

Existence and stability of traveling pulses in a neural field equation with synaptic depression

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Abstract

We examine the existence and stability of traveling pulse solutions in a continuum neural network with synaptic depression and smooth firing rate function. The existence proof relies on geometric singular perturbation theory and blow-up techniques as one needs to track the solution near a point on the slow manifold that is not normally hyperbolic. The stability of the pulse is then investigated by computing the zeros of the corresponding Evans function. This study predicts that synaptic depression leads to the formation of stable traveling pulses with algebraic decay along their back. This characteristic feature differs from the exponential decay of traveling pulses of neural field models with linear adaptation.

Keywords: Neural field equations; Traveling pulse; Geometric singular perturbation theory; Spectral stability; Evans function.

Mathematics Subject Classification: 34E15 - 34D23 - 92B20

1 Introduction

Electrode recordings and imaging studies have revealed that the primary visual cortex can support a variety of cortical waves including standing waves [3, 36], traveling pulses [3, 34, 40] and spiral waves [20, 21, 39]. These traveling waves are not only elicited by localized visual stimuli across the visual cortex but they are also present during spontaneous activity [21, 36]. From a mathematical point of view, much effort has been directed towards the study of one-dimensional cortical waves [6, 8–11, 15, 16, 26, 32, 33, 35, 42]. A popular approach to model cortical waves is to use neural field equations with linear adaptation of the form:

$$\begin{aligned}\frac{\partial u(x, t)}{\partial t} &= -u(x, t) + \int_{\mathbb{R}} J(x - x') S(u(x', t)) dx' - \gamma v(x, t) \\ \frac{1}{\epsilon} \frac{\partial v(x, t)}{\partial t} &= u(x, t) - v(x, t)\end{aligned}\tag{1.1}$$

where $u(x, t)$ represents the local activity of a population of neurons at position $x \in \mathbb{R}$, S is the firing rate function. The neural field $v(x, t)$ represents a form of negative feedback mechanism with γ and ϵ , positive parameters, determining the relative strength and rate of feedback. Motivated by studies in inhibited slices [20, 34], the connectivity function J is assumed to be purely excitatory, isotropic and even.

Ermentrout and McLeod [15], with a homotopy argument, were the first to prove the existence of a traveling front connecting the up state to the down state for equation (1.1) when $\gamma = 0$ and when the firing rate is a

smooth nonlinear function. The asymptotic stability of this traveling front has been studied in [7, 14] using comparison principles. Bressloff and Folias [6] have also investigated the existence of traveling front solutions for equation (1.1) when the firing rate is a smooth function for $\gamma > 0$ and in the limit $0 < \epsilon \ll 1$. Using singular perturbation analysis, it is also possible to construct for $0 < \epsilon \ll 1$ pulse solution for (1.1) with smooth firing rate function [32]. Numerous studies have analyzed the existence, uniqueness and stability (through the construction of Evans functions) of equation (1.1) when the firing rate is assumed to be a Heaviside function [9, 25, 33, 35, 42–44]. The possible bifurcations of traveling front and pulse solutions have also been investigated by Bressloff and Folias [6, 17].

In this paper, we analyze the existence and stability of traveling pulse solution of a neural field model that takes into account another physiological form of negative feedback, namely, synaptic depression. The model is described in Section 2. Using singular perturbation theory and blow-up techniques, we show in Section 3 the existence of a traveling pulse solution (see Figure 1). The existence proof is slightly more involved than in the case of linear adaptation [32]. The difficulty comes from the fact the solution passes close to the knee of the slow manifold that is no longer normally hyperbolic. As consequence, we obtain that the decay along the back of the traveling pulse is only algebraic instead of exponential as is the case with linear adaptation [32]. This type of problem has already been encountered in biological model of electrical cardiac wave [2] and in the propagation of wave in deformable media [19]. We then show in Section 4 that the constructed pulse solution is spectrally stable by the use of Evans functions. Our proof relies on some known results on the stability of traveling front solutions of neural field equation [7, 14] and stability properties of front solutions connecting a normally hyperbolic state to a non normally hyperbolic one [38]. More precisely, we show that the only zero in the right-half plane of the Evans function associated to the linearization of the traveling pulse is zero, and its geometric and algebraic multiplicity is one. Our definition of the Evans function is somewhat different from the one previously used for neural field models with Heaviside firing rate function [9, 33, 35, 42–44]. In our case, the Evans function is not known through an explicit formula due to our choice of the nonlinearity. However, we are still able to collect enough information to determine the location of its zeros.

2 Model and parameters

We consider a neural network which includes synaptic depression [26–28, 41], and system (1.1) is modified according to the following system of equations:

$$\begin{aligned} \tau \frac{\partial u(x, t)}{\partial t} &= -u(x, t) + \int_{\mathbb{R}} J(x - y) q(y, t) S(u(y, t)) dy \\ \frac{1}{\epsilon} \frac{\partial q(x, t)}{\partial t} &= 1 - q(x, t) - \beta q(x, t) S(u(x, t)). \end{aligned} \quad (2.1)$$

The first equation describes the evolution of the synaptic current $u(x, t)$ in the presence of synaptic depression which takes the form of a synaptic scaling factor $q(x, t)$ evolving according to the second equation. This factor can be interpreted as a measure of available presynaptic resources, which are depleted at a rate $\epsilon\beta S$, and recovered on a time scale specified by the constant ϵ . We assume units of time t to be 10ms each and we set $\tau = 1$ (10ms). Experimental recordings [37] suggest that synaptic depression recovers on a timescale of 200 – 800ms, so that $1/\epsilon$ typically ranges from 20 to 80 and thus $\epsilon \sim 0.01 - 0.05$ can be consider as a small parameter in equations (2.1). The range of allowable values for β , as used in used in [26] with $\epsilon \sim 0.01 - 0.05$, is $\beta \sim 1 - 20$. The nonlinear firing-rate function is taken to be the following smooth function

$$S(u) = \frac{1}{1 + e^{-\lambda(u - \kappa)}} \quad (2.2)$$

with threshold κ and gain λ . We take the excitatory weight function J to be a normalized exponential [26],

$$J(x) = \frac{b}{2} e^{-b|x|} \quad (2.3)$$

where $b > 0$ is the effective range of excitatory distribution.

2.1 Traveling wave equation

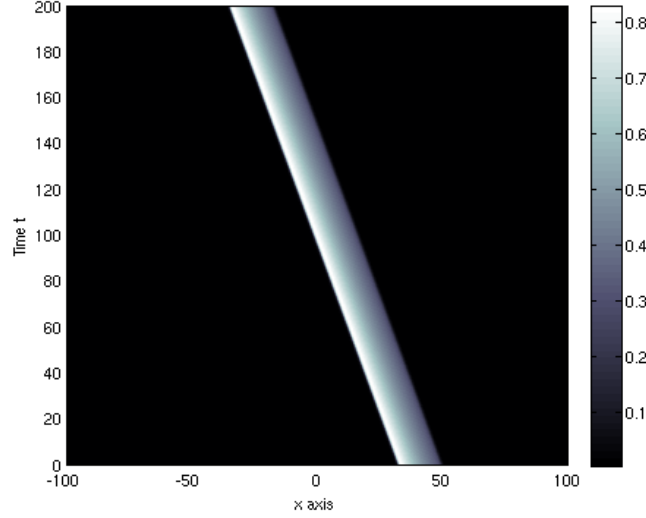


Figure 1: Space-time plot of a traveling pulse solution $u(x, t)$ obtained by solving the system (2.1) numerically with $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$, $\beta = 5$ and $\epsilon = 0.01$. The numerical integration is performed for $t \in [0, 200]$.

In this paper, we want to prove the existence of traveling wave solution for equation (2.1) (see Figure 1). To do so, we introduce a coordinate $\xi = x + ct$ for $c \in \mathbb{R}$ and then express the neural field equation in these coordinates as

$$\begin{aligned} \frac{\partial u(\xi, t)}{\partial t} &= -c \frac{\partial u(\xi, t)}{\partial \xi} - u(\xi, t) + \int_{\mathbb{R}} J(\xi - \xi') q(\xi', t) S(u(\xi', t)) d\xi' \\ \frac{\partial q(\xi, t)}{\partial t} &= -c \frac{\partial q(\xi, t)}{\partial \xi} + \epsilon (1 - q(\xi, t) - \beta q(\xi, t) S(u(\xi, t))). \end{aligned} \quad (2.4)$$

Time independent solutions of these equations satisfy the functional differential equations of mixed type (MFDEs)

$$\begin{aligned} c \frac{d}{d\xi} u(\xi) &= -u(\xi) + \int_{\mathbb{R}} J(\xi - \xi') q(\xi') S(u(\xi')) d\xi' \\ c \frac{d}{d\xi} q(\xi) &= \epsilon (1 - q(\xi) - \beta q(\xi) S(u(\xi))), \end{aligned} \quad (2.5)$$

since they contain both advanced and retarded terms through the convolutional term. This class of equation is notoriously difficult to analyze and appear naturally in problems set on lattice differential equations [22, 30]. In order to overcome this difficulty, we will use the very specific form of the connectivity function J . Indeed, the Fourier transform of this function is given by

$$\widehat{J}(k) = \frac{b^2}{b^2 + k^2}, \quad \forall k \in \mathbb{R}. \quad (2.6)$$

This ensures that if we set $v(\xi) = \int_{\mathbb{R}} J(\xi - \xi') q(\xi') S(u(\xi')) d\xi'$, then v satisfies the ordinary differential equation

$$b^2 v(\xi) - \frac{d^2}{d^2 \xi} v(\xi) = b^2 q(\xi) S(u(\xi)), \quad \forall \xi \in \mathbb{R}. \quad (2.7)$$

This implies that system (2.5) is equivalent to the system of ordinary differential equations

$$\begin{aligned} b^2 v(\xi) - \frac{d^2}{d\xi^2} v(\xi) &= b^2 q(\xi) S(u(\xi)) \\ c \frac{d}{d\xi} u(\xi) &= -u(\xi) + v(\xi) \\ c \frac{d}{d\xi} q(\xi) &= \epsilon (1 - q(\xi) - \beta q(\xi) S(u(\xi))) \end{aligned}$$

which can be converted into a system of first-order equations

$$\begin{aligned} u_\xi &= \frac{1}{c} (-u + v) \\ v_\xi &= w \\ w_\xi &= b^2 (v - qS(u)) \\ q_\xi &= \frac{\epsilon}{c} (1 - q - \beta qS(u)). \end{aligned} \tag{2.8}$$

Here for convenience, u_ξ stands for $\frac{d}{d\xi} u$.

2.2 Fixed points

The fixed points of system (2.8) (which are also stationary homogeneous solutions of (2.1)) satisfy

$$\begin{aligned} 0 &= -u + qS(u) \\ 0 &= 1 - q - \beta qS(u). \end{aligned} \tag{2.9}$$

The following Lemma ensures that this system has a unique solution (u_0, q_0) provided that β is large enough and that (λ, κ) satisfy a certain inequality. Thus, the nullclines of the system (2.8) intersect only at the fixed point as depicted in figure 2.

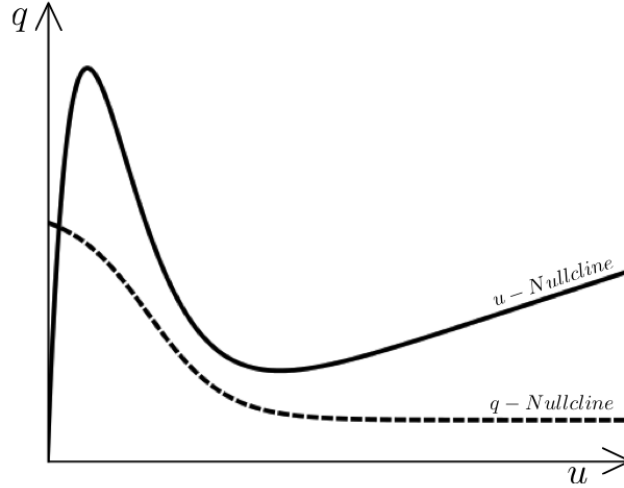


Figure 2: A typical graph of the nullclines of system (2.8) in the (u, q) -plane when the conditions of Lemma 2.1 are satisfied.

Lemma 2.1. *Suppose that $(\lambda, \kappa) \in (0, \infty) \times (0, 1)$ satisfy the relation*

$$2 - 2 \ln(2) \leq \lambda \kappa - \ln(\lambda).$$

Let W_{-1} be the lower branch of the real-valued Lambert function¹. We define

$$\begin{aligned} u_c(\lambda, \kappa) &= -\frac{2}{\lambda} W_{-1} \left(-\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda\kappa}{2}} \right) > 0 \\ \beta_c(\lambda, \kappa) &= \frac{1}{u_c(\lambda, \kappa)} - \frac{1}{S(u_c(\lambda, \kappa))} > 0. \end{aligned}$$

If $\beta > \beta_c(\lambda, \kappa)$ then system (2.9) has a unique solution (u_0, q_0) .

Proof. We postpone to Appendix A the proof of this Lemma. □

2.3 Hypotheses on the parameters

In order to prove the existence of a traveling pulse of equation (2.1), we will need to have some hypotheses on the different parameters of our system $(\lambda, \kappa, \beta, b, \epsilon)$. The following hypothesis, which is a direct consequence of Lemma 2.1, ensures that (u_0, q_0) is the only stationary homogenous solution of system (2.1).

Hypothesis 2.1. We suppose that $(\lambda, \kappa) \in (0, \infty) \times (0, 1)$ satisfy the relation

$$2 - 2 \ln(2) \leq \lambda\kappa - \ln(\lambda)$$

and $\beta > \beta_c(\lambda, \kappa)$ such that (u_0, q_0) is the unique fixed point of system (2.9).

The second hypothesis that we formulate is on the shape of our nonlinear function S .

Hypothesis 2.2. Let g be the C^∞ -smooth function defined through

$$g(u) = \frac{u}{S(u)}. \quad (2.10)$$

We suppose that (λ, κ) are such that there exist $u_+ > u_m > 0$ with $g(u_0) = g(u_m) = g(u_+) = q_0$ together with $g'(u_0) > 0$, $g'(u_m) < 0$ and $g'(u_+) > 0$. We further suppose that (λ, κ) are such that

$$\int_{u_0}^{u_+} -u + q_0 S(u) du > 0. \quad (2.11)$$

See Figure 3 for an illustration.

On account of Hypothesis 2.2, we may choose closed intervals I_L and I_R with $u_0 \in I_L$ and $u_+ \in I_R$, that have nonempty interiors and in addition have $g'(u) > 0$ for all $u \in I_L \cup I_R$. There exist constants $q_{knee} < q_0 < q_{max}$ in such way that we can define two C^∞ -smooth function $s_L : (q_{knee}, q_{max}) \rightarrow I_L$ and $s_R : (q_{knee}, q_{max}) \rightarrow I_R$ with

$$g(s_L(q)) = g(s_R(q)) = q$$

for all $q \in (q_{knee}, q_{max})$. Notice that $s_L(q_0) = u_0$ and $s_R(q_0) = u_+$. We define by continuity $u_{knee} = s_R(q_{knee})$ and $u_- = s_L(q_{knee})$. We thus have the ordering:

$$u_- < u_0 < u_m < u_{knee} < u_+.$$

3 Existence of the traveling pulse

In this section, we prove the existence of traveling pulses for equation (2.1). First, a singular traveling wave solution is constructed for $\epsilon = 0$; section 3.1. Then it is shown that this singular solution persists for small positive values of $\epsilon > 0$; 3.2.

