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WAVE FRONTS IN NEURONAL FIELDS WITH NONLOCAL POST-SYNAPTIC AXONAL CONNECTIONS AND DELAYED NONLOCAL FEEDBACK CONNECTIONS

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Abstract. We consider a neuronal network model with both axonal connections (in the form of synaptic coupling) and delayed non-local feedback connections. The kernel in the feedback channel is assumed to be a standard non-local one, while for the kernel in the synaptic coupling, four types are considered. The main concern is the existence of travelling wave front. By employing the speed index function, we are able to obtain the existence of a travelling wave front for each of these four types within certain range of model parameters. We are also able to describe how the feedback coupling strength and the magnitude of the delay affect the wave speed. Some particular kernel functions for these four cases are chosen to numerically demonstrate the theoretical results.

1. **Introduction.**

Neurons are electrically excitable cells in the nervous system. Chemically connected or functionally associated neurons form neural networks. Signals propagate through such a network in the following manner: When a neuron is stimulated (by another neuron, or by a stimulus such as light), an action potential forms. This action potential travels down the axon (by conductance of the axon) to the synapse, the junction between neurons. The potential travels from the presynaptic ending to post-synaptic receptors of another neuron via certain chemical mechanism. The formation and propagation of certain patterns in synaptically connected neural networks are closely related to the basic information processing in the nervous system ([1, 2, 10]). The occurrence and propagation of such patterns have been observed in experiments and by numeric simulations of the brain in, for example, cortex neurons and in thalamus neurons (see, e.g., [6, 7, 9] and the references there in), in the forms of travelling wave fronts and travelling pulses.

In order to better understand the mechanism of the formation and propagation of activity patterns in neural networks, Hutt [3] recently proposed a model which is a modification and generalization of some existing models (see, e.g., Coombes et. al [1], Coombes and Owen [2], Zhang [10], and the references therein). This new model incorporates both the intral-areal nonlocal axonal connections and nonlocal

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feedback connections with a time delay (see Figure 1 for a demonstration of these two types of connections) and is given by the following integro-differential equation (IDE):

$$u_t + u = \alpha \int_{-\infty}^{\infty} K(x-y)\, H\left(u\left(y, t - \tfrac{1}{c}|x-y|\right) - \theta\right) dy + \beta \int_{-\infty}^{\infty} J(x-y)\, H\left(u(y, t-\tau) - \theta\right) dy. \quad (1)$$

Here, $u(x,t)$ is the effective post-synaptic potential of the neuron population at position x and time t. The first term on the right hand side of (1) represents the synaptic input by axonal connections, while the second term accounts for the delayed nonlocal feedback connections. Thus, the kernels $K(x)$ and $J(x)$ are connectivity functions satisfying some conditions which will be specified later. Under those conditions, the constants α and β are non-negative and represent the synaptic strengths of axonal and nonlocal feedback contributions, respectively. These connectivity functions are similar to a probability density function; however, unlike regular probability density functions, the kernels may be negative at some points to allow for inhibitory behavior in coupling. The conversion from dendritic currents to post-synaptic potential is given by the Heaviside step function $H(u-\theta)$ which activates when u crosses the excitation threshold value $\theta > 0$. The choice of the Heaviside function makes it simpler to perform the analysis but it still reflects the statistical properties of the firing rate of neurons which is sigmoidal in shape [3]. It should be noted that $H(x)$ is chosen to have a value of $\frac{1}{2}$ at $x = 0$, the average of its values on both sides of the discontinuity.

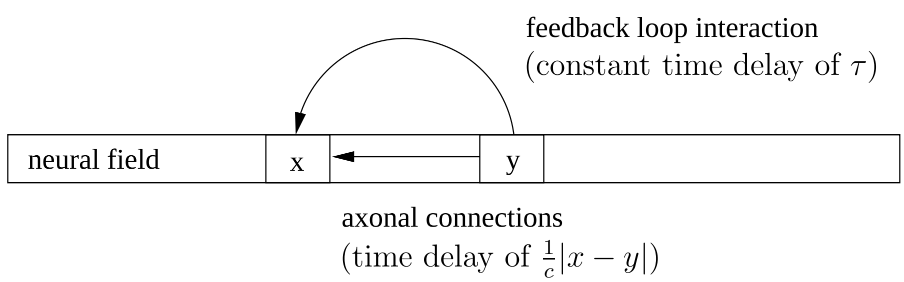

FIGURE 1. Illustration of intra-areal axonal connections and non-local feedback connections

Note that the β-interactions exhibits a constant time delay of τ while the α-type has a delay that depends on both the spatial distance and the finite speed $c \in (0, \infty)$ of the action potential. This is different from the wave speed μ of the post-synaptic potential, which will be discussed in detail in later sections. Experiments on measuring the propagation speeds of neuronal waves have yielded post-synaptic potential speeds of $\mu = 0.06$ m/s and axon potential speeds of $c = 0.5$ m/s [10]. Based on the experimental data, it is naturally expected and we will indeed assume throughout this paper that $0 < \mu < c$.

In Hutt [3], the two kernel functions $K(x)$ and $J(x)$ are assumed to have the following exponential forms:

$$K(x) = \frac{a_e}{2} e^{-|x|} - \frac{a_i r}{2} e^{-r|x|}, \quad J(x) = \frac{1}{2\sigma} e^{-|x|/\sigma} \quad (2)$$

where σ gives the spatial feedback range, a_e and a_i are excitatory and inhibitory weights, and r abbreviates the ratio of excitatory and inhibitory spatial ranges. The above choice for $K(x)$ and $J(x)$ simplifies the Laplacian transform analysis for (1), by which the author was able obtain some results on how the speed of travelling wave front depends on feedback strength μ and the feedback delay τ.

When $\beta = 0$, (1) reduces to the exact form of the model equation in Zhang [10], where synaptic coupling function $K(x)$ is assumed to be continuous at $x = 0$, almost everywhere smooth satisfying

$$\int_{-\infty}^{\infty} K(x)\,dx = 1, \quad \text{and} \quad |K(x)| \le L\exp(-\rho|x|) \ \text{ for } \ x \in (-\infty, \infty), \tag{3}$$

where L and ρ are positive constants. Based on the connectivity feature, Zhang [10] discussed the following three types of functions for $K(x)$:

(A) Pure excitation: $K(x) \ge 0$ for $x \in (-\infty, \infty)$.

(B) Lateral inhibition: $K(x) \ge 0$ for $x \in (-M, N)$ and $K(x) \le 0$ elsewhere for positive constants M and N such that

$$\int_{-\infty}^{0} |x|\, K(x)\, dx \ge 0. \tag{4}$$

This type of kernel functions are called *Mexican hat* kernels.

(C) Lateral excitation: $K(x) \le 0$ on $(-M, N)$ and $K(x) \ge 0$ elsewhere for some positive constants M and N such that

$$\frac{\alpha}{2} + \alpha \int_{-\infty}^{N} K(x)\, dx \ge \theta \tag{5}$$

This type of kernel functions are referred to as *upside down Mexican hat* kernels.

By analyzing the speed index function and the stability index function, Zhang [10] obtained some very interesting and insightful results on the wave speed, and for certain critical cases of some model parameters, he was even able to obtain some concrete results on the stability of the travelling wave fronts.

The goal of this paper is to employ the idea of speed index functions (the main idea in [10] and many existing works) to analyze the more general model equation (1) with $\beta > 0$ and $\tau > 0$, hoping to understand how the delayed feedback term will affect, jointly with the synaptic coupling, the existence as well as the shape of the travelling wave front of the model. We do not confine ourselves to the exponential forms (2) for the kernels, or any other particular forms; instead, we consider general kernels of types (A), (B) and (C). This is important since only for very few functional areas such as the visual cortex, the cerebellum or the prefrontal cortex, the connectivity kernels are known. In response to the co-existence of both synaptic connections and feedback connections, we introduce three speed index functions: the α index function φ_α, the β index function φ_β, and the total index function φ. Note that corresponding to the pure excitation type kernel (Type (A)), there are the pure inhibition type kernels:

(D) Pure inhibition: $K(x) \le 0$ for $x \in (-\infty, \infty)$,

for which the model with $\beta = 0$ does not allow travelling wave fronts. as is mentioned in the introduction of [10]. We will also consider this type for the kernel

$K(x)$, and show that due to the occurrence of feedback connections, the model may also support travelling front for the pure inhibition synaptic coupling. The dependence of wave speed on some parameters will also be discussed, and some numerical examples and their simulations will be given to demonstrate the analytical results.

