TRAVELING WAVES AND SYNCHRONY IN AN EXCITABLE LARGE-SCALE
NEURONAL NETWORK WITH ASYMMETRIC CONNECTIONS.

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Abstract. We study (i) traveling wave solutions, (ii) the formation and spatial spread of synchronous oscillations, and (iii) the effects of variations of threshold in a system of integro–differential equations which describe the activity of large scale networks of excitatory neurons on spatially extended domains. The independent variables are the activity level $u$ of a population of excitatory neurons which have long range connections, and a recovery variable $v$. In the integral component of the equation for $u$ the firing rate function is the heaviside function, and the coupling function $w$ is positive. Thus, there is no inhibition in the system. There is a critical value of the parameter $\beta$ ($\beta_+ > 0$) that appears in the equation for $v$, at which the eigenvalues $\mu^\pm$ of the linearization of the system around the rest state $(u, v) = (0, 0)$ change from real to complex. We focus on the range $\beta > \beta_+$ where $\mu^\pm$ are complex, and analyze properties of wave fronts, 1-pulse and 2-pulse waves when the connection function $w$ is asymmetric. For wave fronts we demonstrate how an initial stimulus evolves into two solutions which propagate in opposite directions with different speeds and shapes. For 1-pulse waves our main theoretical result (Theorem 4.2) shows that there is a range of $\beta > \beta_+$, where two families of waves exist, each consisting of infinitely many solutions. The waves in these two families also propagate in opposite directions with different speeds and shapes. There is a critical value $\theta^* > 0$ such that if $\theta > \theta^*$ then 1-pulse waves can only propagate in one direction. In addition, there is a second critical $\beta$ value, $\beta^* > \beta_+$, where bulk oscillations come into existence and the system becomes bistable. When $\beta \geq \beta_+$ we show how an initial stimulus evolves into a solution with large amplitude oscillations that spread out uniformly from the point of stimulus. The asymmetry in $w$ causes the rate of spread of the ‘region of synchrony’ to be more rapid to the right of the point of stimulus than to the left. When $\theta > \theta^*$ we construct a ‘uni-directional’ circuit where synchronization in one region can trigger synchronization in a distant, second region. However, when synchronization is initially triggered in the second region, it cannot spread to the first region.

Key words. waves, integro–differential equation, nonlocal, excitatory

AMS subject classifications. 34B15, 34C23, 34C11

1. Introduction. Functional behavior of the central nervous system includes such diverse phenomena as information processing from different receptor zones, sleep, and the control of vital autonomic functions [30, 31, 41]. These processes require cooperation between ensembles of cells organized into large scale, spatially extended neuronal networks. The physical laws that govern the behavior of large scale networks are different from those for a system consisting of small numbers of cells [14, 27, 35, 57]. In the study of spatially extended neuronal networks considerable attention has been given to (i) traveling waves of activity, (ii) the formation and spatial spread of synchronous oscillations, and (iii) the effects of variations in the threshold of excitation. This includes

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both experimental [29, 2, 3, 4, 9, 17, 26, 32, 34, 37, 40, 38, 46, 47, 50, 53, 62, 58, 61] and theoretical [1, 11, 12, 13, 16, 18, 19, 20, 22, 23, 25, 33, 36, 39, 41, 43, 59, 60, 63] studies.

In this paper we investigate traveling waves, the spread of synchronous oscillations, and the effects of variations in threshold in the excitable, spatially extended model

\[ \frac{\partial u(x,t)}{\partial t} = -u(x,t) - v(x,t) + \int_{-\infty}^{\infty} w(x-x') f(u(x',t) - \theta) dx' + \zeta(x,t), \]

\[ \frac{\partial v(x,t)}{\partial t} = \epsilon (\beta u(x,t) - v(x,t)). \]

(1.1)

Systems of this form were introduced by Pinto and Ermentrout [43] to model the spread of excitation waves in slices of brain cortex in which synaptic inhibition is pharmacologically blocked [7, 9, 32, 62]. The variable \( u \) denotes the activity level of the population of excitatory neurons with long range connections; \( v \) represents a negative feedback recovery mechanism in which “the negative feedback could represent spike frequency adaptation, synaptic depression or some other process that limits excitation of the network” [43]. The function \( \zeta(x,t) \) represents external input to the system. The parameters \( \epsilon \) and \( \beta \) are positive and control the rate of change of \( v \); \( \theta \) is a positive constant which denotes the threshold level for \( u \). We assume that the coupling function \( w \) is strictly positive. Thus, there is no inhibition in the system. We also assume that \( w \) is continuous, integrable and either symmetric, i.e.

\[ w(x) = w(-x) \forall x \in (-\infty, \infty), \]

(1.2)

or asymmetric, i.e.

\[ w(x) \neq w(-x) \text{ for some } x \in (-\infty, \infty). \]

(1.3)

The firing rate function \( f \) is non-negative and sigmoidal shaped. In order to allow for comparison of our results with those of previous studies, we follow [18, 19, 43, 49, 59] and set

\[ f(u - \theta) = H(u - \theta) = \begin{cases} 1 & \forall u \geq \theta, \\ 0 & \forall u < \theta, \end{cases} \]

(1.4)

and

\[ w(x) = \frac{1}{2} e^{-|x| + \kappa x}, \quad 0 \leq \kappa \leq 1 \text{ and } x \in \mathbb{R}. \]

(1.5)

We will make use of the observation that if \( \kappa > 0 \) then

\[ w(x) > w(-x) \forall x \in (-\infty, \infty). \]

(1.6)
In our numerical studies we employ two methods to initiate a solution such as a traveling wave. The first is to set the external stimulus to zero, i.e. $\zeta(x,0) \equiv 0$, and let $(u(x,0), v(x,0))$ be a perturbation from the rest state $(0,0)$ which has the typical form

$$ (u(x,0), v(x,0)) \equiv (Ae^{-Bx^2}, 0), \quad x \in \mathbb{R}, \quad A > 0 \text{ and } B > 0. $$

Equivalently, we could set $(u(x,0), v(x,0)) = (0,0)$ and set $\zeta(x,0) = Ae^{-Bx^2}$.

**Goals.** We investigate the dynamics of (1.1) when $w$ is asymmetric and the eigenvalues $\mu^{\pm}$ of the linearization of (1.1) around the rest state $(u, v) = (0, 0)$ are complex. Section 2 shows how $\mu^{\pm}$ change from real to complex as $\beta$ passes through the critical value $\beta^* \equiv \frac{(\epsilon-1)^2}{4\epsilon}$ from below. As $\beta$ increases from $\beta_*$ the imaginary part of $\mu^{\pm}$ increases and solutions of the linearization oscillate with increasing frequency. In turn, this causes the dynamics of (1.1) to become more complicated. Thus, we study how the structure of families of traveling waves changes as $\beta$ increases from $\beta_*$. There is a critical value $\beta^* > \beta_*$ where bulk oscillations appear and (1.1) becomes bistable. When $\beta \geq \beta^*$ we investigate the formation and spatial spread of synchronous oscillations. To put our investigation into perspective we summarize previous results in (A.)-(C.) below. Our specific aims are described in (D.).

(A.) **Symmetric couplings and real eigenvalues.** Pinto et al [43, 44, 45] analyzed 1-pulse waves in parameter regimes where $w$ is symmetric and $\mu^{\pm}$ are real. Richardson et al [49] make use of the results in [45] to study the effects of raising electric fields on 1-pulse waves in mammalian cortex. The stability of solutions in the real eigenvalue setting has been studied in [11, 45, 55].

(B.) **Asymmetric couplings and real eigenvalues.** Pinto and Troy [48] analyzed 1-pulse waves when $w$ is asymmetric and $\mu^{\pm}$ are real. The asymmetry in $w$ causes an initial stimulus of the form (1.7) to evolve into two 1-pulse waves which propagate in opposite directions with different amplitudes and speeds. Thus, traveling waves have a preferred direction of propagation when the coupling is asymmetric. In agreement with these theoretical results, we give experimental evidence which indicates that 1-pulse waves in barrel cortex have a preferred direction of propagation.

(C.) **Symmetric couplings and complex eigenvalues.** Troy and Shusterman [59] investigated (1.1) in parameter regimes where the coupling is the symmetric function $w(x) = \frac{1}{2}e^{-|x|}$ and (ii) $\beta > \beta_*$ where $\mu^{\pm}$ are complex. We analyzed one-dimensional wave fronts, single pulse waves, and multi-pulse wave trains. We also explained why multi-pulse waves are expected to exist only in the complex eigenvalue regime. In two dimensions we analyzed the periodic formation of waves, as well as the mechanisms responsible for the formation of spiral waves. Spiral waves were recently discovered in tangential slices of rat brain tissue [32]. Thus, in the complex eigenvalue setting the dynamics of (1.1) are richer than in the real eigenvalue case. Furthermore, these dynamics closely resemble electrophysiological phenomena observed in clinical and experimental studies [41].
Specific aims: Asymmetric couplings and complex eigenvalues.

In this paper we extend the results described in (A.)-(C.) and investigate the dynamics of (1.1) when \( w \) is asymmetric and the eigenvalues \( \mu^{\pm} \) are complex. Our goals are summarized in I - III below.

I. Traveling Waves. Single-pulse and multi-pulse traveling activity waves have been observed in feline cortex [2, 3, 4], in the brain of freely moving mice [17], in tangential and coronal brain slice experiments [32, 62], and in seizure propagation across cortical regions [40, 61]. In Sections 3-5 we analyze wave fronts, 1-pulse waves and 2-pulse waves when \( \beta > \beta^* \) and \( w(x) = \frac{1}{2}e^{-|x|+\kappa x}, \) where \( \kappa \neq 0. \) Wave front solutions cross the threshold level \( u = \theta \) precisely once, whereas N-pulse waves cross threshold exactly 2N times. For a fixed initial stimulus we find that, as \( \beta \) increases, there is a natural evolution from wave fronts to 1-pulse waves, and subsequently to 2-pulse waves. Our main theoretical result (Theorem 4.2) shows that there is a range of \( \beta > \beta^* \) where two families of 1-pulse waves exist, each consisting of infinitely many coexisting solutions. The waves in these two families propagate in opposite directions with different speeds and shapes. Infinite families of solutions with such diverse properties do not exist when \( w \) is asymmetric and \( \mu^{\pm} \) are real. Similar properties hold for wave fronts and 2-pulse waves. Because the eigenvalues are complex, technical difficulties make proofs more challenging than in the real eigenvalue case. These difficulties lead to open problems which are stated as we proceed.

II. Synchronous oscillations. There is a second critical value \( \beta^* > \beta_* \) where spatially independent bulk oscillations come into existence (Section 6). When \( \beta \geq \beta^* \) the system (1.1) is bistable since these oscillations are stable and coexist with the stable rest state \( (u, v) = (0, 0) \). An initial stimulus of the form (1.7) can evolve into a solution which exhibits large amplitude oscillations that spread out uniformly from the point of stimulus. The asymmetry in \( w \) causes the rate of spread of the ‘region of synchrony’ to be more rapid to the right of the point of stimulus than to the left. Eventually, however, the solution oscillates uniformly over the entire spatial region. We also show how an initial stimulus can evolve into a stable 1-pulse wave which coexists with synchronous oscillations and the stable rest state. In Section 6 we compare our theoretical results with clinical observations of epileptiform events.

III. Variations in threshold. In 1936 Hill [29] suggested that the value of threshold might change in response to the state of neuronal tissue. Following Hill’s theoretical ideas, Coombes and Owens [12, 13] studied the effects of a state dependent threshold on bump type solutions in a scalar Wilson-Cowan type model in which \( w \) is of Mexican hat type, i.e. \( w(x) \) is symmetric about \( x = 0 \) and changes sign on \( (-\infty, \infty) \). Recently, Kawai, Lazar and Metherate [36] have given experimental evidence which shows that the threshold of excitation can indeed change. In particular, when they expose axons of thalamocortical mouse neurons to nicotine, the threshold of excitation decreases and the firing rate
of the neurons doubles. In [54] it is suggested that this causes “an increase in the amount of sensory information reaching the cortex,” and that “this is a major reason that nicotine enhances cognitive functioning.” It is also pointed out that in schizophrenia there is poor communication between the thalamus and the cortex, and therefore the high incidence of smoking in schizophrenics might be a method of self medication. In our analysis of traveling waves and synchrony we investigate the effects of both increasing and decreasing the threshold $\theta$, and also the strength $\kappa$ of the the asymmetric coupling. In agreement with [36] we find that the amplitudes and speeds of traveling waves increase dramatically as $\theta$ decreases. Because $w$ is asymmetric there is a critical value $\theta^*$ such that waves can be transmitted in only one direction when $\theta > \theta^*$. In Section 6 we investigate how variations in threshold can affect synchrony. As a first step towards understanding how communication between spatial regions can become inhibited when threshold is too high, we let $\theta > \theta^*$ and study how synchronization in one region can influence synchronization in a distant region. For this we construct a simple “uni-directional neuronal circuit” in which $\theta > \theta^*$ so that waves propagate only to the right. In this setting synchronization in one region causes the formation of a train of waves which propagate to the right and ultimately trigger a second, distant region to undergo synchronization. However, because $\theta > \theta^*$, synchronization in the second region is inhibited from emitting left propagating waves, hence the first region remains at rest.

