

# Speed-up methods for simulations of traveling waves in large-scale integrate-and-fire neural networks

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## Abstract

We consider single and multiple spike traveling waves solutions in an integrate-and-fire neural network. Due to the special properties of this system it is possible to deduce the dynamical state of each neuron in the full network from a small subset, using recurrence relationships. Since the dimension of the subset is equal to the number of the traveling waves, this greatly reduces the computational time required for numerical simulations. These ideas are specific to the class of integrate-and-fire neural network models presented here.

Keywords: *integrate-and-fire, traveling waves, numerical methods*

## 1 Introduction

Synaptically generated traveling waves are one of the most studied large-scale dynamics of cortical tissues [1-11] as they provide insight into their organization and functionality. Computational models usually use reduced models of neurons coupled together via symmetric synapses whose strength decrease with distance. They need to capture the experimental properties of the traveling waves, such as constant shape and speed as well as the increase in speed with the synaptic coupling strength [12]. For these types of models large-scale simulations are needed to test the existence and stability of such traveling waves. As the large-scale simulations are often very time-consuming it is thus important to devise methods that would decrease the overall computation time.

The integrate-and-fire model is one of the widely used models for individual neurons as its simplicity often leads to analytical results that would be very difficult to obtain otherwise. While this model lacks the descriptive power of more detailed models such as Hodgkin-Huxley models it still captures an essential feature needed to model the traveling waves phenomena: the neurons are connected to each other via synapses whose strengths are a function of the firing times.

Due to the instantaneous reset condition the integrate-and-fire models are not continuous in time. This non-linearity needs to be treated carefully in numerical simulations to preserve accuracy. As an example, consider an integrate-and-fire neural network that uses a fixed time step to compute the evolution of its dynamical state. It is then possible for a neuron to spike during a time step and interpolation is one way to decrease the error in the spiking time. For complicated simulations in integrate-and-fire networks elaborate schemes were devised to save computation times while maintaining the desired accuracy [13, 14].

For the particular class of neural networks considered in this paper the firing times of the neurons can be computed “exactly”, that is, with arbitrary accuracy, by solving transcendental equations. A description of the integrate-and-fire neural network is presented in the next section. Considerable computation time can be saved by taking advantage of the special spatial structure of the single and multiple spike traveling waves. In the remaining sections we derive recurrence formulas that allow the computation of the dynamical state of one neuron as a function of the states of its neighbors.

## 2 Neural network description

The neural network we consider is the integrate-and-fire model for a spiking neuron. Each “neuron” is a linear integrator. Upon reaching a predefined threshold,  $V_T$ , the neuron emits a “spike” and the voltage is reset to  $V_R < V_T$ . The effect of a spike on other neurons is to turn on a current whose time dependence is often a simple exponential function and whose magnitude is a function of the distance between the two connected neurons. Thus the system is:

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

along with the reset condition such that if  $V(x, t)$  crosses a threshold,  $V_T$ , it is reset to  $V_R$ .  $g_{syn}$  is the coupling strength. If the domain is two-dimensional, then  $x, y$  are vectors. Here  $\alpha(t)$  is the time-dependent current that arises from an impulse. In the simplest models:

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

$$\alpha(t) = e^{-\frac{t}{\tau_2}} H(t) \quad (3)$$

where  $H(t)$  is the Heaviside step function:  $H(t) = \begin{cases} 0, & t < 0 \\ 1, & t \geq 0 \end{cases}$ .  $t_k(y)$  represents the discrete set of times that the neuron fires. That is, when  $V(x, t)$  crosses  $V_T$ , the threshold for the  $k^{th}$  time, then  $V(x, t^+) = V_R$  (i. e.  $V$  is reset) and  $t_k(x) = t$ . Ermentrout [3], Bressloff [4] and Golomb and Ermentrout [6, 7], 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 assumption (which can be biologically justified by supposing strong synaptic depression or a long refractory period), it is possible to solve (1) for a constant speed traveling wave and obtain an expression for the velocity,  $c$ . The multiple traveling waves problem is much more complicated.

