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Original Article

Traveling wave front solutions in lateral-excitatory neuronal networks

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Abstract

In this paper, we discuss the shape of traveling wave front solutions to a neuronal model with the connection function to be of lateral excitation type. This means that close connecting cells have an inhibitory influence, while cells that are more distant have an excitatory influence. We give results on the shape of the wave fronts solutions, which exhibit different shapes depending on the size of a threshold parameter.

Key words: neural fields, traveling wave solutions, neuronal model, neural networks

1. Introduction

Neuronal systems are very complicated. There are approximately 10^{12} neurons in the human brain and 10^{15} synapses. Abnormal electrical discharges from brain cells result in a recurrent seizure disorder such as epilepsy and migraine. Work on neural fields has its origins in the pioneering work of Beurle (1956), Griffith (1963, 1965), Wilson and Cowan (1972, 1973), Amari (1975, 1977), and Kishimoto and Amari (1979). Beurle (1956) provided a first detailed analysis of the triggering and propagation of large-scale brain activities, considering the proportion of neurons becoming activated per unit time in a given volume element of tissue slice, which is consisting of randomly connected neurons. Beurle dealt only with networks of excitatory neurons without recovery, but confirmed the possibility of large-scale traveling and rotating waves in nervous tissue. Wilson and Cowan (1972, 1973) extended Beurle's work to include both excitatory and inhibitory neurons, as well as incorporating neural refractoriness.

Most of the analytic and computational work on continuous neural field models involves a one-space dimension. As mentioned above, since stationary solutions represent short-term memories, it is still an active research area (Laing and Longtin, 2001; Coombes *et al.*, 2003; Coville and Dupaigne, 2005). Amari (1977) considered the existence and stability of a single bump steady state in the high-gain limiting case, while the two bump solutions seem not to be stable (Laing and Troy, 2003). Modification of the connection function can stabilize or destabilize the bump structures (Laing *et al.*, 2002; Guo and Chow, 2005). Moreover, Rubin and Troy (2004) explored the bump in a single population of spiking neurons on the assumption that the kernel was an off-center coupling function, that is, it was assumed to be continuous, symmetric, and positive on (x_0, x_1), and negative on $(-x_0, x_0)$, and (x_1, ∞) for any arbitrary constants x_0, x_1, such that $0 < x_0 < x_1$. The shape of the connection function can also allow other types of solutions, such as lurching traveling waves (Golomb and Ermentrout, 1999), and other patterns (Price, 1997; Jirsa and Kelso, 2000; Werner and Richter, 2001). There is ongoing bifurcation work to understand what patterns are possible, but the investigations are presently incomplete.

The body of work on propagating fronts and pulses is

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fairly extensive now, see e.g. Jirsa and Haken (1996), Hoppensteadt and Mittelmann (1997), Pinto and Ermentrout (2001a,b), Wennekers (2002), Enculescu (2004), Jalics (2004), Richardson *et al.* (2005), and Ruktamatakul *et al.* (2006). For the scalar problem, Ermentrout and McLeod (1993) proved existence and uniqueness of traveling wave fronts via continuation methods (see also Bates *et al.*, 1997; Chen *et al.*, 1997), and Chen (2003) extended the work. For some specific connection functions and the high-gain limit for the firing rate function, there are specific existence, uniqueness, and stability results available (Pinto and Ermentrout, 2001a; Enculescu, 2004; Zhang, 2004; Ruktamatakul *et al.*, 2006). Chen (1997) used a comparison argument to obtain existence and qualitative properties of solutions. Fife (1995), although his application area is material science, discusses comparison results for related integrodifferential equations. With the cortical layers more properly modeled by neural fields as a 2D structure, then plane waves and wave trains, target patterns (Enculescu and Bestehorn, 2003), spiral waves (Huang *et al.*, 2004), and other patterns can be investigated.

2. Mathematical Model

In this study, we will describe the shape of traveling wave front solutions in a neuronal model. The general neural field model, which is proposed by many works such as Amari (1977), Pinto and Ermentrout (2001a), Coombes *et al.* (2003), Zhang (2004), takes the form

$$\frac{\partial u}{\partial t} + u = \int K(x,x')f(u(x',t))dx' + S(x,t). \quad (1)$$

Here $u = u(x,t)$ can be interpreted as an averaged post-synaptic potential of cells located at space variable x at time t. The function $K(x,x')$ is the strength, or weight, of the connections of neuronal activity at location x' on the activity of the neuron at location x. The strength of the connection is based on the distance between cells, that is, $K(x,x') = K(x-x')$. We also employ the homogeneous and isotropic assumption for the layer so that $K(x-x')$ is an even function of its argument. In general, $K(x-x')$ has four types, which are called excitatory, inhibitory, lateral-inhibitory, and lateral-excitatory. In this paper, we will analyze only case lateral-excitatory. $f(u(x',t))$ represents the firing rate function and $S(x,t)$ is the stimulation from outside the layer. This study we will assume that there is no stimulation from outside the layer. In particular, we will investigate the model (1) with f being the double step function so that we may replace the function f by the Heaviside step function, $H(u-\theta)$, where θ is the fixed threshold value, $H(u-\theta)=1$ for $u \geq \theta$ and $H(u-\theta)=0$ for $u < \theta$. Therefore, the model to be analyzed in this paper as shown in Equation 1 is written as

$$\frac{\partial u(x,t)}{\partial t} + u(x,t) = \alpha\int K(x-y)H(u(y,t)-\theta)dy. \quad (2)$$