Conclusions and directions for future research are given in Section 7.

2. Traveling Waves. Following [45, 59], we set $\zeta(x, t) = 0$ and look for traveling wave solutions of (1.1) of the form $(u, v) = (U(z), V(z))$, where $z = x + ct$. These satisfy

$$
\begin{align*}
&cU'(z) = -U - V + \int_{-\infty}^{\infty} w(z - z')H(U(z') - \theta)dz', \\
&cV'(z) = \epsilon(\beta U - V),
\end{align*}
$$

(2.1)

where

$$
(2.2)
$$

$$
w(z - z') = \frac{1}{2}e^{-|z-z'|+\kappa(z-z')}, \quad 0 \leq \kappa < 1.
$$

Our main focus is on the regime $\kappa \neq 0$ where the coupling is asymmetric. For simplicity we restrict our attention to the case $\kappa > 0$. It is easily verified that (2.1) is equivalent to

$$
(2.3) \quad c^2 U'' + c(1 + \epsilon) U' + \epsilon(\beta + 1)U = c \frac{d}{dz} \int_{-\infty}^{\infty} w(z - z')H(U(z') - \theta)dz' + \epsilon \int_{-\infty}^{\infty} w(z - z')H(U(z') - \theta)dz'.
$$

Linearizing (2.3) around the rest state $U = 0$ leads to

$$
(2.4) \quad c^2 U'' + c(1 + \epsilon) U' + \epsilon(\beta + 1)U = 0.
$$
The eigenvalues associated with (2.4) are

\[ \mu^\pm = \frac{\lambda^\pm}{c} = \frac{-(\epsilon + 1) \pm i\sqrt{4\beta\epsilon - (\epsilon - 1)^2}}{2c}. \]

We restrict our attention to the regime \(0 < \epsilon < 1\). From this and (2.5) it follows that

\[ \mu^\pm \text{ are real } \iff 0 < \beta \leq \beta_* = \frac{(\epsilon - 1)^2}{4\epsilon}. \]

**Remarks.** (i) When \(\mu^\pm\) are real one expects to find only wave fronts or single pulse waves [43, 44, 45, 49, 59]. Our interest is in the regime \(\beta > \beta_*\) where \(\mu^\pm\) are complex and the dynamics of (1.1) are richer.

For example, when \(w\) is symmetric we previously found the coexistence of families of multi-pulse waves in one space dimension, and periodic waves and rotating waves in two dimensions [59].

(ii) We have followed [45, 59] and let the independent variable have the form \(z = x + ct\). Thus, when \(c > 0\), solutions of (2.1)-(2.2) correspond to traveling waves of (1.1) which propagate “to the left” as \(t\) increases. If \(z = x - ct\) then traveling wave solutions propagate “to the right.”

Previous studies analyzed traveling waves when \(w\) is symmetric [18, 19, 20, 43, 45, 49, 59]. In this setting it can be assumed that \(c > 0\), since a wave traveling with speed \(c > 0\) can be transformed into a wave traveling in the opposite direction with the same shape, and with speed \(-c < 0\). Here we study traveling waves when \(\mu^\pm\) are complex and the \(w\) is asymmetric. Our numerical experiments in the next three sections show that an initial perturbation from rest can cause two waves to form which propagate in opposite directions with different speeds and shapes. We will make use of the quantities

\[ \alpha = \text{Re}(\mu^\pm) = \frac{-(\epsilon + 1)}{2c} \quad \text{and} \quad \gamma = \text{Im}(\mu^\pm) = \frac{\sqrt{4\epsilon\beta - (\epsilon - 1)^2}}{2c}. \]

Our investigation indicates that stable traveling waves exist when

\[ 0 < \epsilon, \kappa < 1, \quad 0 < \theta < \min \left( \frac{2\epsilon}{(1 - \kappa^2)(\epsilon + 1)^2}, \frac{1}{4(\epsilon + 1)} \right), \quad \beta > \beta_* = \frac{(\epsilon - 1)^2}{4\epsilon}. \]

The first two sets of inequalities in (2.8) are mild restrictions which allow technical arguments to be completed, and the third inequality means that \(\mu^\pm\) are complex. Throughout the paper we perform numerical experiments for parameters which satisfy (2.8). An important implication of (2.8) is that

\[ \beta_* = \frac{(\epsilon - 1)^2}{4\epsilon} < \beta_1 = \frac{1}{2(1 + \kappa)} - 1 < \beta_2 = \frac{1}{2(1 - \kappa)} - 1 \]

when \(|\kappa|\) is small. In Section 3 we will see that distinct branches of wave fronts come into existence at the critical values \(\beta_1 = \frac{1}{2(1 + \kappa)} - 1\) and \(\beta_2 = \frac{1}{2(1 - \kappa)} - 1\). Our analysis of 1-pulse waves in Section 4 shows that infinitely many wave speeds are possible at \(\beta = \beta_1\) and \(\beta = \beta_2\). Two-pulse solutions are described in Section 5. When \(\mu^\pm\) are complex, underlying oscillatory terms lead to technical difficulties which make the completion of existence proofs especially challenging. These difficulties suggest open problems which are discussed as we proceed.
3. Wave fronts. We analyze wave front solutions when \( w \) is asymmetric. Although the discussion appears lengthy, it is necessary to give complete details in order to obtain a global understanding of the structure of solutions. Our study focuses on the following:

- **A.** The construction of two families of stationary solutions with speed \( c = 0 \) (Figure 3.1).
- **B.** Properties of wavefronts when \( c > 0 \). In this case a family of solutions bifurcates from a stationary solution (Figure 3.1, right panel) as \( c \) increases from \( c = 0 \).
- **C.** Properties of wavefronts when \( c < 0 \). In this case a family of wavefronts with different speeds and shapes bifurcates from a second stationary solution (Figure 3.1, left panel) as \( c \) decreases from \( c = 0 \).
- **D.** The effects of changing the threshold \( \theta \).
- **E.** Open problems.

**A. Stationary solutions.** We set \( c = 0 \) and \( w(x) = \frac{1}{2} e^{-|x-x'| + \kappa(x-x')} \) in (2.3) and investigate the existence of stationary wavefront solutions of the form

\[
(3.1) \quad U(x) = \frac{1}{2(\beta + 1)} \int_{-\infty}^{\infty} e^{-|x-x'| + \kappa(x-x')} H(U(x') - \theta) \, dx'.
\]

We find that there is a range of parameters for which two different solutions exist.

**Fig. 3.1.** Left panel: Stationary front solution of (3.8)-(3.9), with \( U(\infty) = \frac{2\theta}{1+\kappa} = .23 \) when \( (\theta, \kappa) = (.1, .15) \) and \( \beta = \beta_1 = \frac{5}{(\kappa+1)\theta} - 1 = 3.35 \) Right panel: solution with \( U(-\infty) = \frac{2\theta}{1+\kappa} = .173 \) when \( \beta = \beta_2 = \frac{5}{(1-\kappa)\theta} - 1 = 4.88 \)

**The first stationary solution.** The first solution (Figure 3.1, left panel) satisfies

\[
(3.2) \quad \begin{cases} 
U(x) \text{ and } U'(x) \text{ are continuous } \forall x \in (-\infty, \infty), \\
U(x) < \theta \forall x < 0, \; U(0) = \theta \\
U(x) > \theta \forall x \in (0, \infty).
\end{cases}
\]

Without loss of generality we have assumed that \( U(0) = \theta \) in (3.2) since (3.1) is translationally invariant. Then (3.2) reduce (3.1) to

\[
(3.3) \quad U(x) = \frac{1}{2(\beta + 1)} \int_{-\infty}^{\infty} e^{-|x-x'| + \kappa(x-x')} \, dx'.
\]
Solving (3.2)-(3.3) gives

\[ U(x) = \begin{cases} \frac{5}{(\kappa+1)(\beta+1)}e^{(1+\kappa)x} & \forall x \leq 0, \\ \frac{5}{\beta+1} \left( \frac{2}{1-\kappa^2} - \frac{e^{(\kappa-1)x}}{1-\kappa} \right) & x > 0, \end{cases} \]

where \( \beta, \kappa, \theta \) satisfy

\[ 0 < \kappa < 1, \ 0 < \theta < 1, \ \beta = \beta_1 = \frac{5}{(\kappa + 1)\theta} - 1. \]

This and (2.9) imply that

\[ \beta_* < \beta_1 < \frac{1}{2\theta} - 1 \ \forall \kappa \in (0, 1), \ \beta_1 \to \frac{1}{2\theta} - 1 \text{ as } \kappa \to 0^+, \ \beta_1 \to \frac{1}{4\theta} - 1 \text{ as } \kappa \to 1^- . \]

It follows from (3.4)-(3.5) that

\[ U'(x) > 0 \ \forall x \in (-\infty, \infty), \]

\[ (U(x), U'(x)) \to \left( \frac{2\theta}{\kappa}, 0 \right) \text{ as } x \to \infty, \]

\[ (U(x), U'(x)) \to (0, 0) \text{ as } x \to -\infty. \]

The second stationary solution. The second solution (Figure 3.1, right panel) satisfies

\[ \begin{cases} U(x) \text{ and } U'(x) \text{ are continuous } \forall x \in (-\infty, \infty), \\ U(x) > \theta \ \forall x \in (-\infty, 0), \ U(0) = \theta, \\ U(x) < \theta \ \forall x > 0. \end{cases} \]

Conditions (3.8) reduce (3.1) to

\[ U(x) = \frac{1}{2(\beta+1)} \int_{-\infty}^{0} e^{-|x-x'|+\kappa(x-x')} dx'. \]

Solving (3.8)-(3.9) gives

\[ U(x) = \begin{cases} \frac{5}{\beta+1} \left( \frac{2}{1-\kappa^2} - \frac{e^{(\kappa-1)x}}{1-\kappa} \right), & x < 0, \\ \frac{5}{(\beta+1)(1-\kappa)}e^{(\kappa-1)x} & \forall x \geq 0. \end{cases} \]

Conditions (3.8) hold when \( \beta, \kappa, \theta, a \) satisfy

\[ 0 < \kappa < 1, \ 0 < \theta < 1, \ \beta = \beta_1 = \frac{5}{(1-\kappa)\theta} - 1. \]

This implies that

\[ \beta_1 > \frac{1}{2\theta} - 1 \ \forall \kappa \in (0, 1), \ \beta_1 \to \frac{1}{2\theta} - 1 \text{ as } \kappa \to 0^+, \ \beta_1 \to +\infty \text{ as } \kappa \to 1^- . \]
Finally, it follows from (3.10)-(3.11) that $U$ satisfies (3.8), and also
\[
\begin{cases}
U'(x) < 0 \quad \forall x \in (-\infty, \infty), \\
(U(x), U'(x)) \to \left(\frac{2\beta}{1+\kappa}, 0\right) \text{ as } x \to -\infty, \\
(U(x), U'(x)) \to (0,0) \text{ as } x \to +\infty.
\end{cases}
\]

(3.13)

**B. Properties of wavefronts when $c > 0$.** In this and the next two sections we show how distinct branches of solutions bifurcate from the stationary solutions constructed above as $c$ passes through $c = 0$. When $c > 0$ wavefront solutions satisfy
\[
\begin{cases}
U(z) \text{ and } U'(z) \text{ are continuous } \forall z \in (-\infty, \infty), \\
U(z) < \theta \quad \forall z < 0, \\
(U(z), U'(z)) \to (0,0) \text{ as } z \to -\infty, \\
U(0) = \theta, \quad U(z) > \theta \quad \forall z > 0, \quad U'(z) \to 0 \text{ as } z \to \infty.
\end{cases}
\]

(3.14)

Again, without loss of generality we have assumed that $U(0) = \theta$ in (3.2) since (2.3) is translationally invariant. When conditions (3.14) hold equation (2.3) reduces to
\[
c^2 U'' + c(1+\epsilon)U' + \epsilon(\beta+1)U = \frac{c}{2} \frac{d}{dz} \int_{-\infty}^{\infty} e^{-|z-z'|+\kappa(z-z')}dz' + \frac{\epsilon}{2} \int_{-\infty}^{\infty} e^{-|z-z'|+\kappa(z-z')}dz'.
\]

(3.15)

This further reduces to
\[
c^2 U'' + c(1+\epsilon)U' + \epsilon(\beta+1)U = g(z),
\]

where
\[
g(z) = \begin{cases} 
0.5(c + \frac{\epsilon}{1+\kappa})e^{(1+\kappa)z} & \forall z \leq 0, \\
0.5(c - \frac{\epsilon}{1-\kappa})e^{-(1-\kappa)z} + \frac{\epsilon}{1-\kappa} & \text{ if } z > 0.
\end{cases}
\]

(3.17)

A combination of analysis and numerical experiments suggests that two branches of solutions coexist when $c > 0$ (Figure 3.2). To understand how these results are obtained we investigate the following:

- (i) Analysis of solutions on $(-\infty, 0]$.
- (ii) Analysis of solutions on $(0, \infty)$.
- (iii) Numerical evidence for the existence of solutions.