If the specific form of the  $\alpha$  function is given by (3) then by integrating the differential equation (1) one obtains the integral formulation:

$$V(x, t) = \sum_{n=1}^{N(x, t)} \eta(t - t_n^*(x)) + g_{syn} \int_D J(|y - x|) \sum_{m=1}^{N(y, t)} A(t - t_k^*(y)) dy, \quad (4)$$

$N(y, t)$  represents the number of times the neuron at position  $y$  has already fired at time  $t$  and:

$$\eta(t) = \begin{cases} 0, & t < 0 \\ (V_{reset} - V_T) e^{-\frac{t}{\tau_1}}, & t \geq 0 \end{cases} \quad (5)$$

$$A(t) = \begin{cases} 0, & t < 0 \\ \frac{1}{1 - \frac{\tau_1}{\tau_2}} \left( e^{-\frac{t}{\tau_2}} - e^{-\frac{t}{\tau_1}} \right), & t \geq 0 \end{cases} \quad (6)$$

We use the following terminology when referring to the terms of the equation (4): “decaying reset” for the first one and “synaptic sum” for the second one. By using the definition:

$$\beta(t) = e^{-\frac{t}{\tau_1}} H(t) \quad (7)$$

we can re-express  $A(t) = \frac{1}{1 - \frac{\tau_1}{\tau_2}} (\alpha(t) - \beta(t))$ .

### 3 The discretized one-dimensional neural network

In order to simulate equation (4), with the choice of functions from equations (2, 3), one needs to discretize the one-dimensional domain. One way to do that is to use a uniform grid with distance  $\delta$  between nodes. By denoting spatial position of each neuron by  $x = i\delta$ , where  $i \in \mathbf{N}$  represents the numbering of each neuron, we can rewrite equation (4) as:

$$V(i, t) = \sum_{n=1}^{N(i, t)} \eta(t - t_n^*(i)) + g_{syn} \delta \sum_{j=1}^{\infty} J(|i - j|\delta) \sum_{m=1}^{N(j, t)} A(t - t_m^*(j\delta)) \quad (8)$$

Simulating the differential equation (1) directly is extremely time consuming. For every neuron in the network the potential and the synaptic current need to be recalculated at each time step. The integral form (4) takes advantage of the fact that in between spikes the synaptic current does not change at any location. This removes the burden of performing the time integration with fixed or variable step size and it avoids the problem of a spike occurring sometime during the last step of integration. Full advantage of the integral formulation occurs when one knows how to determine the location of the neuron that will fire next.

The firing of any neuron changes the weighted sum from the right-hand side on all other nodes. A brute-force method would recompute this sum every time a neuron spikes, but this would still take considerable time. This problem can be alleviated by maintaining and updating a buffer for the sum at each site. In this way it is possible to compute exactly which neuron would fire first and when this event would take place, saving considerable computational time. Still, the computational time can be further decreased by taking advantage of the symmetries that arise naturally in these types of networks for solitary and multiple traveling waves. We showed [10] that for this type of network the single spiking activity pattern arising after an initial region is brought to firing is monotone, that is neurons closer to the initial “shocked” region fire before neurons further away. As a consequence, as soon as one neuron fires we know that its neighbor spikes next. It is then possible to recompute the weighted sum from the right-hand side of the discrete integral equation (8) for the next neuron to fire based on the weighted sum of the neuron that just fired. Therefore, there is no need to compute the weighted sum for all neurons anymore. Instead one can compute that sum only for the traveling fronts. As soon as one traveling front moves, the dynamical state of the corresponding neuron can be computed using its neighbor’s state.

This is the main idea of the paper. In the next sections we show how this can be implemented for the solitary traveling wave and how this idea can be further extended for multiple traveling waves.

### 4 The solitary traveling wave

Solitary waves can be obtained by resetting the spiking neuron to a very negative potential. The reason why a neuron would not spike again can be explained intuitively in the following fashion: it needs a long time to recover from its resetting. By then its synaptic current wears off considerably and it lacks the strength to make the neuron fire again. Using the single spike assumption and the convention  $t^*(i\delta) = t_i^*$  equation (8) takes the following form:

$$V(i, t) = g_{syn} \delta \sum_{j=1}^{\infty} J(|i - j|\delta) A(t - t_j^*) \quad (9)$$

The decaying reset term is not included in equation (9) as we are not interested in any subsequent spiking.

We show that regardless of the firing times history the voltage outside of the region that already fired has constant shape. We derive a recurrence relationship for the weighted sum from the right-hand side of equation (9). This allows us to compute on the fly the synaptic sum for the neuron that will fire next.