3. Analysis of the Wave Front

In this paper, we will discuss the existence and uniqueness of traveling wave front solutions of the form $u(x,t)=U(z),\ z = x+\upsilon t$, for some constant wave speed υ, and all $x \in \Re$, $t>0$, for a low firing threshold potential, and a high firing threshold potential, and we will give some results on the shape of the wave front solution for all cases possible. For the following analysis, assume

(A1) $K(x)$ is continuous, bounded, even, and integrable on the real line, and $\int_{-\infty}^{\infty} K(x)dx = 1$. Also, because of the lateral excitation assumption, $K(x)<0$ for $|x|<x_0$, and $K(x)>0$ for $|x|>x_0$.

(A2) $U(0)=\theta$.

(A3) $U(z)>\theta$ if and only if $z>0$.

A typical example of such candidate kernel includes $K(x) = a_1 e^{-b_1|x|} - a_2 e^{-b_2|x|}$ where $0<a_1<a_2$, $0<b_1<b_2$ and $\frac{a_1}{b_1} - \frac{a_2}{b_2} = \frac{1}{2}$ as shown in Figure 1.

3.1 Existence and uniqueness of traveling wave front solutions

We will discuss the existence and uniqueness of traveling wave front solutions in the special case of the connection function $K(x)$ such that $K(x)=K_1(x)-K_2(x)$, $K_1(x) \geq -ce^{\mu x}$, $K_2(x) \leq -de^{\rho x}$ for $x<0$ and $K_1(x) \geq -ce^{-\mu x}$, $K_2(x) \leq -de^{-\rho x}$ for $x>0$. By using these properties of $K(x)$, we shall be able to prove Theorem 1.

Theorem 1: Suppose that α and θ are positive constants, such that $0<2\theta<\alpha$. Besides the properties mentioned in (A1), we also assume that $K(x)=K_1(x)-K_2(x)$, $K_1(x) \geq -ce^{\mu x}$, $K_2(x) \leq -de^{\rho x}$ for $x<0$ and $\frac{c}{(1+\mu\upsilon)^2} < \frac{d}{(1+\rho\upsilon)^2}$, where $c>d>0$ and $\mu,\rho>0$. Then, there exists a unique wave front $u(x,t)=U(z)$, where $z=x+\upsilon_0 t$, to the scalar Equation 2, with unique wave speed $\upsilon_0 = \upsilon_0\left(\frac{\theta}{\alpha}\right)>0$ such that $\int_{-\infty}^{0} e^{\frac{x}{\upsilon_0}}K(x)dx = \frac{1}{2} - \frac{\theta}{\alpha}$. Using (A3), the wave front is given by

$$U(z) = \alpha\int_{-\infty}^{z} K(x)dx - \alpha\int_{-\infty}^{z} e^{\frac{x-z}{\upsilon_0}}K(x)dx.$$

Further, we have the limits

$$\lim_{z\to-\infty}(U(z),U'(z)) = (0,0),\ \lim_{z\to+\infty}(U(z),U'(z)) = (\alpha,0).$$

Proof: For traveling front solutions, we consider nontrivial solutions of the form $u(x,t)=U(z)$, $z=x+\upsilon t$, for some wave speeds υ. Substituting this form in Equation 2, we obtain

$$\upsilon U'(z)+U(z)=\alpha\int_{\Re}K(z-y)H(U(y)-\theta)dy. \quad (3)$$

The constant solutions of this equation are $U(z) = \alpha\int_{\Re}K(z-y)H(U(y)-\theta)dy$. By the property of Heaviside step function; that is, $H(x)=1$ for $x\geq 0$ and $H(x)=0$ for $x<0$, we obtain

$$U(z)=\alpha\int_0^{\infty}K(z-y)dy=\alpha\int_{-\infty}^{z}K(x)dx.$$

Thus, the traveling wave front, for $\upsilon>0$, is connecting $U_-\equiv 0<\theta$ at $z=-\infty$ to $U_+\equiv\alpha>\theta$ at $z=+\infty$. Equation 3 then reduces to

$$\upsilon U'(z)+U(z)=\alpha\int_{-\infty}^{z}K(x)dx. \quad (4)$$

Write $f(z)=\alpha\int_{\infty}^{z}K(x)dx$, and the Equation 4 then becomes $\upsilon U'(z)+U(z)=f(z)$ which may be written as $\left(e^{\frac{z}{\upsilon}}U\right)' = \frac{1}{\upsilon}e^{\frac{z}{\upsilon}}f(z)$. Thus,

$$e^{\frac{z}{\upsilon}}U(z)=\frac{1}{\upsilon}\left\{\upsilon e^{\frac{z}{\upsilon}}f(z)-\upsilon\int_z^{\infty}e^{\frac{x}{\upsilon}}f'(x)dx\right\}.$$

So, the bounded solution is

$$U(z)=\alpha\int_{-\infty}^{z}K(x)dx-\alpha\int_{-\infty}^{z}e^{\frac{x-z}{\upsilon}}K(x)dx. \quad (5)$$

Next, we will prove that there is a unique wave front solution by showing that the wave speed is unique. To find the wave speed from the Equation 5, we define an auxiliary function by using the assumption (A2), so that we have

$$\theta\equiv A(\upsilon)=\frac{\alpha}{2}-\alpha\int_{-\infty}^{0}e^{\frac{x}{\upsilon}}K(x)dx.$$

