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Fast computation with spikes in a recurrent neural network

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Neural networks with recurrent connections are sometimes regarded as too slow at computation to serve as models of the brain. Here we analytically study a counterexample, a network consisting of N integrate-and-fire neurons with self excitation, all-to-all inhibition, instantaneous synaptic coupling, and constant external driving inputs. When the inhibition and/or excitation are large enough, the network performs a winner-take-all computation for all possible external inputs and initial states of the network. The computation is done very quickly: As soon as the winner spikes once, the computation is completed since no other neurons will spike. For some initial states, the winner is the first neuron to spike, and the computation is done at the first spike of the network. In general, there are M potential winners, corresponding to the top M external inputs. When the external inputs are close in magnitude, M tends to be larger. If $M>1$, the selection of the actual winner is strongly influenced by the initial states. If a special relation between the excitation and inhibition is satisfied, the network always selects the neuron with the maximum external input as the winner.

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Extensive recurrent connections between neurons exist in the brain. This has inspired researchers to propose recurrent neural network models with multiple feedback loops for many computations done in the brain, such as the winner-take-all (WTA) computation [1]. A WTA results when the dynamics of the network leads to sustained spiking of a single neuron or a group of neurons (the ‘‘winner’’), although all neurons are driven by external inputs and are capable of spiking in the absence of the couplings with other neurons. WTA behavior in the brain's neural networks could be the basis of perceptual decision making [2] and control of visual attention [3,4]. WTA can also be used for implementing universal computations [5] and a hierarchical model of vision [6].

However, recurrent networks are often assumed to be slow in converging to the computational results. Consequently, many researchers believe that recurrent connections are not useful for carrying out brain functions that are experimentally shown to be fast in execution, such as visual scene recognition [7] or orientation selectivity in primary visual cortex [8]. These computations are shown to complete as soon as the first few spikes appear in the networks after the onset of the stimulus. The assumed slowness of the recurrent networks may have come from the use of the rate models in the previous theoretical analysis of recurrent networks [1]. Rate models rely on spike rates averaged over time scales much longer than time between individual spikes; therefore, they are not adequate for addressing transient dynamics over a time scale of a few spikes in the networks. Numerical simulations of recurrent networks with spiking neurons have observed fast convergence of the network dynamics to stable spiking patterns of the neurons, suggesting fast computations with recurrent networks is indeed possible [9,10]. However, theoretical proof of the rapid computations in recurrent network has been lacking [11]. To date, most theoretical works on spiking recurrent networks have only studied synchronous and asynchronous states, in which all neurons have similar spiking patterns [12,13]. Computationally relevant states, such as WTA, often have neurons with completely different spiking patterns, and have been so far neglected in theories of spiking recurrent networks [11].

In this paper, we show that recurrent networks can perform fast computations if the detailed dynamics of individual spikes are considered. Specifically, we analytically analyze a simple spiking recurrent network that performs WTA computation. The network consists of N integrate-and-fire neurons. Each neuron has an excitatory connection to itself, and inhibitory connections to all other neurons [see Fig. 1(a)]. This organization of neurons is an idealization of neuronal structures found in the brain, and has been studied previously with rate models [1] and numerical simulations [9]. To facilitate analysis, we impose a structural symmetry on the network by using neurons with identical parameters, excitatory

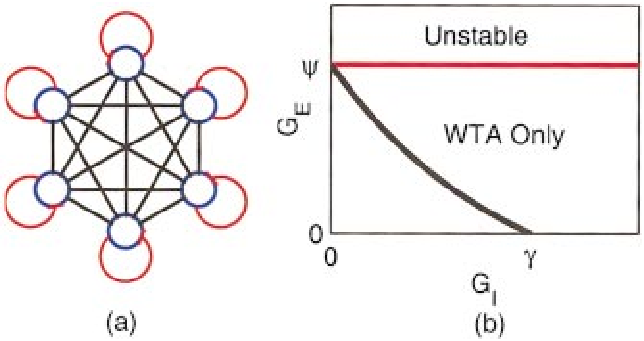

FIG. 1. (Color) (a) Diagram of the network. There are N neurons (blue circles, six shown). The red and black lines are excitatory (strength G_E) and inhibitory connections (strength G_I), respectively. (b) Phase diagram. Here, $\psi=\ln(V_0/V_{th})$, and $\gamma=\ln[I_{th}/(V_0-E_R)]$. The red line is given by $G_E=\psi$, and the black line is given by Eq. (11). When (G_I,G_E) is on the black line, the network always selects the neuron with the maximum input as the winner.

