



Two dimensional synaptically generated traveling waves in a theta-neuron neural network

Remus Osan*, Bard Ermentrout

Department of Mathematics, University of Pittsburgh, Pittsburgh, PA 15260, USA

Abstract

This paper extends some of the previous work on synaptically generated traveling waves from one dimension to two dimensions. Numerical simulations of networks of the so-called theta neurons were used for exploration of the existence, stability and the nature of these waves. The symmetric nature of the traveling waves was justified and a numerical scheme for evaluating the velocity of the traveling waves was constructed. Adding adaptation in the network and imposing special initial conditions gave rise to spiral waves. Moreover, adding delays allowed the formation of the traveling lurching waves. Finally, direction for future work is suggested. © 2001 Published by Elsevier Science B.V.

Keywords: Traveling waves; Spiral waves; Convolutions

1. Introduction

Traveling waves have received much attention lately due to recent experimental and theoretical work [1,5,7,8]. Previous work explored the one-dimensional aspect of the problem as the first step toward a better understanding of the underlying neural circuitry. Traveling activity waves are encountered *in vivo*, either in neurological disorders or in animals drugged with synaptic inhibitors [2,3]. However most of the experimental data are taken from *in vitro* recordings from brain slices since the experimental conditions are more easily controlled this way [2]. Here we use a reduced equation, the theta model, for the individual neurons.

* Corresponding author.

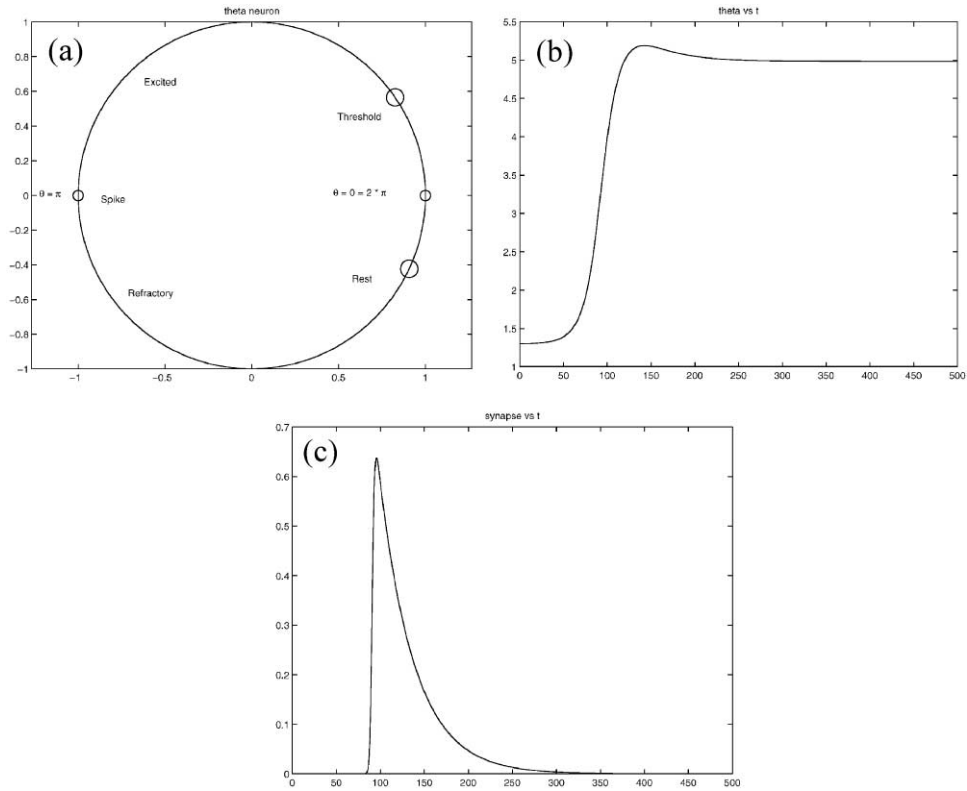


Fig. 1. (a) The θ neuron regimes. (b) Evolution of θ vs time for solitary spike. (c) Evolution of synapse vs time for solitary spike.

