $(\theta_1, W_+(c))$ and $(2\pi - \theta_0, 0)$. The open region enclosed by $\bar{\gamma}_*$, the vertical line $v = \theta_1$, and the horizontal line $w = 0$ is positively invariant, and in it $v' > 0$. Thus, for each $h \in (0, W_+(c))$, the solution of (4.4) satisfies (4.6). On the other hand, if $h > W_+(c)$, the trajectory is above γ_* , and therefore the solution does not satisfy (4.6).

In conclusion, the solution of (4.4) satisfies (4.6) if and only if $c > 2a$ and $h \in (0, W_+(c))$.

2. Now we investigate the function $W_+(\cdot)$, which is a smooth function defined on $(2a, \infty)$. Fix $c > 2a$. We express γ_* by the graph $w = W_*(v, c)$ for $v \in [\theta_1, 2\pi - \theta_0]$. Then $W_+(c) = W_*(\theta_1, c)$ and

$$\begin{aligned} \lim_{s \searrow 2\pi - \theta_0} \frac{W_*(s, c)}{[2\pi - \theta_0] - s} &= \left(1 + a^2\right) \left(\frac{c}{2} - a\right), \\ \frac{dW_*(s, c)}{ds} &= \frac{-cW_*}{F(s, W_*)} < 0 \quad \forall s \in [\theta_1, 2\pi - \theta_0]. \end{aligned}$$

By continuous dependence of solutions with respect to parameters, we have, with $F = F(v, W_*)$,

$$\begin{aligned} \frac{d}{ds} \left(\frac{\partial W_*(s, c)}{\partial c} \right) &= -\frac{cf}{F^2} \frac{\partial W_*}{\partial c} - \frac{W_*}{F}, \\ \lim_{s \searrow 2\pi - \theta_0} \frac{1}{[2\pi - \theta_0] - v} \frac{\partial W_*(s, c)}{\partial c} &= \frac{1 + a^2}{2}. \end{aligned}$$

It then follows that $\frac{\partial W_*(s, c)}{\partial c} > 0$ for every $s \in [\theta_1, 2\pi - \theta_0]$.

3. Next we find a lower bound for W_* . For $s \in [\theta_1, 2\pi - \theta_0]$, set $\phi(s) = \tan \frac{2\pi - s}{2} = -\tan \frac{s}{2}$. Then

$$\frac{dW_*(s, c)}{d\phi} = \frac{cW_*}{W_* + \phi^2 - a^2} \quad \forall \phi \in (a, \infty) \cup (-\infty, -b], \quad W_*|_{\phi=a} = 0.$$

When $\phi \in (a, \infty]$, consider the function

$$\underline{w} = (c - 2a) \frac{(\phi - a)c}{c + \phi - a}.$$

We have $W_* - \underline{w} = O([\phi - a]^2)$ as $\phi \searrow \theta_0$. Also,

$$\frac{d\underline{w}}{d\phi} = \frac{c\underline{w}}{\underline{w} + \phi^2 - a^2} = -\frac{c^2(c - 2a)^2(\phi - a)}{(c + \phi - a)^2(c[c - 2a] + [\phi + a][c + \phi - a])} < 0.$$

It then follows that $W_* > \underline{w}$ when $s \in [\pi, 2\pi - \theta_0]$. This in particular implies that

$$W_*(\pi, c) \geq \underline{w}|_{\phi=\infty} = c^2 - 2ac.$$

Next consider the case $s \in [\theta_1, \pi]$, i.e., $\phi \in (-\infty, -b]$. Since $\phi^2 > a^2$, $\frac{z}{z+\phi^2-a^2}$ is an increasing function of $z > 0$, and $W_*(s, c) > W_*(\pi, c)$ for $s \in [\theta_1, \pi]$, we have

$$\begin{aligned} W_*(\theta_1, c) - W_*(\pi, c) &= \int_{-\infty}^{-b} \frac{cW_*}{W_* + \phi^2 - a^2} d\phi \geq \int_{-\infty}^{-b} \frac{cW_*}{W_*(\pi, c) + \phi^2} d\phi \\ &\geq \int_{-\infty}^{-b} \frac{cW_*(\pi, c)}{W_*(\pi, c) + \phi^2} d\phi \\ &= c\sqrt{W_*(\pi, c)} \left\{ \frac{\pi}{2} - \arctan \frac{b}{\sqrt{W_*(\pi, c)}} \right\} \\ &\geq \frac{c\pi}{2} \sqrt{W_*(\pi, c)} - cb. \end{aligned}$$

