Simulation of Planar I/F Networks with Delayed Connections

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Abstract

This paper studies the synchronization characteristics of a locally connected, planar network of (leaky) integrate-and-fire (I/F) neurons after Hopfield & Hertz [7]. Simulations were conducted using both the Java programming language and the MatLab prototyping language in order to detect implementation errors. Further, two different algorithms were used in the simulations. The first method was a standard numerical simulation using Runge Kutta. The second method was an event-driven algorithm generalized from Campbell et al. Both algorithms yield the same results. Visualizations were included to make qualitative behaviors visually apparent.

We replicated the original Hopfield et al simulation results in which periodic synchronous firing emerged. The Java software displays the activation level of each unit in the planar grid in real time. The software also displays the number of units firing per time step. Since the software runs in real time, user can observe a movie of the network evolution simply by running the simulation. The main result obtained is that when small delays are introduced, synchronized firing takes the form of a traveling wave across the grid. When axon transmission was instantaneous, it was possible to achieve complete synchrony, but when small delays were introduced the largest amount of synchrony possible as less than 10 percent. With larger delays, the synchrony disappears entirely.

1 Introduction

Evidence has emerged within the last 5–15 years, that neuron spike timing is important for brain computations. One aspect of spike timing, synchronized firing, is a prominent feature of cortical neurons [4, 3, 13, 12]. How this synchronization emerges is a subject of intense study [1, 11, 5]. Hopfield and Herz [7] proposed a mechanism by which collections of independently spiking neurons can rapidly (in less than 20 spikes or 200 msec) converge to globally synchronous oscillations. Hopfield and Herz present convergence theorems and simulation studies. Their model uses integrate-and-fire (I/F) neurons, whose history can be traced to [9] (cf., [8]). Their modeling, however, makes the assumption of instantaneous transmission of action potentials. They further assume that a neuron generates an action potential instantly, the moment its membrane potential reaches threshold. Under certain conditions, these assumptions allow a signal to be transmitted across the entire width of a locally connected neuron grid in one time instant. This long-distance-messaging property is not physically or biologically possible. The present paper reproduces the original Hopfield and Herz results, but more important, studies the robustness of the results when an assumption of finite axon transmission speed is imposed on the model.

In related work, Gerstner [6] showed theoretically that integrate-and-fire (I/F) networks with delayed, local, normalized excitatory connections will converge to a periodic solution with phase-locked oscillations. Gerstner’s results depend on the absence of a leakage term in the I/F neurons. Thus, his analytical results can be applied to I/F neurons which have delayed connections, but which do not include leakage. Further, Gerstner did not conduct simulation studies.

Cambell, Wang, and Jayaprakash [2] also reproduced the Hopfield and Herz results but their work studied the speed of convergence and did not use delayed connections. Our work differs from theirs in this respect.

The present paper is an extended version of [10] and describes simulation studies using I/F neurons having delayed connections and leakage. The simulation studies offer intuitions not apparent in the theorems. In particular, the simulations reveal that volleys of synchronized firing travel across the grid in waves.

2 Instantaneous Propagation

This section describes the simulations in which signal propagation is instantaneous. Delayed signal propagation is discussed later. Following Hopfield and Herz, the simulations use 1600 (leaky) I/F neurons arranged on a 40x40 planar grid. Each neuron is locally connected to its four closest neighbors (n,s,e,w) with a fixed positive connection weight of 0.24. The network topology can have either periodic or open boundary conditions. In the open topology, neurons on the grid edges connect only to the interior of the grid so they will have either two or three connections, depending on
whether they are at a corner. In the periodic topology, neurons connect to their counterpart(s) on the opposite grid edge. This latter topology is less biologically realistic but yields a more uniform architecture for theoretical and simulation studies.

Figure 1 shows an I/F neuron. It has a state variable, \( u \), known as a membrane potential. When \( u \) reaches threshold, \( u_{th} = 1 \), the neuron emits an action potential, and \( u \) resets to the resting potential, \( u_{reset} = 0 \). The membrane potential is updated in continuous time. The dynamics of the membrane potential is described by the equation

\[
C \frac{du_i}{dt} = \frac{-1}{R} u_i(t) + I_i(t) \tag{1}
\]

The equation describes the change in \( u \) of the cell body of neuron, \( i \), as a function of its input current, \( I_i(t) \), and leakage term, \( u_i(t) \). The input current depends on two sources as shown in Figure 1 and expressed below.

\[
I_i(t) = \sum_{j=1}^{4} w_{ij} f_j(t) + I_{i}^{ext} \tag{3}
\]

\( I_{i}^{ext} \) is a fixed external input to neuron \( i \) assumed to come from outside of the grid. \( f_j(t) \) is either 0 or 1, depending on whether neuron \( j \) emits an action potential at time \( t \). The values \( j \) correspond to the four presynaptic neurons connecting to neuron \( i \) within the planar grid. \( w_{ij} \) refers to the connection weight from neuron \( j \) to \( i \) and equals 0.24. A neuron emits an instantaneous action potential when \( u_i \) reaches \( u_{th} \), and then \( u_i \) decreases by 1. If \( i \) fires at time instant \( t \), the notation \( u_i(t^-) \) and \( u_i(t^+) \) refers to the membrane potential just before and after that moment.