2. The model

The equation for the theta neuron is

$$\frac{d\theta}{dt} = (1 - \cos \theta) + (1 + \cos \theta)(\beta + I(t)), \quad (1)$$

where θ is the phase variable, $I(t)$ is the time dependent inputs and β is a bias parameter that controls the excitability of the cell. If $I + \beta < 0$, there is a stable rest state. If $I + \beta > 0$ the neuron fires at a rate $\pi/\sqrt{I + \beta}$. The different regimes for the θ -neuron are represented in Fig. 1a. A solitary spike in the phase space is represented in Fig. 1b. A solitary spike in the synapse space is represented in Fig. 1c. Assuming no external current, the rest state is given by

$$\theta_{\text{rest}} = 2\pi - \cos^{-1}\left(\frac{1 + \beta}{1 - \beta}\right), \quad \beta < 0. \quad (2)$$

3. Regular traveling waves

We can generate a traveling wave if we allow each cell to send a signal to the neighboring cells. The strength of the coupling is proportional to a gaussian function of the distance between two cells. Depending on the excitability of the cell it is possible to have one or more spikes for each cell. The equations for the individual neurons become

$$\frac{\partial \theta(x, t)}{\partial t} = (1 - \cos \theta(x, t)) + (1 + \cos \theta(x, t))(\beta + J \otimes s), \tag{3}$$

$$\frac{\partial s(x, t)}{\partial t} = \alpha e^{-\gamma(1 + \cos \theta(x, t))}(1 - s) - \frac{s(x, t)}{\tau}, \tag{4}$$

where $J(x) = e^{-x^2/2\sigma^2}$, $J \otimes s = \int dy J(x - y)s(y, t)$, the synapse obeys (4) (see [6,7]), α , γ , and τ are constants specific to the synapse, and σ is the space constant for the coupling.

Fig. 2a shows a simulation of the one-dimensional traveling wave that contains a line of 150 cells. The first cell (upper left corner) is given an initial depolarization. Time is represented on the horizontal axis, the line of 150 cells is represented on the vertical axis. The phase of the cells is coded in the grayscale and the spiking occurs when the color of the cells becomes white (for illustration purposes the phase is represented from $-\pi$ to π). When a cell spikes its synapse increases and through coupling this increase is propagated to the neighboring cells that start firing too. As a consequence a traveling wave is formed. Note that in this case the cells can fire more than once.

We were interested to see to what extent the subsequent spiking of the neurons influences the speed of the traveling wave. In order to do that we modified Eq. (4) so that the synapses are no longer updated after one spike. Due to this modification the neurons return to the rest state after the first spike. A solitary wave is presented in Fig. 2b.

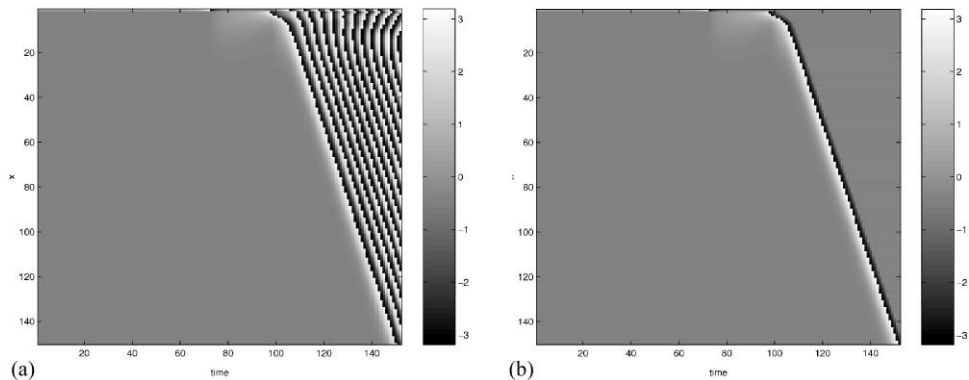


Fig. 2. 1D regular traveling wave: (a) multiple spikes, (b) single spike.