(i) **Analysis of solutions on $(-\infty, 0]$.** On $(-\infty, 0]$ the solution of (3.16) is
\[
U_0(z) = b_1 e^{\alpha z} \cos(\gamma z) + b_2 e^{\alpha z} \sin(\gamma z) + P_0(z),
\]

where $b_1$ and $b_2$ are constants, and $P_0(z)$ is the particular solution
\[
P_0(z) = \frac{0.5(\epsilon + (1+\kappa)c)}{(1+\kappa)((1+\kappa)^2c^2 + (1+\kappa)(1+\epsilon)c + \epsilon(\beta+1))} e^{(1+\kappa)z} \quad \forall z \leq 0.
\]

(3.18)
The oscillatory terms \( b_1 e^{\alpha z} \cos(\gamma z) \) and \( b_2 e^{\alpha z} \sin(\gamma z) \) in (3.18) are due to \( \mu^\pm \) being complex. Recall from (2.7) that \( \alpha = \text{Re}(\mu^\pm) < 0 \) when \( c > 0 \). Thus, to satisfy the condition \( U_0(-\infty) = U'_0(-\infty) = 0 \), we conclude that \( b_1 = b_2 = 0 \), and (3.18)-(3.19) reduce to

\[
U_0(z) = \frac{.5(\epsilon + (1 + \kappa)c)}{(1 + \kappa)((1 + \kappa)^2c^2 + (1 + \epsilon)c + \epsilon(\beta + 1))} e^{(1+\kappa)z} \quad \forall z \leq 0. 
\]

Substituting \( U_0(0) = \theta \) into (3.20) gives the algebraic equation

\[
\frac{.5(\epsilon + (1 + \kappa)c)}{(1 + \kappa)((1 + \kappa)^2c^2 + (1 + \epsilon)c + \epsilon(\beta + 1))} = \theta. 
\]

It follows from (3.20)-(3.21) that

\[
U_0(z) = \theta e^{(1+\kappa)z} < \theta \quad \forall z \leq 0. 
\]

(ii) **Analysis of solutions on** \((0, \infty)\). When \( z > 0 \) the first step in analyzing solutions is to solve (3.21) for wave speed \( c \). This gives the two positive values (Figure 3.2, upper left panel)

\[
c_1 = \frac{.5 - \theta(1 + \kappa)(\epsilon + 1) + \sqrt{(.5 - \theta(1 + \kappa)(\epsilon + 1))^2 - 4\epsilon\theta(1 + \kappa)(\theta(1 + \kappa)(\beta + 1) - .5)}}{2\theta(1 + \kappa)^2}, 
\]

\[
c_2 = \frac{.5 - \theta(1 + \kappa)(\epsilon + 1) - \sqrt{(.5 - \theta(1 + \kappa)(\epsilon + 1))^2 - 4\epsilon\theta(1 + \kappa)(\theta(1 + \kappa)(\beta + 1) - .5)}}{2\theta(1 + \kappa)^2}, 
\]

Recall from (2.8) that \( 0 < \epsilon < 1 \) and \( 0 < \theta < \frac{1}{4(\epsilon + 1)} \). This and (3.23)-(3.24) imply that

\[
\begin{cases} 
  c_1 > 0 & \text{if } 0 < \beta < \frac{1}{2\theta(1 + \kappa)} - 1 + \frac{1}{4\epsilon \theta^2(1 + \kappa)^2}(.5 - \theta(1 + \kappa)(\epsilon + 1))^2, \\
  c_2 = 0 & \text{if } \beta = \frac{1}{2\theta(1 + \kappa)} - 1, \\
  c_2 > 0 & \text{if } \frac{1}{2\theta(1 + \kappa)} - 1 < \beta \leq \frac{1}{2\theta(1 + \kappa)} - 1 + \frac{1}{4\epsilon \theta^2(1 + \kappa)^2}(.5 - \theta(1 + \kappa)(\epsilon + 1))^2, \\
  c_1 \text{ and } c_2 \text{ are complex} & \text{if } \beta > \frac{1}{2\theta(1 + \kappa)} - 1 + \frac{1}{4\epsilon \theta^2(1 + \kappa)^2}(.5 - \theta(1 + \kappa)(\epsilon + 1))^2. 
\end{cases} 
\]

When \( z > 0 \) the solution of (3.16) is

\[
U_1 = k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z) + P_1(z), 
\]

where \( \alpha < 0 \) and \( \gamma > 0 \) are defined in (2.7), and \( P_1(z) \) is the particular solution

\[
P_1(z) = \frac{.5((1 - \kappa)c - \epsilon)}{(1 - \kappa)((1 - \kappa)^2c^2 - (1 - \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} e^{-(1-\kappa)z} + \frac{1}{(\beta + 1)(1 - \kappa^2)}, 
\]

where \( c = c_1 \) or \( c = c_2 \). To preserve continuity at \( z = 0 \) we require that \( (U_1(0), U'_1(0)) = (U_0(0), U'_0(0)) \).

This and (3.26)-(3.27) show that \( k_1 \) and \( k_2 \) are uniquely defined by

\[
k_1 = \theta - P_1(0) \quad \text{and} \quad k_2 = \frac{1}{\gamma} (\theta(1 - \alpha) - P_1'(0) + \alpha P_1(0)). 
\]
(iii) Numerical evidence for the existence of solutions. To complete the proof that a solution satisfies all of the conditions in (3.14) for a traveling wave front we only need to show that

\begin{equation}
U_1(z) > \theta \quad \forall z > 0, \quad \text{and} \quad \lim_{{z \to \infty}} U_1'(z) = 0.
\end{equation}

\[ (3.29) \]
To gain insight we let \( \epsilon = 0.1 \) and \( \beta > \beta_* = 2.025 \), and solve the initial value problem

\[
\begin{align*}
\frac{du}{dt}(x,t) &= -u - v + \frac{1}{2} \int_{-20}^{20} e^{-|x-x'|+\kappa(x-x')} H(u(x',t) - \theta) dx', \\
\frac{dv}{dt}(x,t) &= \epsilon (\beta u - v), \\
u(x,0) &= e^{-x^2} \quad \text{and} \quad v(x,0) = 0 \quad \forall x \in [-20, 20],
\end{align*}
\]

(3.30)

where \((\theta, \kappa)\) satisfy (3.30). The limits \((-\infty, \infty)\) in the integral term have been replaced with \([-20, 20]\).

Other choices for initial conditions give results similar to those described below. A second approach which leads to wave formation is to initially keep \( u \) and \( v \) at their resting levels, i.e. \( u(x,0) = v(x,0) = 0 \), and perturb the system with an external stimulus applied to the right side of the equation for \( u \).

To solve (3.30) we approximate the integral term with a Riemann sum, with step size \( \Delta x = 0.1 \), and use an explicit Euler time step \( \Delta t = 0.05 \). When \( \beta > \beta_* \) the solution of (3.30) evolves into a traveling wavefront (Figure 3.2), a single-pulse wave (Figures 4.1 and 4.3), or an N-pulse wave (Figure 5.1).

Our numerical study of wave fronts suggests that (3.29) does not hold at every point along the curves \( c_1 \) and \( c_2 \) (Figure 3.2, upper left). However, (3.29) does hold along two connected sub-branches \( \Gamma_1 \) and \( \Gamma_2 \) of these curves (Figure 3.2, upper right). Below we describe \( \Gamma_1 \) and \( \Gamma_2 \).

The Lower Branch \( \Gamma_2 \). When \( c = c_2 \) it follows from (3.26), (3.27) and (3.28) that

\[
U_1(z) = k_1 e^{\alpha z \cos(\gamma z)} + k_2 e^{\alpha z \sin(\gamma z)}
\]

(3.31)

\[
\begin{align*}
&= \frac{5(1-\kappa)k_2}{(1-\kappa)(1+\kappa)k_2 - (1-\kappa)(1+\kappa)k_2 + \epsilon(3+\kappa)\Delta x} e^{-(1-\kappa)z} + \frac{1}{(3+\kappa)(1-\kappa)\Delta x}.
\end{align*}
\]

If \( U_1(z) > \theta \ \forall z > 0 \) then (3.31) implies that \( U_1'(z) \to 0 \) as \( z \to \infty \), and therefore both conditions in (3.29) hold. Thus, it is sufficient to show that

\[
U_1(z) > \theta \quad \forall z > 0.
\]

(3.32)

It is difficult to prove (3.32) since the oscillatory component \( k_1 e^{\alpha z \cos(\gamma z)} + k_2 e^{\alpha z \sin(\gamma z)} \) of (3.31) can cause \( U_1(z) \) to dip below the threshold level \( \theta \) at some point in \((0, \infty)\). However, our numerical experiments indicate that there is a branch \( \Gamma_2 \) (Figure 3.2) of solutions satisfying

\[
U(z) = \begin{cases} 
\theta e^{(1+\kappa)z} < \theta & \forall z < 0, \\
U_1(z) > \theta & \forall z > 0.
\end{cases}
\]

(3.33)

Along \( \Gamma_2 \) it follows from (3.23) and (3.25) that

\[
c_2 \to 0^+ \quad \text{as} \quad \beta \to \left( \frac{1}{2(1+\kappa)\theta} - 1 \right)^+.\]

(3.34)

Thus, the left end of \( \Gamma_2 \) begins at \( \beta = \frac{1}{2(1+\kappa)\theta} - 1 \) where \( c_2 = 0 \) and \( U \) is the stationary solution defined by (3.4) (Figure 3.1, left panel). To determine the right end of \( \Gamma_2 \) we substitute the condition
solutions have the form 1 real, and solutions on \( \Gamma \) positive. This branch extends to the left of \( \beta \) since it is tangent to \( U \). Our study also suggests that all solutions on \( \Gamma \) are unstable.

**The Upper Branch** \( \Gamma_1 \). Let \( \Gamma_1 \) denote the upper branch of wave fronts when \( c = c_1 \) (Figure 3.2). This branch extends to the left of \( \beta = \beta_* \) down to \( \beta = 0 \). When \( 0 < \beta \leq \beta_* \) the eigenvalues \( \mu^\pm \) are real, and solutions on \( \Gamma_1 \) are monotone for large \( z \). When \( \beta > \beta_* \) the eigenvalues \( \mu^\pm \) are complex and solutions have the form

\[
U(z) = \begin{cases} 
\theta e^{(1+\kappa)z} & \forall z \leq 0, \\
k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z) + \frac{5(1-(1-\kappa)c_1-\epsilon)(1-\kappa)}{(1-\kappa)(1+\epsilon)(1+c_1+\epsilon(\beta+1))} + \frac{1}{(1-\kappa^2)(\beta+1)} & \forall z > 0,
\end{cases}
(3.35)
\]

where \( \alpha, \gamma, k_1 \) and \( k_2 \) are evaluated at \( c = c_2 \). To complete the proof we need to show that \( U(z) > \theta \) \( \forall z > 0 \). This is difficult to prove, even in the real eigenvalue regime, since \( U \) can dip below \( \theta \) at a positive \( z \) value. In Figure 3.2 (second row, left) we set \( \beta = 4 \) and see that \( U(z) \) is a wave front since \( U(z) > \theta \) \( \forall z > 0 \). In the third row, left panel, we set \( \beta = 6.45 \) and see that \( U(z) \) is not a wave front since it is tangent to \( U = \theta \) at \( z \approx 21 \). When \( \beta > 6.45 \) the function \( U \) cannot be a wave front since it dips below \( \theta \) at a positive \( z \) value. We conjecture that the interval of existence of \( \Gamma_1 \) is approximately \((0, 6.45)\) (Figure 3.2, first row, right). Our study suggests that solutions on \( \Gamma_1 \) are stable.

**C. Properties of wavefronts when** \( c < 0 \). When \( c < 0 \) we investigate solutions which satisfy

\[
\begin{aligned}
& U(\infty) \geq \theta \text{ into (3.33) and obtain } U(\infty) = \frac{1}{(1-\kappa^2)(\beta+1)} \geq \theta. \text{ This implies that } \Gamma_2 \text{ cannot extend past } \\
& \beta = \frac{1}{(1-\kappa^2)\theta} - 1. \text{ Figure 3.2 (fourth row, left panel) shows the solution at the right endpoint of } \Gamma_2 \text{ when } (\epsilon, \theta, \kappa) = (1, 1, 15). \text{ For each } \beta \in \left[ \frac{1}{2(1+\kappa)\theta} - 1, \frac{1}{(1-\kappa^2)\theta} - 1 \right] \text{ our computations indicate that } \\
& U(z) > \theta \text{ } \forall z > 0, \text{ hence we conjecture that the interval of existence of } \Gamma_2 = \left[ \frac{1}{2(1+\kappa)\theta} - 1, \frac{1}{(1-\kappa^2)\theta} - 1 \right].
\end{aligned}
(3.36)
\]

When conditions (3.36) hold equation (2.3) reduces to

\[
c^2 U'' + c(1 + e) U' + \epsilon(\beta + 1) U = \frac{c}{2} \frac{d}{dz} \int_{-\infty}^{0} e^{-|z-z'|+\kappa(z-z')} dz' + \frac{\epsilon c}{2} \int_{-\infty}^{0} e^{-|z-z'|+\kappa(z-z')} dz'.
(3.37)
\]

This further reduces to

\[
c^2 U'' + c(1 + e) U' + \epsilon(\beta + 1) U = g(z),
(3.38)
\]

where

\[
g(z) = \begin{cases} 
-5(c + \frac{\epsilon}{1+\kappa})e^{(1+\kappa)z} + \frac{\epsilon}{1+\kappa} & \forall z \leq 0, \\
-5(c - \frac{\epsilon}{1+\kappa})e^{-(1-\kappa)z} & \text{ if } \ z > 0.
\end{cases}
(3.39)
\]
As in the case $c > 0$, we devote the remainder of this section to the following:

- **(iv)** Analysis of solutions on $[0, \infty)$.
- **(v)** Analysis of solutions on $(-\infty, 0)$.
- **(vi)** Numerical evidence for the existence of solutions.