Then, from the hypotheses, the following limits and inequalities hold:

$$\lim_{\upsilon\to+\infty}A(\upsilon)=0<\theta<\frac{\alpha}{2}=\lim_{\upsilon\to 0^+}A(\upsilon).$$

Furthermore, $A'(\upsilon)=\frac{\alpha}{\upsilon^2}\int_{-\infty}^{0}xe^{\frac{x}{\upsilon}}K(x)dx$. The hypotheses on K are sufficient to show that $A'(\upsilon)<0$. Now,

$$\frac{\upsilon^2}{\alpha}A'(\upsilon)=\int_{-\infty}^{0}xe^{\frac{x}{\upsilon}}\{K_1(x)-K_2(x)\}dx$$

$$\leq\int_{-\infty}^{0}xe^{\frac{x}{\upsilon}}\{ce^{\mu x}\}dx-\int_{-\infty}^{0}xe^{\frac{x}{\upsilon}}\{de^{\rho x}\}dx$$

$$=\frac{c\upsilon^2}{(1+\mu\upsilon)^2}-\frac{d\upsilon^2}{(1+\rho\upsilon)^2}<0.$$

Hence, by continuity and monotonicity of $A(\upsilon)$, there is a unique $\upsilon=\upsilon_0>0$ such that $\frac{\alpha}{2}-\alpha\int_{-\infty}^{0}e^{\frac{x}{\upsilon_0}}K(x)dx=\theta$.

3.2 Analysis of the shape of wave front

In this section, we show that the wave front solution is a non-monotone function for both the "high" and "low" firing threshold potential θ. The difference between the two cases is that the wave shape is monotone on $(0,+\infty)$ for θ being close to 0, but it is not the case when θ is close to $\frac{\alpha}{2}$. We analyze the wave shape by separating the domain into four subintervals, that is $(-\infty,-x_0)$, $(-x_0,0)$, $(0,x_0)$, and (x_0,∞).

Lemma 1: For $2\theta<\alpha$, let $U(z)$ be the wave front solution to Equation 3. Then, $U'(z)>0$ for $z<-x_0$, and therefore $U'(z)>0$ on $z<0$.

Proof: For $z\in(-\infty,-x_0)$, we have $K(x)>0$. So, $U'(z)=\frac{\alpha}{\upsilon}\int_{-\infty}^{z}e^{\frac{(x-z)}{\upsilon}}K(x)dx>0$. Thus, $U(z)$ is monotone increasing on $(-\infty,-x_0)$.

For $z\in(-x_0,0)$, we have

$$\begin{aligned}\frac{\upsilon}{\alpha}U'(z)e^{\frac{z}{\upsilon}} &= \int_{-\infty}^{z}e^{\frac{x}{\upsilon}}K(x)dx\\ &=\int_{-\infty}^{0}e^{\frac{x}{\upsilon}}K(x)dx-\int_{z}^{0}e^{\frac{x}{\upsilon}}K(x)dx\\ &=\frac{1}{\alpha}\left(\frac{\alpha}{2}-\theta\right)-\int_{z}^{0}e^{\frac{x}{\upsilon}}K(x)dx.\end{aligned}$$

Since $\frac{\alpha}{2}>\theta$ and $K(x)<0$ when $x\in(-x_0,0)$, so $\frac{1}{\alpha}\left(\frac{\alpha}{2}-\theta\right)>0$ and $-\int_{z}^{0}e^{\frac{x}{\upsilon}}K(x)dx>0$. Thus, $\frac{\upsilon}{\alpha}U'(z)e^{\frac{z}{\upsilon}}>0$, $U(z)$ is monotone increasing on $(-x_0,0)$. Hence $U'(z)>0$ on $z<0$.

Lemma 2: For $2\theta<\alpha$, assume, besides (A1), that $K(x)$ satisfies the following.

1) $\frac{K(0)x_0}{2}<\frac{1}{\alpha}\left(\theta-\frac{\alpha}{2}\right)$

2) There exist $m_1, \rho_1 > 0$ such that for some $Z_1 > x_0$, it holds that for $x > Z_1$, $K(x) > m_1 e^{-\rho_1 x}$.

3) $\upsilon \rho_1 < 1$.

Then,

a) there is a unique $z = z_1 \in (0, x_0)$ which is a local maximum point for $U(z)$ in that $U'(z) > 0$ on $(0, z_1)$, and $U'(z) < 0$ on (z_1, x_0).

b) there is a unique $z = z_2 \in (x_0, \infty)$ which is a local minimum point for $U(z)$ in that $U'(z) < 0$ on (x_0, z_2), and $U'(z) > 0$ on (z_2, ∞).

Proof: If $z \to 0^+$, then

$$U'(0^+) = \frac{\alpha}{\upsilon} \int_{-\infty}^{0} e^{\frac{x}{\upsilon}} K(x)dx$$

$$= \frac{1}{\upsilon}\left\{\alpha \int_{-\infty}^{0} e^{\frac{x}{\upsilon}} K(x)dx\right\}$$

$$= \frac{1}{\upsilon}\left\{\frac{\alpha}{2} - \theta\right\}$$

since $2\theta < \alpha$ and $\upsilon > 0$. By continuity, then $U'(z) > 0$ for some interval $[0, \delta)$, $\delta > 0$.