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connections with the same strength, and inhibitory connections with the same strength. Also, we neglect the time course of the spikes and the time delay of spike transmissions. The external inputs are modeled as constant currents injected to the neurons.

When inhibition and/or excitation are strong enough, the network performs a WTA computation for all possible external inputs and initial states of the network [see Fig. 1(b)]. The computation is done as soon as *the winner* spikes *once*. This is because the inhibition from the winner prevents other neurons from spiking. In general, the selection of the winner can be strongly influenced by the distribution of the external inputs and by the initial states of the network. When the maximum external input is distinctively larger than all other external inputs, the neuron with the maximum external input will be the winner for all initial states of the network. Other neurons can at most have transient spikes if their initial membrane potentials are high enough. On the other hand, if a group of neurons get external inputs close to the maximum input, the network is multistable, and any neuron in the group can be the winner. As to which neuron will be the actual winner depends largely on their initial membrane potentials. For the network to always select the neuron with maximum input as the winner for all possible external inputs and initial states, the excitation and inhibition must satisfy a special relationship [the black line in Fig. 1(b)]. Previous studies of fast WTA computation in spiking recurrent networks have relied on intuition [3,14] and numerical simulations [9]. These studies have shown that strong inhibition can promote fast WTA computation. However, they have missed the role of the excitation and the complexity of the WTA dynamics. Our analysis shows that a stronger self excitation causes the winner to spike more frequently and inhibit other neurons more effectively, and thus helps to promote a WTA computation even with a weak inhibition. The previous studies all assumed a particular initial state of the networks—all neurons are at the resting membrane potential, and proposed that the winner will be the neuron with the maximum external input. In the brain, this assumption is too restrictive since the membrane potentials of the neurons often deviate from the resting membrane potential because of noise and the inputs from other brain areas. Our analysis shows that initial states of the network can strongly influence the selection of the winner, depending on the distribution of the external inputs.

The dynamics of the network is analyzed by constructing ‘‘spike-timed potential map’’ (STPM). For a network of integrate-and-fire neurons with pulse couplings, the dynamical variables are the membrane potentials. Therefore, we can construct maps between the membrane potentials at different times. A STPM is constructed relative to the spike times of one of the *N* neurons. In particular, the membrane potentials just before the neuron spikes are mapped to those just before the neuron spikes again. Once the map is constructed, we analyze the iteration dynamics of the map to understand the convergence properties of the spiking dynamics. Constructing nonlinear maps is a common technique for analyzing the dynamics of spiking neural networks and pulse-coupled oscillators in general. Over the years, maps between phases or spike times have been proposed by various authors [12,15]. However, these maps are most useful for analyzing synchronous or asynchronous states of the network, since they all assume that neurons spike with the same or nearly the same frequency. STPM is more general, and is especially suitable for analyzing states such as WTA, in which neurons have very different spiking frequencies. Maps similar to STPM may also be useful for analyzing other physical and biological systems that can be modeled as pulse-coupled oscillators [12,16].

We now calculate the STPM relative to neuron *k*, one of the *N* neurons. The membrane potentials $V_j, j=1,\ldots,N$ satisfy the following integrate-and-fire equations:

$$\tau\frac{dV_j}{dt}=E_R-V_j+I_j-g_j^E(t)V_j-g_j^I(t)(V_j-E_R), \qquad (1)$$

where constants E_R and I_j are the membrane resting potential and the external input, respectively, and τ is the membrane time constant. Quantities $g_j^E(t)$ and $g_j^I(t)$ are excitatory and inhibitory conductances, respectively, and satisfy $g_j^E(t)=G_E\Sigma_n\tau\delta(t-t_j^{(n)})$, and $g_j^I(t)=G_I\Sigma_{m,m\neq j}\Sigma_n\tau\delta(t-t_m^{(n)})$. Here, $G_E>0$ is the strength of the self-excitatory connections, $G_I>0$ is the strength of the inhibitory connections between all neurons, and $t_m^{(n)}$ is the nth spike time of neuron *m*. Both G_E and G_I are dimensionless, as they are defined relative to the passive leak conductance of the neuron. We take the reversal potentials of the excitatory and inhibitory connections as 0 and E_R [17], respectively. Neuron *j* spikes when $V_j=V_{th}$, and is reset to $V_j=V_0$. Here, the constants V_{th} and V_0 are the threshold and the reset potentials, respectively, and satisfy $E_R<V_0<V_{th}<0$. The external inputs are assumed to be large enough to make neurons spike in absence of couplings with other neurons, i.e., $I_j>V_{th}-E_R\equiv I_{th}$, where I_{th} is the threshold current.