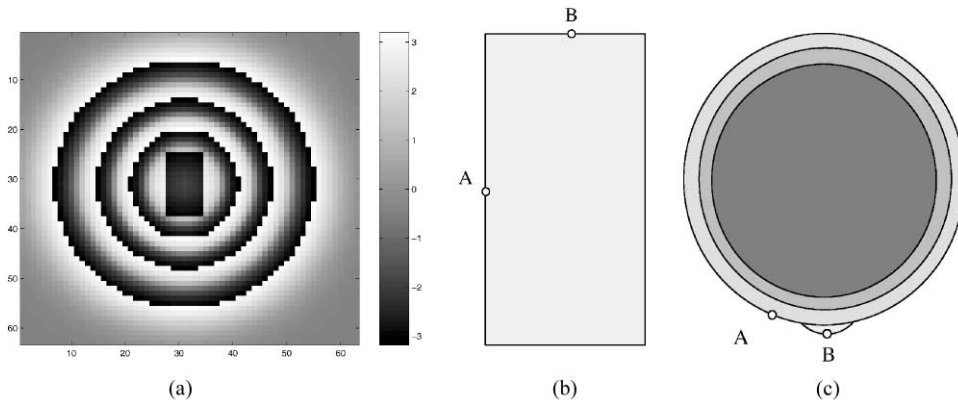


Fig. 3. (a) Two-dimensional regular traveling wave, (b) initial region of excitation will evolve towards a more symmetrical state, (c) the small perturbation is unstable.

For each individual neuron one can record the times when that neuron spikes. The records for all neurons constitute the firing map of the network. The firing maps were recorded for both cases. Suppressing the subsequent spikes has only a small effect on the speed of the traveling wave. For the cases presented in Fig. 2a and b the relative error was 2.6 percent.

Fig. 3a presents a snapshot in the dynamical evolution of the two-dimensional network. A group in the center of the network, in the shape of a rectangle, is given an initial depolarization. The wave starts propagating toward the edges and since the cells may spike more than once, one notices the formation of subsequent traveling waves. Also of interest is the fact that the stable traveling wave is symmetrical, even though the initial conditions were slightly asymmetrical.

This can be understood easier from Fig. 3b. Here the zone that fires at $t = 0$ is a rectangle, similar to the one used as an initial region of excitation in Fig. 3a. The neuron in the middle of the larger side, at point A, receives more input than the neuron in the middle of the smaller side, at point B. Consequently, the neuron A is going to fire faster than the neuron B. Therefore, the speed of the wave is going to be greater on the larger side, on point A, than on the smaller side, on point B. Hence the wave will evolve into to a more symmetrical shape and, eventually, the front will be circular. Once this situation occurs, any small perturbation, as the one described in Fig. 3c, will be unstable, based on similar arguments. The velocity of the wave on the perturbation points will be smaller than on the other points and the perturbation will fall back to the regular circular wavefront.

4. Asymptotic traveling speed

We use the observation from Section 3 that subsequent spikes do not contribute much to the speed of the traveling wave. In this case the temporal evolution of the synapse would have the shape of the one from Fig. 1c. This can be approximate by

a function of form: $\alpha(t) = e^{-a_1 t} - e^{-a_2 t}$, for $t > 0$, and 0, for $t < 0$, where we assume that the neuron spiked at $t = 0$. We can then rewrite Eq. (3), for the one-dimensional case (the two-dimensional case is similar):

$$\frac{\partial \theta(y, t)}{\partial t} = (1 - \cos \theta) + (1 + \cos \theta) \left(\beta + \int dx J(y - x) \alpha(t - t(y)) \right). \quad (5)$$