We point out that the underlying spatial structure for neural systems originates from dendritic arborization of neurons and from the spread of axonal connections, and thus, 3-dimensional or 2-dimensional space would be more realistic. However, to avoid the main idea from being hidden by more complicated calculation due to adoption of higher dimensional space, we will follow Hutt [3], [10] and most of the existing work to consider only 1-dimensional space. Also as in Hutt [3] and [10], here we do not consider external input.

2. **Preliminaries.** In the rest of the paper, we assume that the kernel function $J(x)$ satisfies the following typical conditions: $J(x)$ is non-negative and satisfies

$$\int_{-\infty}^{\infty} J(x)\,dx = 1, \quad \text{and} \quad |J(x)| \leq L\exp(-\rho|x|) \ \text{ for } \ x \in (-\infty,\infty), \tag{6}$$

where L and ρ are positive constants. For simplicity of notation but without loss of generality, we further assume that

$$\int_{-\infty}^{0} J(x)\,dx = \int_{0}^{\infty} J(x)\,dx = \frac{1}{2}. \tag{7}$$

A travelling wave solution of (1) is a solution of the form $u(x,t) = U(x+\mu t)$, where $z = x+\mu t$ is the moving cordinate, $U(z)$ is the profile of the travelling wave and the constant μ is the speed of the travelling wave. If $U_- = \lim_{z\to-\infty} U(z)$ and $U_+ = \lim_{z\to\infty} U(z)$ exist and $U_- \neq U_+$, then the travelling wave solution is called a travelling wave front. If the two limits are identical ($U_- = U_+$), the wave solution corresponds to a travelling pulse.

We are only interested in travelling wave front in this paper. Substituting the wave form $u(x,t) = U(x+\mu t)$ into (1), we obtain

$$\mu U'(z) + U(z) = \alpha \int_{-\infty}^{\infty} K(z-y)\, H\left(U\left(y - \frac{\mu}{c}|z-y|\right) - \theta\right)dy + \beta \int_{-\infty}^{\infty} J(z-y)\, H(U(y-\mu\tau) - \theta)dy. \tag{8}$$

It is easy to see that if the two limits U_- and U_+ exist, they must be constant solutions (equilibria) of (8), or equivalently, of (1).

Note that $U = 0$ is always a constant solution of (8), which serves as U_-. In order for (8)to have another positive constant solution of (8) to serve as U_+, we need some conditions on the kernel function $K(x)$ and some restrictions on the model parameters. In the remainder of the paper, we always assume that $K(x)$ satisfies (3). In addition, for simplicity of notations and similar to (7) for $J(x)$, we also assume that

$$\int_{-\infty}^{0} K(x)\,dx = \int_{0}^{\infty} K(x)\,dx = \frac{1}{2} \quad \text{for} \quad K(x) \quad \text{in types (A)-(B)-(C)}, \tag{9}$$

and

$$\int_{-\infty}^{0} K(x)\,dx = \int_{0}^{\infty} K(x)\,dx = \frac{-1}{2} \quad \text{for} \quad K(x) \quad \text{in type (D).} \tag{10}$$

For kernel function $K(x)$ of types (A), (B) and (C) satisfying (9), it is easily seen that $U = \alpha+\beta$ is a constant solution of (8) if and only if $\theta < \alpha+\beta$. Note that $U = \theta$ is also a constant solution of (8) when $\theta = \frac{\alpha+\beta}{2}$, but since such an identity condition is too sensitive and can hardly hold in reality, we do not consider such a case. In Sections 3 and 4, we will establish the existence and uniqueness of a travelling wave front of (1) with kernel function $K(x)$ of types (A), (B) and (C) respectively, satisfying (10), that connects the two equilibria $U_- = 0$ and $U_+ = \alpha + \beta$.

For kernel function $K(x)$ of types (D) satisfying (10), $U = \beta - \alpha$ give a positive equilibrium for (8) provided that $\alpha < \beta$. In Section 5, we will consider travelling wave front of (1) that connects $U_- = 0$ and $U_+ = \beta - \alpha$.

The parameters α, β, c, τ, and θ are to be collectively called the **explicit parameters** since they all appear explicitly in the model equation (1). For convenience of analysis, we introduce some more parameters which are functions of the explicit parameters as below. Firstly, let

$$\delta = \beta \int_{-\infty}^{-c\tau} \left(1 - e^{\frac{x}{c}+\tau}\right) J(x)\,dx \tag{11}$$

and we call it *feedback effect parameter*. It is easy to see that this parameter is always positive and Theorem 3.2 will show that when it is small enough (smaller than θ), the equation (1) allows travelling wave solutions for specific cases. From the definition of the δ we see that there are two ways to make it small. The first is to make β small, and the second is to make $J(x)$ decay to zero quickly as x goes from $-c\tau \to -\infty$.

Next, we define

$$\varphi_\alpha(\mu) = \alpha \int_{-\infty}^{0} e^{\frac{c-\mu}{c\mu}x} K(x)\,dx \tag{12}$$

$$\varphi_\beta(\mu) = \beta \int_{-\infty}^{-\mu\tau} e^{\frac{x}{\mu}+\tau} J(x)\,dx + \beta \int_{-\mu\tau}^{0} J(x)\,dx \tag{13}$$

$$\varphi(\mu) = \varphi_\alpha(\mu) + \varphi_\beta(\mu), \tag{14}$$

and call them α speed index function, β speed index function and *total* speed index function respectively. We will see later that these functions play an important role in determine the speed of travelling wave fronts for (1).

Finally, for $\mu \in (0, c)$, we define

$$\begin{aligned}\Delta(\mu) &= \beta \int_{-\infty}^{-\mu\tau} \left(1 - e^{\frac{x}{\mu}+\tau}\right) J(x)\,dx \\ &= \beta \int_{-\infty}^{0} \left(1 - e^{\frac{x}{\mu}}\right) J(x-\mu\tau)\,dx.\end{aligned} \tag{15}$$

Considering $\Delta := \Delta(\mu, \tau)$ as a function of $\mu \in (0, c)$ and $\tau \geq 0$, we can easily verify the following properties:

$$\frac{\partial \Delta}{\partial \mu} = \frac{\beta}{\mu^2} \int_{-\infty}^{-\mu\tau} x e^{\frac{x}{\mu}+\tau} J(x)\, dx \leq 0 \tag{16}$$

$$\frac{\partial \Delta}{\partial \tau} = -\beta \int_{-\infty}^{-\mu\tau} e^{\frac{x}{\mu}+\tau} J(x)\, dx \leq 0. \tag{17}$$

Thus, Δ is indeed decreasing in both $\mu \in (0, c)$ and $\tau \geq 0$. It is also obvious that $\Delta(0, \tau) = \frac{\beta}{2}$ and $\Delta(c, \tau) = \delta$, which also implies that

$$\delta < \Delta(\mu, \tau) < \frac{\beta}{2} \quad \text{for} \quad \mu \in (0, c), \quad \tau \geq 0. \tag{18}$$

It is also interesting to explore the relationship between φ_β and Δ. Actually, calculations lead to

$$\begin{aligned}\varphi_\beta(\mu) &= \beta \int_{-\infty}^{-\mu\tau} e^{\frac{x}{\mu}+\tau} J(x)\, dx + \beta \int_{-\mu\tau}^{0} J(x)\, dx \\ &= \beta \int_{-\infty}^{-\mu\tau} \left(e^{\frac{x}{\mu}+\tau} - 1\right) J(x)\, dx + \beta \int_{-\infty}^{0} J(x)\, dx \\ &= -\Delta(\mu, \tau) + \frac{\beta}{2} > 0 \end{aligned} \tag{19}$$

3. **Travelling wave solutions for K(x) of types (A) and (B).** We begin the derivation of the travelling wave fronts by focusing first on those $K(x)$ functions of types (A) and (B). The explicit form of the wave profile function obtained in this section will also be used for other types of $K(x)$ discussed in later sections.