Consider the effects of the nth spike of neuron k at $t=t_k^{(n)}$. Let the membrane potentials right before the spike to be $V_j(t_k^{(n)-})=V_j^{(n)}$, $j=1,\ldots,N$. Obviously, $V_k^{(n)}=V_{th}$. The δ function coupling between neurons cause discontinuous jump of membrane potentials. Following the spike, the membrane potential of neuron *k* is reset, so $V_k=V_0$. The neuron receives an excitatory input immediately because of the excitatory connection to itself, therefore V_k jumps to a new value $V_k(t_k^{(n)+})$. Dividing both sides of Eq. (1) with $V_k(t)$ and integrating from $t_k^{(n)-}$ to $t_k^{(n)+}$, we find $\tau\ln(V_k(t_k^{(n)+})/V_0)=-\tau G_E$ [18]. Therefore,

$$V_k(t_k^{(n)+})=(1-\alpha_E)V_0, \qquad (2)$$

where $\alpha_E\equiv 1-\exp(-G_E)$. Similarly, since all other neurons receive an inhibitory input from neuron *k*, we have

$$V_j(t_k^{(n)+})=(1-\alpha_I)V_j^{(n)}+\alpha_I E_R, \qquad (3)$$

where, $\alpha_I\equiv 1-\exp(-G_I)$. To avoid runaway spiking of neuron *k*, we must have $V_k(t_k^{(n)+})<V_{th}$, or equivalently $\alpha_E<(V_0-V_{th})/V_0$. This imposes an upper bound for G_E [the red line in Fig. 1(b)]. With the constraint on G_E and Eq. (1), it is easy to prove that $E_R<V_j(t)<V_{th}$ for all time.

Now we calculate the membrane potentials $\{V_j^{(n+1)}\}$ just before neuron k spikes again. In between the nth and $(n+1)$-th spikes of neuron k, neuron $j \neq k$ can spike any number of times depending on G_E, G_I and $\{V_j^{(n)}\}$. The simplest case is that all neurons do not spike in this time span. This gives the "0-spike branch" of the STPM relative to neuron k. Other cases, where some neurons spike before neuron k spikes again, are in general more complicated to construct.

To calculate the 0-spike branch, we integrate V_k from $t = t_k^{(n)+}$ until $V_k(t_k^{(n+1)}) = V_{th}$ using Eq. (1), at which point the neuron spikes again. From this we find that the time interval T_k between successive spikes of neuron k is a constant: $T_k = t_k^{(n+1)} - t_k^{(n)} = \tau \ln[(I_k + E_R - V_0 + \alpha_E V_0)/(I_k - I_{th})]$. Integrating V_j from $t_k^{(n)+}$ to $t_k^{(n+1)}$ for all other neurons, we find

$$V_j^{(n+1)} = F_{kj}(V_j^{(n)}) = L_{kj} + M_k V_j^{(n)}, \tag{4}$$

where $L_{kj} = I_j + E_R - (I_j + E_R - \alpha_I E_R)\exp(-T_k/\tau)$, and $0 < M_k = (1-\alpha_I)\exp(-T_k/\tau) < 1$. Equation (4) gives the 0-spike branch. This branch is a linear map. For the 0-spike branch to be valid, we must enforce the consistency condition that all neurons do not spike between $t_k^{(n)+}$ and $t_k^{(n+1)}$. This is equivalent to the requirement that $F_{kj}(V_j^{(n)}) < V_{th}$, or $V_j^{(n)} < V_j^{(k,0)} \equiv (V_{th} - L_{kj})/M_k$ for all $j \neq k$.

It is possible that the STPM relative to neuron k has only the 0-spike branch. For this to happen, we need to show that $V_{th} < V_j^{(k,0)}$. Algebraic manipulations simplify this condition into

$$I_k - I_{th} > \eta (I_j - I_{th}) \tag{5}$$

for all $j \neq k$. Here, $\eta = (V_{th} - V_0 + \alpha_E V_0)/\alpha_I I_{th}$.

