Periodic traveling waves in a one-dimensional integrate-and-fire neural network

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Abstract

We study the existence of one-dimensional periodic traveling waves in a network of coupled integrate-and-fire neurons. We consider two special cases for the kernel of the coupling function, namely finite support and exponential decay. In these cases, we analytically derive a self-consistency equation that generates an explicit dispersion relation between velocity of the traveling waves and their corresponding wavelength. Simulations show how initiation of activity in one part of a network can cause each cell in the network to fire a succession of spikes, with interspike intervals converging toward the spiking period for the periodic regime.

Project description

Traveling waves in networks of synaptically coupled neurons have been the subject of many recent computational modeling studies [1]–[7]. Indeed, the mechanisms underlying these experimentally observed activity patterns may provide clues to the organization and functionality of a variety of neuronal

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systems. Integrate-and-fire networks provide a simple model of excitable neural tissue, which is relatively amenable to simulation and mathematical analysis. In such models, each neuron is a simple integrator; as soon as its voltage reaches a threshold value V_T, it jumps to a reset value V_R.

Although the integrate-and-fire model omits certain aspects of neuronal activity, it does allow for the inclusion of an essential feature needed to model traveling wave patterns: the spatiotemporally varying excitatory synaptic connections between cells. When one cell spikes, this turns on a synaptic current for the cells to which it is coupled. The time dependence of this current is often modeled as a simple exponential function, with magnitude depending on the distance between the two connected neurons.

The neurons in the synaptically-coupled integrate-and-fire network that we consider, on a one-dimensional domain D, obey the equation

$$\tau_1 \frac{\partial V(x,t)}{\partial t} = -V(x,t) + g_{syn} \int_D J(|y-x|) \sum_k \alpha(t - t_k(y))\ dy. \qquad (1)$$

In equation (1), the integral term represents synaptic coupling, with the summation taken over all input spikes to the cell(s) at position x. The function $J(x)$ encodes the spatial dependence of this coupling, while $\alpha(t)$ encodes the time course of the synaptic current due to each spike. Each time that a cell's voltage reaches V_T, it is reset to V_R; that is, if $V(x, \tau^-) = V_T$, then we set $V(x, \tau^+) = V_R$.

Ermentrout [1], Bressloff [2] and Golomb and Ermentrout [3, 4] developed methods for studying the existence of traveling waves of activity in this class of models under the assumption that each cell only fires once. With this

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assumption (which can be biologically justified by supposing strong synaptic depression or a long refractory period), it is possible to find a traveling wave solution and to obtain an expression for its velocity, c.

Bressloff also developed methods for studying periodic traveling waves [5], in which each cell in the network fires periodically and activity propagates through the network at a constant speed. However, his results are based on rather abstract Fourier analysis and cannot be applied directly to the particular cases analyzed in this paper.

Here we propose a different method to study periodic traveling waves. Our approach takes advantage of the spatiotemporal symmetry inherent in this activity pattern. We suppose that a periodic traveling wave, with propagation speed c and interspike interval T, exists as a solution to (1). We then derive a consistency condition which holds if and only if such a periodic solution exists. The derivation is based on the fact that in such a solution, if a cell spikes at times $\tau \pm nT$ for every integer n, then its voltage must equal the threshold level V_T at times $\tau \pm nT$. The condition itself takes the form of a dispersion relation, namely a single equation relating wave speed with spiking period (or equivalently wavelength), for a periodic solution.

The challenge in deriving the dispersion relation is the computation of the synaptic currents (the terms in the integrand of equation (1)). To do this for a fixed point and time, one needs to take into account three contributions. For example, suppose that a cell at $x = 0$ spikes at time $t = 0$ and we wish to compute its total synaptic inputs for some $t \in (0, T)$. The first contribution consists of synaptic currents generated by all spikes from cells on the positive

$(x > 0)$ part of the one-dimensional domain (as well as past spikes by the cell at $x = 0$). Some of these will correspond to spikes fired before $t = 0$, others to spikes fired during time $(0, T)$. The second and third contributions come from synaptic currents generated by traveling waves passing through the negative $(x < 0)$ part of the domain, distinguished into two subsets that take different mathematical forms. The first of these corresponds to waves that have not reached $x = 0$ by time $t = 0$, the second to waves that have.