Theorem 3.1. *Assume that $K(x)$ is of Type (A) or (B). If $\delta < \theta < (\alpha + \beta)/2$, then there exists a unique wave speed $\mu_0 = \mu_0(\alpha, \beta, c, \tau, \theta) \in (0, c)$ and a solution to (1) given by $u(x, t) = U(z)$ where $z = x + \mu_0 t$ where $U(z)$ is the unique solution to the following integral-differential equation*

$$\begin{aligned}\mu_0 U'(z) + U(z) = \alpha \int_{-\infty}^{\infty} K(z-y)\, H\left(U\left(y - \frac{\mu_0}{c}|z-y|\right) - \theta\right) dy \\ + \beta \int_{-\infty}^{\infty} J(z-y)\, H(U(y - \mu_0\tau) - \theta) dy \end{aligned} \tag{20}$$

satisfying the phase conditions

$$U(z) < \theta \text{ for } z < 0; \quad U(z) = \theta \text{ for } z = 0; \quad U(z) > \theta \text{ for } z > 0; \tag{21}$$

and the boundary conditions

$$\lim_{z\to-\infty} U(z) = 0, \quad \lim_{z\to+\infty} U(z) = \alpha + \beta, \quad \lim_{z\to\pm\infty} U'(z) = 0. \tag{22}$$

Indeed, the solution is given by

$$U(z) = \alpha \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx - \alpha \int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(x)}\right) \frac{c}{c+\mu_0 \operatorname{sgn}(x)} dx$$
$$+ \beta \int_{-\infty}^{z} \left(1 - e^{\frac{x-z}{\mu_0}}\right) J(x - \mu_0 \tau)\,dx. \quad (23)$$

To prove this theorem, we first show that for $\mu_0 \in (0, c)$ and with the phase conditions (21), the equation (20) can be simplified.

Let

$$\eta = y - \frac{\mu_0}{c} |z - y|$$

Then,

$$z - \eta = z - y + \frac{\mu_0}{c} |z - y| = (z - y) \left(\frac{c + \mu_0 \operatorname{sgn}(z - y)}{c} \right)$$

and thus

$$\operatorname{sgn}(z - \eta) = \operatorname{sgn}(z - y) \cdot \operatorname{sgn}\left(\frac{c + \mu_0 \operatorname{sgn}(z - y)}{c} \right)$$
$$= \operatorname{sgn}(z - y).$$

From the above, we also obtain

$$z - y = \frac{c}{c + \mu_0 \operatorname{sgn}(z - y)} (z - \eta)$$
$$= \frac{c}{c + \mu_0 \operatorname{sgn}(z - \eta)} (z - \eta).$$

Using these and the (21), we can simplify the first term in the right-hand-side of (20) as follows:

$$\alpha \int_{-\infty}^{\infty} K(z - y) H\left(U\left(y - \frac{\mu_0}{c} |z - y|\right) - \theta\right) dy$$
$$= \alpha \int_{-\infty}^{\infty} \tfrac{c}{c+\mu_0 \operatorname{sgn}(z-\eta)} K\left(\tfrac{c}{c+\mu_0 \operatorname{sgn}(z-\eta)} (z - \eta)\right) H(U(\eta) - \theta)\,d\eta$$
$$= \alpha \int_{0}^{\infty} \tfrac{c}{c+\mu_0 \operatorname{sgn}(z-\eta)} K\left(\tfrac{c}{c+\mu_0 \operatorname{sgn}(z-\eta)} (z - \eta)\right) d\eta$$
$$= \alpha \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx \quad (24)$$

Similarly, the second integral on the right hand side of (20) can also be simplified to

$$\beta \int_{-\infty}^{\infty} J(z - y) H(U(y - \mu_0 \tau) - \theta) dy = \beta \int_{\mu_0 \tau}^{+\infty} J(z - y)\,dy = \beta \int_{-\infty}^{z - \mu_0 \tau} J(x)\,dx \quad (25)$$

Using (24) and (25), (20) can be rewritten as

$$\mu_0 U' + U = \alpha \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx + \beta \int_{-\infty}^{z-\mu_0\tau} J(x)\,dx \tag{26}$$

Now, multiplying this simplified equation by the integration factor e^{z/μ_0} yields

$$\mu_0 \left(U e^{\frac{z}{\mu_0}}\right)' = \alpha e^{\frac{z}{\mu_0}} \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx + \beta e^{\frac{z}{\mu_0}} \int_{-\infty}^{z-\mu_0\tau} J(x)\,dx$$

Integrating the above equation from $-\infty$ to z gives

$$\mu_0 U(z) e^{\frac{z}{\mu_0}} = \int_{-\infty}^{z} \alpha e^{\frac{\xi}{\mu_0}} \int_{-\infty}^{\frac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}} K(x)\,dx\,d\xi + \int_{-\infty}^{z} \beta e^{\frac{\xi}{\mu_0}} \int_{-\infty}^{\xi-\mu_0\tau} J(x)\,dx\,d\xi \tag{27}$$

The right-hand-side can be simplified using integration by parts. The first term can be simplified by writing it as $\int_{-\infty}^{z} f(\xi)\, g'(\xi)\, d\xi$ where

$$f(\xi) = \int_{-\infty}^{\frac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}} K(x)\,dx \quad \text{and} \quad g'(\xi)\,d\xi = \alpha e^{\frac{\xi}{\mu_0}} d\xi$$

Thus

$$\begin{aligned} f'(\xi)\,d\xi &= K\left(\tfrac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}\right) \tfrac{(c+\mu_0 \operatorname{sgn}(\xi))c - c\xi \operatorname{sg}n'(\xi)}{(c+\mu_0 \operatorname{sgn}(\xi))^2} d\xi \\ &= K\left(\tfrac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(\xi)} d\xi \end{aligned}$$

and

$$g(\xi) = \alpha \mu_0 e^{\frac{\xi}{\mu_0}}$$

Then by integration by parts, the first term in (27) becomes

$$\begin{aligned} &\int_{-\infty}^{z} \alpha e^{\frac{\xi}{\mu_0}} \int_{-\infty}^{\frac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}} K(x)\,dx\,d\xi \\ &= \alpha\mu_0 e^{\frac{\xi}{\mu_0}} \int_{-\infty}^{\frac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}} K(x)\,dx \Bigg|_{\xi=-\infty}^{z} - \alpha\mu_0 \int_{\xi=-\infty}^{z} e^{\frac{\xi}{\mu_0}} K\left(\tfrac{c\xi}{c+\mu_0 \operatorname{sgn}(\xi)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(\xi)} d\xi \\ &= \alpha\mu_0 e^{\frac{z}{\mu_0}} \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx - \alpha\mu_0 \int_{-\infty}^{z} e^{\frac{x}{\mu_0}} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(x)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(x)} dx \end{aligned} \tag{28}$$

Similarly, the second term in (27) can be simplified to

$$\int_{-\infty}^{z} \beta e^{\frac{\xi}{\mu_0}} \int_{-\infty}^{\xi-\mu_0\tau} J(x)\,dx\,d\xi = \beta\mu_0 e^{\frac{z}{\mu_0}} \int_{-\infty}^{z-\mu_0\tau} J(x)\,dx - \beta\mu_0 \int_{-\infty}^{z} e^{\frac{x}{\mu_0}} J(x-\mu_0\tau)\,dx$$
$$= \beta\mu_0 \int_{-\infty}^{z} \left(e^{\frac{z}{\mu_0}} - e^{\frac{x}{\mu_0}}\right) J(x-\mu_0\tau)\,dx \tag{29}$$

Thus, going back to (27) and using (28)-(29), we obtain the solution of (26)

$$U(z) = \alpha \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx - \alpha \int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(x)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(x)} dx$$
$$+ \beta \int_{-\infty}^{z} \left(1 - e^{\frac{x-z}{\mu_0}}\right) J(x-\mu_0\tau)\,dx$$

which is (23) and of course, satisfies (20) and (21).

We point out that when $\beta = 0$, the above solution formula reduces to the result in Zhang [10].