¹Here, we consider the real-valued Lambert function defined as solution of the equation $W(x)e^{W(x)} = x$ restricted to real number $x \in \mathbb{R}$. Its lower branch, denoted W_{-1} , is defined for $e^{-1} \leq x \leq 0$ and satisfies $W_{-1}(x) \leq -1$ in that interval (see [13]).

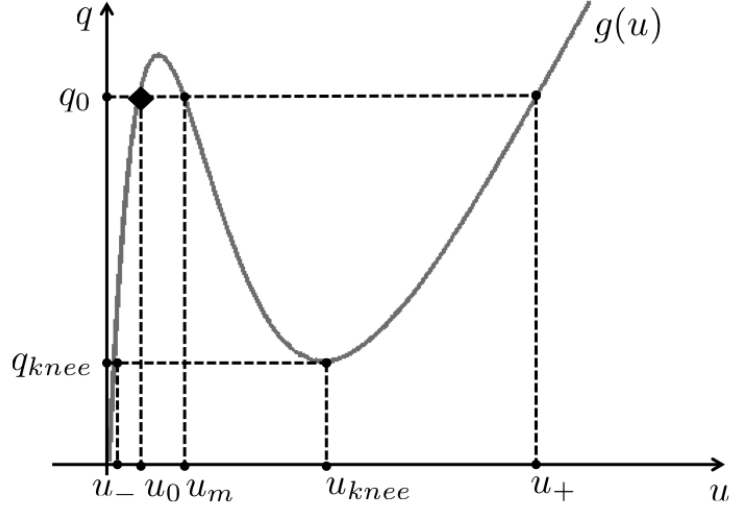


Figure 3: Illustration of the assumptions on the function g of Hypothesis 2.2. The *large diamond* is the fixed point of the system (u_0, q_0) .

3.1 The singular solution

3.1.1 The slow and fast subsystems

We recall that the traveling pulse solution is a stationary solution to the MFDE (2.4) and also a solution of the ODE (2.8). The slow subsystem can be found by a rescaling of the independent variable $z = \epsilon\xi$, and then setting $\epsilon = 0$:

$$\begin{aligned}
 0 &= \frac{1}{c}(-u + v) \\
 0 &= w \\
 0 &= b^2(v - qS(u)) \\
 q_z &= \frac{1}{c}(1 - q - \beta qS(u)).
 \end{aligned} \tag{3.1}$$

By setting $\epsilon = 0$ in (2.8), we obtain the reduced fast system:

$$\begin{aligned}
 u_\xi &= \frac{1}{c}(-u + v) \\
 v_\xi &= w \\
 w_\xi &= b^2(v - qS(u)) \\
 q_\xi &= 0.
 \end{aligned} \tag{3.2}$$

When considering the reduced slow system (3.1), there exists associated leading order slow manifold given by two pieces:

$$\mathcal{M}_L = \{(s_L(q), q)\} \text{ and } \mathcal{M}_R = \{(s_R(q), q)\}.$$

The slow dynamics on these manifolds is given by

$$q_z = \frac{1}{c}(1 - q - \beta qS(u)) \text{ for } (u, q) \in \mathcal{M}_j \quad j = L, R.$$

3.1.2 The front

For $q = q_0$, we seek for a leading order solution connecting the reduced fixed point on \mathcal{M}_L at $(u, v, w, q) = (u_0, u_0, 0, q_0)$ to the fixed point on \mathcal{M}_R at $(u, v, w, q) = (u_+, u_+, 0, q_0)$ for some value of the wave speed c .

Throughout the paper, we shall call this solution the front of the traveling pulse as it corresponds, to leading order, to the front profile of the pulse. In the neural field formalism, this is equivalent to find a traveling wave solution $u(x, t) = u_f(x + c_*t)$ of

$$\frac{\partial u(x, t)}{\partial t} = -u(x, t) + q_0 \int_{\mathbb{R}} J(x - y)S(u(y, t))dy \quad (3.3)$$

for some wavespeed $c_* \in \mathbb{R}$ and profile $u_f \in \mathcal{C}^1(\mathbb{R}, \mathbb{R})$ that satisfies the limits

$$\lim_{\xi \rightarrow -\infty} u_f(\xi) = u_0 \text{ and } \lim_{\xi \rightarrow +\infty} u_f(\xi) = u_+. \quad (3.4)$$

If Hypothesis 2.2 holds, then we know that such a solution exists [15]. Adapting the proof of [15], we obtain the following formula for the wavespeed c_* as a function of q_0 :

$$c_* = c(q_0) = \frac{1}{q_0} \frac{\int_{u_0}^{u_+} -u + q_0 S(u) du}{\int_{-\infty}^{+\infty} (u'_f(\xi))^2 S'(u_f(\xi)) d\xi} > 0. \quad (3.5)$$

A quick look at formula (3.5) shows that there should be a switch from positive to negative $c(q)$ at some value q_{zero} where $c(q_{zero}) = 0$ [15]. Then for all $q > q_{zero}$, $c(q) > 0$.

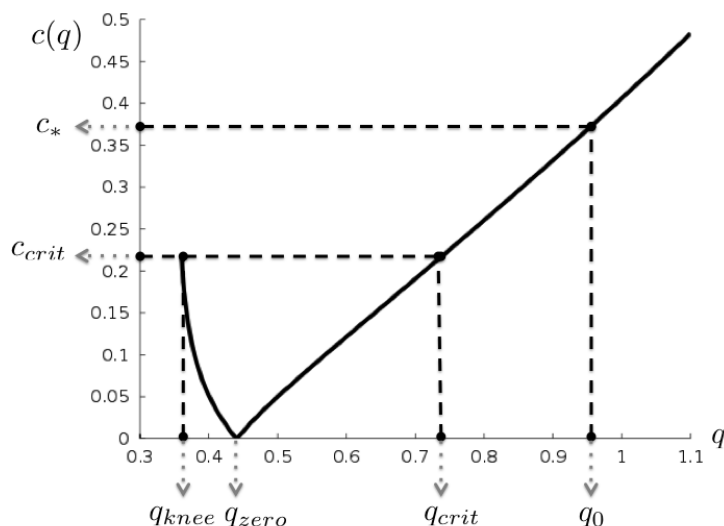


Figure 4: A typical graph of the wave speed $c(q)$ for the front and back of the wave as defined in (3.12), with $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$ and $\beta = 5$. Note that $q_{knee} = 0.3605$, $q_{zero} = 0.4405$, $q_{crit} = 0.7352$ and $q_0 = 0.9527$ with $c_{crit} = 0.2197$ and $c_* = 0.3705$. The reduced model admits traveling front solutions for $q \in [q_{zero}, q_{max}]$ and traveling back solutions for $q \in [q_{knee}, q_{zero}]$. Note that this picture is typical of the homoclinic orbits that we study: no value of $q \in [q_{crit}, q_{max}]$ leads to a singular connection between \mathcal{M}_L and \mathcal{M}_R . Therefore, the jump back must occur at the knee.

3.1.3 The back

The front selects the wavespeed of the pulse. In turn, the wavespeed of the pulse selects the particular value of q for which a jump back exists connecting the right slow manifold to the left slow manifold. In this section, we will need to define the knee of the right slow manifold \mathcal{M}_R . It is easy to see that the knee is given by the value of q for which

$$\begin{aligned} 0 &= -u + qS(u) \\ 0 &= -1 + qS'(u). \end{aligned} \quad (3.6)$$

Lemma 3.1. *Suppose that (λ, κ) satisfy the condition of Hypothesis 2.1, then the values (u_{knee}, q_{knee}) are*

$$\begin{aligned} u_{knee} &= \frac{1}{\lambda} [1 - W_{-1}(-e^{-\lambda\kappa+1})] \\ q_{knee} &= \frac{u_{knee}}{S(u_{knee})}. \end{aligned} \quad (3.7)$$

Proof. The proof of this lemma is moved to the appendix B. \square

For typical values of the parameters, as illustrated in Figure 4, we observe that above a particular value of q , there exists no choice of q for which such a connection between the right slow manifold and left slow manifold can be found. We will label this value of q as $q_{crit} \in [q_{zero}, q_{max}]$. It is defined by the condition that

$$c(q_{crit}) = c(q_{knee}) \stackrel{def}{=} c_{crit}.$$

Therefore, in that case, the only possibility is that the jump back from the right slow manifold to the left slow manifold occurs at the knee. Note that the knee is not a hyperbolic fixed point such that the existence result given in Ermentrout & McLeod [15] is no longer valid. However, the existence of such a connection is well understood in the case of the generalized Fisher-KPP equation of order 2 [4, 5] and can be extended to the neural field formalism.

Proposition 3.1. *For each $c \geq c_{crit}$ there exists a traveling back solution $u_b(x+ct)$ to*

$$\frac{\partial u(x,t)}{\partial t} = -u(x,t) + q_{knee} \int_{\mathbb{R}} J(x-y)S(u(y,t))dy \quad (3.8)$$

with profile $u_b \in C^1(\mathbb{R}, \mathbb{R})$ and that satisfies the limits

$$\lim_{\xi \rightarrow -\infty} u_b(\xi) = u_{knee} \text{ and } \lim_{\xi \rightarrow +\infty} u_b(\xi) = u_-. \quad (3.9)$$

Moreover, u_b satisfies the asymptotic expansions at $\xi = -\infty$

$$u_b(\xi) \sim \begin{cases} u_{knee} - \alpha \exp\left(\frac{-1 + \sqrt{1 + 4b^2 c^2}}{2c} \xi\right) & c = c_{crit} \\ u_{knee} - \left(\frac{q_{knee} S''(u_{knee})}{2c}\right)^{-1} \frac{1}{\xi} & c > c_{crit} \end{cases} \text{ as } \xi \rightarrow -\infty \quad (3.10)$$

with α some positive constant.

Thus, this result ensures that for any $c \geq c_{crit}$ there exists a connection between the knee at $(u_{knee}, u_{knee}, 0, q_{knee})$ and the left branch of the slow manifold at $(u_-, u_-, 0, q_{knee})$. Throughout the paper, we shall refer to this solution as the back of the traveling pulse as it corresponds, to leading order, to the back profile of the pulse.

Proof. The proof of the proposition is divided into three steps. We first show that there exists a traveling back solution for $c = c_{crit}$ and then we show that there still exists a connection between u_{knee} at $-\infty$ and u_- at $+\infty$ for $c > c_{crit}$. We conclude the proof by showing the asymptotic expansions (3.10).

Step-1 We first rewrite (3.8) in ξ -coordinate

$$c \frac{du(\xi)}{d\xi} = -u(\xi) + q \int_{\mathbb{R}} J(\xi - \xi') S(u(\xi')) d\xi' \quad (3.11)$$

and allow $q \in [q_{knee}, q_{max}]$. We know from the study of Ermentrout & McLeod [15], that for each $q \in (q_{knee}, q_{max})$, there exists a traveling solution $(u_b(\xi; q), c(q))$ of (3.11) with limits

$$\lim_{\xi \rightarrow -\infty} u_b(\xi; q) = s_R(q) \text{ and } \lim_{\xi \rightarrow +\infty} u_b(\xi; q) = s_L(q)$$

and an associated wavespeed

$$c(q) = -\frac{1}{q} \frac{\int_{s_L(q)}^{s_R(q)} -u + qS(u) du}{\int_{-\infty}^{+\infty} (u'_b(\xi; q))^2 S'(u_b(\xi; q)) d\xi}. \quad (3.12)$$

Thus, this defines a continuous function $c : (q_{knee}, q_{max}) \rightarrow \mathbb{R}$. Note that for all $q \in (q_{knee}, q_{max})$ the equation

$$F(u; q) \stackrel{def}{=} -u + qS(u) = 0 \quad (3.13)$$

has exactly three solutions given by

$$0 < s_L(q) < u_m(q) < s_R(q).$$

On the other hand, at $q = q_{knee}$, equation (3.13) has only two solutions given by

$$u_- = s_L(q_{knee}) < s_R(q_{knee}) = u_{knee}.$$

We can now use the continuation argument used in Theorem 4.5 [15] and pass to the limit as $q \rightarrow q_{knee}$. We obtain that $u_b^{crit}(\xi) = \lim_{q \rightarrow q_{knee}} u_b(\xi; q)$ is solution of equation (3.8) with the limits:

$$\lim_{\xi \rightarrow -\infty} u_b^{crit}(\xi) = u_{knee} = \lim_{q \rightarrow q_{knee}} s_R(q) \text{ and } \lim_{\xi \rightarrow +\infty} u_b^{crit}(\xi) = u_- = \lim_{q \rightarrow q_{knee}} s_L(q).$$

We thus obtain c_{crit} as the limit of $c(q)$ as $q \rightarrow q_{knee}$ and is given by

$$c_{crit} = -\frac{1}{q_{knee}} \frac{\int_{u_-}^{u_{knee}} -u + q_{knee}S(u)du}{\int_{-\infty}^{+\infty} \left(\frac{du_b^{crit}(\xi)}{d\xi}\right)^2 S'(u_b^{crit}(\xi))d\xi} > 0. \quad (3.14)$$

Step-2 We first write (3.11) has a three-dimensional system of first order differential equations with $q = q_{knee}$:

$$\begin{aligned} u_\xi &= \frac{1}{c}(-u + v) \\ v_\xi &= w \\ w_\xi &= b^2(v - q_{knee}S(u)). \end{aligned} \quad (3.15)$$

We know that this system has only two fixed points given by $U_- = (u_-, u_-, 0)$ and $U_{knee} = (u_{knee}, u_{knee}, 0)$. The linearization at this two points is given by

$$\mathcal{L}_-(c) = \begin{pmatrix} -\frac{1}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2\alpha & b^2 & 0 \end{pmatrix} \text{ and } \mathcal{L}_{knee}(c) = \begin{pmatrix} -\frac{1}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2 & b^2 & 0 \end{pmatrix},$$

where we have set $\alpha = q_{knee}S'(u_-) \in (0, 1)$. $\mathcal{L}_{knee}(c)$ has three real eigenvalues:

- $\mu = 0$ with eigenvector $\zeta = (1, 1, 0)$,
- $\mu_\pm = \frac{-1 \pm \sqrt{1 + 4b^2c^2}}{2c}$ with eigenvector $\zeta_\pm = (1, -c\mu_\mp, cb^2)$.

The three eigenvalues of $\mathcal{L}_-(c)$ are solutions of the cubic equations

$$x^3 + \frac{x^2}{c} - b^2x + \frac{b^2(\alpha - 1)}{c} = 0.$$

As $\alpha < 1$, the above equation has always a positive real solution that we denote ν_3 and the two other solutions (ν_1, ν_2) necessarily have negative real parts. The corresponding eigenvectors are $\zeta_j = (1, 1 + c\nu_j, \nu_j(1 + c\nu_j))$ for $j = 1, 2, 3$. We can then define the two-dimensional stable manifold at the fixed point U_- together with the two-dimensional center unstable manifold at the knee.

We know from the first step that these manifolds intersect for $c = c_{crit}$. Indeed, the connection that departs the right slow manifold along the unstable direction approaches the left slow manifold along its stable manifold is continuous in $q > q_{knee}$. Then, passing to the limit $q \rightarrow q_{knee}$, we obtain a connection that departs the knee of the right slow manifold along the unstable direction and approaches the left slow manifold along its stable manifold with associated wavespeed $c = c_{crit}$. This gives us the desired intersection. At

$q = q_{knee}$, we can use this connection as a separatrix in the two-dimensional center unstable manifold at the knee and then use the trapping region argument of Billingham & Needham [4, 5] to prove that a connection also exists between the knee and the fixed point U_- for all $c > c_{crit}$. Furthermore, this connection can only depart the knee along the center-unstable direction and approaches the left fixed point along its stable manifold. In Figure 5, we present an illustration of the trajectories of the solution of (3.15) for different values of the wavespeed c .

