Wave propagation in mathematical models of striated cortex

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1 Introduction

Transitions from rest to oscillatory behavior can occur in mathematical models of neural networks in a variety of ways. One way is through the disappearance of an impediment to oscillation, such as coalescence and disappearance of stable and unstable rest states lying on a stable limit cycle, resulting in a stable oscillation. This phenomenon is referred to as being a saddle-node bifurcation on a limit cycle (SNLC) [9]. The SNLC and the Hopf bifurcation are the simplest ones exhibiting the onset of oscillations in the sense that they have codimension one; i.e., they have the fewest restrictions.

SNLC bifurcations are observed in the neurobiological models [1], and a canonical model for a SNLC bifurcation is the VCON model developed in [2, 3]. (VCON denotes voltage controlled oscillator neuron model.) The integrate-and-fire model [14] also exhibits this type of bifurcation, and in this sense it is closely related to the VCON.

We describe here some interesting aspects of wave propagation in networks that are near multiple SNLCs by studying networks of VCONs. This work is related to modeling regions of the neocortex and other brain structures [5,7], and these models are similar to many others that have been derived for parts of the neocortex using neurooscillators [8,15]. An advantage of the VCON model is that it enables one to study information flow in networks using routine frequency domain methods.

A VCON network is described by the model [2,3]

$$\dot{\theta}(s,t) = \omega + \int_{\mathcal{D}} K(s-s') f\left(\theta(s,t) - \theta(s',t) - \psi(s-s')\right) ds'$$

where

$s \in E^n$ for $n = 1, 2,$ or 3 addresses sites.

θ is a vector of phase variables taking values in E^N.

$\dot{\theta} = \partial\theta/\partial t$.

The connection matrix kernel $K \in E^{N\times N}$ is L periodic in each dimension of s. We suppose here that K describes isotropic connections: $K = K(s-s')$. It describes the amplitude of connections from s' to s.

ψ describes the polarity of connections from s' to s. It is also L-periodic.

$\mathcal{D}$ is a domain in the space of interest. In our case, we consider this set to be $\mathcal{D} = [-L, L]^n$ for $n = 1, 2,$ or 3.

The vector of functions $f(\phi)$ is 2π-periodic in each component of $\phi \in E^N$.

ω is the vector of center frequencies of the network elements.

This model can be derived from general networks that are operating near a multiple SNLC bifurcation [7]. It has a rich structure of wavelike solutions, and it will be studied in greater detail elsewhere. We wish here to identify steady progressing wave solutions of this system, describe their stability properties, and illustrate them through computer simulations.

2 Steady Progressing Wave Solutions

We consider here only the case where $s \in E^1$ and $\theta \in E^m$ where $m = 1$ or 2 to illustrate several interesting features of such systems. The general case can be treated in similar ways.

The observables of this system are usually not θ, but some periodic wave form or function of θ such as $\cos\theta$ or $\cos_+\theta$. This suggests that we seek a steady progressing wave solution in the form

$$\theta = \alpha s + ct$$

where α is called the wave number and c is a vector of wave speeds.

Direct substitution of the steady progressing wave solution into the equation gives

$$c_\alpha = \omega + \int_{-L}^{L} K(s-s')f(\alpha(s-s') + \psi(s-s'))ds'$$

There is a unique *constant* solution of this equation for c provided the components of α have the form $k\pi/L$ for some integer $k = 0, \pm 1, \pm 2, \cdots$.

Let us fix $\alpha = N\pi/L$ for some integer N. According to the calculation above, there is a steady progressing wave solution of the system having the form

$$\theta = N\pi s/L + c_N t$$

where c_N is given by the formula

$$c_N = \omega + \int_{-L}^{L} K(s-s')f(N\pi(s-s')/L + \psi(s-s'))ds'$$

To test the stability of this steady progressing wave we define

$$x_n(s,t)\delta = \theta(s,t) - N\pi s/L - c_N t$$

The result is

$$\delta\dot{x}(s,t) = \int_{-L}^{L} K(s-s')f(\delta(x(s,t) - x(s',t)) + N\pi(s-s')/L + \psi(s-s'))ds'$$

Expanding the right hand side in powers of δ and ignoring higher order terms gives

$$\dot{x}(s,t) = \int_{-L}^{L} K(s-s')f'(N\pi(s-s')/L + \psi(s-s'))(x(s,t) - x(s',t))ds'$$

Expanding x in its Fourier series

$$x(s,t) = \sum_{n=-\infty}^{\infty} x_n(t)e^{in\pi s/L}$$

and substituting this into the equation gives

$$\dot{x}_n(t) = (A_0 - A_n)x_n$$

where

$$K(s)f'(N\pi s/L+\psi(s))=\sum_{-\infty}^{\infty}A_n e^{in\pi s/L}\equiv A(s)$$

Thus, depending on the properties of the coefficients in A, we get the following stability results for the deviation x: If $K(s)=f(s)=\cos s$ and $\psi(s)\equiv 0$, then the leading components of x are harmonic and the remaining modes are damped. If $\psi\equiv\pi/2$, then all modes (except for $n=0$) are damped.

