Traveling Wave Front Solutions in a Neuronal Model with Lateral-inhibition Type of Connection Function

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Abstract

In this paper, we report on mathematical modeling of signaling mechanism among nerve cells in a neural network. We first investigate the shape of traveling wave front solutions with positive wave speed for a single continuous layer of nerve cells with lateral inhibition type of connection functions. We obtain a characterization of the wave front shapes that depend on the firing threshold potential. We then analyze double continuous layers of nerve cells involving a mutually excitatory layer of cells coupled via excitatory connections to a second layer of cells that provides inhibitory feedback connections to the first layer and derive results on the qualitative behavior of wave front shapes.

KEY WORDS: integro-differential equations, neural network, signal modeling, traveling wave solutions, wave front shape

Introduction

Neurological disorders in human, such as cortical epilepsy and migraine (Connors and Amitai, 1993; Lance, 1993), are characterized by irregular pattern of waves that spread across the surface of the cortex. For this reason, traveling wave solutions constitute biologically an interesting and important concept in the attempt to understand the mechanisms underlying spatially extended networks. Zhang (2004) studied the existence and exponential stability of traveling wave solutions of some integral differential equations arising from neuronal networks in a single layer model. He assumed that the connection kernel function was positive, purely excitatory connection. However, the neural network modeling taken in this paper goes back at least to the work of Amari (1977). The model for a single continuous layer of nerve cells takes the form

\[ u_t(x,t) = -u(x,t) + \alpha \int_{\mathbb{R}} K(x,y) f(u(y,t)) dy, \]  

where \( u(x,t) \), with \( (x,t) \in \mathbb{R} \times \mathbb{R}^+ \), represents the (averaged) synaptic input to the excitable cells located at \( x \) at time \( t \). It is assumed that when the neurons have an average membrane potential \( u \), and \( f \) represents the firing rate, and it is assumed that it only depends on the activity of the neurons located at \( y \) at time \( t \). In this paper, we take the case in which \( f = f_{\max} H(u - \theta) \), where \( \theta \) is the fixed threshold value, \( H(u - \theta) \) being the Heaviside function, that is, where \( H(u - \theta) = 1 \) for \( u \geq \theta \), and \( H(u - \theta) = 0 \) for \( u < \theta \). Here, \( \alpha \) is the synaptic connection strength which is positive. The connection kernel function \( K(x,y) \) in [1], representing the strength, and type, of connection between cells at \( y \) to those at \( x \), only depends on their physical separation \( |x - y| \). Since the cell population typically is made up of excitatory and inhibitory cells, \( K \) takes on both positive and negative values.
The assumption is that nearby neurons excite each other, while more distant pairs have an inhibitory effect. That is, there is local excitatory connections for $|x| \leq x_0$, and long distance inhibitory connections for $|x| \geq x_0$, termed lateral inhibition.

We are interested in traveling wave solutions of the form $u(x,t) = U(z)$, $z = x + vt$, for some constant wave speed $v$, and all $x \in \mathbb{R}$, $t > 0$, and their qualitative behavior, for a continuum neural network model with a lateral inhibition type of connection kernel function. Traveling waves have been considered of the form of spreading depression waves, with velocities in the order of 1-3 mm/minute, and neural activity waves, which have velocities in the 10-90 cm/s range. They represent the movement of information, and could help us to characterize the behavior of more general solutions in a single direction. Therefore, it is appropriate to investigate biological mechanisms of traveling waves, along with other activity patterns in neural models. In the following analysis in this paper, we assume that

(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 inhibition 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 $z > 0$.

**Single layer model**

We consider nontrivial solutions of the form $u(x,t) = U(z)$, $z = x + vt$, for some positive wave speeds $v$. Substituting this form in equation [1], we obtain

$$\nu U'(z) + U(z) = \alpha \int_{-\infty}^{z} K(x)dx. \quad [2]$$

This is a first-order, non-homogeneous linear differential equation. So, the bounded solution is

$$U(z) = \alpha \int_{-\infty}^{z} K(x)dx - \alpha \int_{-\infty}^{z} e^{\frac{x-z}{\nu}} K(x)dx. \quad [3]$$

The traveling wave front is connecting $U_- \equiv 0 < \theta$ at $z = -\infty$ to $U_+ \equiv \alpha > \theta$ at $z = +\infty$.

**Analysis of the wave front shape**

In this section, we show that the wave front solution is a non-monotone function. We analyze the wave shape by separating the domain into four subintervals, that is, $(-\infty, -x_0)$, $(-x_0, 0)$, $(0, x_0)$, and $(x_0, \infty)$.