Step-3 In the case $c = c_{crit}$, the connection departs the knee along the unstable direction with corresponding eigenvalue $\frac{-1 + \sqrt{1 + 4b^2c^2}}{2c}$. Then there exists a constant $\alpha > 0$ such that

$$u_b^{crit}(\xi) \underset{\xi \rightarrow -\infty}{\sim} u_{knee} - \alpha \exp\left(\frac{-1 + \sqrt{1 + 4b^2c^2}}{2c}\xi\right).$$

In the case $c > c_{crit}$, we know that the connection leaves the knee along its center-unstable direction. To leading order, we only need to compute the one-dimensional center manifold at the knee. We know from standard dynamical systems theory (see [18]) that there exists a smooth \mathcal{C}^k ($k \geq 2$) center manifold given as a graph:

$$U = U_{knee} + \beta\zeta + \Psi(\beta), \quad \Psi(\beta) = \beta^2\Psi_1 + \mathcal{O}(\beta^3) \text{ as } \beta \rightarrow 0, \quad (3.16)$$

where $\zeta = (1, 1, 0)$. It is a simple computation to see that the equation on the center manifold is given by

$$\dot{\beta} = \frac{q_{knee}S''(u_{knee})}{2c}\beta^2 + \mathcal{O}(\beta^3) \text{ as } \beta \rightarrow 0.$$

Such that, as $\xi \rightarrow -\infty$, $\beta(\xi) \sim -\left(\frac{q_{knee}S''(u_{knee})}{2c}\right)^{-1}\frac{1}{\xi}$. Plugging back this expansion into (3.16), we deduce the second asymptotic expansion of equation (3.10). This concludes the proof. \square

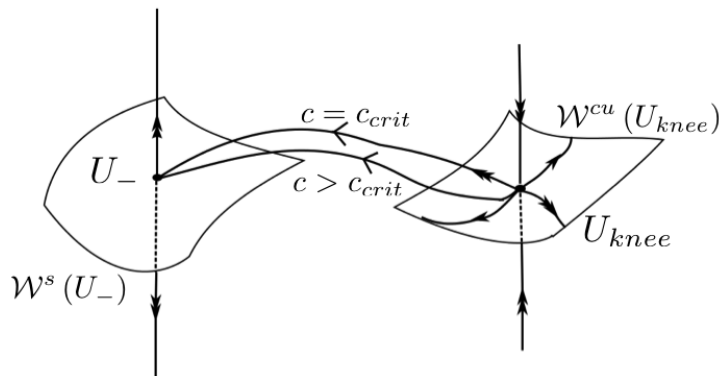


Figure 5: A sketch of the phase portrait of two solution of (3.15) in the (u, v, w) -space for $q = q_{knee}$ for different values of c . The trajectory for $c = c_{crit}$ departs U_{knee} along the unstable direction and approaches U_- along its stable manifold while the trajectory for $c > c_{crit}$ departs U_{knee} along the center-unstable direction and approaches U_- along its stable manifold. $W^s(U_-)$ represents the two-dimensional stable manifold of U_- and $W^{cu}(U_{knee})$ the two-dimensional center-unstable manifold of U_{knee} .

Hypothesis 3.1. We suppose that (λ, κ) are such that the wavespeed selected by the front is strictly greater than the wavespeed selected by the back. Hence, the jump back must occur along the center direction at the knee. See Figure 5.

3.1.4 Summary of the singular solution

Putting the information from the reduced slow and fast dynamics together, the singular solution consists of four pieces as follows:

- (1) a fast jump from $(u_0, u_0, 0, q_0)$ to $(u_+, u_+, 0, q_0)$, which is given by the profile u_f solution of (3.3) with speed $c_* > 0$;
- (2) slow decay along \mathcal{M}_R from $(u_+, u_+, 0, q_0)$ to $(s_R(q_{knee}), s_R(q_{knee}), 0, q_{knee})$;
- (3) a fast jump from $(s_R(q_{knee}), s_R(q_{knee}), 0, q_{knee})$ to $(s_L(q_{knee}), s_L(q_{knee}), 0, q_{knee})$ that departs along the center-unstable manifold;
- (4) slow growth along \mathcal{M}_L back to $(u_0, u_0, 0, q_0)$.

The singular solution, projected onto the (u, q) -plane, is plotted in Figure 6(a). We show, in Figure 6(b), the corresponding singularly perturbed solution projected onto the (u, q) -plane for $\epsilon = 0.005$ with values of the parameters being fixed to $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$ and $\beta = 5$. In Figure 7, we plot the singularly perturbed solution, for the same values of the parameters, in the (u, v, q) -space.

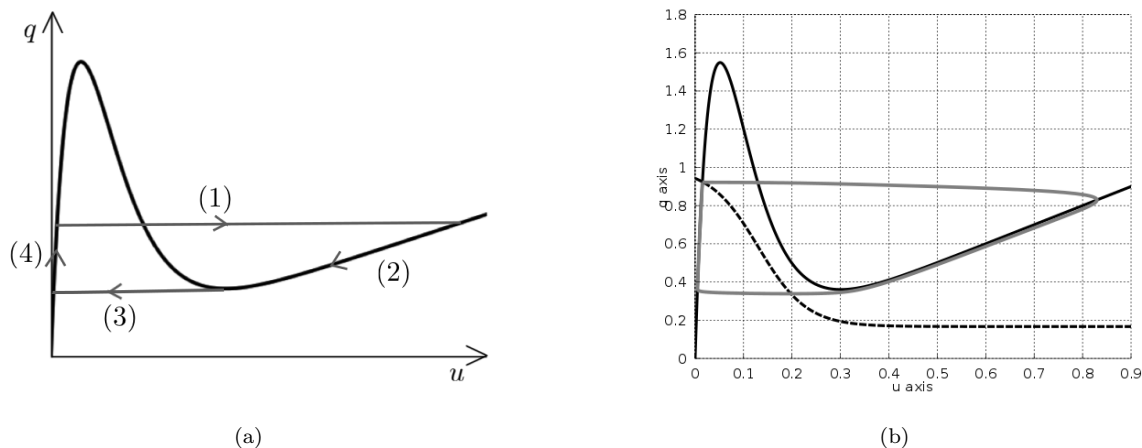


Figure 6: (Left) A sketch of the leading order pulse projected onto the (u, q) -plane, consisting of: (1) a fast jump from $(u_0, u_0, 0, q_0)$ to $(u_+, u_+, 0, q_0)$, (2) slow decay along \mathcal{M}_R , (3) another fast jump connecting $(u_{knee}, u_{knee}, 0, q_{knee})$ to $(u_-, u_-, 0, q_{knee})$ and leaving at the knee, and (4) slow growth along \mathcal{M}_L . (Right) Plot of the pulse solution of (2.8) in the (u, q) -plane, computed numerically with $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$, $\beta = 5$ and $\epsilon = 0.01$.

3.2 Persistence of the pulse

For the simplicity of this paper, we always illustrate our results in the case of $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$ and $\beta = 5$ which are similar to the values used in Kilpatrick & Bressloff [26]. However, the proof holds for much more general parameters values, which we now define.

Definition 3.1. *The set, labelled Π , of allowable parameters $(\lambda, \kappa, b, \beta)$ for the model in (2.1) consists of those parameters such that Hypotheses 2.1, 2.2 and 3.1 are satisfied together with $b > 0$.*

Theorem 3.1. *Suppose that $(\lambda, \kappa, b, \beta) \in \Pi$. Then there exists $\epsilon_1 > 0$ such that for all $0 < \epsilon < \epsilon_1$, there exists $c(\epsilon) = c_* + \mathcal{O}(\epsilon)$ for which problem (2.1) has a traveling pulse solution of the form $(u(x+ct), q(x+ct))$ with $\lim_{\xi \rightarrow \pm\infty} (u, q) = (u_0, q_0)$.*

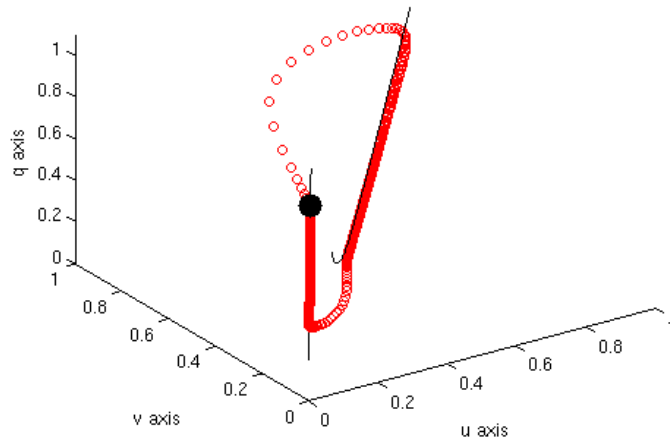


Figure 7: Plot of the traveling pulse solution of (2.8) in the (u, v, q) -space, computed numerically with $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$, $\beta = 5$ and $\epsilon = 0.01$. The *thin curves* represent the slow manifolds to leading order. The *large dot* is the fixed point of the system.

A space-time plot of the $u(x, t)$ -component of a traveling pulse solution, as given in Theorem 3.1, is shown in Figure 1. In Figure 8, we present the corresponding (u, q) -profiles in the traveling wave coordinate $\xi = x + ct$. Note that the decay rate along the back is less than the decay rate along the front. In fact, we will see that the decay along the front is exponential, whereas the decay along the back is only algebraic, as it is already the case for the singular solution at $\epsilon = 0$.

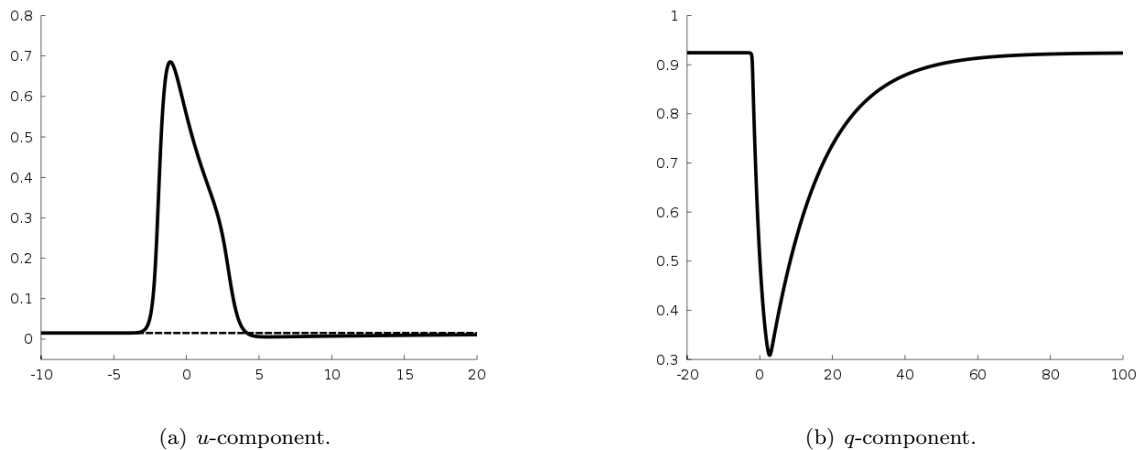


Figure 8: Profiles of a traveling pulse solution $(u(\xi), q(\xi))$ obtained by solving the system (2.1) numerically with $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$, $\beta = 5$ and $\epsilon = 0.01$.

Proof. The idea of the proof is to demonstrate that the singular pulse described above persists for small, positive ϵ . It will be shown that this singular solution lies in the transverse intersection of the stable and unstable manifolds of the equilibrium point $(u_0, u_0, 0, q_0)$ when $\epsilon = 0$.

Persistence of the front

We begin by tracking \mathcal{W}^{cu} , the center-unstable manifold emanating from the unique fixed point of the system, along the first jump. We will show that \mathcal{W}^{cu} intersects transversely the center-stable manifold \mathcal{W}^{cs} of the right slow manifold in the plane $q = q_0$. Consider the reduced fast system (3.2). The plane $q = q_0$ is

invariant, and we want to determine how the unstable manifold of $(u, v, w) = (u_0, u_0, 0)$ intersects the stable manifold of $(u, v, w) = (u_+, u_+, 0)$ as we vary the wavespeed c . To do this, we first augment our traveling wave system with a trivial differential equation for the wavespeed c

$$\begin{aligned} u_\xi &= \frac{1}{c}(-u + v) \\ v_\xi &= w \\ w_\xi &= b^2(v - q_0 S(u)) \\ c_\xi &= 0. \end{aligned} \tag{3.17}$$

Based upon the analysis in subsection 3.1.2, there is a unique c_* for which a unique heteroclinic connection between the saddle $(u_0, u_0, 0)$ at $-\infty$ and the saddle $(u_+, u_+, 0)$ at $+\infty$ exists. We will show that the two-dimensional center-unstable manifold which is a union of the unstable manifolds of $(u, v, w) = (u_0, u_0, 0)$ for values of c near c_* and denoted $\mathcal{W}^{cu}(u_0, u_0, 0)$, intersects the three-dimensional center-stable manifold of $(u_+, u_+, 0)$, defined as a union of the stable manifolds for c near c_* , denoted $\mathcal{W}^{cs}(u_+, u_+, 0)$, and this intersection is transverse in the c direction.

One way to track the evolution of k -dimensional manifolds is using k -forms, as in [24]. Here, it will be enough to use 2-forms. Along the front, the reduced variational equations are given by

$$\begin{aligned} du' &= \frac{1}{c}(-du + dv) - \frac{1}{c^2}(-u + v)dc \\ dv' &= dw \\ dw' &= b^2(dv - q_0 S'(u)du) \\ dc' &= 0. \end{aligned} \tag{3.18}$$

The associated two-forms are $P_{uv} = du \wedge dv$, $P_{uw} = du \wedge dw$, $P_{uc} = du \wedge dc$, $P_{vw} = dv \wedge dw$, $P_{vc} = dv \wedge dc$ and $P_{wc} = dw \wedge dc$, with evolution equations

$$\begin{aligned} P'_{uv} &= -\frac{1}{c}P_{uv} + \frac{1}{c^2}(-u + v)P_{vc} + P_{uw} \\ P'_{uw} &= \frac{1}{c}(-P_{uw} + P_{vw}) + \frac{1}{c^2}(-u + v)P_{wc} + b^2P_{uv} \\ P'_{uc} &= \frac{1}{c}(-P_{uc} + P_{vc}) \\ P'_{vw} &= -b^2q_0 S'(u)P_{uv} \\ P'_{vc} &= P_{wc} \\ P'_{wc} &= b^2(P_{vc} + q_0 S'(u)P_{uc}) \end{aligned} \tag{3.19}$$

The manifolds $\mathcal{W}^{cu}(u_0, u_0, 0)$ and $\mathcal{W}^{cs}(u_+, u_+, 0)$ both have the vector field, $n = (\frac{1}{c}(-u + v), w, b^2(v - q_0 S(u)), 0)$, as one tangent vector. Denote the other one by $\eta^\pm = (du^\pm, dv^\pm, dw^\pm, 1)$, respectively, where we can take $dc = 1$ since $dc' = 0$. This ensures that these two vectors are linearly independent. Based on the dimension of $\mathcal{W}^{cu}(u_0, u_0, 0)$ and $\mathcal{W}^{cs}(u_+, u_+, 0)$, we can also assume that $dw^\pm = 0$. We can compute explicitly that $P_{vc}(n, \eta^\pm) = w$ and $P_{uw}(n, \eta^\pm) = 0$, such that the equation for P_{uv} now reads

$$P'_{uv} = -\frac{1}{c}P_{uv} + \frac{1}{c^2}(-u + v)w.$$

This is solved as

$$P_{uv} = \frac{1}{c}e^{-\frac{\xi}{c}} \int_{-\infty}^{\xi} e^{\frac{\tau}{c}}(-u(\tau) + v(\tau))w(\tau)d\tau.$$

We first note that the sign of $-u + v$ is given by the sign of v_ξ . Secondly, the sign of w is also given by the sign of v_ξ as

$$w(\xi) = v_\xi(\xi) = q_0 \frac{d}{d\xi} \left(\int_{\mathbb{R}} J(\xi') S(u(\xi - \xi')) d\xi' \right) = q_0 \int_{\mathbb{R}} J(\xi') u_\xi(\xi - \xi') S'(u(\xi - \xi')) d\xi'.$$

This ensures that P_{uv} is positive and we conclude that

$$P_{uv}(n, \eta^+) = \frac{1}{c}(-u + v)dv^+ > 0.$$

An analogous computation gives:

$$P_{uv} = -\frac{1}{c}e^{-\frac{\xi}{c}} \int_{\xi}^{\infty} e^{\frac{\tau}{c}} (-u(\tau) + v(\tau))w(\tau)d\tau,$$

from which we deduce that

$$P_{uv}(n, \eta^-) = \frac{1}{c}(-u + v)dv^- < 0.$$

As $-u + v$ does not change sign, this implies that $dv^+ \neq dv^-$ as they have opposite signs. Therefore, the two manifolds $\mathcal{W}^{cu}(u_0, u_0, 0)$ and $\mathcal{W}^{cs}(u_+, u_+, 0)$ intersect transversely.