In the rest of this section, we will show that there is a unique $\mu_0 \in (0, c)$ for which the function $U(z)$ given by (23) satisfies the phase conditions (21) and the boundary conditions (22). We begin with $U(0) = \theta$ in the phase conditions.

Setting $U(0) = \theta$ in (23) leads to

$$\alpha \int_{-\infty}^{0} K(x)\,dx - \alpha \int_{-\infty}^{0} e^{\frac{x}{\mu_0}} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(x)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(x)} dx$$
$$+ \beta \int_{-\infty}^{0} \left(1 - e^{\frac{x}{\mu_0}}\right) J(x-\mu_0\tau)\,dx = \theta$$

$$\Longleftrightarrow \frac{\alpha}{2} - \alpha \int_{-\infty}^{0} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx + \beta \int_{-\infty}^{-\mu_0\tau} \left(1 - e^{\frac{x}{\mu_0}+\tau}\right) J(x)\,dx = \theta$$
$$\Longleftrightarrow \frac{\alpha}{2} - \alpha \int_{-\infty}^{0} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx + \frac{\beta}{2} - \beta \int_{-\mu_0\tau}^{0} J(x)\,dx - \beta \int_{-\infty}^{-\mu_0\tau} e^{\frac{x}{\mu_0}+\tau} J(x)\,dx = \theta$$
$$\Longleftrightarrow \frac{\alpha+\beta}{2} - \varphi(\mu_0) = \theta. \tag{30}$$

The Lemma below shows that if $\delta < \theta < (\alpha+\beta)/2$, then there is a unique μ_0 in $(0, c)$ such that (30) holds.

Lemma 3.2. *Let $K(x)$ be of Type (A) or Type (B). Assume that $\delta < \theta < (\alpha+\beta)/2$. Then there exists a unique $\mu_0 \in (0, c)$ such that*

$$\varphi(\mu_0) = \frac{\alpha+\beta}{2} - \theta. \tag{31}$$

Proof. From the definition of the $\varphi(\mu)$, we can see that the function is continuous for $\mu \in (0,c)$. Note that

$$\lim_{\mu\to 0^+} \varphi(\mu) = 0 < \frac{\alpha+\beta}{2} - \theta; \tag{32}$$

$$\begin{aligned}
\lim_{\mu\to c^-} \varphi(\mu) &= \frac{\alpha}{2} + \beta \int_{-\infty}^{-c\tau} e^{\frac{x}{c}+\tau} J(x)\,dx + \beta \int_{-c\tau}^{0} J(x)\,dx \\
&= \frac{\alpha}{2} + \beta \int_{-\infty}^{0} J(x)\,dx - \beta \int_{-\infty}^{-c\tau} J(x)\,dx + \beta \int_{-\infty}^{-c\tau} e^{\frac{x}{c}+\tau} J(x)\,dx \\
&= \frac{\alpha+\beta}{2} - \beta \int_{-\infty}^{-c\tau} \left(1 - e^{\frac{x}{c}+\tau}\right) J(x)\,dx \\
&= \frac{\alpha+\beta}{2} - \delta \\
&> \frac{\alpha+\beta}{2} - \theta \quad , \quad (\text{since } \delta < \theta)
\end{aligned} \tag{33}$$

By the intermediate value theorem for continuous functions, there is a $\mu_0 \in (0,c)$ such that $\varphi(\mu_0) = \frac{\alpha+\beta}{2} - \theta$.

To prove the uniqueness, we only need to show that $\varphi(\mu)$ is actually an increasing function. To see this, we first compute φ'_α and φ'_β as below:

$$\varphi'_\alpha(\mu) = \alpha \int_{-\infty}^{0} \frac{-x}{\mu^2} e^{\frac{c-\mu}{c\mu}x} K(x)\,dx \tag{34}$$

$$\varphi'_\beta(\mu) = \beta \int_{-\infty}^{-\mu\tau} \frac{-x}{\mu^2} e^{\frac{x}{\mu}+\tau} J(x)\,dx \tag{35}$$

Due to the condition that $J(x) \ge 0$ for all x we know that $\varphi'_\beta(\mu) \ge 0$ for all x. As for the behavior of φ_α, this has to be analyzed on a case-to-case basis depending on the type of $K(x)$.

For Type (A), since $K(x) \ge 0$ for all x and and by the assumption (9), we must have $K(x) > 0$ for some nonempty open interval $I \subseteq (-\infty, 0)$. Thus the integrand $-(x/\mu^2)e^{(c-\mu)x/c\mu} K(x)\,dx \ge 0$ for all negative x and is greater than zero on I. Thus we must have $\varphi'_\alpha(\mu) > 0$ for all $\mu \in (0,c)$.

For Type (B), recall that $K(x) \le 0$ for all $x \in (-\infty, -M) \cup (N, +\infty)$ and $K(x) \ge 0$ elsewhere. Thus for $x \in (-M, 0)$

$$-xe^{\frac{c-\mu}{c\mu}x} K(x) \ge -xe^{-\frac{c-\mu}{c\mu}M} K(x) \ge 0;$$

and for $x \in (-\infty, -M)$

$$0 \ge -xe^{\frac{c-\mu}{c\mu}x} K(x) \ge -xe^{-\frac{c-\mu}{c\mu}M} K(x).$$

By the above, one always have

$$\varphi'_\alpha(\mu) \ge \alpha \int_{-\infty}^{0} -\frac{x}{\mu^2} e^{-\frac{c-\mu}{c\mu}M} K(x)\,dx = \frac{\alpha}{\mu^2} e^{-\frac{c-\mu}{c\mu}M} \int_{-\infty}^{0} |x|\, K(x)\,dx > 0$$

The last step is due to the requirement on Type (A) kernel function listed in Section 1.

Combining the above, we have shown that $\varphi'_\alpha(\mu) > 0$, and hence $\varphi'(\mu) > 0$, for $K(x)$ of either type of (A) or (B). This proves the uniqueness of μ_0 and thus, completes the proof of Lemma 3.2 □

Lemma 3.3. *Let μ_0 be given in Lemma 3.2. Then the function $U(z)$ given in (23) satisfies the boundary conditions (22).*

Proof. It is straightforward to see that $\lim_{z\to-\infty} U(z) = 0$ because all integral terms go to zero. The derivative of U can be found by following the rules of differentiation under an integral sign.

$$U'(z) = \frac{\alpha}{\mu_0}\int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} \frac{c}{c+\mu_0 \operatorname{sgn}(z)} K\left(\frac{cx}{c+\mu_0 \operatorname{sgn}(z)}\right) dx + \frac{\beta}{\mu_0}\int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} J(x-\mu_0\tau)\, dx \quad (36)$$

It is also straightforward to see that $\lim_{z\to\pm\infty} U'(z) = 0$. The remaining limit is $\lim_{z\to+\infty} U(z)$ and this is readily simplified to

$$\begin{aligned}\lim_{z\to+\infty} U(z) &= \alpha - 0 + \beta\int_{-\infty}^{+\infty} (1-0)\, J(x-\mu_0\tau)\, dx\\ &= \alpha + \beta\int_{-\infty}^{+\infty} J(x-\mu_0\tau)\, dx\\ &= \alpha + \beta\end{aligned}$$

Therefore, we have verified that the $U(z)$ given by (23) satisfies all boundary conditions in (22). □

Remark 1. We focused on the travelling waves with $\mu > 0$ that go from $U(-\infty) = 0$ to $U(\infty) = \alpha + \beta$, accounting transition from the rest steady state $U = 0$ to the positive steady state $U = \alpha+\beta$. When $\beta = 0$, Zhang proved that due to symmetry, a travelling wave solution can also be found with $\mu_0 < 0$ and reversed phase and boundary conditions. For $\beta > 0$ however this is not always the case because $J(x)$ may have conditions that are not symmetric with respect to space.

The next lemma verifies all phase conditions in (21).