**(iv) Analysis of solutions on $[0, \infty)$.** Proceeding as above, we find that the solution of (3.38) is

$$U_2(z) = \frac{.5(\epsilon - (1 - \kappa)c)}{(1 - \kappa)(1 - \kappa^2)c^2 + -(1 - \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} e^{-(1 - \kappa)z} \quad \forall z > 0.$$  

Substituting the condition $U_2(0) = \theta$ into (3.40), we obtain

$$\frac{.5(\epsilon - (1 - \kappa)c)}{(1 - \kappa)(1 - \kappa^2)c^2 - (1 - \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} = \theta.$$  

It follows from (3.40)-(3.41) that

$$U_2(z) = \theta e^{-(1 - \kappa)z} < \theta \quad \forall z \geq 0.$$  

Next, solving (3.41) for wave speed $c$ gives the two negative values (Figure 3.2)

$$c_3 = \frac{\theta(1 - \kappa)(\epsilon + 1) - .5 + \sqrt{(.5 - \theta(1 - \kappa)(1 + \epsilon))^2 - 4\epsilon\theta(1 - \kappa)(\beta + 1) - .5)}}{2\theta(1 - \kappa)^2},$$  

$$c_4 = \frac{\theta(1 - \kappa)(\epsilon + 1) - .5 - \sqrt{(.5 - \theta(1 - \kappa)(1 + \epsilon))^2 - 4\epsilon\theta(1 - \kappa)(\beta + 1) - .5)}}{2\theta(1 - \kappa)^2}.$$  

**(v) Analysis of solutions on $(-\infty, 0)$.** When $z < 0$ the solution of (3.16) is

$$U_3 = k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z) + P_2(z),$$  

where $\alpha < 0$ and $\gamma > 0$ are defined in (2.7), and $P_2(z)$ is the particular solution

$$P_2(z) = \frac{-.5((1 + \kappa)c + \epsilon)}{(1 + \kappa)(1 + \kappa^2)c^2 + (1 + \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} e^{(1 + \kappa)z} + \frac{1}{(\beta + 1)(1 - \kappa^2)},$$  

where $c = c_3$ or $c = c_4$. To preserve continuity at $z = 0$ we require that $(U_3(0), U_3'(0)) = (U_2(0), U_2'(0))$. This and (3.45)-(3.46) show that $k_1$ and $k_2$ are uniquely defined by

$$k_1 = \theta - P_2(0) \quad \text{and} \quad k_2 = \frac{1}{\gamma} \left( \theta(1 - \alpha) - P_2'(0) + \alpha P_2(0) \right).$$  

**(vi) Numerical evidence for the existence of solutions.** As in the case $c > 0$, to complete the proof that a solution satisfies all of the conditions in (3.14) for a wave front it suffices to show that

$$U_3(z) > \theta \quad \forall z < 0.$$
Our numerical experiments suggest that conditions (3.48) are not satisfied at every point along the curves $c_3$ and $c_4$ (Figure 3.2). However, (3.48) does hold along two sub-branches $\Gamma_3$ and $\Gamma_4$ of these curves (Figure 3.2). Below we briefly describe properties of solutions along $\Gamma_3$ and $\Gamma_4$.

**The Branch $\Gamma_3$.** When $c = c_3 < 0$ it follows from (3.45), (3.46) and (3.47) that

\[
U_2(z) = k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z)
- \frac{5((1+\kappa)c_3 + \epsilon)(1+\kappa)(1+\epsilon)(c_3 + \epsilon(\beta + 1))}{(\beta+1)(1-\kappa)^2} e^{(1+\kappa)z} + \frac{1}{(\beta+1)(1-\kappa)^2}.
\]

Our numerical experiments indicate that there is a branch $\Gamma_3$ (Figure 3.2) of solutions satisfying

\[
U(z) = \begin{cases} 
\theta e^{-(1-\kappa)z} < \theta & \forall z \geq 0, \\
U_2(z) > \theta & \forall z < 0.
\end{cases}
\]

Along $\Gamma_3$ it follows from (3.43) that

\[
c_3 \to 0^+ \text{ as } \beta \to \left(\frac{1}{2(1-\kappa)\theta} - 1\right)^+.
\]

Thus, the left end of $\Gamma_3$ begins at $\beta = \frac{1}{2(1-\kappa)\theta} - 1$ where $c_3 = 0$ and $U$ is the stationary solution defined by (3.4) (Figure 3.1, right panel). To determine the right end of $\Gamma_3$ we substitute the condition $U(\infty) \geq \theta$ into (3.50) and obtain $U(\infty) = \frac{1}{(1-\kappa)^2(\beta+1)} \geq \theta$. This implies that $\Gamma_3$ cannot extend past $\beta = \frac{1}{(1-\kappa)^2}\theta - 1$. Figure 3.2 (fourth row, right panel) shows the solution at the right endpoint of $\Gamma_3$ when $(\epsilon, \theta, \kappa) = (0.1, 1.1, 1.15)$. For each $\beta \in \left[\frac{1}{2(1-\kappa)\theta} - 1, \frac{1}{(1-\kappa)^2}\theta - 1\right]$ our computations indicate that $U(z) > \theta \forall z < 0$, hence we conjecture that the interval of existence of $\Gamma_3$ is $\left[\frac{1}{2(1-\kappa)\theta} - 1, \frac{1}{(1-\kappa)^2}\theta - 1\right]$. Our study also suggests that all solutions on $\Gamma_3$ are unstable.

**Comparisons.** To obtain $\Gamma_2$ we set $(\epsilon, \theta, \kappa) = (1.1, 1.1, 1.15)$ and let $\beta$ increase from the upper critical value $\beta = \frac{1}{2(1+\kappa)\theta} - 1$ where $c_2 = 0$ and the solution is the stationary front defined by (3.4). $\Gamma_3$ is found by letting $\beta$ increase from the lower critical value $\beta = \frac{1}{2(1+\kappa)\theta} - 1$ where $c_3 = 0$ and the solution is the stationary front defined by (3.10). The eigenvalues $\mu^\pm$ are complex at $\beta = \frac{1}{2(1+\kappa)\theta} - 1$ and $\beta = \frac{1}{2(1-\kappa)\theta} - 1$ since $(\epsilon, \theta, \kappa)$ satisfy (2.8). It is interesting to contrast these bifurcation results with [18] where a similar phenomenon is found when the coupling is symmetric (i.e. $\kappa = 0$) and $(\epsilon, \theta)$ are chosen so that $\mu^\pm$ are real. In that study $(\theta, \beta)$ are kept fixed and counter propagating fronts bifurcate from the stationary solution as $\epsilon$ varies. It would be interesting to analytically determine if a similar phenomenon occurs here where $w$ is asymmetric and $\mu^\pm$ are complex.
The Branch $\Gamma_4$. We let $\Gamma_4$ denote the upper branch of wave fronts when $c = c_4 < 0$ (Figure 3.2). As in the case $c > 0$, this branch extends below $\beta = \beta_4$ down to $\beta = 0$. Solutions on $\Gamma_4$ have the form

$$U(z) = \begin{cases} 
\theta e^{-(1-\kappa)z} & \forall z > 0, \\
k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z) - \frac{5((1+\kappa)c_4+z)\varepsilon^{(1+\kappa)}z}{(1+\kappa)(1+\kappa)\varepsilon^2 + (1+\kappa)(1+\kappa)c_4 + (\beta+1)} + \frac{1}{(1-\kappa^2)(\beta+1)} & \forall z \leq 0,
\end{cases}$$

(3.52)

where $\alpha, \gamma, k_1$ and $k_2$ are evaluated at $c = c_4$. To complete the proof of existence we need to show that $U(z) > \theta \forall z < 0$. Again, this is difficult to prove since $U$ can dip below $\theta$ at a negative value of $z$. In Figure 3.2 (second row, right panel) we set $\beta = 4$ and see that $U(z)$ is a wave front since $U(z) > \theta \forall z < 0$. In the third row, right panel, we set $\beta = 6.45$ and see that $U(z)$ is not a wave front since it is tangent to $U = \theta$ at $z \approx -21$. When $\beta > 6.45$ the function $U$ cannot be a wave front since it dips below $\theta$ at a finite value of $z$. Thus, we conjecture that the interval of existence of $\Gamma_4$ is approximately $(0, 6.45)$. Our study suggests that all solutions on $\Gamma_4$ are stable.

D. The effects of changing the threshold $\theta$. We study how variations in $\theta$ affect wavefront formation when $\mu^\pm$ are complex and $w$ is asymmetric. Figures 3.2 and 3.3 illustrate the differences in the behavior of solutions when $\theta = .1$ and $\theta = .2$, and lead to the following conjectures:

- (i) There is an interval of $\beta$ values, approximately $0 < \beta < 6.75$ when $(\epsilon, \kappa, \theta) = (.1, .15, .1)$, and a second interval $0 < \beta < 4.05$ when $(\epsilon, \kappa, \theta) = (.1, .15, .2)$, over which two stable wavefronts coexist, which propagate in opposite directions, with different speeds and amplitudes.
- (ii) At fixed $(\epsilon, \kappa, \beta)$ the speeds and amplitudes decrease as $\theta$ increases.
- (ii) At fixed $(\epsilon, \kappa)$ the values of $\beta$ at the right endpoints of $\Gamma_1, .., \Gamma_4$ decrease as $\theta$ increases.

E. Open problems. It remains an open problem to prove the existence of wave fronts along the branches $\Gamma_1, .., \Gamma_4$ described above. Whether $\mu^\pm$ are real or complex, new methods are needed in order to overcome the technical difficulties in showing that solutions satisfy $U(z) = \theta$ only once on the interval $(-\infty, \infty)$. Although generalizations and insightful approximations have previously been given [18, 43], this property has not yet been verified for any set of parameters or couplings, even in the real eigenvalue regime. In [59] we considered parameter values where $\mu^\pm$ are real, and developed a comparison method which addresses these issues when $w$ is symmetric. It is hoped that an extensions of our techniques will help complete existence proofs when $w$ is asymmetric, and for a wider range of rate functions and parameter values. The proof of stability of solutions along $\Gamma_1$ and $\Gamma_4$, and the instability of solutions along $\Gamma_2$ and $\Gamma_3$ also remains an open problem. It is possible that this might be accomplished by extensions of Evans function methods developed in [11, 45, 55].

4. 1-pulse traveling waves. We analyze 1-pulse traveling waves when $w$ is asymmetric and $\mu^\pm$ are complex. Our study consists of the following:
Fig. 3.3. Upper left: \(c_1, c_2, c_3\) and \(c_4\) vs. \(\beta\) when \((\epsilon, \theta, \kappa) = (1.1, 2, 15)\). Upper right: \(\Gamma_1, \Gamma_2, \Gamma_3\) and \(\Gamma_4\) in the \((\beta, c)\) plane. Second row: solutions at \(\beta = 3.9\) on \(\Gamma_1\) (left) and at \(\beta = 4.05\), the right endpoint where \(\Gamma_1\) meets \(\Gamma_2\) (right). Third row: solutions at the right endpoints of \(\Gamma_3\) where \(\beta \approx 4.12\) (left) and \(\Gamma_4\) where \(\beta \approx 3.95\) (right). It is conjectured that solutions on \(\Gamma_1\) and \(\Gamma_4\) stable, and those on \(\Gamma_2\) and \(\Gamma_3\) are unstable.

- **A.** The proof of non-existence of stationary, 1-pulse solutions.
- **B.** Positive and negative wave speeds: the statement and proof of Theorem 4.2 concerning the coexistence of two families of infinitely many 1-pulse waves.
- **C.** The effects of changing the threshold and the identification of \(\theta^*\).

**A. Non-existence of stationary solutions.** In the previous section we showed how two distinct families of wavefronts come into existence by means of a bifurcation from stationary solutions when \(\kappa \neq 0\). In [59] we demonstrated how a branch of 1-pulse traveling waves bifurcates from a stationary solution when \(\kappa = 0\) and the coupling is symmetric. Theorem 4.1 below shows that there is a fundamental difference when we consider asymmetric couplings. In particular, we prove that there
is no stationary 1-pulse solution for the class of asymmetric couplings satisfying the general condition

\[(4.1) \quad w(x) - w(-x) > 0 \quad \forall x \in (-\infty, \infty) \quad \text{or} \quad w(x) - w(-x) < 0 \quad \forall x \in (-\infty, \infty).\]

The function \(w(x) = \frac{1}{2}|x+t|+\kappa x\) which we study in this paper falls within this class. Thus, for couplings satisfying condition (4.1) a family of 1-pulse waves cannot come into existence by means of a bifurcation from a stationary solution.