The exchange lemma

We now track \mathcal{W}^{cu} as it passes the right slow manifold. We recall the expressions of u_{knee} and q_{knee} of the knee $(u_{knee}, u_{knee}, 0, q_{knee}, 0)$ (see Lemma 3.1)

$$\begin{aligned} u_{knee} &= \frac{1}{\lambda} [1 - W_{-1}(-e^{-\lambda\kappa+1})] \\ q_{knee} &= \frac{u_{knee}}{S(u_{knee})}. \end{aligned}$$

For any $\delta > 0$, we define a δ -neighborhood of the knee by

$$\mathcal{K}_{\delta} = \{(u, v, w, c) \mid |u - u_{knee}| < \delta, |v - u_{knee}| < \delta, |q - q_{knee}| < \delta, |c - c_*| < \delta\}.$$

Let $\mathcal{B}_R = \mathcal{M}_R \cap \partial\mathcal{K}_{\delta}$. We have the following result.

Lemma 3.2. *For fixed $\delta > 0$, the tracked manifold \mathcal{W}^{cu} is \mathcal{C}^1 , $\mathcal{O}(\epsilon)$ close to $\mathcal{W}^{cu}(\mathcal{M}_R)$ in a neighborhood of \mathcal{B}_R .*

Proof. We have that \mathcal{W}^{cu} intersects $\mathcal{W}^{cs}(\mathcal{M}_R)$ transversely on entry into a neighborhood of \mathcal{M}_R . The proof is then a standard application of the exchange lemma [24]. \square

Analysis at the knee

Consider the ODE for the pulse (2.8) and append to it an equation for ϵ :

$$\begin{aligned} u_{\xi} &= \frac{1}{c}(-u + v) \\ v_{\xi} &= w \\ w_{\xi} &= b^2(v - qS(u)) \\ q_{\xi} &= \frac{\epsilon}{c}(1 - q - \beta qS(u)) \\ \epsilon_{\xi} &= 0. \end{aligned} \tag{3.20}$$

We are interested in the behavior of this equation near the knee, which corresponds to the fixed point $U_{knee} = (u_{knee}, u_{knee}, 0, q_{knee}, 0)$. The Jacobian matrix at this point is given by

$$L = \begin{pmatrix} -\frac{1}{c} & \frac{1}{c} & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ -b^2 & b^2 & 0 & -b^2\alpha & 0 \\ 0 & 0 & 0 & 0 & \gamma \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix},$$

with $\alpha = S(u_{knee})$ and $\gamma = \frac{1}{c}(1 - q_{knee} - \beta q_{knee} S(u_{knee}))$. This matrix has one positive eigenvalue $\lambda_+ = \frac{-1 + \sqrt{1 + 4c^2 b^2}}{2c}$ and one negative eigenvalue $\lambda_- = \frac{-1 - \sqrt{1 + 4c^2 b^2}}{2c}$ with respective corresponding eigenvectors

$$\nu_+ = \left(1, \frac{1 + \sqrt{1 + 4c^2 b^2}}{2}, cb^2, 0, 0\right) \text{ and } \nu_- = \left(1, \frac{1 - \sqrt{1 + 4c^2 b^2}}{2}, -cb^2, 0, 0\right).$$

In addition, $\nu = 0$ is an eigenvalue with algebraic multiplicity three and geometric multiplicity one. The associated eigenvector is $\zeta_1 = (1, 1, 0, 0, 0)$, and the generalized eigenvectors are $\zeta_2 = (0, c, 1, c/\alpha, 0)$ and $\zeta_3 = (0, 0, c, -1/b^2 \alpha, c/\alpha \gamma)$. In order to apply a blow-up technique at the knee, we will need to isolate the nonhyperbolic dynamics which occur on a three-dimensional center manifold denoted \mathcal{W}_{knee} . The vector field $U = (u, v, w, q, \epsilon)$ can be decomposed as

$$U = U_{knee} + A\zeta_1 + B\zeta_2 + C\zeta_3 + \Psi(A, B, C)$$

where the map Ψ is $\mathcal{C}^k(\mathcal{W}_0, \nu_+ \oplus \nu_-)$ and $\Psi(0) = D\Psi(0) = 0$. Furthermore, the Taylor expansion of Ψ is given

$$\Psi(A, B, C) = A^2\Psi_{200} + B^2\Psi_{020} + C^2\Psi_{002} + AB\Psi_{110} + AC\Psi_{101} + BC\Psi_{011} + \mathcal{O}(3)$$

where $\mathcal{O}(3)$ regroup all higher order terms.

Inserting this ansatz into (3.20) gives a set of differential equations that are satisfied by (A, B, C) of the form

$$\begin{aligned} \dot{A} &= \delta_1 B + \delta_2 A^2 + \mathcal{O}(C, B^2, C^2, AB, BC, AC) \\ \dot{B} &= \delta_3 C + \mathcal{O}(AC, BC) \\ \dot{C} &= 0 \end{aligned} \tag{3.21}$$

where δ_1, δ_2 and δ_3 are constants that can be computed explicitly. A straightforward computation shows that

$$\delta_1 = \delta_3 = 1.$$

If we denote $\mathcal{R}(U_1, U_2)$ the following bilinear form on \mathbb{R}^5

$$\mathcal{R}(U_1, U_2) = \begin{pmatrix} 0 \\ 0 \\ -\frac{q_{knee}}{2} S''(u_{knee}) u_1 u_2 - S'(u_{knee}) \frac{u_1 q_2 + u_2 q_1}{2} \\ -\frac{\epsilon_1 q_2 + \epsilon_2 q_1}{2c} - \frac{\beta(\epsilon_1 u_2 + \epsilon_2 u_1)}{2c} - \frac{\beta S(u_{knee})(\epsilon_1 q_2 + \epsilon_2 q_1)}{2c} \\ 0 \end{pmatrix}$$

then we have that:

$$\dot{U} = L(U - U_{knee}) + \mathcal{R}(U - U_{knee}, U - U_{knee}) + \mathcal{O}(\|U - U_{knee}\|^2).$$

If L^* is the adjoint matrix of L , then there exist vectors $(\zeta_3^*, \zeta_2^*, \zeta_1^*)$ such that

$$L^* \zeta_3^* = 0, \quad L^* \zeta_2^* = \zeta_3^*, \quad L^* \zeta_1^* = \zeta_2^* \quad \text{with } \langle \zeta_i, \zeta_j^* \rangle_{\mathbb{R}^5} = \delta_{i,j}.$$

The equation for δ_2 is then given by

$$\delta_2 = \langle L\Psi_{200}, \zeta_1^* \rangle + \langle \mathcal{R}(\zeta_1, \zeta_1), \zeta_1^* \rangle = \langle \mathcal{R}(\zeta_1, \zeta_1), \zeta_1^* \rangle = \frac{q_{knee}}{b^2 c} S''(u_{knee}).$$

Equivalently, the equations satisfied by (u, q, ϵ) on the center manifold are:

$$\begin{aligned} u_\xi &= \frac{q_{knee}}{b^2 c} S''(u_{knee})(u - u_{knee})^2 + \frac{S(u_{knee})}{c}(q - q_{knee}) \\ &\quad + \mathcal{O}(\epsilon, (q - q_{knee})^2, (u - u_{knee})(q - q_{knee}), \epsilon(u - u_{knee}), \epsilon(q - q_{knee})) \\ q_\xi &= \frac{1 - q_{knee} - \beta q_{knee} S(u_{knee})}{c} \epsilon + \mathcal{O}(\epsilon(q - q_{knee}), \epsilon(u - u_{knee})) \\ \epsilon_\xi &= 0. \end{aligned} \tag{3.22}$$

System (3.22) possesses a slow manifold for $\epsilon = 0$, which is given by

$$\mathcal{P} = \left\{ (u, q) \mid \frac{q_{knee}}{b^2 c} S''(u_{knee})(u - u_{knee})^2 + \frac{S(u_{knee})}{c} (q - q_{knee}) = 0 \right\}.$$

This manifold can be divided into an attracting branch \mathcal{P}_a and a repelling branch \mathcal{P}_r . Outside a neighborhood of the fold point $(u, q) = (u_{knee}, q_{knee})$, these manifolds are normally hyperbolic and, therefore, perturb smoothly to locally invariant manifolds \mathcal{P}_a^ϵ and \mathcal{P}_r^ϵ for ϵ positive and sufficiently small. We define the following sets:

$$\begin{aligned} \Delta_{in} &= \{(u, v, w, q, \epsilon) \mid q = q_{knee} - \rho^2\} \\ \Delta_{out} &= \{(u, v, w, q, \epsilon) \mid u = u_{knee} - \rho\} \end{aligned}$$

where $\rho > 0$.

We have the following theorem from [29].

Proposition 3.2. *Let $\pi : \Delta^{in} \rightarrow \Delta^{out}$ be the transition map of the flow of (3.22). Then there exists ϵ_0 , such that for all $\epsilon \in [0, \epsilon_0]$, the following holds:*

1. *The manifold \mathcal{P}_a^ϵ passes through Δ_{out} at a point $(u, q, \epsilon) = (u_{knee} - \rho, q_{knee} + h(\epsilon), \epsilon)$, with $h(\epsilon) = \mathcal{O}(\epsilon^{2/3})$.*
2. *The transition map π is a contraction with contraction constant $\mathcal{O}(\epsilon^{-C/\epsilon})$ with C a positive constant.*

This proposition tells us how to track the manifold \mathcal{W}^{cu} around the knee and that the resulting analysis will be independent of the choice of the center manifold. As already mentioned, for any $q \in (q_{knee}, q_{max})$, the two-dimensional manifold \mathcal{W}^{cu} is spanned by the one-dimensional fast unstable direction of the points $(s_R(q), s_R(q), 0, q)$ and the tangent line in the plane $\{u = v, w = 0\}$ to the one-dimensional slow manifold, given by $q = u/S(u)$. As \mathcal{W}^{cu} enters a neighborhood of the knee, it will intersect the center manifold of the knee \mathcal{W}_{knee} .

Following the notations of [2], we define the following objects:

$$\begin{aligned} I^{u,in} &= \mathcal{W}^{cu} \cap \Delta_{in} \\ p_{knee}^{in} &= I^{u,in} \cap \mathcal{W}_{knee} \\ I^{u,out} &= \mathcal{W}^{cu} \cap \Delta_{out} \\ p_{knee}^{out} &= I^{u,out} \cap \mathcal{W}_{knee} \end{aligned}$$

Near p_{knee}^{in} , the dynamics of each point in \mathcal{W}^{cu} can be decomposed into the flow of a base point $p \in \mathcal{W}_{knee}$ and an expansion in the corresponding unstable fiber $\mathcal{F}_u(p)$ given as a graph over the unstable eigenvector ν_+ . Proposition 3.2 implies that all of the basepoints exit \mathcal{K}_δ at a distance $\mathcal{O}(\epsilon^{-C/\epsilon})$ close to πp_{knee}^{in} . Since the fibers depend smoothly on their basepoints, the exponential contraction of π implies that each unstable fiber will be locally $\mathcal{O}(\epsilon^{2/3})$ close to the unstable fiber at $(u, q, \epsilon) = (u - u_{knee}, q_{knee}, 0)$. Since the unstable fibers are given as a graph over the unstable eigenvector, whose q component is zero, the manifold \mathcal{W}^{cu} will be \mathcal{C}^1 $\mathcal{O}(\epsilon^{2/3})$ close to the plane $q = q_{knee}$. The \mathcal{C}^1 aspect of the perturbation follows from the fact that the center manifold itself is normally hyperbolic, and therefore its unstable fibers perturb smoothly.

Conclusion of the proof

We now follow \mathcal{W}^{cu} along the back and \mathcal{W}^{cs} backward down the left branch of the slow manifold and show they intersect transversely. We have tracked \mathcal{W}^{cu} to an $\mathcal{O}(1)$ distance from the knee and shown that it is \mathcal{C}^1 , $\mathcal{O}(\epsilon^{2/3})$ close to the plane $q = q_{knee}$. Due to the slow q dynamics, this result still hold as \mathcal{W}^{cu} enters an $\mathcal{O}(1)$ neighborhood of \mathcal{M}_L . Due to Fenichel theory, the stable manifold is tangent to the stable eigenspace of \mathcal{M}_L . A direct computation shows that this eigenspace has nonzero q component and, therefore, it must intersect transversely with \mathcal{W}^{cs} . This completes the proof. \square

4 Stability of the pulse

In this section, we will study the spectral stability of the traveling pulse solution constructed in Theorem 3.1. We will linearize the system at the pulse and show that the resulting essential spectrum is bounded to the left of the imaginary axis (note that the bound depends upon ϵ). We will then construct Evans functions associated with the full problem and with the reduced fast pieces along the front and the back of the pulse. We will then show that the eigenvalues of the full Evans function are determined by those of the reduced problems which will allow us to determine the spectral stability of the pulse. More precisely, we will prove the following theorem.

Theorem 4.1. *Suppose that $(\lambda, \kappa, b, \beta) \in \Pi$. Then there exists $\epsilon_2 > 0$ such that for all $0 < \epsilon < \epsilon_2$, the traveling pulse solution from Theorem 3.1 is spectrally stable with a simple zero eigenvalue at $\lambda = 0$ due to translational invariance of the pulse.*

We note that the linear stability of the traveling pulse solution follows directly from a spectral mapping theorem [31] for the strongly continuous semigroup generated by the linear operator in (4.1). In addition, we can use standard center-manifold theory of Bates & Jones [1] and the results for neural field equations of Sandstede [35] to show that the traveling pulse is nonlinearly stable as well. Indeed, the zero eigenvalue found in Theorem 4.1 is isolated.