**Lemma 1** For $2\theta < \alpha$, with $\nu > 0$, let $U(z)$ be the wave front solution to equation [3]. There is a unique local minimum point, $z_1$, in $(-x_0, 0)$ such that $U(z)$ is monotone decreasing on $(-\infty, z_1)$, and is monotone increasing on $(z_1, 0]$, with slope of the wave front being given by $U'(0) = \frac{1}{\nu} \left\{ \frac{\alpha}{2} - \theta \right\} > 0$.

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

1) There exist $m_1, \rho_1 > 0$ such that for some $Z_1 > x_0$, it holds that for $x > Z_1$, $K(x) < -m_1 e^{-\rho_1 x}$.
2) $\nu \rho_1 < 1$. 

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

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

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

2) $\nu \rho_2 > 1$.

Then, $U'(z) > 0$ for $z > x_0$, and therefore $U'(z) > 0$ on $z > 0$.

**Numerical simulation**

Let $K(x) = a_1 e^{-b_1 x} - a_2 e^{-b_2 x}$ where $a_1 > a_2 > 0$, $b_1 > b_2 > 0$ and $\frac{a_1}{b_1} - \frac{a_2}{b_2} = \frac{1}{2}$. We choose $K(x) = 2e^{-2x} \left[ 1 - 0.5 e^{-x} \right]$. For the conditions in Lemma 2, let $\rho_1 = 1$ and $0 < m_1 < \frac{1}{2}$. Then, $K(x) = 2e^{-2x} - 0.5e^{-x} < -m_1 e^{-\rho_1 x}$. Also, $\nu < 1$. Then, $\theta = 1 - \frac{4\nu}{1 + 2\nu} + \frac{\nu}{1 + \nu} = \frac{1}{1 + 3\nu + 2\nu^2} \leq 1$. If $\nu < 1$, $-3\theta + \sqrt{9\theta^2 - 8\theta(\theta - 1)} = \frac{1}{4\theta} < 1$, and so $\theta > \frac{1}{6}$. Thus, if we choose $\frac{1}{6} < \theta < 1$, then $U(z)$ is non-monotone for $z > 0$ as shown in Figure 1(a). On the other hand, for the conditions in Lemma 3, if we choose $0 < \theta < \frac{1}{6}$ then $U(z)$ is monotone increasing function for $z > 0$ as shown in Figure 1(b).

![Figure 1: The graph of $U(z)$ with (a) $\theta = 0.95$, and (b) $\theta = 0.1$.](image)

**Double layer model**

We investigate the case of a mutually excitatory layer of cells coupled via excitatory connections to a second layer of cells that provides inhibitory feedback connections to the first layer. We derive results on the qualitative behavior of wave fronts conditional on parameters that represent the inhibition threshold and time scale of the inhibition process. If $u(x,t)$ represents the potential of a cell in the first layer located at $x$ at time $t$, and $v(x,t)$ represents the potential of a cell in the second layer at location $x$ at time $t$, then the neural network of interest is given, for $(x,t) \in \mathbb{R} \times \mathbb{R}^+$, by
Here, we assume that the following condition holds throughout this section:

\[(A4) \quad K_j(x), \quad j=1,2, \text{ are positive, even, smooth, single humped functions on } \mathbb{R}, \text{ with } \int_{\mathbb{R}} K_j(x)dx = 1, \]

\[\int_{\mathbb{R}} |K'_j(x)|dx < \infty, \text{ and exponentially decay for } |x| \text{ sufficiently large. Also, } K_1(x) > K_2(x) \quad \text{for } |x| < x_0, \]

\[\text{and } K_1(x) < K_2(x) \quad \text{for } |x| > x_0.\]

The equations [4] and [5] are considered non-dimensional, with \(\tau > 0\) representing the ratio of time scales associated with \(u\) and \(v\). We will make a further assumption, motivated by Amari (1977), that the spread of excitatory influence from layer 1 to layer 2 is very narrow. This allows us to idealize the excitatory connection function to \(K_3(x) = k_3 \delta(x)\), where \(\delta(x)\) is the Dirac delta function. A further reduction we do here is to let \(\theta_1 = \theta_3 = \theta\). We want to look for solutions of the form \((u(x,t), v(x,t)) = (U(z), V(z)), \quad z = x + \nu \tau\), for some wave speed \(\nu > 0\). By using the assumptions (A2) and (A3), equations [4] and [5] thus become

\[\nu U' + U = \alpha_1 \int_{-\infty}^{z} K_1(x)dx - \alpha_2 \int_{-\infty}^{z} K_2(y)H(V(y) - \theta_2)dy \quad \text{[6]}\]

and

\[\nu \tau V' + V = k_3 H(z). \quad \text{[7]}\]