2.1 Instantaneous Spike Transmission

We use Hopfield and Herz’s “Model A,” which assumes that synaptic integration times are longer than the duration of the action potential, but that action potentials are instantaneous and propagation delays are zero. Let us clarify the effects of these assumptions. If a neuron \( j \) fires and \( j \) connects to neuron \( i \), then \( i \) receives the action potential when \( j \) fires. In a simulation, time will progress normally using \( \Delta t \) time-steps until some neuron, say \( j \), fires. When this happens, the progress of time is suspended until the effects of the action potential are fully propagated. During this suspended moment, if neurons that receive connections from \( j \) reach threshold as a result of receiving the action potential from \( j \), they also fire (in the same moment) sending an action potential back to \( j \) (in the very same moment). That is, if \( j \) causes \( i \) to fire, it will receive the action potential from \( i \) in the same moment. The membrane potential drops by one at the moment of firing. This raises the question, Can feedback input cause \( j \)’s membrane potential to remain above threshold after firing? As long as \( \sum_j w_{ji} < u_{thresh} = 1 \), \( u_j(t^-) \) will be less than \( u_j(t^-) \). In our simulations, \( \sum_j w_{ji} = 0.96 \).

To illustrate the signal propagation rules, let us apply these assumptions to the network in Figure 2. Assume that neuron \( j \) reaches threshold first, at time \( t \), as a result of receiving external input \( I_{ext} \). Assume \( u(t^-) = 0.9 \) for the other neurons in the network. Neuron \( i \) is the only neuron directly receiving input from \( j \). When \( j \) fires, it boosts \( i \)’s membrane potential by 0.24 to 1.14, driving it above threshold and causing it to emit an action potential, thereby decreasing its membrane potential to 0.14. All of the neurons, \( j \), \( k \), \( l \), and \( m \) receive action potentials as a result of \( i \’s \) firing. Thus, in one instant the action potentials travel a distance of two neural connections (e.g., from \( j \) to \( l \)). Neurons \( k \), \( l \), and \( m \), fire after receiving these action potentials and send return potentials back to \( i \) in the same instant, thus boosting \( i \’s \) membrane potential by another 0.72 to its final value \( u_i(t^+) = 0.86 \). The before-and-after membrane potentials are shown in Table 1.

In Figure 2, if a grid of neuronal connections were uniformly extended to the right, with weights of 0.24 and potentials of 0.9, a signal would propagate across the entire grid in one instant, regardless of the grid size.
Each pixel on the x-axis is one $\Delta t$. The y-axis plots the number of firing neurons per $\Delta t$ (max value is 1600). The network is silent, except when all neurons fire simultaneously. These moments are 443 timesteps apart.

2.2 Simulation Results

In simulations using periodic boundary conditions with parameters given in the method paragraph below, the system converges to complete, periodic global synchrony. Dozens of simulations were run both in Java and MatLab.

Method. A 40x40 neuron grid, modeled using Equations (2) and (3), was initialized to random membrane potentials having values $0 \leq u < 1$. Equation (2) was simulated using Runge-Kutta with a $\Delta t$ of 0.00001. (Corroborating simulations were conducted using an event-driven algorithm generalized from [2]). $I_{ext}$ was set to 10.0 and all $w_{ij}$’s were set to 0.24.

Results. After $\approx$ 45,000 $\Delta t$, the network always converged to a stable solution of periodic, global synchronized firing. This is shown in the synchronous firing graph in Figure 3. The graph displays the number of neurons firing during the $n$-th time step ($\Delta t$). For 443 time steps, there are no action potentials, then all neurons fire during the same time step. When open boundary conditions are used, the network still converges to a periodic solution, but synchrony is not global. For open boundary conditions, the maximum number of synchronous firing neurons in a timestep is about 1200.