4.1 Essential spectrum

In this section, we will denote the traveling pulse solution to (2.4) of Theorem 3.1 by $(U_\epsilon(\xi), Q_\epsilon(\xi))$. Linearizing equation (2.4) at the pulse leads to the system of equations

$$\begin{aligned} \frac{\partial u(\xi, t)}{\partial t} &= -c \frac{\partial u(\xi, t)}{\partial \xi} - u(\xi, t) + \int_{\mathbb{R}} J(\xi - \xi') S(U_\epsilon(\xi')) q(\xi', t) d\xi' + \int_{\mathbb{R}} J(\xi - \xi') Q_\epsilon(\xi') S'(U_\epsilon(\xi')) u(\xi', t) d\xi' \\ \frac{\partial q(\xi, t)}{\partial t} &= -c \frac{\partial q(\xi, t)}{\partial \xi} - \epsilon \beta Q_\epsilon(\xi) S'(U_\epsilon(\xi)) u(\xi, t) - \epsilon (1 + \beta S(U_\epsilon(\xi))) q(\xi, t). \end{aligned} \quad (4.1)$$

The associated eigenvalue problem, when written as a first order system, is given by

$$\begin{aligned} u_\xi &= \frac{1}{c} (-(1 + \sigma)u + v) \\ v_\xi &= w \\ w_\xi &= b^2 (v - qS(U_\epsilon) - Q_\epsilon S'(U_\epsilon)u) \\ q_\xi &= -\frac{\epsilon\beta}{c} Q_\epsilon S'(U_\epsilon)u - \frac{1}{c} (\sigma + \epsilon + \epsilon\beta S(U_\epsilon)) q. \end{aligned} \quad (4.2)$$

Here, we have set $v(\xi) = \int_{\mathbb{R}} J(\xi - \xi') S(U_\epsilon(\xi')) q(\xi', t) d\xi' + \int_{\mathbb{R}} J(\xi - \xi') Q_\epsilon(\xi') S'(U_\epsilon(\xi')) u(\xi', t) d\xi'$. We can write this eigenvalue problem using matrix notation

$$\frac{d}{d\xi} \begin{pmatrix} u \\ v \\ w \\ q \end{pmatrix} = \mathcal{A}(\xi, \sigma) \begin{pmatrix} u \\ v \\ w \\ q \end{pmatrix} \quad (4.3)$$

where

$$\mathcal{A}(\xi, \sigma) = \begin{pmatrix} -\frac{1 + \sigma}{c} & \frac{1}{c} & 0 & 0 \\ 0 & 0 & 1 & 0 \\ -b^2 Q_\epsilon S'(U_\epsilon) & b^2 & 0 & -b^2 S(U_\epsilon) \\ -\frac{\epsilon\beta}{c} Q_\epsilon S'(U_\epsilon) & 0 & 0 & -\frac{1}{c} (\sigma + \epsilon + \epsilon\beta S(U_\epsilon)) \end{pmatrix} \quad (4.4)$$

and the ξ dependence is through the traveling pulse $(U_\epsilon, Q_\epsilon) = (U_\epsilon(\xi), Q_\epsilon(\xi))$.

The location of the essential spectrum is determined by the asymptotic limits of the matrix \mathcal{A} , defined in (4.4), as $\xi \rightarrow \pm\infty$:

$$\mathcal{A}^\infty(\sigma) = \lim_{\xi \rightarrow \pm\infty} \mathcal{A}(\xi, \sigma) = \begin{pmatrix} -\frac{1+\sigma}{c} & \frac{1}{c} & 0 & 0 \\ 0 & 0 & 1 & 0 \\ -b^2 q_0 S'(u_0) & b^2 & 0 & -b^2 S(u_0) \\ -\frac{\epsilon\beta}{c} q_0 S'(u_0) & 0 & 0 & -\frac{1}{c} (\sigma + \epsilon + \epsilon\beta S(u_0)) \end{pmatrix}.$$

The boundary of the essential spectrum is given by all values of σ for which this matrix has purely imaginary eigenvalues. This set is given by

$$\mathcal{S} = \{\sigma \in \mathbb{C} \mid \det [i\nu I - \mathcal{A}^\infty(\sigma)] = 0 \text{ for some } \nu \in \mathbb{R}\}.$$

Proposition 4.1. *The set \mathcal{S} is the union of two curves \mathcal{S}_{-1} and \mathcal{S}_0 in the complex plane with the following properties:*

1. $\mathcal{S}_{-1} = \{\sigma = \omega_1 + i\omega_2 \in \mathbb{C} \mid \omega_1 = F_-(\omega_2^2)\} \subset \{\sigma \in \mathbb{C} \mid -1 < \Re(\sigma) \leq -1 + q_0 S'(u_0)\}$,
2. \mathcal{S}_{-1} is asymptotic to the line $\Re(\sigma) = -1$ as $\Im(\sigma) \rightarrow \pm\infty$,
3. $\mathcal{S}_0 = \{\sigma = \omega_1 + i\omega_2 \in \mathbb{C} \mid \omega_1 = F_+(\omega_2^2)\} \subset \{\sigma \in \mathbb{C} \mid \Re(\sigma) \leq -\epsilon(1 + \beta S(u_0))\}$,
4. \mathcal{S}_0 is $\mathcal{O}(\epsilon)$ -close to the imaginary axis,
5. the functions F_\pm are given through the formula (4.6) in the proof below.

For typical parameters values, the two curves \mathcal{S}_{-1} and \mathcal{S}_0 are shown in Figure 9.

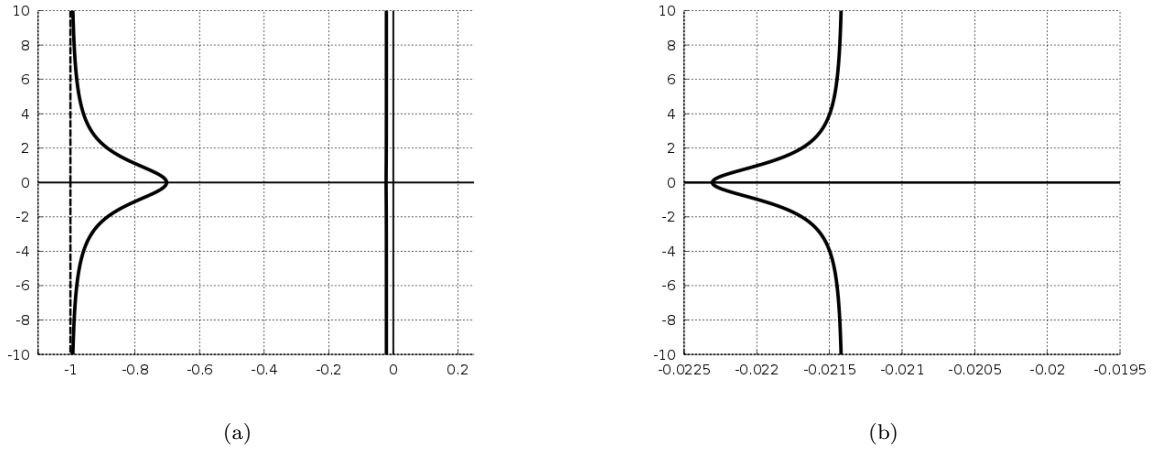


Figure 9: (Left) Plot of the two curves \mathcal{S}_{-1} and \mathcal{S}_0 for values of the parameters: $\lambda = 20$, $\kappa = 0.22$, $b = 4.5$, $\beta = 5$ and $\epsilon = 0.02$. (Right) Zoom on the curve \mathcal{S}_0 close to the imaginary axis.

Proof. Let $\sigma = \omega_1 + i\omega_2$ be a point in the complex plane. The equation $\det [i\nu I - \mathcal{A}^\infty(\sigma)] = 0$ can formally be written as follows:

$$F_r(\nu, \omega_1, \omega_2) + iF_i(\nu, \omega_1, \omega_2) = 0,$$

leading to two equations, with real coefficients,

$$\begin{aligned} F_r(\nu, \omega_1, \omega_2) &= 0 \\ F_i(\nu, \omega_1, \omega_2) &= 0. \end{aligned} \tag{4.5}$$

F_i is given through the formula:

$$F_i(\nu, \omega_1, \omega_2) = \left(\nu + \frac{\omega_2}{c} \right) (-2\nu^2\omega_1 - \nu^2 - \nu^2\epsilon\beta S(u_0) - \epsilon\nu^2 - b^2\epsilon\beta S(u_0) - b^2 + b^2q_0S'(u_0) - 2b^2\omega_1 - b^2\epsilon).$$

Substituting $\nu = -\omega_2/c$ in the first equation of the above system gives an implicit equation of the form:

$$F_r \left(-\frac{\omega_2}{c}, \omega_1, \omega_2 \right) = 0.$$

This equation can be written as a quadratic polynomial in ω_1

$$A(\omega_2^2) \omega_1^2 + B(\omega_2^2) \omega_1 + C(\omega_2^2) = 0$$

where

$$\begin{aligned} A(x) &= x + c^2b^2 \\ B(x) &= x + c^2b^2(1 - q_0S'(u_0)) + \epsilon(1 + \beta S(u_0))(1 + x) \\ C(x) &= \epsilon [c^2b^2(1 - q_0S'(u_0) + \beta S(u_0)) + (1 + \beta S(u_0))x]. \end{aligned}$$

We define the functions F_{\pm} as follows:

$$F_{\pm}(x) = \frac{-B(x) \pm \sqrt{B(x)^2 - 4A(x)C(x)}}{2A(x)}. \quad (4.6)$$

Note that $B(x)^2 - 4A(x)C(x) = (x + c^2b^2(1 - q_0S'(u_0)))^2 + \mathcal{O}(\epsilon)$ such that, for small enough ϵ , F_{\pm} are well defined for all $x \geq 0$. This implies the following asymptotic expansions in ϵ

$$F_-(x) = -1 + \frac{c^2b^2q_0S'(u_0)}{x + c^2b^2} + \mathcal{O}(\epsilon) \text{ and } F_+(x) = \mathcal{O}(\epsilon).$$

We deduce from the expansion of F_- that $-1 < F_-(x)$ for all $x \geq 0$, provided that ϵ is small enough. As $1 - q_0S'(u_0) > 0$, we have that $B(x) > 0$ and $C(x)$ for all $x \geq 0$, such that $F_+(x) < 0$. Straightforward computations show that

$$\lim_{x \rightarrow +\infty} F_-(x) = -1, \quad F_-(x) \leq F_-(0) \leq -1 + q_0S'(u_0) \text{ and } F_+(x) \leq \lim_{x \rightarrow +\infty} F_+(x) = -\epsilon(1 + \beta S(u_0)).$$

To complete the proof, we need to show that there does not exist any other solutions of system (4.5). From the expression of F_i , we have that other potential solutions should verify the equation:

$$-2\nu^2\omega_1 - \nu^2 - \nu^2\epsilon\beta S(u_0) - \epsilon\nu^2 - b^2\epsilon\beta S(u_0) - b^2 + b^2q_0S'(u_0) - 2b^2\omega_1 - b^2 = 0.$$

This can be written in a more convenient form as

$$\nu^2 = -b^2 \frac{1 + 2\omega_1 + \epsilon(1 + \beta S(u_0)) - q_0S'(u_0)}{1 + 2\omega_1 + \epsilon(1 + \beta S(u_0))} \stackrel{\text{def}}{=} D(\omega_1).$$

This equation gives two curves in the (ν, ω_1) -plane parametrized by:

$$\mathcal{F}_{\pm} = \left\{ (\nu, \omega_1) \in \mathbb{R}^2 \mid \nu = \pm \sqrt{D(\omega_1)} \text{ for } \frac{-1 - \epsilon(1 + \beta S(u_0))}{2} < \omega_1 \leq \frac{q_0S'(u_0) - 1 - \epsilon(1 + \beta S(u_0))}{2} \right\}.$$

Plugging back $\nu = \pm \sqrt{D(\omega_1)}$ into the first equation of system (4.5), one finally needs to solve:

$$\begin{aligned} F_r \left(\pm \sqrt{D(\omega_1)}, \omega_1, \omega_2 \right) &= 0 \\ \frac{-1 - \epsilon(1 + \beta S(u_0))}{2} < \omega_1 &\leq \frac{q_0S'(u_0) - 1 - \epsilon(1 + \beta S(u_0))}{2}. \end{aligned}$$

We only prove that $F_r \left(\sqrt{D(\omega_1)}, \omega_1, \omega_2 \right) = 0$ does have any real solutions (ω_1, ω_2) (the same analysis applies for $F_r \left(-\sqrt{D(\omega_1)}, \omega_1, \omega_2 \right) = 0$). This equation can be written as a quadratic polynomial in ω_2 with coefficients as functions of ω_1 of the form

$$F_r \left(\sqrt{D(\omega_1)}, \omega_1, \omega_2 \right) = \delta_1(\omega_1)\omega_2^2 + \delta_2(\omega_1)\omega_2 + \delta_3(\omega_1)$$

where δ_1, δ_2 and δ_3 satisfy the relation

$$\delta_2^2(\omega_1) - 4\delta_1(\omega_1)\delta_3(\omega_1) = -4(\epsilon^2\beta S(u_0) - \epsilon\beta S(u_0) + \epsilon^2 + 2\omega_1\epsilon + \omega_1^2)(\epsilon\beta S(u_0) + 2\omega_1 + \epsilon)^2.$$

For $\frac{-1-\epsilon(1+\beta S(u_0))}{2} < \omega_1 \leq \frac{q_0 S'(u_0) - 1 - \epsilon(1+\beta S(u_0))}{2}$, the above expression is negative. This ensures that $F_r(\sqrt{D(\omega_1)}, \omega_1, \omega_2)$ does not have any real solutions ω_2 . This completes the proof of the proposition. \square

We know that the essential spectrum lies to the left of the above boundary, that is:

$$\Sigma_{ess} \subset \{\sigma \in \mathbb{C} \mid \Re(\sigma) \leq -\epsilon(1 + \beta S(u_0))\}.$$

In the limit $\epsilon \rightarrow 0$, the essential spectrum will approach the imaginary axis. We define $\Omega(\epsilon)$ the open region in the complex plane that lies to the right of the essential spectrum, containing the right half plane.