When Eqs. (5) are satisfied, neuron k becomes a winner, i.e., the only neuron that spikes in subsequent time, as soon as it spikes *once*. Moreover, the membrane potentials of all other neurons quickly settle down to periodic subthreshold oscillations. To see this, we note that the iteration dynamics of the STPM has one fixed point. This fixed point is globally stable, since the slope M_k of the STPM, now a linear map, is positive but smaller than one. The spiking of neuron k is periodic right from the start, since its dynamics is unaffected by other neurons. Equations (5) carves out a subspace in the N-dimensional Euclidean space of the external inputs $I_j > I_{th}, j = 1, \ldots, N$. In this subspace, neuron k is the winner if it spikes once.

When $\eta < 1$, or equivalently

$$\alpha_E(-V_0) + \alpha_I I_{th} > V_{th} - V_0, \tag{6}$$

the network operates completely in a WTA mode [see Fig.1(b)]. In other words, for all possible external inputs, the network always settles down to a WTA state. We can easily show this by the following proof-by-contradiction argument. Suppose that there are $M > 1$ neurons spike in the steady state. We can label these spiking neurons according to the external inputs, so that $I_1 \geqslant I_2 \geqslant \cdots \geqslant I_M$. It follows, then, $I_1 - I_{th} > \eta(I_j - I_{th})$ for all $2 < j < M$. But the above relations are nothing but Eqs. (5), according to which neuron one should be a winner over the other spiking neurons as soon as it spikes once. Hence, the assumption that more than one neuron are spiking in the steady state is wrong, and the network is indeed operating in a WTA mode. From Eq. (6), we see that both strong inhibition and strong excitation helps to promote the WTA computation.

It is easy to prove that the neuron with the maximum external input will be the winner as soon as it spikes once. For convenience of discussion, in the rest of the paper we will label neurons such that $I_1 \geqslant I_2 \geqslant \cdots \geqslant I_N$. We find $I_1 - I_{th} > \eta(I_j - I_{th})$ for all $2 < j < N$ since $\eta < 1$. Therefore, neuron one, which has the maximum external input, satisfies Eqs. (5), and will be the winner if it spikes once. If the maximum input is so large that no other external inputs can satisfy Eqs. (5), the neuron with the maximum input will be the winner for all possible initial conditions of the network. With our labeling scheme, this condition can be expressed as

$$I_1 - I_{th} > (I_2 - I_{th})/\eta. \tag{7}$$

In this case, other neurons can *at most* have transient spikes if their initial membrane potentials are high enough. The WTA is *likely* done as soon as the *first spike* appears in the network, since usually membrane potentials of the neurons are near the resting membrane potential initially, and the neuron with the maximum input will be the first to spike. Equation (7) is the condition for the winner to be completely determined by the external inputs.

If several external inputs satisfy Eqs. (5) (this is possible since $\eta < 1$), more than one neuron can be the winner, i.e., the network can be multistable. In this case, the winner is determined by both the external inputs and the initial membrane potentials. The conditions for $M < N$ neurons to be potential winners are

$$I_M - I_{th} > (I_{M+1} - I_{th})/\eta, \tag{8}$$

$$I_M - I_{th} > \eta(I_1 - I_{th}). \tag{9}$$

Equation (8) ensures that neurons $M+1, \ldots, N$ are losers to one of the neurons $1, \ldots, M$, and Eq. (9) ensures that all neurons $1, \ldots, M$ can be potential winners. The losing neurons can at most have transient spikes, whereas the potential winners will be the only neuron spiking after it spikes once. The initial states of the network can strongly influence which of the neurons $1, \ldots, M$ spikes first, hence, will be important for selecting the winner. A special case of multistability is when

$$I_N - I_{th} > \eta(I_1 - I_{th}). \tag{10}$$

This condition is satisfied near $I_1 = I_2 = \cdots = I_N$. Here, Eqs. (5) hold for all neurons in the network. Therefore, whoever spikes first will be the winner, and the WTA computation is *always* done as soon as the *first spike* appears in the network. The initial membrane potentials have strong influence on determining the winner.

When $\eta = 1$, or equivalently

$$\alpha_E(-V_0) + \alpha_I I_{th} = V_{th} - V_0, \tag{11}$$

the network operates in a WTA mode unless the maximum of the external inputs is shared by more than one neuron. Moreover, the neuron with the maximum input will always be the winner regardless of the initial states of the network. In this case, the network is a robust maximum input selector. The spiking frequency of the winner monotonically increases with the increase of the maximum input. This mode of computation is useful for implementing universal computation [5] or a hierarchical model of vision [6]. From Eq. (11) we see that robust maximum selector requires a careful tuning of the strength of the excitation and inhibition. Previous intuitive and numerical studies of WTA spikes have all missed this point [3,9,14].