The solution to equation [7] is \(V(z) = \frac{k_3}{\tau} \left(1 - \frac{z}{\nu \tau} \right) H(z) \text{ with } V'(z) > 0\). Then, there exists a unique \(z = z_1 > 0\) such that \(V(z_1) = \theta_2\), so that \(z_1 = \nu \tau \ln \left(\frac{k_3}{k_3 - \theta_2}\right)\) provided \(k_3 > \theta_2\). Now, equation [6] thus becomes

\[\nu U' + U = \alpha_1 \int_{-\infty}^{z} K_1(x)dx - \alpha_2 \int_{-\infty}^{z} K_2(x)dx \quad \text{[8]}\]

and the solution to equation [8] becomes

\[U(z) = \alpha_1 \int_{-\infty}^{z} K_1(x)dx - \alpha_1 \int_{-\infty}^{z} e^{\frac{(x-z)}{\nu \tau}} K_1(x)dx - \alpha_2 \int_{-\infty}^{z} K_2(x)dx + \alpha_2 \int_{-\infty}^{z} e^{\frac{(x-z)}{\nu \tau}} K_2(x)dx \quad \text{[9]}\]

Analysis of wave shape with respect to \(z_1(\tau)\)

We give a schematic summary of these different behaviors of traveling wave front solutions as shown in Figure 2.
Figure 2: The shapes of $U(z)$ with respect to $\theta_2$ and $\tau$ for each region in $(\theta_2, \tau)$-plane ahead of the wave front ($z < 0$) and behind the wave front ($z > 0$).

Lemma 4 For $0 < 2\theta < \alpha_1 - \alpha_2$, $0 < \theta_2 < k_3$, let $(U(z), V(z))$ be a traveling wave solution to equations [6], [7], with $\nu > 0$. Then, for all $\varepsilon > 0$, there exists a $\delta > 0$ such that whenever

$$0 < \tau < \frac{\alpha_2 K_2'(-x_0) \nu \ln \frac{k_3}{k_3 - \theta_2}}{\delta},$$

there is a unique $z = z_2 \in (-x_0, 0)$, which is a local minimum point for $U(z)$ in that $U(z)$ is monotone decreasing on $(-\infty, z_2)$, non-monotone (Lemma 4) $(z_2, 0)$, with steepness of the wave front being given by $U'(0) = \frac{1}{\nu} \left( \frac{\alpha_1}{2} - \frac{\alpha_2}{2} \int_{-\infty}^{z_2} K_2(x) dx - \theta \right) > 0$.

Lemma 5 For $0 < 2\theta < \alpha_1 - \alpha_2$, $0 < \theta_2 < k_3$ and for all $\varepsilon > 0$, there exists a $\delta > 0$ such that whenever

$$0 < \tau < \frac{\alpha_2 \inf_{(-x_0, 0)} K_2'(x) \nu \ln \frac{k_3}{k_3 - \theta_2}}{\delta},$$

$\equiv \bar{\tau}_{m_1}^*, z < 0$, $U'(z) > 0$ on $z < 0$.

Lemma 6 For $0 < 2\theta < \alpha_1 - \alpha_2$, $\theta_2$ sufficiently small, and for all $\varepsilon > 0$, there exists a $\delta > 0$ such that whenever

$$0 < \tau < \frac{\alpha_2 \inf_{[0, z_0]} K_2'(x) \nu \ln \frac{k_3}{k_3 - \theta_2}}{\delta},$$

$\equiv \bar{\tau}_{m_2}^*, z > 0$, $U'(z) > 0$ on $z > 0$.

Lemma 7 For $0 < 2\theta < \alpha_1 - \alpha_2$, $\theta_2 \to k_3^-$, assume, besides (A4), that $K_1(x)$ and $K_2(x)$ satisfy the followings.

1) There exist $m_1, m_2, \rho_1, \rho_2 > 0$, such that $K_1(x) < m_1 e^{-\rho_1 x}$, $K_2(x) < m_2 e^{-\rho_2 x}$ for $x > 0$.

2) $\nu \neq \frac{1}{\rho_1}$ and $\nu \neq \frac{1}{\rho_2}$.

3) $\inf_{[0, \infty)} K_2'(x) > -\infty$.