4.2 Evans function

For $\sigma \in \Omega(\epsilon)$, $\mathcal{A}^\infty(\sigma)$ has only one eigenvalue of positive real part. This is easy to check this for $\epsilon = 0$. Indeed, eigenvalues of $\mathcal{A}^\infty(\sigma)$, with $\epsilon = 0$, are solutions of

$$\left(\frac{\sigma}{c} + X\right) \left(X^3 + \frac{1+\sigma}{c}X^2 - b^2X - \frac{b^2}{c}(1 - q_0 S'(u_0) + \sigma)\right) = 0.$$

For all real positive $\sigma = \omega_1 \in \mathbb{R}^+$, it is clear that the above equation has only one positive real eigenvalue as $-\frac{b^2}{c}(1 - q_0 S'(u_0) + \sigma) < 0$. Let $\omega_1 \geq 0$ be fixed, and let $\sigma = \omega_1 + i\omega_2$ with now $\omega_2 \in \mathbb{R}$. Then, a direct numerical computation with values of the parameters in the set Π of Definition 3.1 shows that the above equation has only one eigenvalue with positive real part. It therefore follows that for $\epsilon > 0$ and $\sigma \in \Omega(\epsilon)$, $\mathcal{A}^\infty(\sigma)$ has only one eigenvalue of positive real part. We denote $\nu^+(\sigma)$ the corresponding eigenvector. One can also check that there exists a constant ρ , independent of ϵ , such that, $\nu^+(\sigma)$ remains the unique eigenvalue with largest real part for all ϵ sufficiently small and $\bar{\Omega} = \{\sigma \in \mathbb{C} \mid -\rho < \Re(\sigma)\}$. The eigenvector associated to $\nu^+(\sigma)$ can be written

$$X^+(\sigma) = \left(1, 1 + \sigma + \nu^+(\sigma), \nu^+(\sigma)(1 + \sigma + \nu^+(\sigma)), -\frac{\epsilon\beta q_0 S'(u_0)}{\sigma + \epsilon + \epsilon S(u_0) + c\nu^+(\sigma)}\right).$$

As a result, there exists a unique solution $\zeta(\xi, \sigma)$ to (4.3) that satisfies:

$$\lim_{\xi \rightarrow -\infty} \zeta(\xi, \sigma) e^{-\nu^+(\sigma)\xi} = X^+(\sigma). \quad (4.7)$$

We can consider the adjoint problem

$$\frac{d}{d\xi} \begin{pmatrix} u \\ v \\ w \\ q \end{pmatrix} = -\bar{\mathcal{A}}(\xi, \sigma)^T \begin{pmatrix} u \\ v \\ w \\ q \end{pmatrix}. \quad (4.8)$$

Similarly, for $\sigma \in \bar{\Omega}$, there exists a unique eigenvalue of the associated asymptotic matrix with smallest real part. This eigenvalue is given by $\mu^-(\sigma) = -\bar{\nu}^+(\sigma)$ and we denote $Y^-(\sigma)$ its associated eigenvector. Then there exists a unique solution to (4.8), $\eta(\xi, \sigma)$, such that

$$\lim_{\xi \rightarrow +\infty} \eta(\xi, \sigma) e^{-\mu^-(\sigma)\xi} = Y^-(\sigma). \quad (4.9)$$

The Evans function is then defined by

$$\mathcal{E}(\sigma) = \langle \zeta(\xi, \sigma), \eta(\xi, \sigma) \rangle_{\mathbb{C}^4}. \quad (4.10)$$

Here $\langle \cdot, \cdot \rangle_{\mathbb{C}^4}$ stands for the Hermitian scalar product of \mathbb{C}^4 . One checks easily that $\mathcal{E}(\sigma)$ is independent of ξ :

$$\begin{aligned} \frac{d}{d\xi} \mathcal{E}(\sigma) &= \left\langle \frac{d}{d\xi} \zeta(\xi, \sigma), \eta(\xi, \sigma) \right\rangle_{\mathbb{C}^4} + \left\langle \zeta(\xi, \sigma), \frac{d}{d\xi} \eta(\xi, \sigma) \right\rangle_{\mathbb{C}^4} \\ &= \langle \mathcal{A}(\xi, \sigma) \zeta(\xi, \sigma), \eta(\xi, \sigma) \rangle_{\mathbb{C}^4} - \langle \zeta(\xi, \sigma), \bar{\mathcal{A}}(\xi, \sigma)^T \eta(\xi, \sigma) \rangle_{\mathbb{C}^4} \\ &= 0 \end{aligned}$$

Following [23], $\zeta(\xi, \sigma)$ and $\eta(\xi, \sigma)$ can be shown to be \mathbb{C}^4 -valued analytic function of $\sigma \in \bar{\Omega}$ for each fixed ξ , and thus $\mathcal{E}(\sigma)$ is an analytic function on $\bar{\Omega}$.

4.3 Proof of Theorem 4.1

In this section, we complete the proof of Theorem 4.1. We will show that the only zero of $\mathcal{E}(\sigma)$ with $\Re(\sigma) \geq 0$ is $\sigma = 0$, and that its geometric and algebraic multiplicity is one. The argument will closely follow the one presented in [2] which is an extension of the primary argument exposed in [23]. We collect only the relevant results and do not repeat all the proofs here.

4.3.1 Reduced Evans function along the front

We first consider the reduced Evans functions for the fast equation along the front and back of the pulse. The reduced fast equation that governs the dynamics of the front is given to leading order by

$$\frac{\partial u(\xi, t)}{\partial t} = -c \frac{\partial u(\xi, t)}{\partial \xi} - u(\xi, t) + q_0 \int_{\mathbb{R}} J(\xi - \xi') S(u(\xi', t)) d\xi'. \quad (4.11)$$

The corresponding traveling wave equation is

$$\begin{aligned} u_\xi &= \frac{1}{c} (-u + v) \\ v_\xi &= w \\ w_\xi &= b^2 (v - q_0 S(u)). \end{aligned} \quad (4.12)$$

As mentioned in 3.1.2, there exists c_* so that (4.12) possesses a solution $(u_f(\xi), v_f(\xi), w_f(\xi))$ so that

$$\lim_{\xi \rightarrow -\infty} (u_f(\xi), v_f(\xi), w_f(\xi)) = (u_0, u_0, 0) \text{ and } \lim_{\xi \rightarrow -\infty} (u_f(\xi), v_f(\xi), w_f(\xi)) = (u_+, u_+, 0).$$

Linearize (4.11) about this wave:

$$\mathcal{L}_f [u(\xi, t)] = -c \frac{\partial u(\xi, t)}{\partial \xi} - u(\xi, t) + q_0 \int_{\mathbb{R}} J(\xi - \xi') S'(u_f(\xi')) u(\xi', t) d\xi'. \quad (4.13)$$

The associated eigenvalue problem $(\mathcal{L}_f - \sigma I)u = 0$ can be written as a system

$$\frac{d}{d\xi} \begin{pmatrix} u \\ v \\ w \end{pmatrix} = \mathcal{A}_f(\xi, \sigma) \begin{pmatrix} u \\ v \\ w \end{pmatrix} \quad (4.14)$$

where

$$\mathcal{A}_f(\xi, \sigma) = \begin{pmatrix} -\frac{1+\sigma}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2 q_0 S'(u_f) & b^2 & 0 \end{pmatrix} \quad (4.15)$$

and the ξ dependence is through the traveling front $(u_f(\xi), v_f(\xi), w_f(\xi))$. This has an asymptotic system at $\pm\infty$ given by the matrices:

$$\mathcal{A}_f^{-, \infty}(\sigma) = \begin{pmatrix} -\frac{1+\sigma}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2 q_0 S'(u_0) & b^2 & 0 \end{pmatrix} \text{ and } \mathcal{A}_f^{+, \infty}(\sigma) = \begin{pmatrix} -\frac{1+\sigma}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2 q_0 S'(u_+) & b^2 & 0 \end{pmatrix}. \quad (4.16)$$

We set $\mathcal{S}^\pm = \left\{ \sigma \in \mathbb{C} \mid \det \left[i\nu I - \mathcal{A}_f^{\pm, \infty}(\sigma) \right] = 0 \text{ for some } \nu \in \mathbb{R} \right\}$. We denote G_f the component of $\mathbb{C} \setminus \mathcal{S}^- \cup \mathcal{S}^+$ containing the right half-plane. Then if we denote the spectrum of \mathcal{L}_f $\Sigma(\mathcal{L}_f)$, we have $\Sigma(\mathcal{L}_f) \cap G_f \subset \Sigma_p(\mathcal{L}_f)$ (here $\Sigma_p(\mathcal{L}_f)$ denotes the point spectrum). $\mathcal{A}_f^{-, \infty}(\sigma)$ has only one eigenvalue with positive real part that we denote $\sigma_f^+(\sigma)$ with associated eigenvector

$$X_f^+(\sigma) = \left(1, 1 + \sigma + \nu_f^+(\sigma), \nu_f^+(\sigma)(1 + \sigma + \nu_f^+(\sigma)) \right).$$

As a result, there exists a unique solution $\zeta_f(\xi, \sigma)$ to (4.14), analytic in $\sigma \in G_f$ that satisfies:

$$\lim_{\xi \rightarrow -\infty} \zeta_f(\xi, \sigma) e^{-\nu_f^+(\sigma)\xi} = X_f^+(\sigma). \quad (4.17)$$

We can consider the adjoint problem

$$\frac{d}{d\xi} \begin{pmatrix} u \\ v \\ w \end{pmatrix} = -\bar{\mathcal{A}}_f(\xi, \sigma)^T \begin{pmatrix} u \\ v \\ w \end{pmatrix}. \quad (4.18)$$

Similarly, for $\sigma \in G_f$, there exists a unique eigenvalue of the associated asymptotic matrix with smallest real part. This eigenvalue is given by $\mu_f^-(\sigma) = -\bar{\nu}_f^+(\sigma)$ and we denote $Y_f^-(\sigma)$ its associated eigenvector. Then there exists a unique solution to (4.18), $\eta_f(\xi, \sigma)$, such that

$$\lim_{\xi \rightarrow +\infty} \eta_f(\xi, \sigma) e^{-\mu_f^-(\sigma)\xi} = Y_f^-(\sigma). \quad (4.19)$$

The Evans function is then defined by

$$\mathcal{E}_f(\sigma) = \langle \zeta_f(\xi, \sigma), \eta_f(\xi, \sigma) \rangle_{\mathbb{C}^3} \quad (4.20)$$

and it has domain G_f .

The stability of the traveling wave is well understood. De Masi *et al* [14] and Chen [7] have separately shown that the front is globally stable modulo translations. This result translates into properties for $\mathcal{E}_f(\sigma)$ that are stated in the following proposition.

Proposition 4.2. *Let $\mathcal{E}_f(\sigma)$ denote the reduced Evans function that one obtains from the stability analysis of the heteroclinic front of (4.11). Then \mathcal{E}_f is analytic in $\bar{\Omega}$ and*

1. $\mathcal{E}_f(0) = 0$,
2. $\mathcal{E}_f(\sigma) \neq 0$ for all $\sigma \in \bar{\Omega} \setminus \{0\}$,
3. $\frac{d}{d\sigma} \mathcal{E}_f(\sigma)|_{\sigma=0} \neq 0$.

The first point of the proposition follows from the standard feature of translation of waves, the second and third point come from the stability analysis of [7, 14]. Here, it may be necessary to take ρ in the definition of $\bar{\Omega}$ to be slightly smaller than above.

4.3.2 Reduced Evans function along the back

Next, consider the reduced equation for the back:

$$\frac{\partial u(\xi, t)}{\partial t} = -c \frac{\partial u(\xi, t)}{\partial \xi} - u(\xi, t) + q_{knee} \int_{\mathbb{R}} J(\xi - \xi') S(u(\xi', t)) d\xi', \quad (4.21)$$

where $c = c_*$ is the wavespeed selected in the analysis of the front. The corresponding wave equation is

$$\begin{aligned} u_\xi &= \frac{1}{c} (-u + v) \\ v_\xi &= w \\ w_\xi &= b^2 (v - q_{knee} S(u)). \end{aligned} \quad (4.22)$$

As already seen in 3.1.3, the back solution is a heteroclinic solution between $(u_{knee}, u_{knee}, 0)$ at $-\infty$ and $(u_-, u_-, 0)$ at $+\infty$ where $u_- = s_L(q_{knee})$. It is asymptotic to a stable manifold at $+\infty$, but a center manifold at $-\infty$, where it decays only algebraically. It is an easy computation to see that the essential spectrum of the associated linearized operator is contained in the region of the left plane delimited by the curve $\mathcal{S}_b = \left\{ \sigma = \omega_1 + i\omega_2 \in \mathbb{C} \mid \omega_1 = -\frac{\omega_2^2}{\omega_2^2 + c^2 b^2} \right\}$. As this region touches the imaginary axis at the origin, the stability of the back and the construction of the associated reduced Evans function is more involved. However, this analysis has been carried out in [38] for the Fisher-type equation which can straightforwardly be extended to our type of nonlinearity. We quote their result.

Proposition 4.3. *Let $\mathcal{E}_b(\sigma)$ denote the reduced Evans function that one obtains from the stability analysis of the heteroclinic solution of (4.21). Then*

1. \mathcal{E}_b is analytic in $\bar{\Omega}$,
2. $\mathcal{E}_b(\sigma) \neq 0$ for all $\sigma \in \bar{\Omega}$.

Again, it may be necessary to take ρ in the definition of $\bar{\Omega}$ to be slightly smaller than above.

4.3.3 Approximate location of eigenvalues

In the following proposition, we recall a result from [2] where it is demonstrated that any zeros of the Evans function $\mathcal{E}(\sigma)$ in $\bar{\Omega}$ must be near a unique zero of $\mathcal{E}_f(\sigma)$ and $\mathcal{E}_b(\sigma)$ near $\sigma = 0$.

Proposition 4.4. *$\mathcal{E}(\sigma) \neq 0$ for all $\sigma \in G = \bar{\Omega} \setminus \mathcal{B}_\delta$, where \mathcal{B}_δ denotes the ball of radius δ centered at 0 in the complex plane with $\delta > 0$ such that $\mathcal{B}_\delta \subset \bar{\Omega}$.*

Proof. The proof of the proposition relies essentially on the fact that it is possible to track $\zeta(\xi, \sigma)$ around the pulse until ξ is large enough and then show that it cannot be orthogonal to $\eta(\xi, \sigma)$. This proof was originally presented in [23] for the FitzHugh-Nagumo pulse and then adapted in [2] in the presence of a knee. Here we will only sketch the proof and we refer to [2, 23] for more details.

In order to track $\zeta(\xi, \sigma)$ around the pulse, we couple the traveling wave system (2.8) with the eigenvalue system (4.2) and follow the combined solution $(Z(\xi), z(\xi)) \stackrel{def}{=} (U(\xi), V(\xi), W(\xi), Q(\xi), u(\xi), v(\xi), w(\xi), q(\xi)) \in \mathbb{R}^4 \times \mathbb{C}^4$ of

$$\begin{aligned}
U_\xi &= \frac{1}{c}(-U + V) \\
V_\xi &= W \\
W_\xi &= b^2(V - QS(U)) \\
Q_\xi &= \frac{\epsilon}{c}(1 - Q - \beta QS(U)) \\
u_\xi &= \frac{1}{c}(-(1 + \sigma)u + v) \\
v_\xi &= w \\
w_\xi &= b^2(v - qS(U) - QS'(U)u) \\
q_\xi &= -\frac{\epsilon\beta}{c}QS'(U)u - \frac{1}{c}(\sigma + \epsilon + \epsilon\beta S(U))q.
\end{aligned} \tag{4.23}$$

The natural setting for (4.23) is the complexified tangent bundle to \mathbb{R}^4 , denoted $T\mathbb{R}^4$. Since (4.23) is linear in $z = (u, v, w, q) \in \mathbb{C}^4$, the induced flow can be projectivized in the second component. We define $(y_1, y_2, y_3) := \pi(u, v, w, q) = \left(\frac{v}{u}, \frac{w}{u}, \frac{q}{u}\right)$. Thus, $\pi : \{(u, v, w, q) \in \mathbb{C}^4 : u \neq 0\} \rightarrow \mathbb{CP}^3$. The evolution of (y_1, y_2, y_3) is governed by

$$\begin{aligned}
\frac{d}{d\xi}y_1 &= y_2 + \frac{1 + \sigma}{c}y_1 - \frac{1}{c}y_1^2 \\
\frac{d}{d\xi}y_2 &= b^2(y_1 - S(U)y_3 - QS'(U)) + \frac{1 + \sigma}{c}y_2 - \frac{1}{c}y_1y_2 \\
\frac{d}{d\xi}y_3 &= -\frac{\epsilon\beta}{c}QS'(U) - \frac{1}{c}(-1 + \epsilon + \epsilon\beta S(U))y_3 - \frac{1}{c}y_1y_3.
\end{aligned} \tag{4.24}$$

Using a scaling argument, we need only to consider a bounded region $\hat{G} = \{\sigma \in G \mid |\sigma| < M\}$ within G , for some fixed M independent of ϵ . For $\sigma \in \hat{G}$, we denote respectively $\hat{\zeta}$ and $\hat{\eta}$ the projectivized version of ζ and η . Similarly, we can construct the projectivized version of the reduced equation (4.12) and define $\hat{\zeta}_f$. For $\sigma \in \hat{G}$, we know that the reduced system (4.12) does not have an eigenvalue and thus, when the pulse enters a neighborhood of the invariant slow manifold, to leading order, $\hat{\zeta} = (\hat{\zeta}_f, 0)$ will be equal to the direction of the unstable fiber of the manifold. Along the slow manifold, $\hat{\zeta}$ will remain close to the direction of the unstable fibers until it enters a neighborhood of the knee. Based on the analysis conducted in [38], for $\sigma \in \hat{G}$, in the neighborhood of the knee, $\hat{\eta}$ is still attracted to the direction of its corresponding eigenvector. When it emerges from a neighborhood of the knee, $\hat{\zeta}$ is \mathcal{C}^1 $\mathcal{O}(\epsilon)$ -close to the strong unstable direction. The evolution of $\hat{\zeta}$ along the back is similar to that of the front. As the linearization around the back does not have an eigenvalue in \hat{G} , $\hat{\zeta}$ must be still $\mathcal{O}(\epsilon)$ -close to the unstable fibers as the pulse enters a neighborhood of the slow invariant manifold. Thus, $\hat{\zeta}$ can be followed along the slow manifold \mathcal{M}_L and we can conclude that it is not orthogonal to $\hat{\eta}$ when it enters a neighborhood of the fixed point $(u_0, u_0, 0, q_0)$. This proves that ζ and η are not orthogonal as well. \square

4.3.4 Winding number computation

From Proposition 4.3, any potential unstable eigenvalues must lie in \mathcal{B}_δ . Here, we choose δ small enough such that zero is the only eigenvalue of either reduced systems along the front or the back that is contained in \mathcal{B}_δ . Following [2, 23], we will compute the winding number of $\mathcal{E}(\sigma)$ along $K = \partial\mathcal{B}_\delta$ and show that it is one.