When $\eta > 1$, the network does not operate completely in a WTA mode. The network will still settle down to a WTA state if Eq. (7) is satisfied. Otherwise, the network settles to cospiking states with more than one neuron spiking. These states are in general quite complicated to analyze completely. Special cases with a few neurons spiking can be analyzed by constructing STPM beyond the 0-spike branch. Details will be published elsewhere.

In summary, we have exhibited a recurrent network that performs a fast winner-take-all computation. To facilitate analytical calculations, we made simplifications that are not completely biological. For example, the mutual inhibitions between the neurons are really mediated by interneurons in the brain. However, as long as the response time of the interneurons is much faster than the spike time intervals of the neurons, our results should still apply. Similarly, the omission of the time course of the spikes and the time delay of spike transmissions are not important, provided that these times are much smaller than the interspike intervals of the neurons.

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[1] S. Grossberg, Stud. Appl. Math. **L11**, 213 (1973); S. Amari and M. A. Arbib, in *Systems Neuroscience*, edited by J. Metzler (Academic Press, Boston, 1977), p. 119; B. Ermentrout, Neural Networks **5**, 415 (1992); J. Feng and K. P. Hadeler, J. Phys. A **29**, 5019 (1996); R. H. Hahnloser *et al.*, Nature (London) **405**, 947 (2000).
[2] C. D. Salzman and W. T. Newsome, Science **264**, 231 (1994).
[3] E. Niebur and C. Koch, in *NIPS*, edited by D. Touretzky *et al.* (MIT, Cambridge, MA, 1996), Vol. 8, p. 802.
[4] D. K. Lee *et al.*, Nat. Neurosci. **2**, 375 (1999).
[5] W. Maass, Neural Comput. **12**, 2519 (2000).
[6] M. Riesenhuber and T. Poggio, Nat. Neurosci. **2**, 1019 (1999).
[7] S. Thorpe *et al.*, Nature (London) **381**, 520 (1996).
[8] S. Celebrini *et al.*, Visual Neurosci. **10**, 811 (1993).
[9] R. Coultrip *et al.*, Neural Networks **5**, 47 (1992).
[10] F. P. Battagelia and A. Treves, Neural Comput. **10**, 431 (1998).
[11] J. J. Hopfield and A. V. Herz, Proc. Natl. Acad. Sci. U.S.A. **92**, 6655 (1995).
[12] R. E. Mirollo and S. H. Strogatz, SIAM (Soc. Ind. Appl. Math.) J. Appl. Math. **50**, 1645 (1990).
[13] L. F. Abbott and C. van Vreeswijk, Phys. Rev. E **48**, 1483 (1993); M. Tsodyks *et al.*, Phys. Rev. Lett. **71**, 1280 (1993); S. Bottani, *ibid.* **74**, 4189 (1995); P. C. Bressloff and S. Coombes, *ibid.* **81**, 2168 (1998); C. C. Chow, Physica D **118**, 343 (1998); C. van Vreeswijk, Phys. Rev. Lett. **84**, 5110 (2000); D. Hansel and G. Mato, *ibid.* **86**, 4175 (2001).
[14] S. J. Thorpe, in *Parallel Processing in Neutral Systems and Computers*, edited by R. Eckmiller, G. Hartmann, and G. Hauske (Elsevier Science, New York, 1990), p. 91.
[15] W. Gerstner, Phys. Rev. E **51**, 738 (1995); D. Hansel *et al.*, Neural Comput. **7**, 307 (1995).
[16] Z. Olami *et al.*, Phys. Rev. Lett. **68**, 1244 (1992); C. Peskin, *Mathematical Aspects of Heart Physiology* (Courant Institute of Mathematical Sciences, New York University, New York, 1975); A. V. M. Herz and J. J. Hopfield, Phys. Rev. Lett. **75**, 1222 (1995).
[17] This choice of the reversal potential for the inhibition makes it a shunting inhibition. This is mainly for convenience of analytical calculation. With other choices of the reversal potential, analysis similar to the case of shunting inhibition can be done. The conclusions of the paper do not depend on the particular use of shunting inhibition.
[18] This way of integrating over the δ functions is suggested to us by Dr. Ken Miller.