3 Computer simulations

We performed numerical simulations of these models using the method of lines. In this, we model the integrodifferential equation using a set of 200 ordinary differential equations. In the cases presented here, the connection polarities are taken to be $\psi\equiv 0$, the components of f and of K are cosines, and we solved the system

$$\dot{\theta}_j=\omega_j+\frac{1}{200}\sum_{i=1}^{200}K_{i,j}\cos(\theta_j-\theta_i)$$

for $j=1,\cdots,200$.

A series of computations was done for the single and double layer cases. In the two examples presented here, the initial data had the form

$$\theta_j(0)=j2\pi/200+R_j$$

for $j=1,\cdots,200$, where R_j is a uniformly distributed random variable having $|R_j|\leq 2\pi/10$.

We calculate the solutions to time $t=1000\pi$ using an adaptive step Runge-Kutta scheme of orders 7 and 8 [12], and by that time the solution had achieved the form $\theta\approx s+ct$ and the wave speed (c) is estimated by evaluating $\theta_1(1000\pi)/1000\pi$.

The results of the single layer simulation are shown in the Figure 1. In this, $\omega=1, N=1, L=\pi$ and the predicted wave speed is $1+\pi$. In Figure 2 we plot the numerical error, which is deviation of our calculated solution from the theoretical solution derived above

$$\left|1-\frac{\theta_{computed}(s,T)-\theta(0,T)}{s}\right|$$

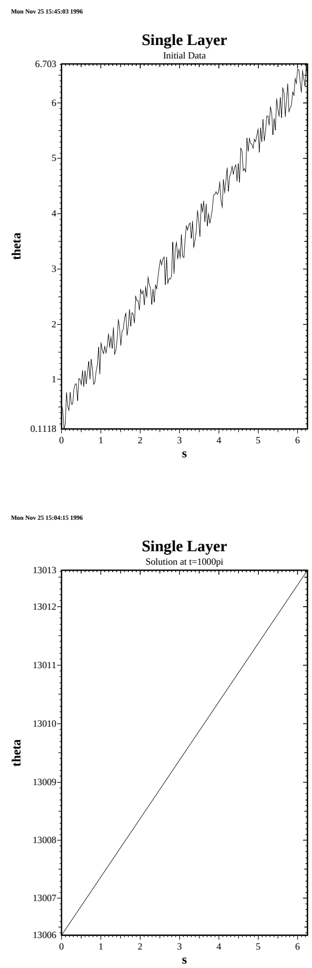


Figure 1: Initial data (top) and calculated solution $\theta_j(1000\pi)$ (bottom). In this case, $c_{obs} \approx 4.14$ and $c_{calc} = 1 + \pi$.

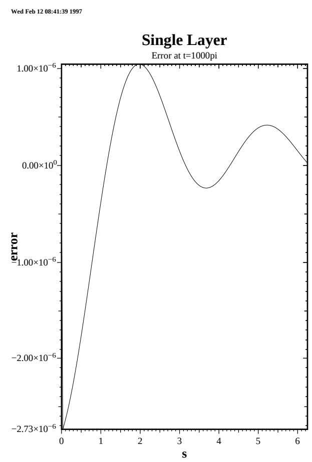


Figure 2: Error of our computer simulation of the single layer model shown in Figure 1.

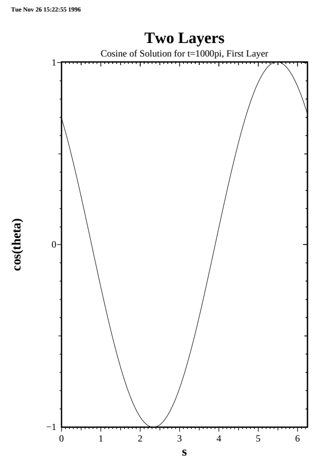
at $T = 1000\pi$. We see there that the error is $O(10^{-6})$ for this simulation.

In the case of two layers, we take similar initial data for each of the two layers as described above, but we take $\omega_1/\omega_2 = 0.01$. The results are shown in Figure 3 This simulation demonstrates that a striated structure can support different wave speeds.

4 Conclusions

The models and simulations here demonstrate that steady progressing waves are possible in networks whose elements are near SNLC bifurcations. Such networks arise in studies of the neocortex, and cortical waves of this kind have been observed [11,15]. There are many areas of the brain whose function is based on propagation of activity, such as sound location in the nucleus laminaris [3]. It is also possible that propagation of neural activity in the hippocampus is important for navigation and memorization [10].

We have shown here that striated structures can support waves having different speeds which is not possible in single layer structures. These waves in striated structures moving at different speeds can create dynamic patterns with brief intervals of coincidence that are believed to play important roles in brain function [13].



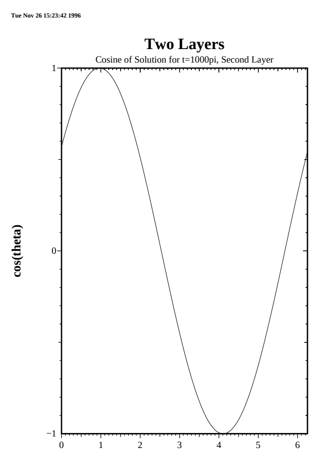


Figure 3: Plotted here are $\cos\theta_{1,j}(1000\pi)$ (top) and $\cos\theta_{2,j}$ (bottom). The estimated wave speeds in these cases are $c_1 = 5.01$ and $c_2 = 0.264$.

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