We use the one-dimensional version of the previous equation for clarity, but the two-dimensional case is similar. Using the same technique described in [5], we look for traveling wave solutions of the previous equation, that is $\theta(x, t) = \theta(vt - x)$. Denoting $vt - x \equiv \xi$, we obtain $s(x, t) = \alpha(t - x/v) = \alpha(\xi/v)$. For this model the cells cross the threshold at $\xi = 0$, so cells with positive ξ already fired and the ones with negative ξ have not fired yet. The net input to cell at position x will be $J \otimes s = \int_0^\infty d\xi' J(\xi - \xi') \alpha(\xi'/v)$, and the equation in θ will be now

$$v \frac{d\theta}{d\xi} = (1 - \cos \theta) + (1 + \cos \theta) \left(\beta + \int_0^\infty d\xi' J(\xi - \xi') \alpha(\xi'/v) \right). \quad (6)$$

This equation has to satisfy the following conditions:

- (i) $\theta \rightarrow \theta_{\text{rest}}$, as $\xi \rightarrow -\infty$;
- (ii) $\theta(0) = \pi$;
- (iii) $\theta \rightarrow \theta_{\text{rest}} + 2\pi$, as $\xi \rightarrow \infty$;

There is no analytic solution to the boundary problem. However this can be solved numerically using shooting procedures since the integral can be evaluated.

5. Spiral waves

Spiral-like and rotating waves have been observed in the visual cortex of the turtle [9]. Because the strong excitability of the theta model, adaptation is added in order to increase the refractory period and make it less excitable. This allows the propagation of solitary pulses in one dimension and spiral waves in two dimensions. The spiral wave presented in Fig. 4a rotates clockwise. After the initial transient state the spiral wave continues to rotate around. This model can be used to suggest suitable initial conditions for producing a spiral wave as long as the time constant of adaptation is not too long. On the other hand, if adaptation is too short lasting then synaptic re-excitation occurs through the mechanism of Fig. 3a, also destroying the spiral. The modified equations plus the equation for the adaptation z are

$$\frac{\partial \theta}{\partial t} = (1 - \cos \theta) + (1 + \cos \theta) (\beta + J \otimes s - g_a z), \quad (7)$$

$$\frac{\partial s}{\partial t} = \alpha e^{-\gamma(1 + \cos \theta)} (1 - s) - \frac{s}{\tau}, \quad (8)$$

$$\frac{\partial z}{\partial t} = \alpha_a e^{-\gamma_a(1 + \cos \theta)} (1 - z) - \frac{z}{\tau_a}. \quad (9)$$

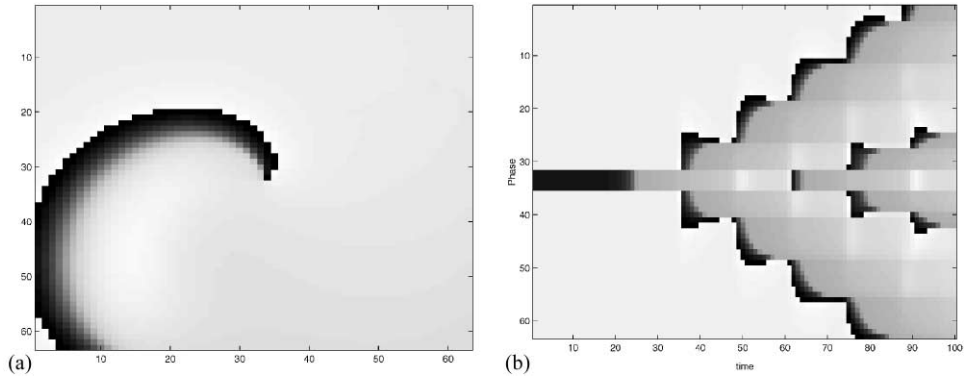


Fig. 4. (a) Spiral wave, (b) 1D section of the 2D lurching wave.