**Theorem 4.1.** If \(w\) satisfies (4.1) then (2.3) does not have a stationary 1-pulse solution.

**Proof.** If a stationary solution \(U\) exists then \(c = 0\) and (2.3) reduces to

\[(4.2) \quad U(x) = \frac{1}{\beta+1} \int_{-\infty}^{\infty} w(x-x')dx'.\]

We assume, for contradiction, that \(U(x)\) satisfies

\[(4.3) \quad \begin{cases} 
U(x) \text{ and } U'(x) \text{ are continuous } \forall x \in (-\infty, \infty), \\
U(x) < \theta \quad \forall x < 0, \quad U(0) = \theta, \\
U(x) > \theta \quad \forall x \in (0, a), \quad \text{for some } a > 0, \\
U(a) = \theta, \quad U(x) < \theta \quad \forall x > a, \\
(U(x), U'(x)) \to 0 \text{ as } |x| \to \infty.
\end{cases}\]

Without loss of generality we have assumed that \(U(0) = \theta\) in (4.3) since (4.2) is translationally invariant. Conditions (4.3) reduce (4.2) to

\[(4.4) \quad U(x) = \frac{1}{\beta+1} \int_0^a w(x-x')dx'.\]

The substitution \(\eta = x - x'\) changes (4.4) into

\[(4.5) \quad U(x) = \frac{1}{\beta+1} \int_{x-a}^{x} w(\eta)d\eta.\]

Setting \(x = 0\) and \(x = a\) in (4.5), we conclude from (4.3) that

\[(4.6) \quad U(0) = \frac{1}{\beta+1} \int_{-a}^{0} w(\eta)d\eta = \theta \quad \text{and} \quad U(a) = \frac{1}{\beta+1} \int_{0}^{a} w(\eta)d\eta = \theta.\]

From this it follows that \(\int_{-a}^{0} w(\eta)d\eta = \int_{0}^{a} w(\eta)d\eta\), hence

\[(4.7) \quad \int_{0}^{a} [w(\eta) - w(-\eta)]d\eta = 0.\]

However, condition (4.1) implies that either

\[(4.8) \quad \int_{0}^{a} [w(\eta) - w(-\eta)]d\eta > 0 \quad \text{or} \quad \int_{0}^{a} [w(\eta) - w(-\eta)]d\eta < 0,\]

which contradicts (4.7). This completes the proof.
B. Positive and negative wave speeds. In this section we study properties of 1-pulse traveling waves for both positive and negative wave speeds.

**Positive wave speeds.** When \( c > 0 \) we investigate the existence of 1-pulse waves which satisfy

\[
\begin{align*}
U(z) \text{ and } U'(z) & \text{ are continuous } \forall z \in (-\infty, \infty), \\
U(z) & < \theta \ \forall z < 0, \ U(0) = \theta, \\
U(z) > \theta \ \forall z \in (0, a), & \text{ for some } a = a(c) > 0, \\
U(a) & = \theta \text{ and } U'(z) < \theta \ \forall z \in (a, \infty), \\
(U(z), U'(z)) & \to (0, 0) \text{ as } |z| \to \infty.
\end{align*}
\]

Again we have assumed that \( U(0) = \theta \) since (2.3) is translationally invariant. When conditions (4.9) hold, equation (2.3) reduces to

\[
(4.10) \quad c^2 U'' + c(1 + \epsilon)U' + \epsilon(\beta + 1)U = c \frac{d}{dz} \int_0^a w(z - z')dz' + \epsilon \int_0^a w(z - z')dz'.
\]

Because \( w(x) = \frac{1}{2} e^{-|x|+\kappa x} \), equation (4.10) can be written in the equivalent form

\[
(4.11) \quad c^2 U'' + c(1 + \epsilon)U' + \epsilon(\beta + 1)U = f(z),
\]

where

\[
(4.12) \quad f(z) = \begin{cases} 
\frac{5}{1+\kappa} (c(1+\kappa) + \epsilon) (1 - e^{-(1+\kappa)a}) e^{(1+\kappa)z} & \forall z \leq 0, \\
\frac{5}{1+\kappa} (\epsilon - c(1+\kappa))(e^{1-\kappa a} - 1) e^{-(1+\kappa)z} & \forall z \geq a,
\end{cases}
\]

**Negative wave speeds.** When \( c < 0 \) a 1-pulse traveling wave satisfies

\[
\begin{align*}
U(z) \text{ and } U'(z) & \text{ are continuous } \forall z \in (-\infty, \infty), \\
U(z) & < \theta \ \forall z \in (-\infty, a), \text{ for some } a = a(c) < 0, \ U(a) = 0, \\
U(z) > \theta \ \forall z \in (a, 0), & \ U(0) = \theta, \\
U(z) & < \theta \ \forall z > 0, \\
(U(z), U'(z)) & \to (0, 0) \text{ as } |z| \to \infty.
\end{align*}
\]

When conditions (4.13) hold, equation (2.3) reduces to

\[
(4.14) \quad c^2 U'' + c(1 + \epsilon)U' + \epsilon(\beta + 1)U = c \frac{d}{dz} \int_0^a w(z - z')dz' + \epsilon \int_0^a w(z - z')dz'.
\]

Because \( w(x) = \frac{1}{2} e^{-|x|+\kappa x} \), equation (4.14) can be written in the equivalent form

\[
(4.15) \quad c^2 U'' + c(1 + \epsilon)U' + \epsilon(\beta + 1)U = h(z),
\]
where

\[
(4.16) \quad h(z) = \begin{cases}
\frac{5}{1 - \kappa} (c(1 - \kappa) - c) (e^{(1 - \kappa)z} - 1) e^{-(1 - \kappa)z} & \forall z \geq 0, \\
0.5 \left( c + \frac{1}{\kappa + 1} \right) e^{(\kappa + 1)z} + \frac{c}{1 - \kappa} & \text{if } a < z < 0, \\
\frac{5}{1 - \kappa} (c + (1 + \kappa)) (e^{-(1 + \kappa)z} - 1) e^{(1 + \kappa)z} & \forall z \leq a.
\end{cases}
\]

We prove the following:

**Theorem 4.2.** Let \((c, \theta)\) satisfy (2.8) If \(\kappa > 0\) is small and \(\beta = \frac{1}{2(1 - \kappa + \mu)} - 1\) then

(i) there are infinitely many \(c \in (c_2, c_1)\) and \(a(c) > 0\), and solutions \(U\) of (4.11)-(4.12) such that

\[
U(z) = \theta e^{(1 + \kappa)z} \forall z < 0, \quad U(0) = U(a(c)) = \theta \quad \text{and} \quad U'(0) = 1 + \kappa,
\]

\[
(U(z), U'(z)) \to (0,0) \quad \text{as} \quad z \to -\infty,
\]

(ii) there are infinitely many \(c \in (c_4, c_3)\) and \(a(c) < 0\), and solutions \(U\) of (4.11)-(4.12) such that

\[
U(z) = \theta e^{-(1 - \kappa)z} \forall z > 0, \quad U(a(c)) = U(0) = \theta \quad \text{and} \quad U'(0) = \kappa - 1,
\]

\[
(U(z), U'(z)) \to (0,0) \quad \text{as} \quad z \to -\infty.
\]

**Remarks.** (i) The proof of Theorem 4.2 relies heavily on sine and cosine terms which arise due to \(\mu^\pm\) being complex. Such terms are not present in the real eigenvalue case and therefore we conjecture that the Theorem 4.2 does not hold when \(\mu^\pm\) are real.

(ii) The positive wave speed solutions described in Theorem 4.2 have monotone tails as \(z \to -\infty\), and oscillatory tails as \(z \to \infty\). By contrast, the speeds and amplitudes of the negative wave speed solutions are larger than those of the positive speed solutions, they have oscillatory tails as \(z \to -\infty\), and monotone tails as \(z \to \infty\). The oscillatory tails are due to \(\mu^\pm\) being complex.

(iii) To prove that the solutions in Theorem 4.2 are 1-pulse waves we must also prove that \(z = 0\) and \(z = a(c)\) are the only solutions of \(U(z) = \theta\), and that \((U(z), U'(z)) \to (0,0)\) as \(z \to \infty\). Because \(\mu^\pm\) are complex, technical difficulties arise which make the verification of these properties a challenging problem which remains open.

**Proof of Theorem 4.2.** We prove part (i) for the case \(c > 0\). The details for the case \(c < 0\) are similar and are omitted for brevity. On the interval \((-\infty, 0)\) the system (4.11)-(4.12) reduces to

\[
(4.19) \quad c^2 U'' + c(1 + \epsilon) U' + \epsilon (\beta + 1) U = \frac{5}{1 + \kappa} (c(1 + \kappa) + \epsilon) (1 - e^{-(1 + \kappa)z}) e^{(1 + \kappa)z} \forall z \leq 0.
\]

The general solution of (4.19) is

\[
U_3(z) = k_1 e^{\alpha z} \cos(\gamma z) + k_2 e^{\alpha z} \sin(\gamma z)
\]

\[
+ \frac{5((1 + \kappa)c + \epsilon)(1 - e^{-(1 + \kappa)z})}{(1 + \kappa)((1 + \kappa)\beta + c(\beta + 1))} e^{(1 + \kappa)z}.
\]
We need to show that there are values $c \in (c_2, c_1)$ and $\alpha > 0$ such that

\[(4.21) \quad U_3(z) < \theta \quad \forall z \in (-\infty, 0), \quad U_3(-\infty) = U_3'(\infty) = 0 \quad \text{and} \quad U_3(0) = \theta.\]

Recall from (2.7) that $\alpha = \Re(\mu^{\pm}) < 0$. Thus, to satisfy $U_3(-\infty) = U_3'(\infty) = 0$ we conclude that $k_1 = k_2 = 0$, and therefore

\[(4.22) \quad U_3(z) = \frac{.5((1 + \kappa)c + \epsilon)(1 - e^{-(1+\kappa)\alpha})}{(1 + \kappa)((1 + \kappa)\kappa c^2 + (1 + \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} e^{(1+\kappa)z}\]

Substituting the continuity requirement $U_3(0) = \theta$ into (4.22) gives

\[(4.23) \quad \frac{.5((1 + \kappa)c + \epsilon)(1 - e^{-(1+\kappa)\alpha})}{(1 + \kappa)((1 + \kappa)\kappa c^2 + (1 + \kappa)(1 + \epsilon)c + \epsilon(\beta + 1))} = \theta.\]

Combining (4.22) and (4.23) gives $U_3(z) = \theta e^{(1+\kappa)z} \quad \forall z \leq 0$.

The interval $(0, a)$. On the interval $(0, a)$ the system (4.11)-(4.12) reduces to

\[(4.24) \quad c^2U'' + c(1+\epsilon)U' + \epsilon(\beta+1)U = .5 \left( c + \frac{\epsilon}{\kappa - 1} \right) e^{(\kappa-1)z} - .5 \left( c + \frac{\epsilon}{\kappa + 1} \right) e^{(\kappa+1)(z-a)} + \frac{\epsilon}{1 - \kappa^2}.\]

The general solution of (4.24) is

\[(4.25) \quad U_4(z) = m_1 e^{\alpha z} \cos(\gamma z) + m_2 e^{\alpha z} \sin(\gamma z) + P_4(z),\]

where $\alpha$ and $\gamma$ are defined in (2.7), and $P_4$ is the particular solution

\[(4.26) \quad P_4(z) = \frac{.5((1 + \epsilon)c + \epsilon)(\kappa - 1)z}{(1 + \kappa)((1 + \kappa)\kappa c^2 - (1 + \epsilon)(1 + \kappa)c + \epsilon(\beta + 1))} e^{(\kappa-1)z} - \frac{.5((1 + \epsilon)c + \epsilon)(\kappa + 1)z}{(1 + \kappa)((1 + \kappa)\kappa c^2 + (1 + \epsilon)(1 + \kappa)c + \epsilon(\beta + 1))} e^{(\kappa+1)(z-a)} + \frac{1}{(\beta + 1)(1 - \kappa^2)}.\]

Continuity at $z = 0$ requires that $(U_4(0), U_4'(0)) = (U_3(0), U_3'(0)) = (\theta, (1 + \kappa)\theta)$. Combining this with (4.25) and (4.26) shows that the coefficients $m_1$ and $m_2$ in (4.25) are defined by

\[(4.27) \quad m_1 = \theta - P_4(0) \quad \text{and} \quad m_2 = \frac{1}{\gamma} (\theta (1 + \kappa - \alpha) - P_4'(0) + \alpha P_4(0)).\]
Next, solve (4.23) for $e^{-(1+\kappa)a}$ and get
\begin{equation}
(4.28) \\
e^{-(1+\kappa)a} = \frac{5(\epsilon + c(1 + \kappa)) - \theta(1 + \kappa) ((1 + \kappa)^2c^2 + (1 + \epsilon)c(1 + \kappa) + \epsilon(\beta + 1))}{5(\epsilon + c(1 + \kappa))}.
\end{equation}