Let $y_1(x) = \dfrac{K(0)}{x_0}(x_0 - x)$ such that $K(x) \le y_1(x)$ on $(0, x_0)$. Since

$$\int_0^{x_0} K(x)dx < \int_0^{x_0} y_1(x)dx$$

$$= \frac{K(0)}{x_0}\int_0^{x_0}(x_0 - x)dx = \frac{K(0)x_0}{2}$$

we have

$$\frac{\upsilon}{\alpha}U'(x_0)e^{\frac{x_0}{\upsilon}} = \int_{-\infty}^{x_0} e^{\frac{x}{\upsilon}} K(x)dx$$

$$= \int_{-\infty}^{0} e^{\frac{x}{\upsilon}} K(x)dx + \int_{0}^{x_0} e^{\frac{x}{\upsilon}} K(x)dx$$

$$< \frac{1}{\alpha}\left(\frac{\alpha}{2} - \theta\right) + \int_0^{x_0} K(x)dx$$

$$< \frac{1}{\alpha}\left(\frac{\alpha}{2} - \theta\right) + \frac{K(0)x_0}{2} < 0.$$

Then, $U'(x_0) < 0$. Therefore, there exists a $z = z_1$, $z_1 \in (0, x_0)$, such that $U'(z_1) = 0$ and $U(z_1)$ is a local maximum.

Next, we prove z_1 is unique. Suppose not, then there are at least two different $z's$, say z_1 and z_1', such that $U'(z_1) = 0$, $U'(z_1') = 0$ and $z_1, z_1' \in (0, x_0)$. Then, one is larger, say $0 < z_1 < z_1' < x_0$. Since $U'(z_1) = \dfrac{\alpha}{\upsilon}\displaystyle\int_{-\infty}^{z_1} e^{\frac{(x - z_1)}{\upsilon}} K(x)dx = 0$, we have

$$\int_{-\infty}^{z_1} e^{\frac{x}{\upsilon}} K(x)dx = 0. \tag{6}$$

Also, $U'(z_1') = \dfrac{\alpha}{\upsilon}\displaystyle\int_{-\infty}^{z_1'} e^{\frac{(x - z_1')}{\upsilon}} K(x)dx = 0 = U'(z_1)$. Then

$$e^{-\frac{z_1'}{\upsilon}} \int_{-\infty}^{z_1} e^{\frac{x}{\upsilon}} K(x)dx + e^{-\frac{z_1'}{\upsilon}} \int_{z_1}^{z_1'} e^{\frac{x}{\upsilon}} K(x)dx = e^{-\frac{z_1}{\upsilon}} \int_{-\infty}^{z_1} e^{\frac{x}{\upsilon}} K(x)dx$$

that is

$$\int_{z_1}^{z_1'} e^{\frac{x}{\upsilon}} K(x)dx = \left(e^{\left(\frac{z_1' - z_1}{\upsilon}\right)} - 1\right)\int_{-\infty}^{z_1} e^{\frac{x}{\upsilon}} K(x)dx.$$

Since $z_1' > z_1$, $e^{\left(\frac{z_1' - z_1}{\upsilon}\right)} - 1 > 0$, and $\displaystyle\int_{z_1}^{z_1'} e^{\frac{x}{\upsilon}} K(x)dx < 0$. This contradicts Equation 6. Hence $z_1 = z_1'$, that is, z_1 is unique. Now, consider the case when $z >> x_0$. We find

$$\upsilon U'(z)e^{\frac{z}{\upsilon}} = \alpha \int_{-\infty}^{z} e^{\frac{x}{\upsilon}} K(x)dx$$

$$= \left(\frac{\alpha}{2} - \theta\right) + \alpha\int_0^{x_0} e^{\frac{x}{\upsilon}} K(x)dx + \alpha\int_{x_0}^{Z_1} e^{\frac{x}{\upsilon}} K(x)dx + \alpha\int_{Z_1}^{z} e^{\frac{x}{\upsilon}} K(x)dx.$$

Letting $\Omega_1 \equiv \left(\dfrac{\alpha}{2} - \theta\right) + \alpha\displaystyle\int_0^{x_0} e^{\frac{x}{\upsilon}} K(x)dx + \alpha\int_{x_0}^{Z_1} e^{\frac{x}{\upsilon}} K(x)dx$, which is bounded, we have

$$\upsilon U'(z)e^{\frac{z}{\upsilon}} = \Omega_1 + \alpha\int_{Z_1}^{z} e^{\frac{x}{\upsilon}} K(x)dx$$

$$> \Omega_1 + \alpha\int_{Z_1}^{z} e^{\frac{x}{\upsilon}}\{m_1 e^{-\rho_1 x}\}dx$$

$$= \Omega_1 + \frac{m_1 \alpha \upsilon}{1 - \rho_1 \upsilon}\left\{e^{\left(\frac{1 - \rho_1 \upsilon}{\upsilon}\right)z} - e^{\left(\frac{1 - \rho_1 \upsilon}{\upsilon}\right)Z_1}\right\}.$$

Thus, when $z \to +\infty$,

$$\frac{m_1 \alpha \upsilon}{1 - \rho_1 \upsilon}\left\{e^{\left(\frac{1 - \rho_1 \upsilon}{\upsilon}\right)z} - e^{\left(\frac{1 - \rho_1 \upsilon}{\upsilon}\right)Z_1}\right\} \to \infty.$$

Hence, $U'(z) > 0$ when z is sufficiently large, given conditions 2) and 3). So, there exists a $z = z_2$, $z_2 \in (x_0, \infty)$, such that $U'(z_2) = 0$ and $U(z_2)$ is a local minimum. The claim now is that z_2 is unique. The uniqueness argument is the same as that given in the Lemma above.