Discussion. By observing that a neuron fires exactly once per period, Hopfield & Herz manipulate the exact solution for Equation (3) (assuming $I(t)$ is constant), to conclude that the predicted period, $P_{pred}$, is

$$P_{pred} = \ln(I - 4\alpha) - \ln(I - 1),$$

where $\alpha = w_{ij} = 0.24$. With our simulation parameters $P_{pred} = .00443$. The formula for the observed period, $P_{obs}$, is

$$P_{obs} = n\Delta t,$$

where $n$ is the number of time steps in a period. Our simulations yielded $n = 443$ using $\Delta t = 0.00001$. Thus $P_{pred} = P_{obs}$ providing strong support for correctness of the implemented simulation.

What mechanism underlies the synchronized firing? As the network converges to a stable solution, the initially random membrane potentials converge to values near threshold. When the grid is in this state, the firing of any neuron is analogous to setting a fire in a field of dry grass where the flames travel instantly across the entire grid. The firing of some trigger neuron $i$ ignites its four neighbors which in turn ignite their neighbors, continuing across the grid. The causal process is depicted in Figure 6. Because the synchronized firing yields intense excitatory feedback, the membrane potential of each neuron in the network drops by a mere 0.04. That is, for any neuron, $u(t^+) = u(t^-) - 0.04$. When the trigger neuron $i$ fires, $u_i(t^-) = u_{thresh} = 1$. Consequently, $u_i(t^+) = 0.96$.

3 Rate of Convergence

With I/F neurons, firing rate increases linearly with $I_{ext}$. This relationship can be confirmed by plotting the reciprocal of Equation (4) with $\alpha = 0$. Setting $\alpha = 0$ describes an uncoupled neuron. Since the firing rate of biological neurons shows a saturating non-linearity as stimulus intensity increases, it is problematic to interpret $I_{ext}$ as stimulus intensity. An alternative interpretation is to view $I_{ext}$ as a parameter to control the operating range of the neuron.

When $I_{ext} = 10$, the operating range of the membrane potential response is very nearly linear because the non-linear portion of the curve is above $u_{th} = 1$. When $I_{ext} = 1.1$, non-linearity becomes a significant factor. When time is normalized, the rate of convergence is higher with lower values of $I_{ext}$.

For the following discussion, assume that a neuron’s membrane potential is between 0 and 0.76. When a neuron receives a spike, its membrane potential increases by 0.24. This translates into a time savings to reach threshold and the neuron will fire sooner than it would otherwise. When the membrane potential response curve is saturating non-linear, the amount of savings depends on when the neuron receives the action potential. If the neuron is near the beginning of the response curve, the time savings is less than if the neuron is later in the response curve.

Consider a system of two neurons, $i$ and $j$, with mutually excitatory couplings. Let us assume these neurons do not fire simultaneously and that neuron $i$ fires before $j$. Assume that $j$’s membrane potential is slightly less than 0.76. When $i$ fires, $j$ will enjoy a time savings and fire sooner. When $j$ fires, $i$ will be early in its membrane potential curve. Neuron $i$ will also enjoy a time savings but to a lesser extent than $j$. Since $j$ fired later than $i$, but enjoyed a greater time savings, the amount by which $j$ follows $i$ on the next cycle will be less. That is $i$ and $j$ will be closer in synchrony. This catch-up effect is what causes the neurons to synchronize and it depends on the non-linear membrane potential response curve. Thus, convergence should be slower for high values of $I_{ext}$ then for lower values of $I_{ext}$ if time is properly normalized.

The above discussion gives intuitions about how a system of two neurons may synchronize. We now ask the question, How does a large grid of neurons synchronize? Figure 4 shows a simulation of a 20x20 grid at an intermediate stage of synchrony. Except for the grid size, the simulation parameters are the same as for the earlier simulations. Groups of synchronized neurons form spatially adjacent clusters. The frame on the left shows the neural firings at 9,478 steps into the simulation. The frame in the middle shows the neural firings at 9,649 steps into the simulation. These clusters eventually merge at 20,218 steps into the simulation as shown in the frame on the right. The merge happens suddenly. The two
4 Delayed Signal Propagation

To improve the biological relevance of the model, this section introduces axon transmission delays. The simulations in the previous section do not use physical time units. To introduce delays, it is useful to provide a real-time interpretation of the simulation results in the previous section. A lower time bound can be set by observing that a neuron in the simulation fires once per period and that the maximum sustainable firing rate of a biological neuron is on the order of 100 Hz. This gives us the interpretation that 0.00443 (i.e., 443Δt) non-physical units is at least 10 msec. For concreteness, we shall assume that a period is 10 msec in duration. Using Equation (5), Δt from the previous simulation approximates 0.023 msec. Thus the simulations in the previous section took about 1.04 sec (i.e., 45,000Δt) to fully converge.

To study signal propagation delays, we repeated the previous simulations, but introduced propagation delays of 1, 2, and 3 Δt units. Because the connectivity in the grid is highly localized, the effect of longer propagation delays was not studied.