It then follows that, since $W_*(\pi, c) > (c - 2a)c$ and $W_+(c) = W_*(\theta_1, c)$,

$$W_+(c) \geq W_*(\pi, c) + \frac{c\pi}{2} \sqrt{W_*(\pi, c)} - cb \geq c \left\{ c - 2a - b + \frac{\pi}{2} \sqrt{c^2 - 2ac} \right\}.$$

Finally, $\lim_{c \searrow 2a} W_+(c)$ exists since $W'_+ > 0$ on $(2a, \infty)$. The limit must be zero since otherwise the solution of (4.4) with $c = 2a$ and $h = \lim_{c \searrow 2a} W_+(c)$ would satisfy (4.6), contradicting the nonexistence conclusion from linear analysis for the equilibrium $(2\pi - \theta_0, 0)$. This completes the proof of Lemma 2. \square

Proof of Lemma 3.

Proof. By the upper bound of $W_-(c)$ in (4.10) and the lower bound of $W_+(c)$ in (4.13), we find that, for each $c > 2a$,

$$W_+(c) - W_-(c) > c \left\{ c - 2a - b + \frac{\pi}{2} \sqrt{[c^2 - 2ac]} \right\} - \frac{(c + 2a)(a + b)}{1 + \frac{a+b}{2a+2c}} = \frac{H(a, b, c)}{1 + \frac{a+b}{2a+2c}},$$

where

$$H(a, b, c) = \left(c + \frac{(a + b)c}{2a + 2c} \right) \left\{ c - 2a - b + \frac{\pi}{2} \sqrt{[c^2 - 2ac]} \right\} - (c + 2a)(a + b).$$

When $c \geq b + 2a$, we have $\frac{\partial H}{\partial c} > c - (a + b) > 0$. Hence, setting $\varrho = a/b \in (0, 1)$, we have

$$\begin{aligned} \frac{H(a, b, c)}{b^2} &\geq \frac{H(a, b, b + 2a)}{b^2} \\ &= (1 + 2\varrho) \left(1 + \frac{1 + \varrho}{2(1 + 3\varrho)} \right) \frac{\pi}{2} \sqrt{1 + 2\varrho} - (1 + 3\varrho)(1 + \varrho) > 1.3. \end{aligned}$$

Here the lower bound 1.3 is obtained by plotting the function of ϱ for $\varrho \in [0, 1]$. Thus, when $c \geq b + 2a$, $W_-(c) < W_+(c)$. \square