Lemma 3.4. *Let the kernel function $K(x)$ be of Type (A) or (B), and μ_0 be the positive number given in Lemma 3.2. Then the function $U(z)$ given in (23) satisfies the phase conditions (21).*

Proof. Lemma 3.2 has confirmed $U(0) = \theta$. The other two phase conditions require more work to prove. We first separate the terms involving α from those involving β in the expression for $U(z)$ by letting

$$U(z) = \alpha U_\alpha(z) + \beta U_\beta(z) \quad (37)$$

where

$$U_\alpha = \int_{-\infty}^{\frac{cz}{c+\mu_0 \operatorname{sgn}(z)}} K(x)\,dx - \int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(x)}\right) \tfrac{c}{c+\mu_0 \operatorname{sgn}(x)} dx \tag{38}$$

$$U_\beta = \int_{-\infty}^{z} \left(1 - e^{\frac{x-z}{\mu_0}}\right) J(x - \mu_0\tau)\,dx. \tag{39}$$

It follows from (36) that

$$U'_\alpha(z) = \frac{1}{\mu_0} \int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} \tfrac{c}{c+\mu_0 \operatorname{sgn}(z)} K\left(\tfrac{cx}{c+\mu_0 \operatorname{sgn}(z)}\right) dx \tag{40}$$

$$U'_\beta(z) = \frac{1}{\mu_0} \int_{-\infty}^{z} e^{\frac{x-z}{\mu_0}} J(x - \mu_0\tau)\,dx \tag{41}$$

For $K(x)$ of Type (A), Since $K(x), J(x) \geq 0$ for all x and they both have to integrate to $\frac{1}{2}$ on $(-\infty, 0)$ then there must be a nonempty open interval $I \subseteq (-\infty, 0)$ such that $K(x)$ or $J(x)$ or both are positive on I. Pick the leftmost point z_* such that z_* is a left endpoint of such an interval I (allow for $z_* = -\infty$). Since both kernels are always non-negative then $U' = \alpha U'_\alpha + \beta U'_\beta$ starts off at zero at $-\infty$ and stays at zero until it hits z_*. Past this point $U' > 0$. Thus U behaves in the following manner: it starts of at zero and stays there until z_* after which it starts strictly increasing and approaching $\alpha + \beta$ as $z \to \infty$ (Lemma 3.3). This strictly increasing nature of $U(z)$ guarantees all of the remaining phase conditions.

For $K(x)$ of Type (B), the proof for this case is much more involved. Recall that $K(x) \leq 0$ for all $x \in (-\infty, -M) \cup (N, +\infty)$ and ≥ 0 everywhere else. Substitute the case $z = 0$ in equation (40) and using substitution and splitting of the integral derive

$$\mu_0 e^{\frac{z}{\mu_0}} U'_\alpha(0) = \int_{-\infty}^{-M} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx + \int_{-M}^{0} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx. \tag{42}$$

From $\int_{-\infty}^{0} K(x)\,dx = \frac{1}{2}$, one obtains

$$0 \leq -\int_{-\infty}^{-M} K(x)\,dx < \int_{-M}^{0} K(x)\,dx$$

and

$$0 \leq -\int_{-\infty}^{-M} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx \leq -\int_{-\infty}^{-M} e^{-\frac{c-\mu_0}{c\mu_0}M} K(x)\,dx$$
$$< \int_{-M}^{0} e^{-\frac{c-\mu_0}{c\mu_0}M} K(x)\,dx \leq \int_{-M}^{0} e^{\frac{c-\mu_0}{c\mu_0}x} K(x)\,dx$$

Using this in (42), we find that $U'_\alpha(0) > 0$. Now, since $K(x) \leq 0$ for all $x \in (-\infty, -M)$ then $U'_\alpha(z) < 0$ for all $z \in (-\infty, -M)$. Thus U'_α must change sign from negative to positive at some point z_* in $(-M, 0)$. This can only happen once because of the form $K(x)$. Also because of the form of $K(x)$, $U'_\alpha > 0$ on (z_*, N). Past N, φ'_α may change signs again but only once.

From (41) it is obvious that $U'_\beta \geq 0$. Now express $U_\alpha(0)$ using speed index functions

$$\alpha U_\alpha(0) = \frac{\alpha}{2} - \varphi_\alpha(\mu_0) > 0 \quad \text{since } 0 \leq \varphi_\alpha(\mu) \leq \frac{\alpha}{2} \tag{43}$$

Recall that $U(0) = \alpha U_\alpha(0) + \beta U_\beta(0) = \theta$. Thus $\beta U_\beta(0) < \theta$ and since $U'_\beta \geq 0$ then $\beta U_\beta(z) < \theta$ for all $z < 0$ and particularly, for all $z < z_*$.

The results above show that $U = \alpha U_\alpha + \beta U_\beta$ cannot cross θ before $z_* \in (-M, 0)$ because αU_α started from zero and is decreasing while βU_β by itself is less than θ. On the interval (z_*, N) both $U'_\alpha > 0$ and $U'_\beta > 0$ so $U' > 0$ and U is strictly increasing (and crosses θ at 0). Past N, U'_α may change signs once and $U'_\beta > 0$. This means U' may change signs a maximum of once also. In the case that it does not change signs then the proof is finished. In the case that it does change signs, we apply the $+\infty$ boundary conditions in Lemma 3.3. Since $U \to \alpha + \beta$ then $U' < 0$ implies that U crossed above $\alpha + \beta$ and then approaches it from above. In this case, U cannot cross θ again either and this completes the proof of the this lemma. ☐

Combining the derivation of (23) and Lemmas 3.2, 3.3 and 3.4, we have proved Theorem 3.1.

4. **Travelling wave solutions for $\mathbf{K}(\mathbf{x})$ of type (C).** Here it is shown that for $K(x)$ of Type (C), with the same conditions as in Theorem 3.1 if the existence and uniqueness of the μ_0 wave speed can be guaranteed then the model also yields travelling wave solutions.

Theorem 4.1. *Assume that $K(x)$ is of Type (C) and $\theta < (\alpha+\beta)/2$. If there exists a unique $\mu_0 \in (0, c)$ such that $\varphi(\mu_0) = \frac{\alpha+\beta}{2} - \theta$ then there exists a solution to (1) given by $u(x,t) = U(z)$ where $z = x + \mu_0 \tau$ and $U(z)$ is the solution to the ODE (20) with phase conditions (21). The solution is given by (23) and also satisfies the boundary conditions (22).*

Proof. In the proof of Theorem 3.1, the only parts that depended on the type of $K(x)$ is that pertaining to μ_0 and the phase conditions. The uniqueness of μ_0 is a requirement of Theorem 4.1 and it also guarantees that $U(0) = \theta$. Thus all that remains is to prove that $U < \theta$ on $(-\infty, 0)$ and $U > \theta$ on $(0, +\infty)$ as required in (21).

This proof will be performed in a similar manner to the proof in Lemma 3.4 for Type (B) kernels. Firstly, separate the terms involving α from those involving β like in (37)-(41). We re-arrange the expression for U'_α from (40) here for convenience:

$$\begin{aligned} \mu_0 e^{\frac{z}{\mu_0}} U'_\alpha &= \int_{-\infty}^{z} e^{\frac{x}{\mu_0}} \frac{c}{c+\mu_0 \operatorname{sgn}(z)} K\left(\frac{cx}{c+\mu_0 \operatorname{sgn}(z)}\right) dx \\ &= \int_{-\infty}^{\frac{c+\mu_0 \operatorname{sgn}(z)}{c\mu_0} z} e^{\frac{c+\mu_0 \operatorname{sgn}(z)}{c\mu_0} x} K(x)\, dx. \end{aligned} \tag{44}$$

Recall that Type (C) kernels have the following properties: $K(x) \leq 0$ if $x \in (-M, N)$ and $K(x) \geq 0$ if $x \in (-\infty, -M) \cup (N, +\infty)$. Thus, from the above expression we see that $\mu_0 e^{\frac{z}{\mu_0}} U'_\alpha$ starts at zero at $z = -\infty$ and monotonically increases up until $z = -\frac{c\mu_0}{c-\mu_0}M$. Past this it decreases until it hits $z = \frac{c\mu_0}{c-\mu_0}N$ and then starts increasing again. From all this we can infer that $U'_\alpha(z) \geq 0$ for $z \in \left(-\infty, -\frac{c\mu_0}{c-\mu_0}M\right)$ and may change signs to negative on $\left(-\frac{c\mu_0}{c-\mu_0}M, \frac{c\mu_0}{c-\mu_0}N\right)$.