#### 4.1 Computing the voltage in the vicinity of the traveling front

Let us consider a traveling wave moving towards the positive direction of the one-dimensional domain. We assume that at time  $t_{i_0-1}$  the traveling front reaches position  $(i_0 - 1)\delta$ , that is, the neuron located there fires and its potential is reset from  $V_T$  to  $V_R$ . The neuron situated at  $i_0 \delta$  fires at  $t_{i_0}$ . We use (9) and the equation  $A(0) = 0$  to compute the potential at position  $j_0 > i_0$  at time  $t_{i_0}$ :

$$\begin{aligned} V(j_0\delta, t_{i_0}) &= g_{syn}\delta \sum_{j=1}^{i_0} J((j_0 - j)\delta)A(t_{i_0} - t_j) = \\ e^{-\frac{(j_0-i_0)\delta}{\sigma}} g_{syn}\delta \sum_{j=1}^{i_0-1} J((i_0 - j)\delta)A(t_{i_0} - t_j) &= V_T e^{-\frac{(j_0-i_0)\delta}{\sigma}} \end{aligned} \quad (10)$$

It follows from equation (10) that regardless of the details of the firing map, the potential on the right of the traveling front decays exponentially from  $V_T$  to zero as  $j_0$  increases. Since the neuron one position ahead of the traveling front has the highest potential and receives the highest synaptic current it follows that it will fire next. This is the intuitive explanation for the firing times monotonicity proof we used in [10].

#### 4.2 Recurrence formula for the synaptic sum

We can obtain a recurrence relationship between the synaptic sum from different spatial locations. At time  $t_{i_0-1} < t < t_{i_0}$  the synaptic sums at positions  $x = i_0\delta$  and  $y = j_0\delta > x$  are:

$$V(i_0\delta, t) = \frac{g_{syn}\delta}{1 - \frac{\tau_1}{\tau_2}} \sum_{j=1}^{i_0-1} J((i_0 - j)\delta) (\alpha(t_{i_0} - t_j)\alpha(t - t_{i_0}) - \beta(t_{i_0} - t_j))\beta(t - t_{i_0}) \quad (11)$$

$$V(j_0\delta, t) = S_\alpha(i_0, t_{i_0-1})e^{-\frac{(j_0-i_0)\delta}{\sigma}} \alpha(t - t_{i_0-1}) - S_\beta(i_0, t_{i_0-1})e^{-\frac{(j_0-i_0)\delta}{\sigma}} \beta(t - t_{i_0-1})$$

where

$$S_\gamma(i_0, t_{i_0-1}) = \frac{g_{syn}\delta}{1 - \frac{\tau_1}{\tau_2}} \sum_{j=1}^{i_0-1} J((i_0 - j)\delta) \gamma(t_{i_0-1} - t_j), \quad \gamma = \alpha, \beta$$

We use equations (11) to compute the potential at position  $y = (i_0 + 1)\delta$  for  $t \in (t_{i_0}, t_{i_0+1}]$ , that is, after neuron at  $x = i_0\delta$  fires:

$$V((i_0 + 1)\delta, t) = S_\alpha(i_0 + 1, t_{i_0}) \alpha(t - t_{i_0}) - S_\beta(i_0 + 1, t_{i_0}) \beta(t - t_{i_0}) \quad (12)$$

where  $S_\alpha(i_0 + 1, t_{i_0})$  and  $S_\beta(i_0 + 1, t_{i_0})$  are given by the recurrence formulas:

$$S_\gamma(i_0 + 1, t_{i_0}) = S_\gamma(i_0, t_{i_0-1}) e^{-\frac{\delta}{\sigma}} \gamma(t_{i_0} - t_{i_0-1}) + \frac{g_{syn}}{1 - \frac{\tau_1}{\tau_2}} \delta J\left(\frac{\delta}{\sigma}\right) \quad (13)$$

We obtained a relationship (13) which allows us to compute the coefficients  $S_\alpha(i_0 + 1, t_{i_0})$  of the synaptic sum (12) (which for the solitary traveling wave case is also the voltage) at location  $x = (i_0 + 1)\delta$ , as a function of previous synaptic components  $S_\alpha(i_0, t_{i_0-1})$  and  $S_\beta(i_0, t_{i_0-1})$  and of the difference  $\Delta t = t_{i_0} - t_{i_0-1}$ . The intuitive meaning of this relationship is that the  $\alpha$  and  $\beta$  components of the synaptic sum at the new location are obtained by right “shifting” the components at the previous location and adding the effects of the last spike. Note that shifting decreases the synaptic components by a factor of  $e^{-\frac{\delta}{\sigma}}$ . The decaying terms  $\gamma(t_{i_0} - t_{i_0-1})$  also decrease the synaptic components, while the effects of the last spike lead to an increase in the overall synaptic sum.

