

## Synchronized Firing in a Time-delayed Neural Network

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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 (1995). Hopfield & Herz showed that, with the assumption of instantaneous signal transmission, locally connected networks converge to periodic, synchronized oscillations. We verify these results as well as study their robustness when signal transmission delays are introduced. Our simulation results are consistent with the theoretical work of Gerstner (1996) but the simulation studies offer intuitions not apparent in the theorems. In particular, the simulations reveal that volleys of synchronized firing travel across the network in waves.

### Introduction

Sequential computations in a computer are paced by a global clock. A brain also performs sequential computations, but its computing elements (neurons) operate in parallel and asynchronously, without an apparent global clock. There is, however, ample EEG evidence of synchronized computation in the brain. Further evidence has emerged within the last 5-15 years, that the timing of neuron spikes is also important for brain computations (Malsburg & Schneider 1986). How this synchronization emerges is a subject of intense study (R. Eckhorn & Reitboeck 1992).

Hopfield and Herz (1995) have proposed a mechanism by which collections of independently spiking neurons can rapidly (in less than 20 spikes or 200 ms) converge to globally synchronous oscillations. Their results are supported by convergence theorems and simulation studies. Their modeling, however, makes the assumption of instantaneous transmission of the action potential from one neuron to another. 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 planar grid of neurons in one time instant. This long-distance-messaging property is not physically possible and if the global synchronization results depend on this property, they will have little practical import.

Consequently, it is important to know how robust the Hopfield and Herz results are under less idealized conditions. 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 (1996) 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 (1996) results depend on the absence of a leakage term in the I/F neurons. Thus, his analytical results can be applied to Hopfield/Herz I/F neurons which have delayed connections, but which do not include leakage. Further, Gerstner did not conduct simulation studies.

Cambell, Wang, and Jayaprakash (1999) 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.

Our work conducts simulation studies using I/F neurons having delayed connections and leakage terms. In this respect, the work is unique. Further, 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.

### 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 very uniform architecture for theoretical and simulation studies.

Figure 1 shows a Hopfield and Herz I/F neuron. It differs from standard artificial neural network (ANN) neurons in

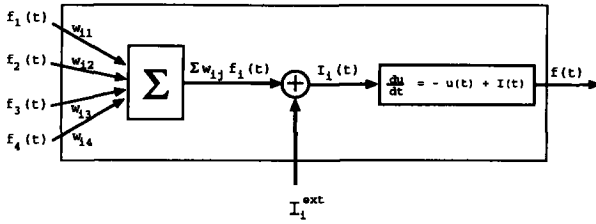


Figure 1: Integrate-and-fire (I/F) neuron with four inputs and an external input.

two ways. First, it has a state variable,  $u$ , known as a membrane potential. When  $u$  reaches threshold,  $u_{thresh} = 1$ , the neuron emits an action potential, and  $u$  resets to the resting potential,  $u_{reset} = 0$ . The membrane potential is updated in continuous time and this is the second difference from an ANN neuron. The dynamics of the membrane potential is described by the differential equation below.

$$C \frac{du_i}{dt} = -\frac{1}{R} u_i(t) + I_i(t) \quad (1)$$

In the model  $R = C = 1$ , thereby yielding the equation

$$\frac{du_i}{dt} = -u_i(t) + I_i(t). \quad (2)$$

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.

$$I_i(t) = \sum_{j=1}^4 w_{ij} f_j(t) + I_i^{ext} \quad (3)$$

$I_i^{ext}$  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  $u_{thresh}$ , and then  $u_i$  decreases by 1. If  $i$  fires at time instant  $t$ , we shall use the notation  $u_i(t^-)$  and  $u_i(t^+)$  to refer to the membrane potential just before and after that moment.

### 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 at the moment  $j$  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

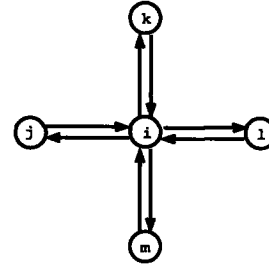


Figure 2: All connection weights are 0.24. At time  $t$ , neuron  $j$  reaches threshold. At time  $t$ , all other neurons have a membrane potential of  $u = 0.9$ .

neuron	$u(t^-)$	$u(t^+)$
$i$	0.9	0.86
$j$	1.0	0.24
$k$	0.9	0.14
$l$	0.9	0.14
$m$	0.9	0.14

Table 1: Membrane potentials immediately before and after neuron  $j$  fires at time  $t$ .

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  $\sum_i w_{ji} < u_{thresh} = 1$ ,  $u_j(t^+)$  will be less than  $u_j(t^-)$ . In our simulations,  $\sum_i w_{ji} = 0.96$ .

Let us apply these assumptions to the five-unit network in Figure 2. It is not an example of a grid but serves to illustrate the signal propagation rules. 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 their 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. This is the feature that makes the global synchronization possible.

### 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

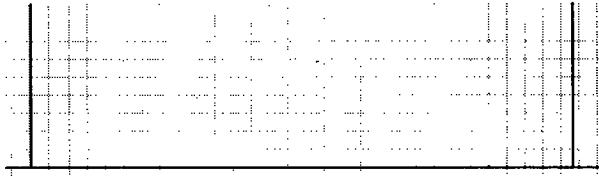


Figure 3: Synchronization plot for instantaneous transmission. Each pixel on the x-axis is a  $\Delta t$  timestep. The y-axis plots the number of neurons which fire during a timestep (max value is 1600). The network is silent, except for moments when all 1600 neurons fire simultaneously. These moments are 443 timesteps apart.

of simulations were run, all with identical results.