3.1 Simulation Results for Delays

The synchronization results appear in Figure 5. Initial global synchronization required about 50,000 Δt ≈ 1.15 sec. It took approximately three to four times longer to reach the stable oscillations shown in Figure 5. We note that Figure 5 shows the number of synchronously firing neurons for each timestep after converging completely. In the periods before convergence, the order of neural firings changes randomly as the system behavior develops.

For the three delays, the oscillation periods are virtually identical to each other, and to the simulations in the previous section. The time required for the synchronous wave front to spread across the grid is proportional to the propagation delay. The area under each triangle is 1600, the number of neurons in the network, because each neuron fires once. The width of the triangle bases are 40, 80, and 120, increasing by 40 for each increase of Δt. The maximum number of synchronized firing neurons at any time step is 78, corresponding to the perimeter of the largest diamond which can be embedded in the grid. Figure 6 shows the synchronous wave fronts, which form concentric diamonds (for a 7x7 grid) whose trigger neuron is in the center.

At full convergence, the firing patterns organize to the stable form such as that shown in Figure 6. This figure depicts the action potentials traveling in concentric, diamond-shaped, wave fronts across the grid. The mechanism of wave propagation is as follows. If a network has converged completely, then the membrane potentials of all the neurons in the grid approach threshold uniformly. The first neuron, i, to fire will “ignite” the grid. The immediate neighbors of i will fire when they receive i’s action potential in the next timestep. These neighbors will in turn ignite their neighbors in the succeeding timestep. The wave will travel outward in concentric diamonds. The wave cannot travel inward because the relevant neurons have just fired and their membrane potentials have not recharged.

For a square grid whose dimensions are odd, we more formally describe the synchronous wave fronts when the network has completely converged. The description is similar when the dimensions are even. We assume complete convergence and noiseless dynamics. Suppose we have a dxd grid with periodic boundary conditions, where d is odd. Let k = (d − 1)/2. k is the number of squares on a side of the largest diamond that fits in the grid. Let t₀ be the time step in which some unique neuron ignites the grid. At this timestep,
The period of oscillation is preserved with delays and is only one neuron fires. Let \( \text{Tot}(n) \) denote the number of neurons firing at integer \( n \) timesteps after \( t_0 \), where \( 1 \leq n < d \). For \( n \leq k \), then \( \text{Tot}(n) = 4n \). For \( k < n \leq 2k \), then \( \text{Tot}(n) = 4(2k + 1 - n) \).

The total number of neurons that fire in the volley is given by

\[
1 + \sum_{n=1}^{2k} \text{Tot}(n) = 1 + 2 \sum_{n=1}^{k} 4n = d^2. \tag{6}
\]

Each term in the sum on the left represents the number of neurons in a concentric wavefront. The duration of the wave propagation episode is \( d \) timesteps.

For example, if \( d = 41 \), then \( k = 20 \), then the duration of the wave propagation episode is 41 timesteps. The total number of neurons firing in the episode is given below. This is, of course, all of the neurons in the grid.

\[
1 + 2 \sum_{n=1}^{k} 4n = 1 + 4k(k + 1) = 1681 = 41^2. \tag{7}
\]

Our results concerning time delays are summarized below and assume periodic boundary conditions.

1. The period of oscillation is preserved with delays and is described by Equation (4).
2. After convergence, firing of a neuron ignites a wavefront that travels across the grid, in concentric diamonds, at a rate inversely proportional to the signal transmission delay. For a delay of one \( \Delta t \), the duration of the propagation event is \( d \), were \( d \) is the number of neurons on a grid edge.
3. The maximum number of neurons firing in an instant corresponds to the number of neurons in the perimeter of the largest diamond that fits within the grid. This is \( 2(d - 1) \), or 78 in the case of a 40 x 40 grid.

5 Conclusions

The simulations in which signals were transmitted instantaneously were consistent with the results reported in [7]. With instantaneous signal transmission, all the neurons in the grid can fire at the same moment. When small transmission delays are introduced, the qualitative nature of the synchronization changes. It takes the form of a wave of synchronous firing that travels over the grid. With a transmission delay of 0.023 msec, the wave travels across a 40 x 40 grid in less than 1 msec. In biological terms, this is fast enough to be classified as a volley of synchronized firing. Time to convergence remains an issue. Convergence time in all cases was on the order of 1 sec or more. This seems too slow to describe the emergence of synchronized firing in the brain.

In software systems, it is possible to build architectures which axon signal transmission is instantaneous. Consequently, the Hopfield et al synchronization results are easy to apply. Since the synchronization characteristics are fragile when axon transmission delays are introduced, the application to biological systems must be done cautiously.

References