## 5 Multiple traveling waves

The simple scheme outlined for the single spike traveling waves solution does not work for multiple spike waves. While the potential outside the region where neurons spiked at least once still decays exponentially with the spatial width of the gaussian  $J$ , the voltage in the region between successive traveling waves does not have a simple formula. However, for the traveling waves case, it is possible to devise a numerical scheme that extends the same basic ideas and allows the computation of firing times based on recurrence formulas. More precisely we require that the firing map  $t_k^*(y)$  is monotone in  $y$ , that is,  $t_k^*(y) > t_k^*(x)$ ,  $y > x$ . We then show how the numerical scheme can be implemented for the particular choice of the cortical-cortical connectivity function from equation (2).

### 5.1 Computing the decaying reset term

The decaying reset term depends only on the local history of the neuron and it can be computed as needed.

$$\eta(i_0, t) = \sum_{n=1}^{N(i_0, t)} \eta(t - t_n^*(i)) \quad (14)$$

### 5.2 Recurrence relationships for the synaptic sum

Let us assume again that the neuron located at position  $x = (i_0 - 1)\delta$  is the last one to fire, at time  $t_{i_0-1}$  and the neuron located at  $x = i_0\delta$  is the next one to fire, at time  $t_{i_0}$ . We then rewrite the synaptic sum at the node  $i_0$ ,  $S(i_0, t) = g_{syn}\delta \sum_{j=1}^{\infty} J(|i_0 - j|\delta) \sum_{m=1}^{N(j, t)} A(t - t_m^*(j\delta))$  as a sum of left and right plus the central spatial contributions evaluated at the time of the last spike  $t_{i_0-1}$  (the central contribution refers to the self-contribution, that is the effects of the neuron's spikes onto itself):

$$S(i_0, t) = \sum_{\gamma \in \{\alpha, -\beta\}} (S_{\gamma L}(i_0, t_{i_0-1}) + S_{\gamma C}(i_0, t_{i_0-1}) + S_{\gamma R}(i_0, t_{i_0-1})) \gamma(t - t_{i_0-1}) \quad (15)$$

where

$$\begin{aligned} S_{\gamma L}(i_0, t_{i_0-1}) &= g_{syn}\delta \sum_{j=1}^{i_0-1} J(|i_0 - j|\delta) \sum_{m=1}^{N(j, t_{i_0-1})} \gamma(t_{i_0-1} - t_m^*(j\delta)) \\ S_{\gamma C}(i_0, t_{i_0-1}) &= g_{syn}\delta J(0) \sum_{m=1}^{N(i_0, t_{i_0-1})} \gamma(t_{i_0-1} - t_m^*((i_0)\delta)) \end{aligned} \quad (16)$$

$$S_{\gamma R}(i_0, t_{i_0-1}) = g_{syn}\delta \sum_{j=i_0+1}^{\infty} J(|i_0 - j|\delta) \sum_{m=1}^{N(j, t_{i_0-1})} \gamma(t_{i_0-1} - t_m^*(j\delta))$$

The synaptic contribution for a neuron located at  $y = (i_0 + 1)\delta$ , for  $t \in [t_{i_0-1}, t_{i_0}]$  is then:

$$S(i_0 + 1, t) = \sum_{\gamma \in \{\alpha, -\beta\}} \left( (S_{\gamma L}(i_0, t_{i_0-1}) + S_{\gamma C}(i_0, t_{i_0-1})) e^{-\frac{\delta}{\sigma}} + S_{\gamma R}(i_0, t_{i_0-1}) e^{\frac{\delta}{\sigma}} \right) \gamma(t - t_{i_0-1})$$