Now note that since $K(x)$ has to integrate to $\frac{1}{2}$ then it is easy to prove the for $z >> N$ we must have $U'_\alpha > 0$ (the proof is similar to that in Lemma 3.4. Thus if U'_α did go negative on $\left(-\frac{c\mu_0}{c-\mu_0}M, \frac{c\mu_0}{c-\mu_0}N\right)$ then it has to turn positive again somewhere on $\left(\frac{c\mu_0}{c-\mu_0}N, +\infty\right)$.

From the equation (44), we can evaluate

$$U'_\alpha(0) = \frac{1}{\mu_0}\int_{-\infty}^{0} e^{\frac{(c-\mu_0)x}{c\mu_0}} K(x)\,dx = \frac{1}{\alpha}\varphi_\alpha(\mu_0) > 0 \quad \text{since } \varphi_\alpha \in \left(0, \frac{\alpha}{2}\right).$$

This means that U_α is monotonically increasing on $(-\infty, 0)$. From here we consider two cases.

Case 1 : $U'_\alpha\left(\frac{c\mu_0}{c-\mu_0}N\right) \geq 0$. Since at $z > \frac{c\mu_0}{c-\mu_0}N$, $\mu_0 e^{\frac{z}{\mu_0}} U'_\alpha$ is increasing (and therefore cannot go negative) then $U'_\alpha \geq 0$ for $(0, +\infty)$. Thus in this case $U'_\alpha \geq 0$ for all $x \in \mathbb{R}$. Since $U'_\beta \geq 0$ for all x as well, then $U' > 0$ also for all x and we have a monotonically increasing wavefront. Given already that $U(0) = \theta$, this proves the phase conditions.

Case 2 : $U'_\alpha\left(\frac{c\mu_0}{c-\mu_0}N\right) < 0$. For this case to happen, there must exist one and only one $z_1 \in \left(0, \frac{c\mu_0}{c-\mu_0}N\right)$ such that $U'_\alpha(z_1) = 0$ corresponding to a relative maximum for U_α. Since $U'_\alpha \geq 0$ for large enough z, there must exist a $z_2 \in \left(\frac{c\mu_0}{c-\mu_0}N, +\infty\right)$ such that $U'_\alpha(z_2) = 0$ corresponding to a relative minimum:

$$\begin{aligned}\alpha U_\alpha(z_2) &= \frac{\alpha}{2} + \alpha\int_0^N K(x)\,dx + \alpha\int_N^{\frac{c\mu_0}{c-\mu_0}z_2} K(x)\,dx \\ &> \frac{\alpha}{2} + \alpha\int_0^N K(x)\,dx \geq \theta - \delta \quad \text{from the requirements of type C kernels.}\end{aligned} \tag{45}$$

Now recall that

$$\begin{aligned}\beta U_\beta(0) &= \frac{\beta}{2} - \varphi_\beta(\mu_0) \\ &= \Delta(\mu_0) \geq \delta \quad \text{from the properties of} \quad \Delta(\mu).\end{aligned}$$

Since $U(0) = \alpha U_\alpha(0) + \beta U_\beta(0) = \theta$, $\alpha U_\alpha(0) = \theta - \Delta(\mu_0) \leq \theta - \delta$.

From (45) we find that $\alpha U_\alpha(z_2) > \alpha U_\alpha(0)$. Thus we now have a complete description of the behavior of U_α. It is increasing on $(-\infty, z_1)$ (where $z_1 > 0$), and decreasing on (z_1, z_2) and increasing again on $(z_2, +\infty)$. It attains a local maximum at z_1 and a local minimum at z_2 for which $U_\alpha(z_2) > U_\alpha(0)$. Thus if we consider that $U'_\beta > 0$ for all z then we find that U behaves in the following manner: it is increasing from $(-\infty, z_1)$. $U(0) = \theta$ and on $(-\infty, z_1)$ it could not have crossed it again. However U may be increasing or decreasing on the interval (z_1, z_2). Since

U_β is still increasing here then closest U may come back down to θ is at z_2 if $U_\beta(z_2) = U_\beta(0)$. However,

$$\alpha U_\alpha(z_2) > \alpha U_\alpha(0),$$
$$\alpha U_\alpha(z_2) + \beta U_\beta(0) > \alpha U_\alpha(0) + \beta U_\beta(0) = \theta.$$

Thus U cannot possibly cross θ again in (z_1, z_2). On $(z_2, +\infty)$, U is increasing again.

The above completes the proof of Theorem 4.1. □

Remark 2. A special case that can be considered for this section is that when $\delta < \theta$ (as required in Section 3). This requirement guarantees the existence of μ_0 but not its uniqueness. If we perform analysis similar to Lemma 3.2, we find that in this case φ_α starts off decreasing, reaches a minimum and then goes on increasing. φ_β on the other hand is always increasing. Some choices for $K(x)$ and $J(x)$ may allow for the possibility of non-unique μ_0. It is also possible to ensure the uniqueness of μ_0 under some condition(s). One such condition is the requirement that $\varphi_\beta < \frac{\alpha+\beta}{2} - \theta$ on the entire interval $(0, c)$. This means requiring

$$\max_{\mu\in(0,c)} \varphi_\beta(\mu) = \varphi_\beta(c) = \frac{\beta}{2} - \delta < \frac{\alpha+\beta}{2} - \theta, \tag{46}$$

that is, $\delta > \theta - \alpha/2$. Thus if

$$\theta - \alpha/2 < \delta < \theta, \tag{47}$$

then we are guaranteed existence of a travelling wave solution for kernel $K(x)$ of Type C, with the wave speed uniquely determined by $\phi(\mu_0) = (\alpha + \beta)/2 - \theta$.

5. Travelling wave solutions for $\mathbf{K}(\mathbf{x})$ of type (D).

For this type of kernel function $K(x)$, it has been pointed out in [10] that (1) does not allow travelling wave front when $\beta = 0$. Now in the presence of the nonlocal feedback connections (i.e., $\beta > 0$), we will see in this section that travelling wave front becomes possible. Indeed, if $\beta > \alpha$, then (PDEU) has the positive equilibrium $U = \beta - \alpha$. Following the same lines as in Sections 5, we can obtain the following theorem.

Theorem 5.1. *Let $K(x)$ be of Type (D). Assume that $\beta > \alpha$ and $0 < \theta < \frac{\beta-\alpha}{2}$. If there exists a unique $\mu_0 \in (0, c)$ such that $\varphi(\mu_0) = \frac{\beta-\alpha}{2} - \theta$, then there exists a solution to (1) given by $u(x,t) = U(z)$ where $z = x + \mu_0\tau$ and $U(z)$ is the solution to the ODE (20) with phase conditions (21). The solution is given by (23) and also satisfies the boundary conditions*

$$\lim_{z\to-\infty} U(z) = 0, \quad \lim_{z\to+\infty} U(z) = \beta - \alpha, \quad \lim_{z\to\pm\infty} U'(z) = 0. \tag{48}$$

We omit the proof of this theorem because it is similar to that for Theorems 3.1 and 5.1 (with some portions being exactly the same). Travelling wave fronts may also be found under less strict conditions but that is beyond the scope of this study. In the next session, an example will be given for $K(x)$ of Type (D), for which numeric simulations will be performed to show the existence of a travelling wave front.

6. **Conclusions and discussion.** In the previous sessions, we have established the existence of travelling wave fronts for the model (1) with both synaptic input by axonal connections (α connections) and the delayed nonlocal feedback connections (β connections). We have seen that the existence of the wave front is characterized by the total speed index function $\varphi(\mu)$: under some restrictions on the model parameters, for kernel $K(x)$ of types (A),(B) and (C), the wave speed μ_0 is the unique solution of

$$\varphi(\mu) = \frac{\beta + \alpha}{2} - \theta, \quad \mu \in (0, c); \tag{49}$$

while for kernel $K(x)$ of type (D), the wave speed μ_0 is determined by

$$\varphi(\mu) = \frac{\beta - \alpha}{2} - \theta, \quad \mu \in (0, c). \tag{50}$$

From the results in the above sessions, we see the wave speed μ_0, if any, is indeed smaller than the axon potential speed c as is observed experimentally. We have also seen that the wave obeys the phase conditions (21); this means that once a neuron at position x is activated beyond its threshold value θ it does not relax back down again to a value below θ. But this does not imply that the wave front has to be monotone, see the examples 3 and 4 in the next section.