Lemma 3: For $2\theta < \alpha$, and $\upsilon > 0$, assume, besides (A1), that $K(x)$ satisfies the following.

1) $\frac{K(0)x_0}{2} > \frac{1}{\alpha}\left(\theta - \frac{\alpha}{2}\right)$

2) There exist $m_2, \rho_2 > 0$ such that for $x > x_0$, $K(x) > m_2 e^{-\rho_2 x}$.

3) $\upsilon\rho_2 > 1$.

Then, $U'(z) > 0$ on $z > 0$.

Proof: Let $y_2(x) = \frac{K(0)}{X}(X - x)$ for $0 < x < X$, where X is the largest x in the interval $(0, x_0]$ such that $K(x) \geq y_2(x)$ on $(0, x_0)$. Then, for $0 < x < x_0$, let $y = \max\{0, y_2\}$. Hence, $K(x) \geq y(x)$ on $[0, x_0]$. Since

$$\int_0^X K(x)dx > \int_0^X y(x)dx$$

$$= \frac{K(0)}{X}\int_0^X (X - x)dx = \frac{K(0)X}{2}$$

for $z \in (0, x_0)$, we have

$$\frac{\upsilon}{\alpha}U'(z)e^{\frac{z}{\upsilon}} = \int_{-\infty}^{z} e^{\frac{x}{\upsilon}} K(x)dx$$

$$= \int_{-\infty}^{0} e^{\frac{x}{\upsilon}} K(x)dx + \int_0^z e^{\frac{x}{\upsilon}} K(x)dx$$

$$> \frac{1}{\alpha}\left(\frac{\alpha}{2} - \theta\right) + \int_0^z K(x)dx$$

$$> \frac{1}{\alpha}\left(\frac{\alpha}{2} - \theta\right) + \frac{K(0)x_0}{2} > 0.$$

Let $\Omega_2 \equiv \frac{1}{\alpha}\left(\frac{\alpha}{2} - \theta\right) + \frac{K(0)x_0}{2}$, which is bounded. For $z \in (x_0, \infty)$,

$$\frac{\upsilon}{\alpha}U'(z)e^{\frac{z}{\upsilon}} > \Omega_2 + \int_{x_0}^{z} e^{\frac{x}{\upsilon}} K(x)dx$$

$$> \Omega_2 + \int_{x_0}^{z} e^{\frac{x}{\upsilon}}\left\{m_2 e^{-\rho_2 x}\right\}dx$$

$$> \Omega_2 + \frac{m_2\upsilon}{1 - \rho_2\upsilon}\left\{-e^{\left(\frac{1-\rho_2\upsilon}{\upsilon}\right)x_0}\right\} > 0.$$

Hence $U'(z) > 0$ on $z > 0$, given conditions 1) to 3).

Example: Let $K(x) = a_1 e^{-b_1|x|} - a_2 e^{-b_2|x|}$ where $0 < a_1 < a_2$, $0 < b_1 < b_2$ and $\frac{a_1}{b_1} - \frac{a_2}{b_2} = \frac{1}{2}$. From the Equation 5 and the assumption (A2),

$$\theta = \frac{\alpha}{2} - \alpha\int_{-\infty}^{0} e^{\frac{x}{\upsilon}}\left\{a_1 e^{-b_1 x} - a_2 e^{-b_2 x}\right\}dx = \frac{\alpha}{2} - \frac{\alpha a_1 \upsilon}{1 + \upsilon b_1} + \frac{\alpha a_2 \upsilon}{1 + \upsilon b_2}.$$

So, $2\theta b_1 b_2 \upsilon^2 + \{(2\theta - \alpha)(b_1 + b_2) - 2\alpha(a_2 - a_1)\}\upsilon + (2\theta - \alpha) = 0$. If we let $a = 2\theta b_1 b_2 > 0$, $b = (2\theta - \alpha)(b_1 + b_2) - 2\alpha(a_2 - a_1)$ and $c = (2\theta - \alpha) < 0$, then $4ac < 0$, which implies $\sqrt{b^2 - 4ac} > b$. Since $\upsilon > 0$, we obtain $\upsilon = \frac{-b + \sqrt{b^2 - 4ac}}{2a}$.