It follows from (3.21) that the right side of (4.28) is zero at $c = c_1$ and $c = c_2$, and that (Figure 4.2)
\begin{equation}
(4.29) \\
a(c) > 0 \ \forall c \in (c_2, c_1) \ \text{and} \ \lim_{c \to c_1^+} a(c) = \lim_{c \to c_1^-} a(c) = \infty.
\end{equation}

We will use (4.29) to help prove that there exist values $c \in (c_2, c_1)$, and $a = a(c) > 0$, such that
\begin{equation}
(4.30) \\
U_4(a(c)) = \theta
\end{equation}

Substituting (4.25) into (4.30) gives
\begin{equation}
(4.31) \\
m_1e^{a(c)}\cos(\gamma a(c)) + m_2e^{a(c)}\sin(\gamma a(c)) + P_4(a(c)) = \theta.
\end{equation}

Thus, it remains to show that there are infinitely many $c \in (c_2, c_1)$ such that the function
\begin{equation}
(4.32) \\
g(c) = m_1e^{a(c)}\cos(\gamma a(c)) + m_2e^{a(c)}\sin(\gamma a(c)) + P_4(a(c)) - \theta
\end{equation}
satisfies $g(c) = 0$. The first step is to write (4.28) as
\begin{equation}
(4.33) \\
\frac{5(\epsilon + c(1 + \kappa))}{(1 + \kappa)^2c^2 + (1 + \epsilon)(1 + \kappa)c + \epsilon(\beta + 1)} = \frac{5(\epsilon + c(1 + \kappa))e^{-(1+\kappa)a}}{(1 + \kappa)^2c^2 + (1 + \epsilon)(1 + \kappa)c + \epsilon(\beta + 1)} + \theta(1 + \kappa).
\end{equation}

Substituting (4.33) into (4.26), and using the hypothesis $\beta = \frac{1}{2(1-\kappa^2)^\theta} - 1$ we obtain
\begin{equation}
(4.34) \\
P_4(a(c)) - \theta = e^{-(1-\kappa)a(c)} \left( \frac{5(\epsilon(1-\kappa)-\epsilon)}{(1-\kappa)((1-\kappa)^2c^2-(1+\epsilon)(1-\kappa)c+\epsilon(\beta+1))} \right) \\
- e^{-(1+\kappa)a(c)} \left( \frac{5(\epsilon+(1+\kappa))}{(1+\kappa)((1+\kappa)^2c^2+(1+\epsilon)(1+\kappa)c+\epsilon(\beta+1))} \right).
\end{equation}

Next, substitute (4.34) into (4.32) and get
\begin{equation}
(4.35) \\
g(c) = e^{a(c)}g_1(c),
\end{equation}
\begin{equation}
\begin{aligned}
g_1 &= m_1 \cos(\gamma a(c)) + m_2 \sin(\gamma a(c)) + e^{-(1+\alpha-\kappa)a(c)} \left( \frac{5(c(1-\kappa)-\delta)}{(1-\kappa)(1-\kappa)c+\epsilon(1+\kappa)c+\epsilon(\beta+1)} \right) \\
&\quad - e^{-(1+\alpha+\kappa)a(c)} \left( \frac{5(c+\epsilon(1+\kappa))}{(1+\kappa)(1+\kappa)c+\epsilon(1+\kappa)c+\epsilon(\beta+1)} \right).
\end{aligned}
\end{equation}

Because \( e^{\alpha a(c)} > 0 \), it suffices to show that \( g_1(c) \) changes sign infinitely often on \((c_2, c_1)\). To analyze \( g_1(c) \) we need to determine the limiting behavior, as \( c \to c_1^- \), of the terms on the right side of (4.36).

For this we need the five basic estimates developed below.

(i) **The behavior of** \( e^{-(1+\alpha-\kappa)a(c)} \) **and** \( e^{-(1+\alpha+\kappa)a(c)} \) **as** \( c \to c_1^- \).

From (2.7) it follows that

\begin{equation}
\lim_{c \to c_1^-} (1 + \alpha - \kappa) = \frac{2c_1 (1 - \kappa) - 1 - \epsilon}{2c_1}.
\end{equation}

It follows from (3.23), and the hypothesis \( \beta = \frac{1}{2(1-\kappa)^2} - 1 \), that

\begin{equation}
c_1 = \frac{0.5 - \theta(1+\kappa)(\epsilon + 1) + \sqrt{(0.5 - \theta(1+\kappa)(1+\epsilon))^2 - \frac{2\epsilon \theta_c(1+\kappa)}{1-\kappa} \beta}}{2\theta(1+\kappa)^2}.
\end{equation}

We substitute (4.38) into (4.37) and conclude from an algebraic manipulation, and the restriction

\( 0 < \theta < \frac{1}{4(\epsilon + 1)} \)

given in (2.8), that

\begin{equation}
\lim_{(c,\kappa) \to (c_1^- , 0)} (1 + \alpha - \kappa) = \frac{1 - 3\theta(1 + \epsilon)}{1 - 2\theta(1 + \epsilon)} > 0.
\end{equation}

From (4.39) and continuity it follows that if \( \kappa > 0 \) is small then

\begin{equation}
\lim_{c \to c_1^-} (1 + \alpha - \kappa) > 0.
\end{equation}

Thus, if \( \kappa > 0 \) is small, then (4.29) and (4.40) imply that

\begin{equation}
\lim_{c \to c_1^-} e^{-(1+\alpha-\kappa)a(c)} = \lim_{c \to c_1^-} e^{-(1+\alpha+\kappa)a(c)} = 0.
\end{equation}

(ii) **The behavior of** \( \gamma a(c) \) **as** \( c \to c_1^- \).

Recall that \( \beta = \frac{1}{2(1-\kappa)^2} - 1 \). This and (2.7)-(2.8) imply that

\begin{equation}
\gamma = \frac{(\epsilon + 1)}{2c\sqrt{(1-\kappa)^2 \theta}} \sqrt{\frac{2x}{(\epsilon + 1)^2} - (1-\kappa^2)\theta} > 0 \ \forall c \in [c_2, c_1] \ \text{and} \ \forall \kappa \in [0, 1).
\end{equation}

From this and (4.29) we conclude that \( \gamma a(c) \) is continuous in \( c \), and that

\begin{equation}
\gamma a(c) > 0 \ \forall c \in (c_2, c_1), \ \text{and} \ \lim_{c \to c_1^-} \gamma a(c) = \infty \ \forall \kappa \in [0, 1).
\end{equation}

(iii) **The behavior of** \( (1-\kappa)^2c^2 - (1+\epsilon)(1-\kappa)c + \epsilon(\beta+1) \) **as** \( c \to c_1^- \).
We show that
\[ \lim_{c \to c_1^-} \left( (1 - \kappa)^2 c^2 - (1 + \epsilon)(1 - \kappa)c + \epsilon(\beta + 1) \right) > 0 \quad \forall \kappa \in [0, 1). \] (4.44)

It follows from (2.8) that the discriminant of the limiting term
\[ (1 - \kappa)^2 c_1^2 - (1 + \epsilon)(1 - \kappa)c_1 + \epsilon(\beta + 1) \]

satisfies
\[ \text{Discriminant} = (1 - \kappa)^2 \left( (1 + \epsilon)^2 - 4\epsilon(\beta + 1) \right) < 0 \quad \forall \kappa \in [0, 1), \]

since \( \epsilon > 0 \) and \( \beta > \frac{(\epsilon - 1)^2}{4\epsilon} \). This and continuity imply that (4.44) holds.

(iv) The behavior of \( m_1 \) as \( c \to c_1^- \).

We show that \( m_1 \) is bounded away from 0 as \( c \to c_1^- \) when \( \kappa > 0 \) is small. Since \( a(c) \to \infty \) as \( c \to c_1^- \), it follows from (4.26) and the definition of \( m_1 \) given in (4.27), that \( m_1 \) is continuous in \( \kappa \) and \( c \), and
\[ \lim_{c \to c_1^-} m_1 = \theta - \frac{.5(c_1(1 - \kappa) - \epsilon)}{(1 - \kappa)((1 - \kappa)^2 c_1^2 - (1 + \epsilon)(1 - \kappa)c_1 + \epsilon(\beta + 1))} - \frac{1}{(\beta + 1)(1 - \kappa^2)}. \] (4.46)

We solve (3.21) for \( c^2 \), substitute the resultant expression into (4.46), and obtain the limiting value
\[ \lim_{(\kappa,c) \to (0,c_1^-)} m_1 = \frac{\theta(\epsilon - 2\theta(1 + \epsilon)c_1)}{(5 - 2\theta(1 + \epsilon))c_1 + .5\epsilon} - \frac{1}{\beta + 1}. \] (4.47)

where, by (3.23), \( c_1 \) has the limiting value
\[ c_1 = \frac{5 - \theta(1 + \epsilon)}{\theta} > 0. \] (4.48)

Substituting (4.48) into the numerator of the first term in (4.47) gives the limiting value
\[ \lim_{(\kappa,c) \to (0,c_1^-)} m_1 = \frac{\theta(-1 + 2\theta(1 + \epsilon)^2)}{(5 - 2\theta(1 + \epsilon))c_1 + .5\epsilon} - \frac{1}{\beta + 1}. \] (4.49)

Recall from (2.8) that \( 0 < \epsilon < 1 \) and \( 0 < \theta < \frac{1}{4(\epsilon + 1)} \). This implies that \(-1 + 2\theta(1 + \epsilon)^2 < .5(\epsilon - 1) < 0 \) and \(.5 - 2\theta(1 + \epsilon) > 0 \). Thus, the first term in (4.49) is negative, and therefore
\[ \lim_{(\kappa,c) \to (0,c_1^-)} m_1 < -\frac{1}{\beta + 1} = -2\theta. \] (4.50)

Finally, it follows from (4.50) and continuity that if \( \kappa > 0 \) is small, then
\[ \lim_{c \to c_1^-} m_1 < -2\theta. \] (4.51)

(v) The behavior of \( g_1(c) \)
We now use the estimates given above to determine the behavior of \( g_1(c) \) when \( \kappa > 0 \) is small. It follows from (4.43) that, for small \( \kappa > 0 \), there is an increasing sequence \( \{c_n\} \) such that
\[
(4.52) \quad c_n \to c^-_2 \text{ as } n \to \infty, \quad \text{and} \quad \gamma a(c_n) = 2n\pi \text{ for large } n.
\]
Let \( c = c_n \) in (4.36). Then \( \sin(\gamma a(c_n)) = 0 \), \( \cos(\gamma a(c_n)) = 1 \), and (4.36) reduces to
\[
(4.53) \quad g_1(c_n) = m_1 + e^{-(1+\alpha+\kappa)a(c_n)} \left( \frac{5(e_{\kappa-1}-\epsilon)}{(1-\kappa)^2e_{\kappa-1}^2 - (1+\epsilon)(1-\kappa)e_{\kappa} + \epsilon(\beta+1))} \right) - e^{-(1+\alpha+\kappa)a(c_n)} \left( \frac{5(e+c_{\kappa+1})}{(1+\kappa)^2e_{\kappa+1}^2 + (1+\epsilon)(1+\kappa)e_{\kappa} + \epsilon(\beta+1))} \right).
\]
Combining the estimates in (4.41), (4.44), (4.51) and (4.52), we conclude from (4.53) that
\[
(4.54) \quad g_1(c_n) < -\theta \text{ for } n >> 1.
\]
Likewise, for small \( \kappa > 0 \), there is an increasing sequence \( \{c^n\} \) such that
\[
(4.55) \quad c^n \to c^-_2 \text{ as } n \to \infty \quad \text{and} \quad \gamma a(c^n) = (2n+1)\pi \text{ for } n >> 1.
\]
Let \( c = c^n \) in (4.36). Then \( \sin(\gamma a(c^n)) = 0 \) and \( \cos(\gamma a(c^n)) = -1 \). From this, (4.41), (4.44), (4.51) and (4.55) it follows that
\[
(4.56) \quad g_1(c^n) > \theta \text{ for large } n >> 1.
\]
It follows from (4.54) and (4.56) and continuity that \( g_1(c) \), and therefore \( g(c) \), have infinitely many zeros on \((c_1, c_2)\) when \( \kappa > 0 \) is small. Thus, we have proved that there are infinitely many \( c \in (c_1, c_2) \) and \( a(c) > 0 \), and corresponding solutions \( U \) of (2.3), such that
\[
(4.57) \quad U(z) = \begin{cases} 
\theta e^{(1+\kappa)z} & \forall z \leq 0, \\
U_4(z) & 0 < z < a(c),
\end{cases}
\]
where \( U_4(z) \) is defined in (4.25)-(4.26), and satisfies
\[
(4.58) \quad U_4(0) = U_4(a(c)) = \theta \quad \text{and} \quad U'_4(0) = 1 + \kappa.
\]
This completes the first part of the proof of (4.17). It remains to show that the solution satisfies \((U(z), U'(z)) \to (0, 0)\) as \( z \to \infty \). This is addressed below.