**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 Forward Euler with a  $\Delta t$  of 0.00001.  $I^{ext}$  was held fixed at 10.0 and all  $w_{ij}$ 's were held fixed at 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

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

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

$$P_{obs} = n\Delta t, \quad (5)$$

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, such as 0.9. 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. 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 5. 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,  $u_i(t^+) = u_i(t^-) - 0.04$ . When the trigger neuron  $i$  fires,  $u_i(t^-) = u_{thresh} = 1$ . Consequently,  $u_i(t^+) = 0.96$ .

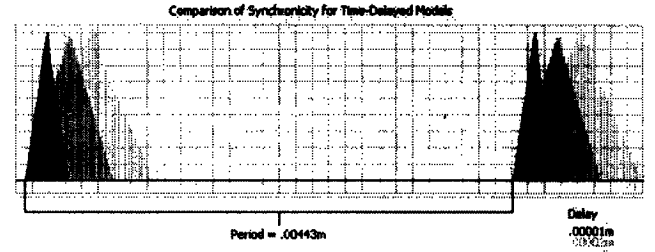


Figure 4: Synchronization plot for signal propagation delays of 1, 2, and 3  $\Delta t$ 's. All three runs are superimposed on the same plot. Wider triangles reflect longer delays. Each pixel on the x-axis is a  $\Delta t$  timestep. The period is 0.00443, but the synchronization is dispersed over time. The maximum neurons firing in a timestep is about 80. The narrowest triangle was generated using a propagation delay of 1  $\Delta t \approx 0.023$  msec. The width of the narrowest triangle is 40  $\Delta t \approx 1$  msec.

## Delayed Signal Propagation

This section describes the simulations that use propagation delays. The simulations in the previous section do not use physical time units. To introduce time 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 Hertz. This gives us the interpretation that 0.00443 (i.e.,  $443\Delta t$ ) non-physical units is at least 10 msec. For concreteness, we shall assume that a period is 10 msec in duration. Using Equation (5), we may conclude that, in the previous simulation,  $\Delta t \approx 0.023$  msec. Thus the simulations in the previous section took about 1.04 sec (i.e.,  $45,000\Delta t$ ) to completely converge.

To study effects of signal propagation delays on the model, we repeated the simulations in the previous section, but introduced propagation delays of 1, 2, and 3  $\Delta t$  units. Because the connectivity in the grid is highly localized, the effect of longer propagation delays was not studied.

## Simulation Results for Delays

The synchronization results appear in Figure 4. Initial global synchronization required about  $50,000 \Delta t \approx 1.15$  sec. It took approximately three to four times longer to reach the stable oscillations shown in Figure 4. We note that Figure 4 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 delay periods, the periods of these oscillations are 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  $\Delta t$ . The maximum number of synchronized firing neurons at any time step is

6	5	4	3	4	5	6
5	4	3	2	3	4	5
4	3	2	1	2	3	4
3	2	1	0	1	2	3
4	3	2	1	2	3	4
5	4	3	2	3	4	5
6	5	4	3	4	5	6

Figure 5: Locus of synchronous wave fronts over seven  $\Delta t$  for a 7x7 neural grid with periodic boundary conditions. The firing wavefronts form concentric diamonds. The trigger neuron, in the grid center, fires at  $t_0$ . Numbers in other squares describe time of firing in  $\Delta t$  units after  $t_0$ .

78, corresponding to the perimeter of the largest diamond which can be embedded in the grid. Figure 5 shows the synchronous wave fronts, which form concentric diamonds (for a 7x7 grid) whose trigger neuron is in the center.

At complete convergence, the firing patterns organize to the stable form such as that shown in Figure 5. 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  $d \times d$  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  $t_0$  be the time step in which some unique neuron ignites the grid. At this timestep, only one neuron fires. Let  $Tot(n)$  denote the number of neurons firing at integer  $n$  timesteps after  $t_0$ , where  $1 \leq n < d$ . For  $n \leq k$ , then  $Tot(n) = 4n$ . For  $k < n \leq 2k$ , then  $Tot(n) = 4(2k + 1 - n)$ .

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

$$1 + \sum_{n=1}^{2k} Tot(n) = 1 + 2 \sum_{n=1}^k 4n = d^2. \quad (6)$$

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.

$$1 + 2 \sum_{n=1}^k 4n = 1 + 4k(k + 1) = 1681 = 41^2. \quad (7)$$

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  $1\Delta t$ , the duration of the propagation event is  $d$ , where  $d$  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.

## Conclusions

The simulations in which signals were transmitted instantaneously were consistent with the results reported in (Hopfield & Herz 1995). 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.

## References

- Campbell, S. R.; Wang, D. L.; and Jayaprakash, C. 1999. Synchrony and desynchrony in integrate-and-fire oscillators. *Neural Computation* 11(7):1505–1619.
- Gerstner, W. 1996. Rapid phase locking in systems of pulse-coupled oscillators with delays. *Physical Review Letters* 76(10):1755–1758.
- Hopfield, J. J., and Herz, A. V. M. 1995. Rapid local synchronization of action potentials: Toward computation with coupled integrate-and-fire neurons. *Proceedings of the National Academy of Sciences* 92:6655–6662.
- Malsburg, C., and Schneider, W. 1986. A neural cocktail-party processor. *Biological Cybernetics* 54:29–40.
- R. Eckhorn, P. Dicke, M. A., and Reitboeck, H. J. 1992. Feature linking of visual features by stimulus-related synchronizations of model neurons. In Basar, E., and Bullock, T. H., eds., *Induced Rhythms in the Brain*. Birkhäuser. 397–416.