REFERENCES

- [1] S.-I. AMARI, *Dynamics of pattern formation in lateral-inhibition type neural fields*, Biol. Cybernet., 27 (1977), pp. 77–87.
- [2] P. C. BRESSLOFF, *Waves in Neural Media*, Lecture Notes on Mathematical Modelling in the Life Sciences, Springer, New York, (2014).
- [3] G. A. CARPENTER, *A geometric approach to singular perturbation problems with applications to nerve impulse equations*, J. Differential Equations, 23 (1977), pp. 335–367.
- [4] X. CHEN, *Existence, uniqueness, and asymptotic stability of traveling waves in nonlocal evolution equations*, Adv. Differential Equations, 2 (1997), pp. 125–160.
- [5] S. COOMBES, *Waves, bumps, and patterns in neural field theories*, Biol. Cybernet., 93 (2005), pp. 91–108.
- [6] B. ERMENTROUT, *Type I membranes, phase resetting curves, and synchrony*, Neural Comput., 8 (1996), pp. 979–1001.
- [7] B. ERMENTROUT, *Simulating, Analyzing, and Animating Dynamical Systems: A Guide to XPPAUT for Researchers and Students*, Software Environ. Tools 14, SIAM, Philadelphia, 2002.
- [8] G. B. ERMENTROUT AND J. B. MCLEOD, *Existence and uniqueness of travelling waves for a neural network*, Proc. Roy. Soc. Edinburgh Sect. A, 123 (1993), pp. 461–478.
- [9] G. B. ERMENTROUT AND J. RINZEL, *Waves in a simple, excitable or oscillatory, reaction-diffusion model*, J. Math. Biol., 11 (1981), pp. 269–294.
- [10] G. FAYE, *Existence and stability of traveling pulses in a neural field equation with synaptic depression*, SIAM J. Appl. Dynam. Syst., 12 (2013), pp. 2032–2067, <https://doi.org/10.1137/130913092>.
- [11] G. FAYE AND A. SCHREL, *Existence of pulses in excitable media with nonlocal coupling*, Adv. Math., 270 (2015), pp. 400–456.
- [12] S. E. FOLIAS, *Traveling waves and breathers in an excitatory-inhibitory neural field*, Phys. Rev. E, 95 (2017), 032210.
- [13] D. GOLOMB AND Y. AMITAI, *Propagating neuronal discharges in neocortical slices: Computational and experimental study*, J. Neurophysiol., 78 (1997), pp. 1199–1211.
- [14] L. R. GONZÁLEZ-RAMÍREZ, O. J. AHMED, S. S. CASH, C. E. WAYNE, AND M. A. KRAMER, *A biologically constrained, mathematical model of cortical wave propagation preceding seizure termination*, PLOS Comput. Biol., 11 (2015), e1004065.
- [15] S. HASTINGS, *Existence of Traveling Waves in a Neural Model*, preprint, <https://arxiv.org/abs/1503.04057>, 2015.
- [16] M. W. HIRSCH, C. C. PUGH, AND M. SHUB, *Invariant Manifolds*, Lecture Notes in Math. 583, Springer, New York, 1977.
- [17] A. L. HODGKIN AND A. F. HUXLEY, *A quantitative description of membrane current and its application to conduction and excitation in nerve*, J. Physiol., 117 (1952), pp. 500–544.
- [18] F. C. HOPPENSTEADT AND E. M. IZHKEVICH, *Weakly Connected Neural Networks*, Appl. Math. Sci. 126, Springer, New York, 1997.
- [19] E. M. IZHKEVICH, *Neural excitability, spiking and bursting*, Internat. J. Bifur. Chaos Appl. Sci. Engrg., 10 (2000), pp. 1171–1266.
- [20] G. KATRIEL, *Rotating Waves in the Theta Model for a Ring of Synaptically Connected Neurons*, preprint <https://arxiv.org/abs/nlin/0405029>, 2004.
- [21] C. R. LAING AND W. C. TROY, *PDE methods for nonlocal models*, SIAM J. Appl. Dynam. Syst., 2 (2003), pp. 487–516, <https://doi.org/10.1137/030600040>.
- [22] R. MILLER AND J. RINZEL, *The dependence of impulse propagation speed on firing frequency, dispersion, for the Hodgkin-Huxley model*, Biophys. J., 34 (1981), pp. 227–259.
- [23] R. OSAN, J. RUBIN, AND B. ERMENTROUT, *Regular traveling waves in a one-dimensional network of theta neurons*, SIAM J. Appl. Math., 62 (2002), pp. 1197–1221, <https://doi.org/10.1137/S0036139901387253>.
- [24] D. J. PINTO AND G. B. ERMENTROUT, *Spatially structured activity in synaptically coupled neuronal networks: I. Traveling fronts and pulses*, SIAM J. Appl. Math., 62 (2001), pp. 206–225, <https://doi.org/10.1137/S003613990346453>.
- [25] D. J. PINTO, S. L. PATRICK, W. C. HUANG, AND B. W. CONNORS, *Initiation, propagation, and termination of epileptiform activity in rodent neocortex in vitro involve distinct mechanisms*, J. Neurosci., 25 (2005), pp. 8131–8140.
- [26] J. RINZEL AND G. B. ERMENTROUT, *Analysis of neural excitability and oscillations*, Methods Neuronal Model., 2 (1998), pp. 251–292.

- [27] G. TESCHL, *Ordinary Differential Equations and Dynamical Systems*, Grad. Stud. Math. 140, AMS, Providence, RI, 2012.
- [28] G. WEN, Y. YU, Z. PENG, AND W. HU, *Traveling wave solutions in a one-dimension theta-neuron model*, in *Advances in Neural Networks-ISNN 2009*, Springer, Berlin, 2009, pp. 909–918.