**The interval** \((a, \infty)\). On the interval \((a, \infty)\) the system (4.11)-(4.12) reduces to
\[
(4.59) \quad c^2U'' + c(1+\epsilon)U' + \epsilon(\beta+1)U = \frac{5}{1-\kappa}(\epsilon - c(1-\kappa))(e^{(1-\kappa)a} - 1)e^{-(1-\kappa)z} \quad \forall z > a.
\]
The general solution of (4.59) is
\[
(4.60) \quad U_5(z) = q_1 e^{\alpha z} \cos(\gamma z) + q_2 e^{\alpha z} \sin(\gamma z) + P_5(z),
\]
where $\alpha$ and $\gamma$ are defined in (2.7), and $P_5$ is the particular solution

$$
P_5(z) = \frac{(\epsilon-c(1-\kappa)(1-(1-\kappa)z_0)-1)e^{-(1-\kappa)z}}{(1-\kappa)(1-\kappa)c^{(1-\kappa)z_0}(1+c(1-\kappa)z_0+c^{(1-\kappa)z_0})}.
$$

(4.61)

The coefficients $q_1$ and $q_2$ in (4.60) are uniquely defined by the continuity conditions

$$
U_5(a(c)) = U_4(a(c)) = \theta \quad \text{and} \quad U_5'(a(c)) = U_4'(a(c)).
$$

(4.62)

Finally, it follows from (4.60)-(4.61), and the fact that $\alpha < 0$, that

$$
(U_5(z), U_5'(z)) \to (0, 0) \quad \text{as} \quad z \to \infty.
$$

(4.63)

This completes the proof of part (i) Theorem 4.2.

C. The effects of changing threshold and the identification of $\theta^*$. To understand how solutions change as $\theta$ varies we proceed as in Section 3 and compare the behavior of solutions when $\theta = .1$ and $\theta = .2$ For these values our numerical experiments suggest that all conditions for a 1-pulse wave are satisfied along a branch $\Lambda_1$ of solutions when $c > 0$, and also along a second branch $\Lambda_2$ when $c < 0$. Solutions along $\Lambda_1$ and $\Lambda_2$ are stable and propagate in opposite directions with different speeds and amplitudes. Figure 4.3 (top row) illustrates these branches when $(\epsilon, \kappa) = (.1, .15)$.

(i) The case $\theta = .1$ Figure 4.3 (second row, first panel) shows two solutions which coexist at the right endpoints of $\Lambda_1$ and $\Lambda_2$ where $\beta \approx 12.75$

(i) The case $\theta = .2$ The middle panel of the second row shows two solutions which coexist when $\beta = 3.35$ The right endpoint of $\Lambda_1$ occurs at $\beta \approx 3.5$ where the positive wave speed solution ceases to exist. When $\beta > 3.5$ the negative wave speed solution continues to exist until $\beta \approx 7.5$, where the branch $\Lambda_2$ comes to an end. The third panel illustrates the solution at $\beta = 7.5$.

Our experiments lead to the following conjectures whose proofs remain open problems:

- At fixed $(\epsilon, \kappa, \beta)$ the amplitudes and speeds of 1-pulse solutions decrease as $\theta$ increases.
- At fixed $(\epsilon, \kappa)$ the right endpoint of $\Lambda_1$ decreases more rapidly than the right endpoint of $\Lambda_2$ as $\theta$ increases. Thus, there is an interval $I$ of $\beta$ values such that if $\beta \in I$ is fixed then a critical value $\theta^* = \theta^*(\epsilon, \kappa, \beta)$ exists such that there are two stable solutions when $0 < \theta \leq \theta^*$, and only one solution when $\theta > \theta^*$.

Experimental implications. By controlling the electric field in disinhibited slices of mammalian cortex, Richardson et al [49] can determine properties of 1-pulse waves for different values of threshold. Our results show that, when threshold has a low value, an appropriate stimulus causes waves to form which propagate in opposite directions with different amplitudes and speeds. The methods in [49]
Fig. 4.3. First row: bifurcation curves \( \Lambda_1 \) and \( \Lambda_2 \) in the \((\beta, c)\) plane for families of 1-pulse waves when \((\epsilon, \kappa, \theta) = (1, 1.5, 1)\) (left) and \((\epsilon, \kappa, \theta) = (1, 1.5, 2)\) (right). Second row. Solutions at specific points along \( \Lambda_1 \) and \( \Lambda_2 \). Please click on each figure in the second row to view the movies.

might allow one to determine if similar properties hold for low electric field values, and also whether there is a critical value of the field where one of the waves disappears. This, together with an analysis of the speeds and amplitudes of waves as a function of electric field strength could provide a plausible method to obtain a measure of the asymmetry in the connectivity between neuronal groups.

5. 2-pulse waves. To understand how 2-pulse waves form when \( \beta > \beta_* \) we analyze the linearization of (2.3) around the rest state \( U = 0 \):

\[
(5.1) \quad c^2 H'' + c(1 + \epsilon)H' + \epsilon(\beta + 1)H = 0.
\]

When \( \mu^\pm \) are complex the general solution of (5.1) is

\[
(5.2) \quad H(z) = b_1 e^{\alpha z} \sin(\gamma z) + b_2 e^{\alpha z} \cos(\gamma z),
\]

where

\[
(5.3) \quad \alpha = \text{Re}(\mu^\pm) = \frac{-(\epsilon + 1)}{2c} < 0 \quad \text{and} \quad \gamma = \text{Im}(\mu^\pm) = \frac{\sqrt{4c\beta - (\epsilon - 1)^2}}{2c} > 0.
\]

It follows from (5.2)-(5.3) that the frequency of oscillation of \( H(z) \) increases as \( \beta \) increases from \( \beta_* \). In turn, this causes solutions of (1.1) to become more oscillatory as \( \beta \) increases, making it increasing
likely that an initial perturbation will evolve into an 2-pulse traveling wave. It follows from (2.3) that a 2-pulse traveling wave satisfies

\[
c^2U'' + c(1 + \epsilon)U' + \epsilon(\beta + 1)U = c \frac{d}{dx} \int_0^a w(z - z')dz' + \epsilon \int_0^a w(z - z')dz' + \epsilon \int_0^d w(z - z')dz',
\]

(5.4)

where

\[
\begin{align*}
U(0) &= U(a) = U(b) = U(d) = \theta \text{ for some } d > b > a > 0, \\
U(z) &\neq \theta \text{ if } z \notin \{0, a, b, d\}, \\
(U(z), U'(z)) &\to (0, 0) \text{ as } |z| \to \infty. 
\end{align*}
\]

(5.5)

In Figure 5.1 we consider the representative parameter set \(\epsilon = .1\) and \(\beta = 7.5\), and illustrate three different types of 2-pulse waves. For this we solve the initial value problem

\[
\begin{align*}
\frac{\partial u}{\partial t}(x, t) &= -u - v + \frac{1}{2} \int_{-120}^{120} e^{-|z-x'|+\kappa(x-x')}H(u(x', t) - \theta)dx', \\
\frac{\partial v}{\partial t}(x, t) &= \epsilon(\beta u - v), \\
u(x, 0) &= .6e^{-x^2} \text{ and } v(x, 0) = 0 \forall x \in [-120, 120].
\end{align*}
\]

(5.6)

In the left panel we let \(\theta = .1\) and set \(\kappa = 0\) so that \(w\) is symmetric. The initial stimulus splits into two 2-pulse waves which propagate outward from \(x = 0\). The wave propagating to the left has the same speed and shape as the wave propagating to the right. In the second panel we keep \(\theta = .1\) and set \(\kappa = .15\) so that \(w\) is asymmetric. The initial stimulus again splits into two waves. The wave traveling to the left is slower than the one traveling to the right, and its shape is also different. In the third panel we keep \(\kappa = .15\), and raise \(\theta\) to \(\theta = .17\) Once again the initial perturbation splits into

\[5.1.\text{Two-pulse waves when } \beta = 7.5 \text{ and } (\epsilon, \theta, \kappa) = (.1, .1, 0) \text{ (left), } (.1, .1, .15) \text{ (middle), } (.1, .17, .15) \text{ (right). In the right panel the wave propagates only to the right since } \theta = .17 > \theta^* \text{ when } (\epsilon, \kappa) = (.1, .15). \text{ Click on each panel to see the movie.} \]
two waves which begin to propagate outward from the \( x = 0 \). However, because \( \theta = .17 > \theta^* \), the ‘weaker’ wave propagating to the left cannot be sustained and it quickly shrinks and collapses onto the steady state \((u, v) = (0, 0)\). The wave propagating to the right persists indefinitely. We note that (i) other choices for initial conditions give the same results, and (ii) similar properties were observed for 1-pulse waves (see Figures 4.1 and 4.3).

For general \( N \geq 2 \) a simple extension of (5.4)-(5.5) gives the criteria satisfied by N-pulse traveling waves. In particular, it is necessary to prove that the solution intersects \( U = \theta \) exactly 2N times. However, as with 1-pulse waves, the non-local terms in the equation lead to technical difficulties in proving this key property, and therefore existence proofs remain a challenging open problem. Finally, we note that our numerical study suggests that the traveling waves in Figure 5.1 are all stable as solutions of (1.1). It would be of interest to develop Evans function methods to prove this conjecture.

6. Synchronous oscillations.. In this section we investigate the formation and spread of uniformly synchronous oscillations when \( \beta \) increases past a second critical value \( \beta^* > \beta \), where (1.1) becomes bistable. In particular, we show how \( \beta^* \) arises and study the following when \( \beta \geq \beta^* \):

- A. Bistability: the coexistence of bulk oscillations and a stable rest state.
- B. Synchrony: the formation of uniformly synchronous oscillations which spread outwards from a point of stimulus.
- C. The coexistence of synchronous oscillations and 1-pulse waves.
- D. How synchronization in one region can trigger synchronization in another.

A. Bistability: the coexistence of bulk oscillations and a stable rest state.

Our goal here is to show that there is a critical value \( \beta^* \) where spatially independent bulk oscillations come into existence. Such solutions depend only on the variable \( t \) and satisfy

\[
\begin{align*}
\frac{du}{dt} &= -u - v + f(u - \theta) \int_{-\infty}^{\infty} w(\eta) d\eta, \\
\frac{dv}{dt} &= \epsilon (\beta u - v).
\end{align*}
\]

In [59] we considered symmetric couplings and showed that periodic solutions of (6.1) come into existence at a critical \( \beta^* \). Figure 6.1 illustrates how this happens for the parameter set \((\epsilon, \theta, \kappa) = (.1, 1, 0)\). In the first row we let \( \beta = 12.6 \) and see that the solution with initial condition \((u(0), v(0)) = (4, 0)\) returns to the rest state \((u, v) = (0, 0)\) as \( t \to \infty \). The same behavior occurs when \( 0 < \beta < 12.6 \), and for all other initial conditions. Thus, the rest state is globally stable when \( 0 < \beta \leq 12.6 \) at \( \beta = \beta^* \approx 12.61 \) a periodic solution comes into existence (second row, right panel). Its trajectory forms a closed loop in the \((u, v)\) plane and intersects the \( u' = 0 \) nullcline at the ‘threshold point’ \((u, v) = (\theta, -\theta)\) (left panel). This property causes the periodic solution to be semi-stable. That is, solutions of (6.1) whose initial conditions lie outside its trajectory approach a translate of the periodic
solution as $t \to \infty$, and solutions with initial conditions inside the trajectory satisfy $(u, v) \to (0, 0)$ as $t \to \infty$. As $\beta$ increases from $\beta^*$ a family of stable periodic orbits bifurcates from the periodic solution at $\beta^*$. The third row shows such a solution at $\beta = 17$. Our study shows that this mechanism also occurs when $\kappa \neq 0$, and over a wide range of $\theta$, which includes the critical value $\theta^*$. For small $\theta > 0$ a phase plane approach can be used to prove the existence of periodic solutions. General proofs remain open.

**B. Synchrony** When $\beta \geq \beta^*$ our numerical experiments on the full system (1.1) show that uniformly synchronous oscillations can form and spread outwards from a point of stimulus. In Figure 6.2 we set $(\beta, \epsilon, \theta, \kappa) = (17, .1, 1.15, .15)$ and consider the initial condition

$$(u(x, 0), v(x, 0)) = (0.6e^{-x^2}, 0), \ x \in \mathbb{R}. \tag{6.2}$$

The stimulus (6.2) is sufficiently strong so that the bulk oscillations affect the solution and cause it to begin oscillating at the center of the stimulus. The oscillations are spatially uniform and in phase over an ever expanding "region of synchrony." Our study suggests the following:

- (i) During each oscillation the region of synchrony expands outward by an amount proportional to the speed of a 1-pulse wave.
During each oscillation the expanding region sheds a traveling wave. Since $\theta > \theta^*$ for our choice of parameters, these waves can propagate only to the right. Because of the asymmetry in $w$, the expansion of the region of synchrony is most rapid in the direction to the right of the point of initial stimulus, and less rapid to the left. Eventually, however, the solution oscillates uniformly over the entire spatial region, and with the same period as the bulk oscillation.