Since the main feature of the model (1) is the presence of the delayed nonlocal feedback connections, it is interesting and worthwhile to discuss impact of delayed feedback on the existence of wave front. First of all, as mentioned in the introduction, for the pure inhibitory type axon connection (kernel $K(x)$ of type (D)), in the absence of feedback connections, there will be no travelling wave front. Now, for this type of kernel $K(x)$, the incorporation of the delayed non-local feedback connections with appropriate chosen kernel $J(x)$, travelling wave front becomes possible. Although analytically determining the existence of a unique root for speed equation (50) remains an open problem, the Example 4 in the next section does show that for $\beta > \alpha$ it is possible for (1) to have travelling waves.

We may also discuss the dependence of the travelling wave speed μ_0 on on the connection strength β and the magnitude of the delay τ. Take the kernel $K(x)$ of types (A) or (B) as an example, by (12)-(14), (17) and (19), we know that the root of (49) is *decreasing in* $\tau > 0$, meaning that the *larger* the delay τ, the *smaller* the wave speed μ_0. To see the impact of β on μ_0, we rewrite (49) as

$$\varphi(\mu) - \frac{\beta}{2} = \frac{\alpha}{2} - \theta. \tag{51}$$

Now by(12)-(14), (19) and (15), we obtain

$$\frac{\partial}{\partial \beta}\left(\varphi(\mu) - \frac{\beta}{2}\right) = \frac{\partial}{\partial \beta}\left(\varphi_\beta(\mu) - \frac{\beta}{2}\right) = \frac{\partial}{\partial \beta}\left(-\Delta(\mu)\right) \tag{52}$$

$$= \int_{-\infty}^{0}\left(1 - e^{x/\mu}\right) J(x - \mu\tau)\, dx < 0. \tag{53}$$

Noting that the right hand side of (51) is independent of β, we conclude that the wave speed (the root of (51)) is *increasing in* β. Of course, when $\beta = 0$ the wave speed μ_0 reduces to the wave speed purely determined by the α speed index function $\varphi_\alpha(\mu)$.

7. **Examples.** This section intends to give examples to numerically demonstrate the results obtained in the previous sections. To this end, we fix the kernel $J(x)$ as below

$$J(x) = \frac{1}{\sqrt{\pi}} e^{-x^2}, \tag{54}$$

which obviously satisfies conditions (6) and (7). Then, for each of the types (A)-(D), we choose the following particular kernels for $K(x)$:

- Example 1 (type (A)): $K(x) = \frac{1}{2}\exp(-|x|)$.
- Example 2 (type (B)): $K(x) = 4|x|\exp^{-4|x|} - |x|\exp^{-2|x|}$.
- Example 3 (type (C)): $K(x) = \frac{5}{2}|x|\exp^{-|x|} - 4|x|\exp^{-\sqrt{2}|x|}$.
- Example 4 (type (D)): $K(x) = -\frac{1}{2}\exp(-|x|)$.

The explicit model parameters for Examples 1-3 are chosen as below:

$$\alpha = 3.0; \ \ \beta = 0.75, \ \ c = 2.0, \ \ \tau = 0.25, \ \ \theta = 1.00. \tag{55}$$

Then the related indirect parameters are numerically determined to be
(i) $\delta \approx 0.0042$, $\mu_0 \approx 0.565$ for Example 1;
(ii) $\delta \approx 0.0042$, $\mu_0 \approx 0.146$ for Example 2;
(iii) $\delta \approx 0.0042$, $\mu_0 \approx 1.398$ for Example 3.
For Example 4, the explicit parameters are given by

$$\alpha = 0.50; \ \ \beta = 3.00, \ \ c = 2.0, \ \ \tau = 0.25, \ \ \theta = 1.00, \tag{56}$$

which numerically determine
(iv) $\delta \approx 0.0042$, $\mu_0 \approx 0.138$.

For the purpose of comparison with results for the model without delayed non-local feedback connection (i.e., $\beta = 0$), we denote the wave speed for $\beta = 0$ by μ_α. That is, for Examples 1-3, μ_α solves $\varphi_\alpha(\mu) = \alpha/2 - \theta$ in for μ in $\mu \in (0, c)$, while for Example 4 there is no such μ_α. The determinations of wave speed for each of the four examples are demonstrated in Figures 1-4.

With the above explicit parameters given and indirect parameters determined, the wave equation (8) can be numerically solved, giving travelling wave front as illustrated in Figures 5-8 for Examples 1-4 respectively. Observe that the travelling wave fronts for Example 2 are non-monotone. More interestingly, in Example 3, for $\beta = 0$ the travelling wave front is non-monotone while for $\beta = 0.75 > 0$, the wave front becomes monotone. This observation suggests that the β connection not only affects the waves speed but also has an impact on the shape of the wave fronts.

Finally, we point out that although in the end of Section 6, we are able to show that the wave speed is decreasing in the delay τ only for Types A and B, numerical simulations seem to support this conclusion for Types C and D as well. Figure 10 is the numerical result for type D, showing the dependence of μ_0 on τ, from which we can see that the wave speed μ_0 decreases asymptotically to zero as τ is increased. One possible explanation for this is that the assumption of non-negativeness of the kernel $J(x)$ guarantees a *positive* global feedback from the whole neural fields which is delayed by τ time units. Such a *positive* global feedback is advantageous to the propagation of signals represented by the traveling wave fronts, and thus, the larger the delay, the longer it takes for a location to receive the global feedback, and hence, the slower the propagation would be. The same conclusion has been obtained for travelling wave fronts in reaction-diffusion models for population growth with a maturation delay, see, e.g., Zou [11] and the references therein. However, as τ

varies, the shape of the wavefront does not change significantly, and we omit the simulation results here.

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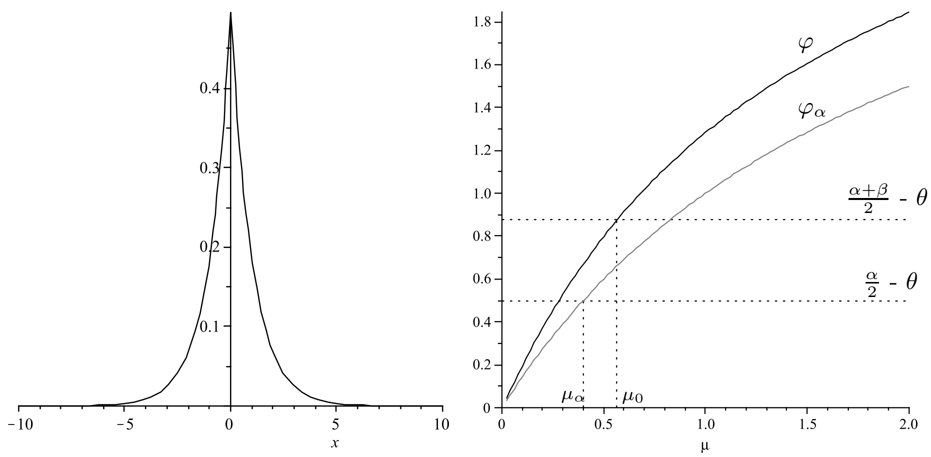
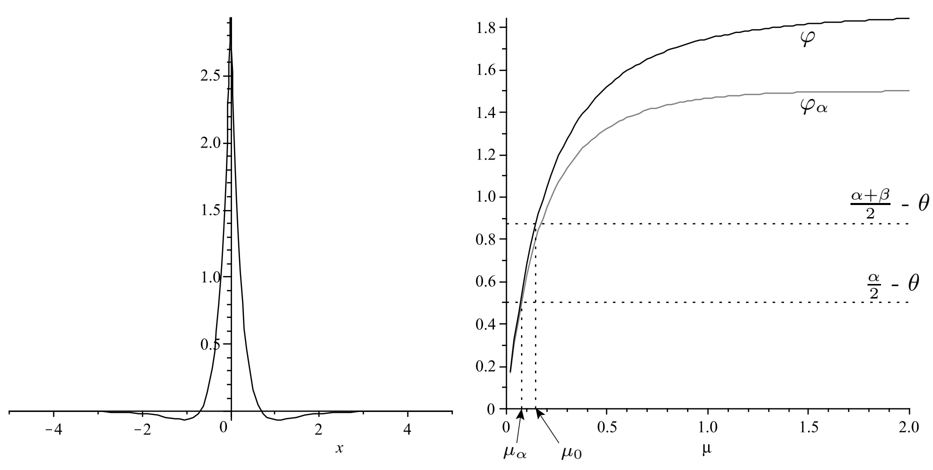