Then, for all $\varepsilon > 0$, there exists a $\delta > 0$ such that whenever

$$0 < \tau < \frac{\alpha_2 \inf_{[0, z_3]} K_2'(x) \nu \ln \frac{k_3}{k_3 - \theta_2}}{\delta},$$

there is a unique $z = z_3 \in (x_0, \infty)$ which is a local maximum point for $U(z)$ in that $U'(z) > 0$ on $[0, z_3)$, and $U'(z) < 0$ on $(z_3, \infty)$.
Lemma 8 For $0 < 2\theta < \alpha_1 - \alpha_2$, $0 < \theta_2 < k_3$, assume that there exist $m_1, m_2, \rho_3, \rho_4 > 0$, such that $K_1(x)$ and $K_2(x)$ satisfy the same conditions 1)-3) as in Lemma 7. Then, for all $\varepsilon > 0$, there exists a $\delta > 0$ such that whenever $\tau < -\frac{\delta}{\alpha_2 \inf_{(0,x_0)} K'_2(x)} \ln \left[ \frac{k_3}{k_3 - \theta_2} \right] = \tau^{**}$, there is a unique $z = z_4 \in (x_0, z_1)$ which is a local maximum point for $U(z)$ in that $U'(z) > 0$ on $[0,z_4)$, and $U'(z) < 0$ on $(z_4, \infty)$.

Numerical simulation

Let $K_1(x) = a_1 e^{-b_1 |x|}$ and $K_2(x) = a_2 e^{-b_2 |x|}$ where $a_1 > a_2 > 0$, $b_1 > b_2 > 0$, $a_1 = \frac{b_1}{2}$ and $a_2 = \frac{b_2}{2}$. We choose $K_1(x) = e^{-x}$ and $K_2(x) = 0.5e^{-x}$. In order to satisfy the conditions in Lemma 4 and Lemma 6, we let $\tau = 0.01$, $\theta_2 = 0.1$, $\theta = 0.1$ and $k_3 = 0.9$. Thus, $z_1 = 0.01 \nu \ln \left( \frac{9}{8} \right)$, yielding $\nu = 2.691$. The function $U(z)$ is non-monotone on $z \in (-\infty,0)$ and monotone on $z \in (0,\infty)$ as shown in Figure 3(a). In order to satisfy the conditions in Lemma 4 and Lemma 7, we let $\tau = 0.01$, $k_3 = 1.0$, $\rho_1 = \rho_2 = 1$, $1 > m_1 > e^{-x}$ and $m_2 > \frac{1}{2}$ for $x > 0$. Then, $K_1(x) = e^{-2x} < m_1 e^{-\rho_1 x}$ and $K_2(x) = 0.5e^{-x} < m_2 e^{-\rho_2 x}$ on $x \in (x_0, \infty)$. Also, $\nu \neq 1$. Thus, if we choose $\theta_2 = 0.95$ and $\theta = 0.95$, then $U(z)$ is non-monotone as shown in Figure 3(b). In order to satisfy the conditions in Lemma 5 and Lemma 8, we let $\tau = 10$, $\theta_2 = 0.95$, $\theta = 0.95$, $k_3 = 1.0$, $\rho_1 = \rho_2 = 1$, $1 > m_1 > e^{-x}$ and $m_2 > \frac{1}{2}$ for $x > 0$. Then, $K_1(x) = e^{-2x} < m_1 e^{-\rho_1 x}$ and $K_2(x) = 0.5e^{-x} < m_2 e^{-\rho_2 x}$ on $x \in (x_0, \infty)$. Also, $\nu \neq 1$. So, $U(z)$ is monotone for $z < 0$ but non-monotone for $z > 0$ as shown in Figure 3(c).

Figure 3: The graph of $U(z)$ with (a) $\theta_2 = 0.1$, $\tau = 0.01$, $x_0 = 0.693$, $z_1 = 0.00317$ and $\nu = 2.691$, (b) $\theta_2 = 0.95$, $\tau = 0.01$, $x_0 = 0.693$, $z_1 = 0.00063$ and $\nu = 0.021$, and (c) $\theta_2 = 0.95$, $\tau = 10$, $x_0 = 0.693$, $z_1 = 8.67$ and $\nu = 0.289$. 

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Conclusions

We have examined the shape of traveling wave-front solutions in a neuronal model with lateral-inhibition type of connection function. We give a characterization of the wave front shape. The fronts are found here to be non-monotone for various ranges of the system parameters and the wave front shape depends on the relationship between the firing threshold and a measure of synaptic strength for single layer model. For double layer model, the wave fronts are non-monotone function too and the wave front shape depends on the threshold behavior and time scales.

References


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