There are similarities between the theoretical spread of a region of synchrony and clinical observations of epileptiform events. Milton and Jung ([41], pp. 346-347) point out that “during a seizure there is a propagation of synchrony over the cortical surface” (see Figures 5.7, 5.8 in [41]), and that optical imaging shows wavelike properties of epileptic propagation. In electocorticographic studies, Towel et al [58] show how spatially uniform synchronous oscillations develop in a region behind the leading edge of a seizure as it propagates across the cortex (see Figures 6.2, 6.5 and 6.11 in [58]). Milton ([40], pp. 18-19) notes that a seizure spreads relatively slowly when compared with spike propagation rates.

Our numerical study indicates the the region of synchrony also spreads slowly, at a rate which is only a fraction of the speed of a traveling wave. An important challenge for future research is to extend the methods in [59] and derive a theoretical formula for the rate of expansion which takes into account asymmetric couplings as well as variations in the threshold $\theta$.

**C. The coexistence of of synchronous oscillations and 1-pulse waves.** Wright and Sergejew [61] have demonstrated the presence of traveling waves in EEG studies of seizure propagation. In [59] we found that a similar phenomenon occurs theoretically, i.e. 1-pulse traveling waves can form.
in the same parameter regime as synchronous oscillations when $\kappa = 0$ and $\theta > 0$ is small. Here we examine the robustness of this property when $\kappa \neq 0$, and for larger values of $\theta$. For this we consider the representative parameter set $(\beta, \epsilon, \theta, \kappa) = (17, 1, 0.15, 0.15)$. At these values the system is bistable and synchronous oscillations form and spread outwards in response to a sufficiently strong initial stimulus. However, synchrony is not always the outcome. For example, Figure 6.3 illustrates how the solution with the smaller amplitude initial perturbation
\[
(u(x, 0), v(x, 0)) = (0.18 e^{-x^2}, 0), \quad x \in \mathbb{R}
\]
evolves into a 1-pulse wave. It propagates only to the right since $\kappa = 0.15$ and $\theta = 0.15 > \theta^*$. Our study suggests that synchronous oscillations and stable 1-pulse waves coexist for a broad range of parameters. Proofs remain an open problem.

\[\text{Fig. 6.3. A small amplitude stimulus } (u(x, 0), v(x, 0)) = (0.18 e^{-x^2}, 0) \text{ evolves into a 1-pulse wave when } (\beta, \epsilon, \theta, \kappa) = (17, 1, 0.15, 0.15). \text{ Its speed } c \approx |c_4| = 0.257 \text{ is computed from (3.43). Click on the first panel to view the movie.}\]

**D. How synchronization in one region can trigger synchronization in another.**

We investigate how synchronous oscillations in one region can spread and initiate synchronization in distant regions. This aspect of our study is motivated by two diverse settings.

(i) In Section 1 we described recent experiment results which show that exposure to nicotine reduces the threshold of excitation in thalamocortical mouse neurons, and that this dramatically increases their firing rates ([36, 54]). It is suggested that in the brains of schizophrenics, the poor communication between thalamus and cortex might be improved by such lowering of threshold.

(ii) Chkhenkeli and Milton [6] describe how seizures in one region of the brain can trigger seizure onset in another. In particular, they give evidence which shows how rhythmic oscillations in the amygdala can trigger a seizure in the hippocampus (see Figure 3.4. in [6]). They also show how a seizure which starts in the hippocampus does not necessarily spread to the amygdala (see Figure 3.4. in [6]).

Our goal here is to understand how similar phenomena occur in our model when $\kappa \neq 0$ and the threshold $\theta$ varies. In particular, we find that when $\theta$ increases past the critical value $\theta^*$, synchronization
in one region can trigger the onset of synchronization in another, but the reverse is not true. To see how this happens we let \( \beta \) vary as a function of \( x \), and define

\[
\beta(x) = \begin{cases} 
17 & \forall x \in [-100, -35) \\
10 & \forall x \in [-35, 35) \\
17 & \forall x \in [35, 100]. 
\end{cases}
\]

(6.4)

As in (B.) and (C.) above, we set \((\epsilon, \theta, \kappa) = (0.1, 0.15, 0.15)\). Since \( \beta = 17 \) in \([-100, 35) \) and \([35, 100] \) the results of part (B.) show that spatially uniform synchronous oscillations can develop in these intervals. However, since \( \beta = 10 < \beta^* \) when \( x \in [-35, 35) \), synchronization cannot occur in this interval. Thus, the interval \([-35, 35) \) forms a 'buffer' region separating the two outer intervals where synchronization can occur. Furthermore, \( \theta > \theta^* \) for our choice of parameters, hence waves can propagate only to the right in any of the three subintervals. To understand the behavior of this “uni-directional neuronal circuit” we performed three simple experiments.

**I.** In the first row of Figure 6.4 a small initial stimulus centered at \( x = -50 \) evolves into a 1-pulse wave propagating to the right (left panel). When the wave enters the interval \([-35, 35) \) its amplitude and speed increase since \( \beta \) has the lower value \( \beta = 10 \) (middle panel). As the wave crosses into the interval \([35, 100] \) it is not sufficient to trigger synchronization. Instead, its amplitude and speed decrease and the wave passes through the interval \([35, 100] \) as time \( t \) increases (right panel). Thus, a small amplitude stimulus centered in the interval \([-100, -35) \) evolves into a 1-pulse wave which propagates through the entire circuit without triggering synchronization.

**II.** In the second row a stimulus centered at \( x = -50 \) (left panel) is sufficiently strong to trigger the formation and spread of synchronous oscillations in the interval \([-100, -35) \). During each cycle the region of synchrony expands by a small amount and a wave is emitted. Thus, a train of waves is created. These waves propagate to the right and enter \([-35, 35) \) where their amplitudes and speeds increase (middle panel). As the waves pass the point \( x = 35 \) they are sufficient to initiate synchronization in the interval \([35, 100] \) (right panel). Thus, synchronization in the region \([-100, -35) \) causes the formation of a train of waves which eventually trigger synchronization in the region \([35, 100] \).

**Remark.** We have found that at least three waves must pass the point \( x = 35 \) in order to initiate synchronization in the region \([35, 100] \). To test this we found that the initial stimulus \((u(x, 0), v(x, 0)) = (10e^{-(x+20)^2}, 0) \) evolves into a 2-pulse wave which propagates to the right and passes right on through the interval \([35, 100] \) without initiating synchronization.

**III.** In the third row we test whether synchronization in the right end interval \([35, 100] \) can ultimately trigger synchronization in the left end interval \([-100, 35) \). An initial stimulus centered at \( x = 50 \) (left panel) initiates synchronous oscillations which spread uniformly over the entire interval
Fig. 6.4. First row: A small amplitude stimulus \((u(x,0),v(x,0)) = (.18e^{-(x+50)^2},0)\) evolves into a 1-pulse wave. The wave propagates through the entire circuit without triggering any part of it to undergo synchronization. Parameters are \((\epsilon, \theta, \kappa) = (.1, .15, .15)\).

Second row: a larger amplitude stimulus \((u(x,0),v(x,0)) = (e^{-(x+50)^2},0)\) triggers synchronization in the interval \([-100, -35)\). The train of waves emitted by the synchronizing region propagates through the circuit and initiates synchronization in the interval \([35, 100]\).

Third row: a stimulus \((u(x,0),v(x,0)) = (e^{-(x-50)^2},0)\) triggers synchronization in the interval \([35, 100]\). Since waves cannot propagate to the left, there can be no initiation of synchronization in the left end interval \([-100, -35)\). Click on the first figure in each row to view the movies.

[35, 100] (second and third panels). However, our choice or parameters does not allow left propagating waves, hence there is no initiation of synchrony in \([-100, -35]\) where the solution remains in the rest state \(u = v = 0\).

Remarks. The results described in (I.)-(III.) still hold when \(\beta\) has different values in the outer intervals \([-100, 35]\) and \([35, 100]\). In this setting, when synchronous oscillations are initiated in these intervals, their frequencies do not necessarily entrain. Analytical proofs of the numerical experiments described in parts (A.)-(D.) remain a challenging open problem.
7. Conclusions. In this paper we analyzed the dynamic behavior of a system of integro-differential equations that models the activity of excitatory neurons on large-scale, spatially extended domains. The independent variables represent the activity level of a population of excitatory neurons with long range connections \( u \), and recovery \( v \). We considered positive, asymmetric coupling functions \( w \) and a Heaviside firing rate \( f \).

There is a critical value of the parameter \( \beta (\beta_* > 0) \) that appears in the equation for \( v \), at which the eigenvalues \( \mu^\pm \) of the linearization of the system around the rest state \((u,v) = (0,0)\) change from real to complex. If \( 0 < \beta \leq \beta_* \) then \( \mu^\pm \) are real and both wave fronts and 1-pulse traveling waves can exist. In [59] we explained why multi-pulse waves are not expected in the real eigenvalue case. By contrast, when \( \beta > \beta_* \) and \( \mu^\pm \) are complex the range of behavior is much richer. For example, our analysis provides evidence for the coexistence of at least two distinct families of stable wave fronts. Because \( w \) is asymmetric, these solutions propagate in opposite directions with different speeds and shapes. We have also found a range of \( \beta > \beta_* \) where two families of 1-pulse traveling wave solutions exist (Theorem 4.17). Each family consists of infinitely many coexisting solutions, and solutions in the two families propagate in opposite directions with different speeds and shapes. We also study the effects of variations of threshold \( \theta \) on the dynamics of the system. As \( \theta \) increases the speeds and amplitudes of the waves in each family decrease until a critical value \( \theta^* > 0 \) is reached where solutions in the first family disappear. That is, left propagating 1-pulse waves cease to exist when \( \theta > \theta^* \). In addition there is a range \( \theta > \theta^* \) where 2-pulse waves can propagate only in one direction. This phenomenon does not occur when the coupling is asymmetric function. To our knowledge this is the first description of such uni-directional wave propagation in this class of nonlocal model.

There is a second critical value \( \beta^* > \beta_* \) where (1.1) becomes bistable and a family of spatially independent bulk oscillations come into existence. These solutions influence the global dynamics of (1.1). For example, when \( \beta \geq \beta^* \) a strong initial stimulus evolves into uniformly synchronous oscillations which spread outwards from the point of stimulus. However, a weak stimulus does not trigger synchronization and merely evolves into a 1-pulse traveling wave. We also study how variations in \( \theta \) affect the spread of synchrony. In particular, we let \( \kappa > 0 \) be fixed and allow \( \beta > \beta^* \) to be a function of the spatial coordinate \( x \). We then raise \( \theta \) to a value above the critical value \( \theta^* \) so that waves propagate only to the right. In the resulting uni-directional circuit we show how synchronization in one region can trigger synchronization in a second, distant region. However, when synchronization is triggered in the second region, it cannot spread to the first region and the first region remains at rest.

In all cases formidable technical difficulties preclude the completion of the the final step of existence proofs. It remains an open problem to extend our methods so that existence proofs can be completed for a wider range of parameters, and also for more general coupling and firing rate functions.
Our numerical experiments were performed when the firing rate is the Heaviside function. To test the robustness of our results we have considered more general, sigmoidal shaped firing rates of the form

\[ f(u) = \frac{1}{1 + Ke^{-r(u-\theta)}}, \quad K > 0, r > 0 \]  

(7.1)

and

\[ f(u) = Ke^{-r(u-\theta)^2}H(u - \theta), \quad K > 0, r > 0. \]  

(7.2)

With \( f \) given by (7.1) or (7.2) our numerical results continue to hold when \( M \) is of moderate size and \( R \) is large (e.g. \( K \approx 1 \) and \( R \geq 50 \)). It remains an open problem to determine the maximal range of parameters, firing rate and coupling functions over which the numerical results are valid.

Our theoretical results might have important implications for experimental and clinical neurophysiology. In particular, our finding that the dynamics of (1.1) undergo qualitative transitions when \( \mu^\pm \) become complex, or \( \theta \) exceeds \( \theta^* \), offers a plausible explanation of trailing-end instabilities and wave speed variations observed in cortical experiments [36, 46, 47]. Further explanation of observed variability in cortical waves might be provided by our findings that the asymmetry in \( w \) leads to the coexistence of entire families of traveling waves which propagate in opposite directions with different shapes and speeds. The unpredictable variation in trailing ends and wave speeds could be caused by solutions switching from one member of the family to another. A possible biophysical mechanism of such switching may involve a variable neurohormonal concentration affecting neuronal recovery and strength of inter-cellular connections [32].

Our observation that bifurcations of the system behavior occur at the critical values \( \beta = \beta_* \) or \( \theta = \theta^* \) also has important practical correlates. It predicts that by pushing the system above or below one of these values one can qualitatively change the system behavior and obtain a broad range of dynamical phenomena. One experimental example of such macrobehavior is an evoked response, which might persist long after the stimulus [47]. Understanding the cellular mechanisms responsible for such important functional changes in neuronal networks requires further study.

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