Exploiting this classification allows us to compute all synaptic currents, in the case that $J(x)$ has finite support or decays exponentially. In the finite support case,

$$J(x) \begin{cases} 0, & |x| > \sigma \\ \frac{1}{2\sigma}, & |x| \geq \sigma \end{cases}$$

where $H(t)$ is the Heaviside step function. For exponential support, we take

$$J(x) = \frac{e^{-\frac{|x|}{\sigma}}}{2\sigma}$$

For both of these forms of $J(x)$, equation (1) can be integrated. For the standard choice of alpha function

$$\alpha(t) = e^{-\frac{t}{\tau_2}} H(t) = \begin{cases} 0, & t < 0 \\ e^{-\frac{t}{\tau_2}}, & t \geq 0 \end{cases}$$

this leads to a single nonlinear algebraic equation relating the speed of the traveling waves c and the period T.

In addition to computing formulas analytically, we conducted numerical simulations to explore the initiation of multi-spike traveling waves and to study how well such solutions approximate periodic waves. In these simulations, an initial region is "shocked", that is, is brought to firing by an

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application of current. A traveling wave of spiking activity starts propagating away from the shocked region. The neurons in the shocked region, due to the synaptic current received from all the neurons that fire (including the shocked cells themselves), fire again, generating a second wave. This wave generation repeats faster and faster (as the accumulated synaptic current becomes greater and greater), driving the network towards the periodic firing regime (see Figure 1). We find that the interspike interval for each cell converges towards some fixed value. The intuition behind this convergence is that synaptic current accumulates more and more as firing rates increase, but the reset procedure provides an effective delay time that prevents firing rates from going to infinity.

When the times between spikes have become constant (up to a tolerance level), the speed of the traveling waves is numerically computed. For this speed, the analytical dispersion relation for the periodic regime predicts a certain period. We find very good agreement between the asymptotic value for the interspike intervals generated in our simulations and the predicted periods.
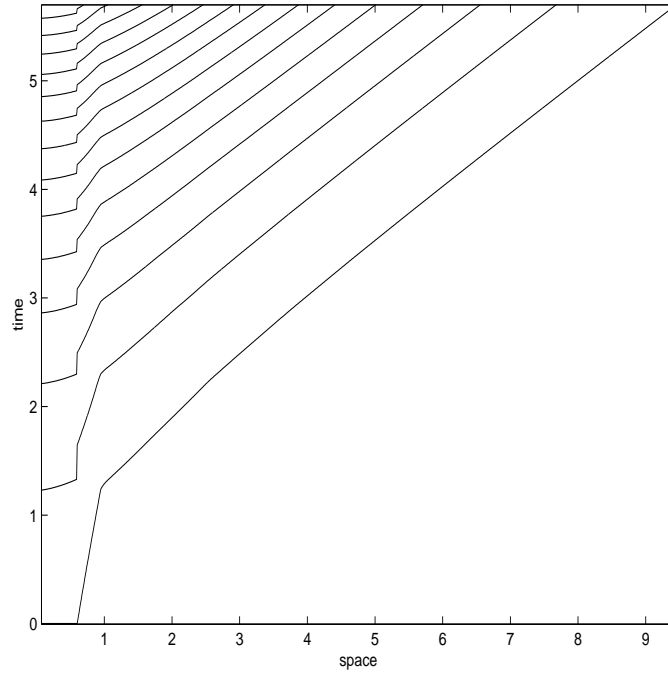
Figure 1: Multi-spike traveling waves from simulation of equation (1). Space is represented on the horizontal axis and time on the vertical axis. The region near the spatial coordinate 0 was given a single excitatory input at time 0. All subsequent waves were generated by the dynamics of equation (1). The times between successive spikes at each spatial point decrease, approaching a limiting value away from the shocked region.

References

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