If we take an element $\hat{z} = \left(\frac{v}{u}, \frac{w}{u}, \frac{q}{u}\right) \in \mathbb{CP}^3$, then we can associate it an element in \mathbb{C}^4 using

$$\pi^{-1}(\hat{z}) = \left(1, \frac{v}{u}, \frac{w}{u}, \frac{q}{u}\right) := \tilde{z}.$$

One can easily check that for any ξ such that $u(\xi, \sigma) \neq 0$,

$$\zeta(\xi, \sigma) = u(\xi, \sigma) \left[\pi^{-1}(\hat{\zeta}) \right] (\xi, \sigma) = u(\xi, \sigma) \tilde{\zeta}(\xi, \sigma).$$

Here and in the following of the sequel, $u(\xi, \sigma)$ always stands for the first component of the eigenvector $\zeta(\xi, \sigma)$ defined in (4.7). As the Evans function is independent of ξ , we can evaluate it at any value of ξ that we choose. Hence, we pick $T_4 > 0$, a sufficiently large value of ξ , such that

$$\Re \left(\left\langle \tilde{\zeta}(T_4, \sigma), \tilde{\eta}(T_4, \sigma) \right\rangle_{\mathbb{C}^4} \right) > 0,$$

for all $\sigma \in K$. The proof of this fact follows closely that in [23], and so we do not repeat here. As T_4 is large enough, from the definition of $\eta(\xi, \sigma)$ in (4.9), we also have

$$e^{\nu^+(\sigma)T_4} \eta(T_4, \sigma) = \tilde{\eta}(T_4, \sigma) + \epsilon(T_4, \sigma)$$

where $|\epsilon(T_4, \sigma)| \rightarrow 0$ as $T_4 \rightarrow +\infty$, uniformly for $\sigma \in K$. As $\mathcal{E}(\sigma)$ is independent of ξ , we have

$$\mathcal{E}(\sigma) = u(T_4, K) e^{-\nu^+(\sigma)T_4} \left(\left\langle \tilde{\zeta}(T_4, \sigma), \tilde{\eta}(T_4, \sigma) \right\rangle_{\mathbb{C}^4} + \left\langle \tilde{\zeta}(T_4, \sigma), \epsilon(T_4, \sigma) \right\rangle_{\mathbb{C}^4} \right),$$

and thus

$$\begin{aligned} W(\mathcal{E}(\sigma)) &= W(u(T_4, \sigma)) + W \left(e^{-\nu^+(\sigma)T_4} \right) + W \left(\left\langle \tilde{\zeta}(T_4, \sigma), \tilde{\eta}(T_4, \sigma) \right\rangle_{\mathbb{C}^4} + \left\langle \tilde{\zeta}(T_4, \sigma), \epsilon(T_4, \sigma) \right\rangle_{\mathbb{C}^4} \right) \\ &= W(u(T_4, \sigma)) + 0 + 0 \\ &= W(u(T_4, \sigma)), \end{aligned}$$

for all $\sigma \in K$ where W denotes the winding number. Here we have used the fact that δ is small enough so that $\nu^+(\sigma)$ is approximated by $\nu^+(0)$ for all $\sigma \in K$, thus $W \left(e^{-\nu^+(K)T_4} \right) = 0$. We then have that $W(\mathcal{E}(K)) = W(u(T_4, K))$. It now remains to track the evolution of $u(\xi, \sigma)$ around the underlying pulse for $\sigma \in K$ and to evaluate the corresponding winding number at well chosen times T_i . Thus, we introduce the following intermediary values of ξ :

- T_0 is the value for which the traveling pulse exits a neighborhood of $(u_0, u_0, 0, q_0)$,
- T_1 is the value at which it enters a neighborhood of $(u_+, u_+, 0, q_0)$,
- T_2 is the value at which it exists a neighborhood of the knee $(u_{knee}, u_{knee}, 0, q_{knee})$,
- T_3 is the value at which it enters a neighborhood of $(u_-, u_-, 0, q_{knee})$.

We shall prove that as $u(\xi, \sigma)$ moves along the pulse, the corresponding winding number increases by one as it moves along the front and it remains constant along the rest of the wave.

Proposition 4.5. 1. $W(u(T_0, K)) = 0$,

2. $W(u(T_1, K)) = 1$,

3. $W(u(T_2, K)) = 1$,

4. $W(u(T_3, K)) = 1$,

5. $W(u(T_4, K)) = 1$.

Proof. Similar computations of winding numbers have been conducted in [2, 23] so that we only sketch the proof. Because of the presence of the knee, the main difficulty will be to check that $W(u(T_2, K)) = 1$.

1. $W(u(T_0, K)) = 0$. From its definition we have

$$e^{-\nu^+(\sigma)\xi}\zeta(\xi, \sigma) = X^+ + \epsilon_0(\xi, \sigma)$$

with $|\epsilon_0(\xi, \sigma)| \rightarrow 0$ as $\xi \rightarrow -\infty$, uniformly in $\sigma \in K$. Then, if $\xi = T_0$ is negative enough we have

$$\Re(u(T_0, \sigma)) > 0,$$

and then $W(u(T_0, K)) = 0$.

2. $W(u(T_1, K)) = 1$. Using the same kind of argument as given earlier, we can easily show that $W(\mathcal{E}_f(K)) = W(u_f(T_1, K))$, where \mathcal{E}_f is the Evans function associated to the front solution. From Proposition 4.2, we know that $\mathcal{E}_f(0) = 0$ with $\mathcal{E}_f(\sigma) \neq 0$ for all $\sigma \in K$, and $\frac{d}{d\sigma}\mathcal{E}_f(\sigma)|_{\sigma=0} \neq 0$, which gives $W(\mathcal{E}_f(K)) = 1$ and thus $W(u_f(T_1, K)) = 1$. Here u_f stands for the first component of the eigenvector $\zeta_f(\xi, \sigma)$ defined in (4.17). Following the argument of Lemma 6.2 in [23], one can show that $\left| \frac{u(T_1, \sigma)}{u(T_0, \sigma)} - \frac{u_f(T_1, \sigma)}{u_f(T_0, \sigma)} \right|$ can be made as small as desired uniformly in $\sigma \in K$ so that $\left| u(T_1, \sigma) - \frac{u_f(T_1, \sigma)}{u_f(T_0, \sigma)}u(T_0, \sigma) \right|$ can also be made small and

$$W(u(T_1, K)) = W\left(\frac{u_f(T_1, K)}{u_f(T_0, K)}\right) + W(u(T_0, K)) = 1 + 0 = 1.$$

3. $W(u(T_2, K)) = 1$. The idea is to construct a homotopy between $u(T_1, K)$ and $u(T_2, K)$ which would imply that their winding numbers are equal. The projectivized system (4.24), near the knee, to leading order in ϵ , reads

$$\begin{aligned} \frac{d}{d\xi}y_1 &= y_2 + \frac{1+\sigma}{c}y_1 - \frac{1}{c}y_1^2 \\ \frac{d}{d\xi}y_2 &= b^2(y_1 - S(u_{knee})y_3 - 1) + \frac{1+\sigma}{c}y_2 - \frac{1}{c}y_1y_2 \\ \frac{d}{d\xi}y_3 &= \frac{1}{c}y_3 - \frac{1}{c}y_1y_3. \end{aligned}$$

This system has four fixed points given by $(1, -\sigma/c, -\sigma^2/c^2b^2S(u_{knee}))$ and $(x(\sigma), -(1+\sigma)x(\sigma)/c + x(\sigma)^2/c, 0)$ where $x(\sigma)$ is solution of the cubic equation

$$X^3 - 2(1+\sigma)X^2 - (c^2b^2 - (1+\sigma)^2)X + c^2b^2 = 0.$$

This equation has three solutions that we denote $x_1(\sigma)$, $x_2(\sigma)$ and $x_3(\sigma)$ with $\Re(x_1(\sigma)) < 0$, $\Re(x_2(\sigma)) > 0$ and $\Re(x_3(\sigma)) > 0$. As $\sigma \rightarrow 0$, the above equation reduces to

$$X^3 - 2X^2 - (c^2b^2 - 1)X + c^2b^2 = 0,$$

and the corresponding solutions are $x_1(0) = \frac{1 - \sqrt{1 + 4c^2b^2}}{2}$, $x_2(0) = \frac{1 + \sqrt{1 + 4c^2b^2}}{2}$ and $x_3(0) = 0$. Thus, $(1, -\sigma/c, -\sigma^2/c^2b^2S(u_{knee}))$ coincides with $(x_3(\sigma), -(1 + \sigma)x_3(\sigma)/c + x_3(\sigma)^2/c, 0)$ in the limit $\sigma \rightarrow 0$, while the other fixed points remain separate, uniformly in σ . The direction along x_2 defines the attractor that $\hat{\zeta}$ follows as it moves along the wave. Since fast unstable directions always point along vector with nonzero u component, this shows that $u(\xi) \neq 0$ for all $\xi \in [T_1, T_2]$, uniformly for σ near zero. Then $W(u(T_2, K)) = W(u(T_1, K)) = 1$.

4. $W(u(T_3, K)) = 1$. We now use the information collected for the back solution. Once again, using similar argument as already given earlier, we can easily show that $W(\mathcal{E}_b(K)) = W(u_b(T_3, K))$, where \mathcal{E}_b is the Evans function associated to the front solution. Here u_b stands for the first component of the eigenvector $\zeta_b(\xi, \sigma)$. From Proposition 4.3, we know that $\mathcal{E}_b \neq 0$ for all $\sigma \in K$, which gives $W(\mathcal{E}_b(K)) = 0$ and thus $W(u_b(T_3, K)) = 0$. Using the same argument as in 2., we have

$$W(u(T_3, K)) = W\left(\frac{u_b(T_3, K)}{u_b(T_2, K)}\right) + W(u(T_2, K)) = 0 + 1 = 1.$$

5. $W(u(T_4, K)) = 1$. As $u(\xi, \sigma) \neq 0$ for all $\sigma \in K$ and $T_3 \leq \xi \leq T_4$, $u(\xi, \sigma)$ defines a homotopy from $u(T_3, K)$ to $u(T_4, K)$ and therefore $W(u(T_3, K)) = W(u(T_4, K)) = 1$.

□

4.3.5 Conclusion of the proof of Theorem 4.1

We can now conclude the proof of Theorem 4.1.

Proof. [of Theorem 4.1] As $W(\mathcal{E}(K)) = W(u(T_4, K)) = 1$, this proves that there is only one zero of the Evans function in $\bar{\Omega}$, since we know there exists a zero at the origin due to the translations, it must be the only one. □

5 Discussion

In this paper, we have shown the existence of traveling pulse solutions for a neural field model with synaptic depression and smooth firing rate function. We have first constructed a singular traveling solution for $\epsilon = 0$ and then proved that this singular solution persists for small positive value of ϵ . Contrary to neural field models with linear adaptation [32], the jump back from the right slow manifold to the left slow manifold must occur at the knee of the right slow manifold for models with synaptic depression and for typical values of parameters. This implies that one needs to use a blow-up technique in order to follow the solution near this non normally hyperbolic point. As a consequence, the decay along the back of the constructed traveling pulse is only algebraic. Note also that our existence proof does not rely on an explicit construction of the traveling solution as it is often the case with models with Heaviside firing rate function [26].

We have also investigated the stability of the traveling pulse solution. We have constructed an associated Evans function and studied its zero in the complex plane. More precisely, we have shown that the only zero of the Evans function in the right-half plane is zero, and its geometric and algebraic multiplicity is one. The crucial step in this analysis is to show that the knee does not produce any additional eigenvalue which can be shown through winding number computations. That part of the proof relies essentially on the results

presented in [2, 38]. Our definition of the Evans is somewhat different from the one previously used for neural field models with Heaviside firing rate function [9, 33, 35, 42–44]. In our case, the Evans function is not known through an explicit formula due to our choice of the nonlinearity. However, we can collect enough information to determine the location of its zeros.

As it has already been highlighted in other studies, synaptic depression has fundamental repercussion on the spatiotemporal dynamics of neuronal networks. For example, Kilpatrick [28] has recently shown that synaptic depression improves information transfer in perceptual multistability. In their seminal work [26], Kilpatrick & Bressloff have demonstrated that synaptic depression plays a major role, compared to adaptation, in determining the characteristics of the traveling waves. In our study, we have presented another determinant role that synaptic depression plays on the characteristic of traveling wave. Indeed, we have seen that the decay along the back of the constructed traveling pulse is only algebraic while it is exponential in the case of adaptation. We believe that this prediction could be verified experimentally and further assess the validity of the model.

In [26], Kilpatrick & Bressloff have used a Heaviside firing rate function instead of the smooth firing rate function (2.2). It is important to note that the singular perturbation analysis presented in this paper breaks down if one uses a Heaviside function as Hypothesis 2.2 is no longer satisfied. However, Kilpatrick & Bressloff have explicitly derived formula for the traveling pulse solution. Their constructive approach predicts the existence of two types of traveling pulse solutions: a fast pulse (with a wide profile) and a slow pulse (with a narrow profile). The fast traveling pulse solution, obtained with a Heaviside function, is qualitatively similar to the pulse found in our study. Indeed, in both models, the fast pulse is found to be spectrally stable. Both fast pulses have a wide profile. Note however that the Heaviside model predicts an exponential decay along the back of the pulse while our model predicts only an algebraic decay, so that there still exists a slight difference in the profile of the solution. As we have used singular perturbation theory, it is not possible to directly predict the existence of the slow pulse without doing some modifications that we now outline. In order to prove the existence of a slow pulse, one needs to rescale the wave speed c . We anticipate that the wave speed will scale as $c = \tilde{c}\epsilon^\alpha$ with $\tilde{c} = \mathcal{O}(1)$ and for some $0 < \alpha < 1$ to be determined. With this new scaling, one can use singular perturbation theory to prove the existence of a traveling pulse solution along the lines of this paper. As for the Heaviside model, we expect this slow pulse solution to be unstable. We keep this analysis for future work.