By computing the central self-contribution at the node  $i_0 + 1$  at time  $t = t_{i_0}$ :

$$S_{\gamma C}(i_0 + 1, t_{i_0}) = g_{syn}\delta J(0) \sum_{m=1}^{N(i_0+1, t_{i_0})} \gamma(t_{i_0} - t_m^*((i_0 + 1)\delta))$$

and taking into account the effect of the last spike we find the recurrence formulas that advance formula (15) from  $i_0$  to  $i_0 + 1$ :

$$S_{\gamma L}(i_0 + 1, t_{i_0}) = (S_{\gamma L}(i_0, t_{i_0-1}) + S_{\gamma C}(i_0, t_{i_0-1})) e^{-\frac{\delta}{\sigma}} \gamma(t_{i_0} - t_{i_0-1}) + \frac{g_{syn}}{1 - \frac{\tau_1}{\tau_2}} \delta J\left(\frac{\delta}{\sigma}\right) \quad (17)$$

$$S_{\gamma R}(i_0 + 1, t_{i_0}) = S_{\gamma R}(i_0, t_{i_0-1}) e^{\frac{\delta}{\sigma}} \gamma(t_{i_0} - t_{i_0-1}) - S_{\gamma C}(i_0 + 1, t_{i_0})$$

Note that the computation of the self-contribution  $S_{\gamma C}(i_0 + 1, t_{i_0})$  is not really needed in order to compute synaptic sum  $S(i_0 + 1, t)$ . However the self-contribution will be needed next time a “shifting” procedure is required on that neuron.

### 5.3 Evolution of the firing maps for the multispiking traveling waves

In order to save computation time we monitor only the neurons one position ahead of the traveling fronts of the traveling waves. The previous recurrence formulas (17) along with the equation for the reset (14) allows one to compute the synaptic sum for the neuron closest to the one that fired last. We need to account for the changes in the synaptic sum for the other neurons that are monitored. Let us assume, without loss of generality that one of those neurons, located at  $y = j_0\delta$ , is situated on the right of the last spiking neuron, located at  $x = i_0\delta$ . We denote by  $t_k$  the previous firing time of the network. The updated equations for the neuron  $j_0$  are:

$$\begin{aligned} \eta(j_0, t_{i_0}) &= \eta(j_0, t_{i_k})\beta(t_{i_0} - t_k) \\ S_{\gamma L}(j_0, t_{i_0}) &= S_{\gamma L}(j_0, t_k) \gamma(t_{i_0} - t_k) + \frac{g_{syn}}{1 - \frac{\tau_1}{\tau_2}} \delta J\left(-\frac{(j_0 - i_0)\delta}{\sigma}\right) \\ S_{\gamma S}(j_0, t_{i_0}) &= S_{\gamma S}(j_0, t_k) \gamma(t_{i_0} - t_k), \quad S = C, R \end{aligned} \tag{18}$$

The computation of the firing times of the network can be performed now in the following manner. Only the dynamical state of a small subset of the network is computed by monitoring just the fronts of the traveling waves. As a new neuron spikes the focus shifts to its right neighboring neuron for which the synaptic sums can be computed using equations (17) along with the reset term equation (14). For all the other neurons from the monitored set the synaptic sums are updated by the use of equations (18). Similarly to the single spike wave case the left components of the synaptic sum components are “right shifted” (which decreases the left components by a factor of  $e^{\frac{\delta}{\sigma}}$ ). However, in contrast to the solitary wave case, a “left shift” is also needed (which increases the right components by a factor of  $e^{\frac{\delta}{\sigma}}$ ). The updating of the synaptic sums is completed by taking into account the time decays and the effects of the last spike.

## 6 Conclusions

We showed how the special spatial structure of the traveling waves can be used to decrease the simulation time for an integrate-and-fire network, for both single and multiple spike waves. The results of this paper apply to the specific forms of the synaptic  $\alpha$  function (3) and cortical-cortical connectivity (2). These functions are widely used in many computational models.

Effectively this allows simulations where the computation for the state of thousands or more neurons is reduced down to computations on the order of the number of traveling waves. As an example, this procedure was used in numerical simulations with 50,000 neurons where the number of synaptically generated waves was 50, hence the speed-up was around 1000.

For the one-dimensional domain the use of a gaussian function instead of the exponential one for the connectivity kernel  $J$  (2) would void the shifting property, rendering equations (13) and (17) wrong. Also, it is not possible to directly extend the results of this paper from the one-dimensional domain to the two-dimensional one as the shifting procedure is not valid in the two-dimensional domain. This is possible only if the “manhattan distance” is used as a measure of the distance between two neurons. In this case the generalization is straightforward, but this choice of the cortical-cortical function is a rather unnatural one. For the other two-dimensional

cases (euclidian distance, exponential or gaussian kernel) the speed-up procedure used in this paper cannot be implemented and the dynamical state two-dimensional neural network needs to be computed at the level of each individual neuron.

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