Now,

$$U(z) = \alpha\int_{-\infty}^{z} K(x)dx - \alpha\int_{-\infty}^{z} e^{\frac{x-z}{\upsilon}} K(x)dx$$

$$= \alpha\int_{-\infty}^{z}\left\{a_1 e^{b_1 x} - a_2 e^{b_2 x}\right\}dx - \alpha\int_{-\infty}^{z} e^{\frac{x-z}{\upsilon}}\left\{a_1 e^{b_1 x} - a_2 e^{b_2 x}\right\}dx$$

$$= \frac{\alpha a_1}{b_1(1 + \upsilon b_1)}e^{b_1 z} - \frac{\alpha a_2}{b_2(1 + \upsilon b_2)}e^{b_2 z}, \text{ when } z < 0.$$

For $z > 0$,

$$U(z) = \alpha\int_{-\infty}^{0} K(x)dx + \alpha\int_0^z K(x)dx - \alpha e^{\frac{-z}{\upsilon}}\int_{-\infty}^{0} e^{\frac{x}{\upsilon}} K(x)dx - \alpha e^{\frac{-z}{\upsilon}}\int_0^z e^{\frac{x}{\upsilon}} K(x)dx$$

$$= \alpha\int_{-\infty}^{0}\left\{a_1 e^{b_1 x} - a_2 e^{b_2 x}\right\}dx + \alpha\int_0^z\left\{a_1 e^{-b_1 x} - a_2 e^{-b_2 x}\right\}dx - \alpha e^{\frac{-z}{\upsilon}}\int_{-\infty}^{0} e^{\frac{x}{\upsilon}}\left\{a_1 e^{b_1 x} - a_2 e^{b_2 x}\right\}dx$$

$$- \alpha e^{\frac{-z}{\upsilon}}\int_0^z e^{\frac{x}{\upsilon}}\left\{a_1 e^{-b_1 x} - a_2 e^{-b_2 x}\right\}dx$$

$$= \alpha + \alpha\left(-\frac{a_1}{b_1} - \frac{a_1\upsilon}{1 - \upsilon b_1}\right)e^{-b_1 z} + \alpha\left(\frac{a_2}{b_2} + \frac{a_2\upsilon}{1 - \upsilon b_2}\right)e^{-b_2 z} - h(\upsilon)e^{\frac{-z}{\upsilon}}$$

where $h(\upsilon) = \alpha\left\{\frac{a_1\upsilon}{1 + \upsilon b_1} - \frac{a_2\upsilon}{1 + \upsilon b_2} - \frac{a_1\upsilon}{1 - \upsilon b_1} + \frac{a_2\upsilon}{1 - \upsilon b_2}\right\}$.

For a numerical example, let $a_1 = 1$, $b_1 = 1$, $a_2 = 1.5$, $b_2 = 3$, and $\alpha = 2$. Then, $K(x) = e^{-|x|} - 1.5e^{-3|x|}$ whose graph is shown in Figure 1 and we have $x_0 = -0.5\ln\left(\frac{2}{3}\right) \approx 0.2027$, and $K(0) = -0.5$.

In order to satisfy the conditions in Lemma 2, we let

1. $\rho_1 = 1$ and $0 < m_1 < 1$. Then, $K(x) = e^{-x} - 1.5e^{-3x} > m_1 e^{-\rho_1 x}$.

2. $\frac{1}{\upsilon} > \rho_1 = 1$, so that $\upsilon < 1$. Then, for $\upsilon > 0$,

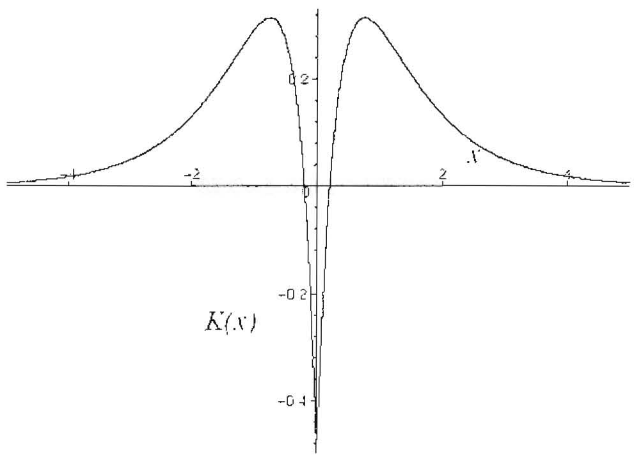

Figure 1 Graph of $K(x) = e^{-|x|} - 1.5e^{-3|x|}$

$\theta = 1 - \dfrac{2\upsilon}{1+\upsilon} + \dfrac{1.5\upsilon}{1+3\upsilon} = \dfrac{1 + 3.5\upsilon - 1.5\upsilon^2}{1 + 4\upsilon + 3\upsilon^2}$ or $(6\theta + 3)\upsilon^2 + (8\theta - 7)\upsilon + (2\theta - 2) = 0$.

Thus,

$$\upsilon = \frac{-(8\theta - 7) + \sqrt{(8\theta - 7)^2 - 4(6\theta + 3)(2\theta - 2)}}{2(6\theta + 3)}$$

$$= \frac{-(8\theta - 7) + \sqrt{16\theta^2 - 88\theta + 25}}{2(6\theta + 3)}$$

Since $\upsilon < 1$, $\dfrac{-(8\theta - 7) + \sqrt{16\theta^2 - 88\theta + 25}}{2(6\theta + 3)} < 1$ or $16\theta^2 + 2\theta - 1 > 0$.

We obtain $\theta > \dfrac{-2 + \sqrt{68}}{32} \approx 0.2$. If we let $\theta = 0.9741$ then $\dfrac{K(0)x_0}{2} \approx -0.05$, and $\dfrac{1}{\alpha}\left(\theta - \dfrac{\alpha}{2}\right) = -0.013$ which satisfies the condition 1) in Lemma 2. Thus, if we choose $\dfrac{-2 + \sqrt{68}}{32} < \theta < 1$, then $U(z)$ is non-monotone for $z > 0$ as shown in Figure 2.