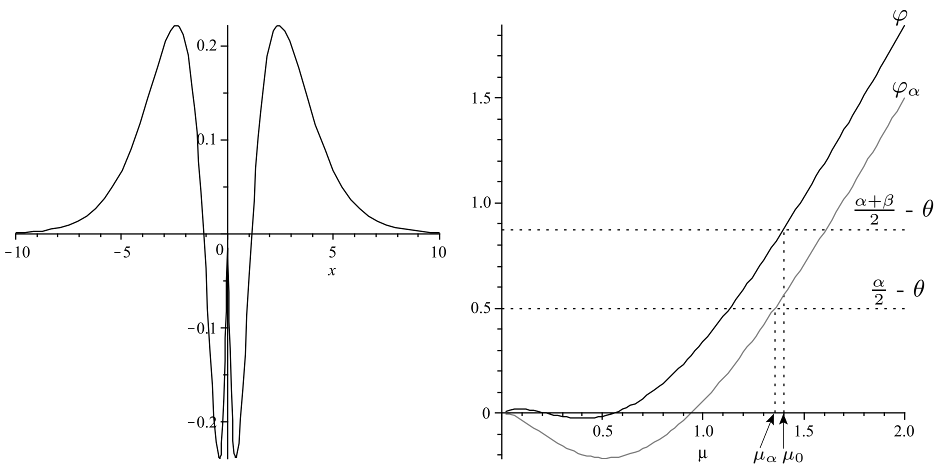
(a) $K(x) = \frac{1}{2}\exp(-|x|)$ (b) Comparison of φ and φ_α

FIGURE 2. Determination of wave speed for Example 1.



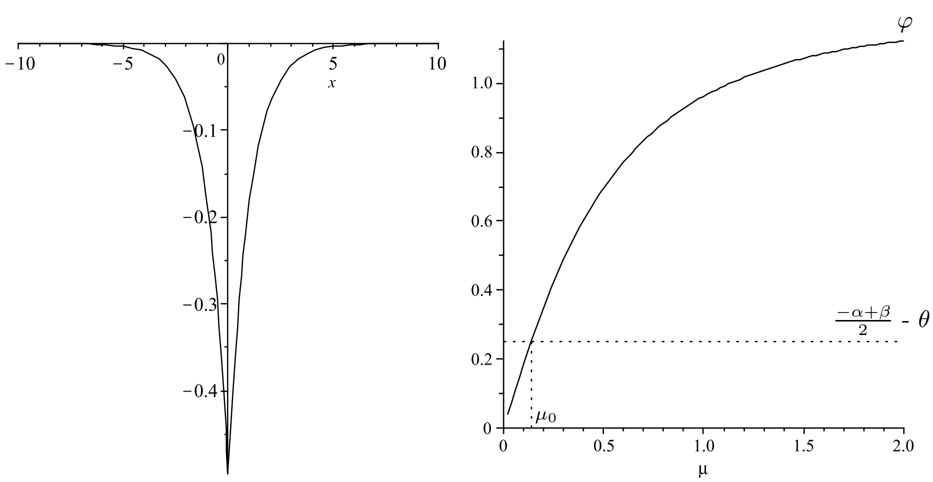
(a) $K(x) = 4|x|\exp^{-4|x|} - |x|\exp^{-2|x|}$ (b) Comparison of φ and φ_α

FIGURE 3. Determination of wave speed for Example 2.



(a) $K(x) = \frac{5}{2}|x|\exp^{-|x|} - 4|x|\exp^{-\sqrt{2}|x|}$ (b) Comparison of φ and φ_α

FIGURE 4. Determination of wave speed for Example 3.



(a) $K(x) = -\frac{1}{2}\exp(-|x|)$ (b) Speed index function φ

FIGURE 5. Determination of wave speed for Example 4.

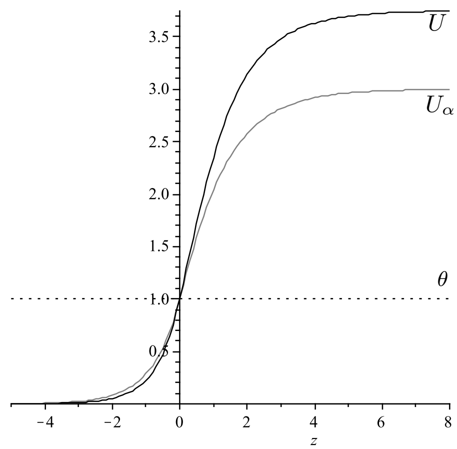


FIGURE 6. Plots of travelling wave solution for Example 1.

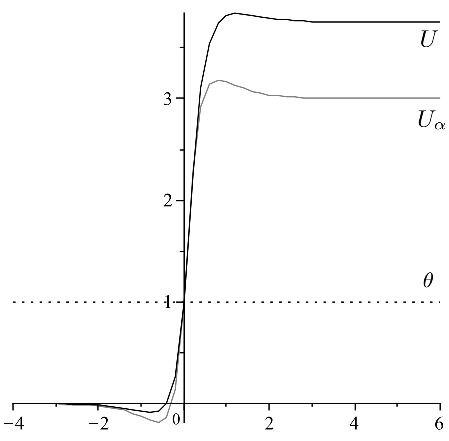


FIGURE 7. Plots of travelling wave solution for Example 2.

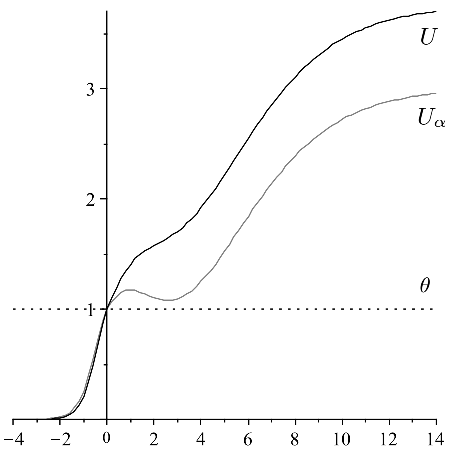


FIGURE 8. Plots of travelling wave solution for Example 3.

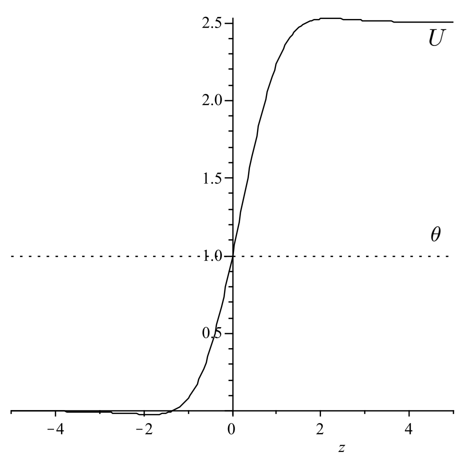


FIGURE 9. Plots of travelling wave solution for Example 4.

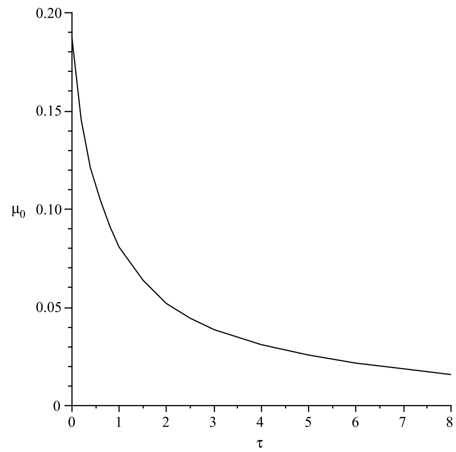


FIGURE 10. In Example 4, wave speed μ_0 decreases as τ increases.

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