Finally, the particular choice of our connectivity function has allowed us to transform a functional differential equation of mixed type (with infinite delays in backward and forward time) into a system of four first order ordinary differential equations. It seems that the existence of a stable pulse solution is robust with respect to the choice of the connectivity function. Indeed, a simple numerical exploration shows that for Gaussian ($J(x) = e^{-x^2}/\sqrt{\pi}$) or slowly algebraically decaying ($J(x) = \frac{1}{\pi(1+x^2)}$) connectivity functions, where no simple transformation to a first order system of ordinary differential equations is possible, there still exists a traveling pulse solution. We expect that the existence of such a traveling pulse solution will hold true with the following general conditions on J :

- (i) $J : \mathbb{R} \rightarrow \mathbb{R}$ is continuous, positive and even;
- (ii) $J \in L^1(\mathbb{R})$ and $J' \in L^1(\mathbb{R})$;
- (iii) $\int_{\mathbb{R}} J(x)dx = 1$.

The assumptions (i) are natural from a biological point of view as we are modeling a purely excitatory network, the technical assumptions (ii) are necessary to prove the existence of the front solution and the properties of its linearization [7, 15]. The last assumption is only a normalization condition. Note that in the case of linear adaptation, Pinto & Ermentrout [32] have constructed the singular traveling solution for $\epsilon = 0$, but not proved that it persists for small positive value of ϵ . We think that ideas developed in [22, 30] can provide insights for proving the persistence of such waves. It will be the subject of forthcoming research.

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APPENDIX

A Proof of Lemma 2.1

Lemma A.1. *Suppose that $(\lambda, \kappa) \in (0, \infty) \times (0, 1)$ satisfy the relation*

$$2 - 2 \ln(2) \leq \lambda \kappa - \ln(\lambda).$$

We define

$$\begin{aligned} u_c(\lambda, \kappa) &= -\frac{2}{\lambda} W_{-1} \left(-\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda \kappa}{2}} \right) > 0 \\ \beta_c(\lambda, \kappa) &= \frac{1}{u_c(\lambda, \kappa)} - \frac{1}{S(u_c(\lambda, \kappa))} > 0. \end{aligned}$$

If $\beta > \beta_c(\lambda, \kappa)$ then system (2.9) has a unique solution (u_0, q_0) .

Proof. If we define $h(u) = -u + \frac{S(u)}{1 + \beta S(u)}$, then looking for solutions to the system (2.9) is equivalent to finding real roots to the equation $h(u) = 0$. Due to the boundedness of S , we have for all parameters values

$$\lim_{u \rightarrow +\infty} h(u) = -\infty.$$

As $h(0) > 0$, this ensures the existence of $u_0 > 0$ such that $h(u_0) = 0$. We want to find the critical value β_c , as a function of (λ, κ) , such that for $\beta > \beta_c$, u_0 is the only positive real root of h . In order to compute this critical value, let first solve the following system:

$$\begin{aligned} 0 &= h(u) \\ 0 &= h'(u). \end{aligned}$$

The first equation gives the relation:

$$u = \frac{1}{1 + \beta + e^{-\lambda(u-\kappa)}}$$

which can be plugged into the second equation to obtain the transcendental equation

$$1 = u^2 \lambda e^{-\lambda(u-\kappa)}. \tag{A.1}$$

This equation can be solved in terms of the Lambert function W as follows. We rewrite equation (A.1) as

$$\frac{\lambda}{4} e^{-\lambda \kappa} = \left(\frac{-\lambda u}{2} e^{-\frac{\lambda u}{2}} \right) \left(\frac{-\lambda u}{2} e^{-\frac{\lambda u}{2}} \right)$$

We introduce the intermediary variable $y = \frac{-\lambda u}{2} e^{-\frac{\lambda u}{2}}$ such that the previous equation reduces to

$$\frac{\lambda}{4} e^{-\lambda \kappa} = y^2.$$

Taking the square root, we have

$$-\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda \kappa}{2}} = \frac{-\lambda u}{2} e^{-\frac{\lambda u}{2}}. \tag{A.2}$$

If (λ, κ) satisfy the relation

$$2 - 2 \ln(2) \leq \lambda \kappa - \ln(\lambda)$$

then the following equality holds

$$-\frac{1}{e} \leq -\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda\kappa}{2}}.$$

Then for this choice of parameters, equation (A.2) is equivalent to

$$-\frac{\lambda u}{2} = W_{-1} \left(-\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda\kappa}{2}} \right)$$

which gives

$$u = -\frac{2}{\lambda} W_{-1} \left(-\frac{\sqrt{\lambda}}{2} e^{-\frac{\lambda\kappa}{2}} \right) = u_c(\lambda, \kappa).$$

From $0 = h(u_c)$ we deduce that β_c is given by

$$\beta_c(\lambda, \kappa) = \frac{1}{u_c(\lambda, \kappa)} - \frac{1}{S(u_c(\lambda, \kappa))}.$$

We can now complete our proof. For (λ, κ) such that $2 - 2 \ln(2) \leq \lambda\kappa - \ln(\lambda)$, $h'(u) < 0$ for all $u > 0$ provided that $\beta > \beta_c(\lambda, \kappa)$. This implies that u_0 is the unique positive root of h for $\beta > \beta_c(\lambda, \kappa)$. The fact that $\beta_c(\lambda, \kappa) > 0$ for all $(\lambda, \kappa) \in (0, \infty) \times (0, 1)$ that satisfy $2 - 2 \ln(2) \leq \lambda\kappa - \ln(\lambda)$ is checked numerically. \square

B Proof of Lemma 3.1

Lemma B.1. *Suppose that (λ, κ) satisfy the condition of Hypothesis 2.1, then the values (u_{knee}, q_{knee}) are*

$$\begin{aligned} u_{knee} &= \frac{1}{\lambda} [1 - W_{-1}(-e^{-\lambda\kappa+1})] \\ q_{knee} &= \frac{u_{knee}}{S(u_{knee})}. \end{aligned}$$

Proof. We look for a solution (u_c, q_c) of system (3.6). Replacing the value of q_c into the second equation gives:

$$\lambda u_c (1 - S(u_c)) = 1$$

which is equivalent to

$$(\lambda u_c - 1) e^{-\lambda(u_c - \kappa)} = 1.$$

Multiplying each side by $-e^{-\lambda\kappa+1}$, we obtain

$$(-\lambda u_c + 1) e^{-\lambda u_c + 1} = -e^{-\lambda\kappa+1}.$$

This transcendental equation can be solved using Lambert W function. Noticing that if (λ, κ) satisfy condition of Hypothesis 2.1 then automatically the following inequality is also satisfied

$$-\frac{1}{e} \leq -e^{-\lambda\kappa+1}$$

Finally, one can invert the previous equation and obtain

$$-\lambda u_c + 1 = W_{-1}(-e^{-\lambda\kappa+1}),$$

which gives the desired formula. \square

References

- [1] P. W. Bates and C. K. R. T. Jones. *Invariant manifolds for semilinear partial differential equations*. Dynamics Reported, 2, pp. 1–38, 1989.
- [2] M. Beck, C.K.R.T Jones, D. Schaeffer and M. Wechselberger. *Electrical waves in a one-dimensional model of cardiac tissue*. SIAM J. Applied Dynamical Systems, vol 7, no 4, pages 1558–1581, 2008.
- [3] A. Benucci, R. A. Frazor, and M. Carandini. *Standing waves and traveling waves distinguish two circuits in visual cortex*. Neuron, 55, pages 103–17, 2007.
- [4] J. Billingham and D.J. Needham. *A note on the properties of a family of traveling-wave solutions arising in cubic autocatalysis*. Dynamics and Stability of Systems, vol 6, no 1, pages 33–49, 1991.
- [5] J. Billingham and D.J. Needham. *The development of traveling waves in quadratic and cubic autocatalysis with unequal diffusion rates. I. Permanent form traveling waves*. Phil. Trans. R. Soc. Lond. A, vol 334, pages 1–24, 1991.
- [6] P.C. Bressloff and S.E. Folias. *Front bifurcations in an excitatory neural network*. SIAM J. Appl. Math., vol 65, no 1, pages 131–151, 2004.
- [7] X. Chen *Existence, uniqueness, and asymptotic stability of traveling waves in nonlocal evolution equations*. Advances in Differential Equations, 2, pages 125–160, 1997.
- [8] S. Coombes, G.J. Lord and M.R. Owen. *Waves and bumps in neuronal networks with axo-dendritic synaptic interactions*. Physica D: Nonlinear Phenomena, vol. 178, no. 3-4, pages 219–241, 2003.
- [9] S. Coombes and M. R. Owen. *Evans functions for integral neural field equations with heaviside firing rate function*. SIAM J Appl. Dyn. Syst., 3 , pages 574–600, 2004.
- [10] S. Coombes and M. R. Owen. *Bumps, Breathers, and Waves in a Neural Network with Spike Frequency Adaptation*. Phys. Rev. Lett., vol. 94, no. 14, 2005.
- [11] S. Coombes. *Waves, bumps, and patterns in neural fields theories*. Biological Cybernetics, vol. 93, no. 2, pages 91–108, 2005.
- [12] S Coombes, N A Venkov, L Shiau, I Bojak, D T J Liley and C R Laing. *Modeling electrocortical activity through improved local approximations of integral neural field equations*. Physical Review E, vol. 76, 051901–8, 2007.
- [13] R.M. Corless, G.H. Gonnet, D.E.G. Hare, D.J. Jeffrey and D.E. Knut. *On the Lambert W function*. Advances in Computational Mathematics, vol 5, pages 329–359, 1996.
- [14] A. De Masi, T. Gobron and E. Presutti. *Traveling fronts in non-local evolution equations*. Arch. Rat. Mech. Anal, 132, pp 143–205, 1995.
- [15] G. B. Ermentrout and J. B. McLeod. *Existence and uniqueness of travelling waves for a neural network*. Proc. Roy. Soc. Edin., 123A, pp. 461–478, 1993.
- [16] G. B. Ermentrout, S.E. Folias and Z.P. Kilpatrick. *Spatiotemporal pattern formation in neural fields with linear adaptation*. Springer, in Neural Field Theory, 2012.
- [17] S.E. Folias. *Nonlinear Analysis of Breathing Pulses in a Synaptically Coupled Neural Network*. SIAM J. Appl. Dyn. Syst, vol 10, no 2, pages 744–787, 2011.
- [18] M. Haragus and G. Iooss. *Local bifurcations, center manifolds, and normal forms in infinite dimensional systems*. EDP Sci. Springer Verlag UTX series, 2010.

- [19] M. Holzer, A. Doelman and T.J. Kaper. Existence and stability of traveling pulses in a reaction-diffusion-mechanics system. *J. Nonlinear Sci*, DOI 10.1007/s00332-012-9147-0, online first, 2012.
- [20] X. Huang, W. C. Troy, Q. Yang, H. Ma, C. R. Laing, S. J. Schiff, and J.-Y. Wu. *Spiral waves in disinhibited mammalian neocortex*. *J. Neurosci.*, 24, pages 9897–9902, 2007.
- [21] X. Huang, W. Xu, J. Liang, K. Takagaki, X. Gao and J.-Y. Wu. *Spiral wave dynamics in neocortex*. *Neuron*, 69, pages 978–990, 2010.
- [22] H.J. Hupkes and B. Sandstede. *Traveling pulse solutions for the discrete FitzHugh-Nagumo system*. *SIAM J. Applied Dynamical Systems*, vol 9, no 3, pages 827–882, 2010.
- [23] C.K.R.T Jones. *Stability of the traveling wave solution of the Fitzhugh-Nagumo system*. *Trans. Amer. Math. Soc.*, 286, pages 431–469, 1984.
- [24] C.K.R.T Jones and N. Kopell. *Tracking invariant manifolds with differential forms in singularly perturbed systems*. *J. of Differential Equations*, 108(1), pages 64–88, 1994.
- [25] Z.P. Kilpatrick, S.E. Folias and P.C. Bressloff. *Traveling pulses and wave propagation failure in inhomogeneous neural media*. *SIAM Journal on Applied Dynamical Systems*, vol. 7, no. 1, pages 161–185, 2008.
- [26] Z.P. Kilpatrick and P.C. Bressloff. *Effects of synaptic depression and adaptation on spatiotemporal dynamics of an excitatory neuronal network*. *Physica D: Nonlinear Phenomena*, vol. 239, no. 9, pages 547–560, 2010.
- [27] Z. P. Kilpatrick and P. C. Bressloff. *Binocular rivalry in a competitive neural network with synaptic depression*. *SIAM J Appl Dyn Syst*, 9, pages 1303–1347, 2010.
- [28] Z.P. Kilpatrick *Short term synaptic depression improves information transfer in perceptual multistability*. *Frontiers in Computational Neuroscience*, vol 7, pp. 1–16, 2013.
- [29] M. Krupa and P. Szmolyan. *Extending geometric singular perturbation theory to non hyperbolic points fold and canard points in two dimensions*. *SIAM J. Math. Anal.*, 33(2), pages 91–138, 2001.
- [30] J. Mallet-Paret. *The global structure of traveling waves in spatially discrete dynamical systems*. *Journal of Dynamics and Differential Equations*, 11, 1, pages 49–127, 1999.
- [31] A. Pazy. *Semigroups of Linear Operators and Applications to Partial Differential Equations*. Springer-Verlag, New-York, 1983.
- [32] D.J. Pinto and G.B. Ermentrout. *Spatially structured activity in synaptically coupled neuronal networks: 1. Traveling fronts and pulses*. *SIAM J. of Appl. Math.*, vol. 62, pages 206–225, 2001.
- [33] D. J. Pinto, R. K. Jackson, and C. E. Wayne. *Existence and stability of traveling pulses in a continuous neuronal network*. *SIAM J. Appl. Dyn. Syst.*, 4, pages 954–984, 2005.
- [34] 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*. *Journal of Neuroscience*, 25 , pages 8131–8140, 2005.
- [35] B. Sandstede. *Evans functions and nonlinear stability of traveling waves in neuronal network models*. *International Journal of Bifurcation and Chaos*, Vol. 17, No. 8 (2007), 2693-2704.
- [36] T.K. Sato, I. Nauhaus and M. Carandini. *Traveling waves in visual cortex*. *Neuron Review*, 75, pages 218–229, 2012.
- [37] M.V. Tsodyks and H. Markram. *The neural code between neocortical pyramidal neurons depends on neurotransmitter release probability*. *P.N.A.S.*, vol. 94, no. 2, pp. 719–723, 1997.

- [38] Y. Wu, X. Xing and Q. Ye. *Stability of traveling waves with algebraic decay for n -degree Fisher-type equations*. Discrete Contin. Dynam. Systems, 16, pages 47–66, 2006.
- [39] J.-Y. Wu, X. Huang and C. Zhang. *Propagating waves of activity in the neocortex: What they are, what they do*. Neuroscientist, 14, pages 487–502, 2008.
- [40] W. Xu, X. Huang, K. Takagaki, and J.-Y. Wu. *Compression and reflection of visually evoked cortical waves*. Neuron, 55, pages 119–129, 2007.
- [41] L.C York and M.C.W. van Rossum. *Recurrent networks with short term synaptic depression*. J Comput. Neurosci., 27, pages 607–620, 2009.
- [42] L. Zhang. *Existence, uniqueness, and exponential stability of traveling wave solutions of some integral differential equations arising from neuronal networks*. Differential Integral Equations, 16, pages 513–536, 2003.
- [43] L. Zhang. *Traveling Waves of a Singularly Perturbed System of Integral-Differential Equations Arising from Neuronal Networks*. Jour. Dynamics and Diff. Equ., vol 17, no 3, 2005.
- [44] L. Zhang. *How Do Synaptic Coupling and Spatial Temporal Delay Influence Traveling Waves in Non-linear Nonlocal Neuronal Networks?*. SIAM J. Appl. Dyn. Syst., vol 6, no 3, pages 597–644, 2007.