On the other hand, in order to satisfy the conditions in Lemma 3, we let

1. $\rho_2 = 1$ and $0 < m_2 < 1$. Then, $K(x) = e^{-x} - 1.5e^{3x} > m_2 e^{-\rho_2 x}$.

2. $\dfrac{1}{\upsilon} < \rho_2 = 1$, so that $\upsilon > 1$, that is, $0 < \theta < \dfrac{-2 + \sqrt{68}}{32}$.

If we let $\theta = 0.1033$ then $\dfrac{K(0)x_0}{2} \approx -0.05$, and $\dfrac{1}{\alpha}\left(\theta - \dfrac{\alpha}{2}\right) = -0.448$ which satisfies the condition 1) in Lemma 3. Then, $U(z)$ is monotone increasing function for $z > 0$ as shown in Figure 3.

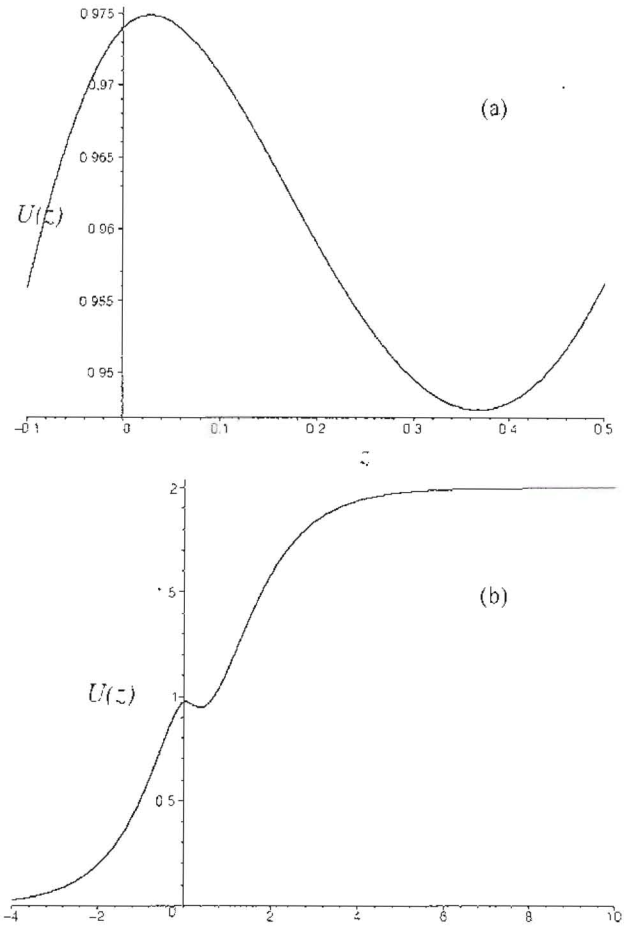

Figure 2. Graph of $U(z)$ with $\theta = 0.9741$, (a) $z \in (-0.1, 0.5)$ and (b) $z \in (-4, 10)$

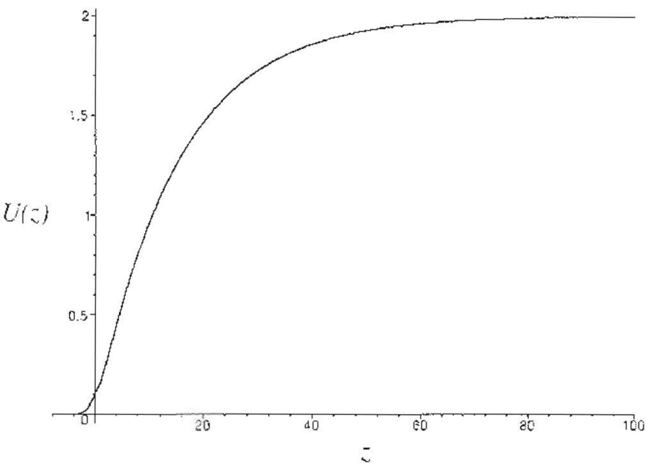

Figure 3. Graph of $U(z)$ with $\theta = 0.1033$

4. Stability Analysis

We will extend the results in a lemma in Zhang (2004), which described the stability of the traveling wave fronts due to a positive connection kernel function, to analyze the stability of the fronts in the case, where the connection kernel function is of a lateral excitation type. Zhang defined a linear operator, L, on the space of bounded, continuous, complex-valued functions on $\Re$, whose derivative was also defined on $\Re$, bounded, and continuous. Zhang then went on to characterize the solution to the eigenvalue problem, which led to an eigenvalue (or Evans) function

$$E(\lambda) = 1 - \frac{\alpha}{\upsilon U'(0)} \int_{-\infty}^{0} K(z) e^{\frac{(\lambda+1)z}{\upsilon}} dz . \qquad (7)$$

Lemma 4: (Zhang, 2004) The Evans function is a complex analytic function, and it is real-valued if the eigenvalue parameter λ is real. The complex number λ is an eigenvalue of the operator L if and only if $E(\lambda) = 0$.

From Evans' theorem, for exponential stability we need $\lambda = 0$ to be a simple eigenvalue and the spectrum of L to be in the left half space, i.e. $\max\{\mathrm{Re}(\lambda) | \lambda \in \sigma(\mathrm{L}), \lambda \neq 0\} \leq -k$ for some $k > 0$. In terms of the Evans function, the degree of the zero of E is equal to the order of the eigenvalue, so we need $E'(0) \neq 0$, and for $E(\lambda) = 0,\ \lambda \neq 0,$ then $\mathrm{Re}(\lambda) < 0$.