6. Lurching waves

Adding delays to the propagation of the signal from one cell to its neighboring cells may lead to the formation of lurching waves by choosing the appropriate delay times [4,8]. The characteristic of the lurching waves is the existence of segregated regions that fire almost simultaneously. The evolution of a symmetrical 2D lurching wave is presented in a 1D section taken along the central horizontal line of the 2D network (Fig. 4b). The middle region belongs to the original excited region. The equations for the individual neurons are now

$$\frac{\partial \theta}{\partial t} = (1 - \cos \theta) + (1 + \cos \theta)(\beta + J \otimes s - g_a z), \quad (10)$$

$$\frac{\partial s}{\partial t} = \alpha e^{-\gamma(1 + \cos \theta(t - \text{delay}))}(1 - s) - \frac{s}{\tau}, \quad (11)$$

$$\frac{\partial z}{\partial t} = \alpha_a e^{-\gamma_a(1 + \cos \theta)}(1 - z) - \frac{z}{\tau_a}. \quad (12)$$

7. Proposed future work

Using the numerical scheme from (6) one can find the velocity of the traveling front, but this is not the only feature of interest. We would like to know how big the initial region of excitation should be to evoke a wave and how much time it would take the process to “ignite”. For the lurching wave the interesting features that we would like to be able to compute are the average speed of the front and the lurching length.

References

- [1] P.C. Bressloff, Synaptically generated wave propagation in excitable neural media, *Phys. Rev. Lett.* 82 (1999) 2972–2982.
- [2] R.D. Chervin, P.A. Pierce, B.W. Connors, Periodicity and directionality in the propagation of epileptiform discharges across neurocortex, *J. Neurophysiol.* 60 (1988) 1695–1713.
- [3] B.W. Connors, Y. Amitai, Generation of epileptiform discharge by local circuits of neurocortex, in: P.A. Schwartzkroin (Ed.), *Epilepsy: Models, Mechanisms and concepts*, Cambridge University Press, Great Britain, 1993, pp. 388–423.
- [4] D. Contreras, A. Destexhe, T.J. Sejnowski, M. Steriade, Spatiotemporal patterns of spindle oscillations in cortex and thalamus, *J. Neurosci.* 17 (1997) 1179–1713.
- [5] B. Ermentrout, The analysis of Synaptically Generated Traveling Waves, *J. Comp. Neurol.* 5 (1998) 191–208.
- [6] D. Golomb, X.-J. Wang, J. Rinzel, Propagation of spindle waves in a thalamic slice model, *J. Neurophysiol.* 75 (1996) 750–769.
- [7] D. Golomb, Y. Amitai, Propagating neuronal discharges in neocortical slices: computational and experimental study, *J. Neurophysiol.* 78 (1997) 1199–1211.
- [8] D. Golomb, B. Ermentrout, Continuous and lurching traveling pulses in neuronal networks with delay and spatially decaying connectivity, *Proc. Natl. Acad. Sci. USA* 96 (23) (1999) 13480–13485.
- [9] J.C. Prechtl, L.B. Cohen, P.P. Mitra, D. Kleinfeld, Visual stimuli induce waves of electrical activity in turtle cortex, *Proc. Natl. Acad. Sci.* 94 (1997) 7621–7622.



Remus Osan has a B.Sc. in Physics from University of Bucharest, and a M.Sc. in Computer Science from University of Pittsburgh, where he is currently completing a Ph.D. in the Department of Physics and Astronomy. His research focuses on synaptically generated waves in visual cortex. He also has research interests on ocular dominance and orientation columns' pattern formation in visual cortex.



Bard Ermentrout is a Professor of Mathematics at University of Pittsburgh where he has toiled away for the last 18 years on a variety of problems in mathematical biology and dynamical systems. In addition to his scientific work, he is a parrot fancier and renowned limericist.