Since $E(0) = 0$ implies $\upsilon U'(0) = \alpha \int_{-\infty}^{0} K(z) e^{\frac{z}{\upsilon}} dz$,

we can rewrite in Equation 7 as

$$E(\lambda) = 1 - \frac{\int_{-\infty}^{0} K(z) e^{\frac{(\lambda+1)z}{\upsilon}} dz}{\int_{-\infty}^{0} K(z) e^{\frac{z}{\upsilon}} dz} .$$

Thus, $E(\lambda) = 0$ if and only if $\int_{-\infty}^{0} K(z) e^{\frac{(\lambda+1)z}{\upsilon}} dz = \int_{-\infty}^{0} K(z) e^{\frac{z}{\upsilon}} dz$.

Note that $E'(0) \neq 0$ only if $\int_{-\infty}^{0} zK(z) e^{\frac{z}{\upsilon}} dz \neq 0$, and this follows from our existence result since we have imposed hypotheses guaranteeing $A'(\upsilon) < 0$ for all $\upsilon > 0$.

Now, we consider the zeros of E for $K(x) = a_1 e^{-b_1|x|} - a_2 e^{-b_2|x|}$ where $0 < a_1 < a_2$, $0 < b_1 < b_2$ and $\frac{a_1}{b_1} - \frac{a_2}{b_2} = \frac{1}{2}$. We will rescale by letting $a_1 = 1$, $b_2 = a$ and $b_1 = 1$ such that $a > 1$. We then obtain $a_2 = \frac{3}{2} a$. So, $K(x) = e^{-|x|} - \frac{3}{2} a e^{-a|x|}$, $a > 1$. Here, $K(0) = 1 - 1.5a$ and $x_0 = \frac{\ln(1.5a)}{a-1}$. Since if and only if

$$\int_{-\infty}^{0} K(z) e^{\frac{(\lambda+1)z}{\upsilon}} dz = \int_{-\infty}^{0} K(z) e^{\frac{z}{\upsilon}} dz ,$$

we may define

$$f(\lambda, a) = \int_{-\infty}^{0} K(z) e^{\frac{(\lambda+1)z}{\upsilon}} dz . \qquad (8)$$

Given α and θ, $0 < 2\theta < \alpha$, from Theorem 1, υ is given by $\int_{-\infty}^{0} K(z) e^{\frac{z}{\upsilon}} dz = \frac{1}{2} - \frac{\theta}{\alpha}$. Thus,

$$f(\lambda, a) = \frac{-\frac{1}{2} a\upsilon^2 - \upsilon(1.5a - 1)(1+\lambda)}{\lambda^2 + (2 + \upsilon + a\upsilon)\lambda + 1 + \upsilon + a\upsilon + a\upsilon^2} = \frac{1}{2} - \frac{\theta}{\alpha} \qquad (9)$$

where the integral in Equation 8 assumes $\mathrm{Re}(\lambda) + 1 + \upsilon > 0$.

If now we define

$$A = 2 + \upsilon + a\upsilon + \frac{\upsilon(1.5a - 1)}{0.5 - \frac{\theta}{\alpha}},$$

and

$$B = 1 + \upsilon + a\upsilon + a\upsilon^2 + \frac{a\upsilon^2 + (3a - 2)\upsilon}{1 - \frac{2\theta}{\alpha}}.$$

Thus, Equation 9 can be written as the quadratic equation

$$\lambda^2 + A\lambda + B = 0 . \qquad (10)$$

For any root $\lambda = \rho + \sigma i$, $\rho, \sigma \in \Re$, the real and imaginary parts of the left hand side of Equation 10 must be zero, namely

$$\rho^2 - \sigma^2 + A\rho + B = 0 \qquad (11)$$

and

$$A\sigma + 2\rho\sigma = 0 . \qquad (12)$$

For Equation 12 to hold, either $\sigma = 0$, so λ is real, which implies $\rho^2 + A\rho + B = 0$, or else $\sigma \neq 0$, so that $\rho = -\frac{A}{2}$.

From Equation 11, this implies

$$\sigma^2 = \rho^2 + A\rho + B = B - \frac{A^2}{4}.$$

But $\lambda = 0$ must be a solution to Equation 9, hence Equation 10 becomes $B = 0$, which gives $\sigma^2 = -\frac{A^2}{4}$. But this contradicts σ being a real number, so the only roots are $\rho = 0$ and $\rho = -A$.

For stability we need $A > 0$. From the definition of A as before, we have $A > 0$. Thus, for this class of kernel functions, the wave front solutions are stable.

5. Conclusion and Discussion

In this study we have examined the shape of traveling wave front solutions for a neural network model with lateral excitatory connectivity. We give a characterization of the wave front shape that depending on the size of a threshold parameter . We found that in the case of a high threshold potential or low wave speeds the wave shape is non-monotone, but in case of a low threshold potential or high wave speeds the wave shape becomes monotone.

This study analyzed the theoretical model for networks of nerve cells that is important for the progress in understanding spatially structured activity seen in neural tissues such as how the activity patterns are generated, and suggesting new types of medications to treat some neurological diseases.

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