# Spike propagation in driven chain networks with dominant global inhibition

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Spike propagation in chain networks is usually studied in the synfire regime, in which successive groups of neurons are synaptically activated sequentially through the unidirectional excitatory connections. Here we study the dynamics of chain networks with dominant global feedback inhibition that prevents the synfire activity. Neural activity is driven by suprathreshold external inputs. We analytically and numerically demonstrate that spike propagation along the chain is a unique dynamical attractor in a wide parameter regime. The strong inhibition permits a robust winner-take-all propagation in the case of multiple chains competing via the inhibition.

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Synfire chain activity, in which synchronous spikes propagate along a chain of successive groups of neurons connected unidirectionally via excitatory synaptic connections [1], has been extensively studied [2] and suggested as the underlying mechanism for precisely timed sequential firings of neurons observed in a number of neural systems, including songbirds [3–5], cortical activity [6], and primate motor cortex [7]. Synfire activity requires the excitation be in a restricted regime: the excitation must be strong enough for the synaptic activity to evoke spikes in subsequent groups of neurons, but weak enough to avoid runaway instability [4,8].

In this paper, we demonstrate that precisely timed spike propagation in chain networks can be robustly established beyond the synfire regime. Instead of the synaptic activation, neural activity is sustained by suprathreshold external inputs. The activity is controlled by a strong global feedback inhibition and shaped by the unidirectional excitatory connections between the groups. The inhibition dominates the excitation and the synfire activity is suppressed. We show that spike propagation is a unique attractor to which the dynamics flows from all initial conditions when the external inputs are on. This mechanism is robust, with a large working parameter regime for the excitation and inhibition strengths. The strong inhibition also permits a robust winner-take-all selection of a single chain for spikes to propagate when there are multiple chains competing for the activity, which could be a mechanism for action selection if each chain encodes an action element such as a song syllable in songbirds [4,5].

Our results in the "driven-chain" regime are obtained through analytical analysis and numerical simulations of chain networks of leaky integrate-and-fire neurons. The analytical analysis is aided with three simplifications: the groups of neurons are replaced by single neurons, the global inhibition is modeled with all-to-all inhibitory connections between the neurons, and the synaptic interactions are approximated as pulse coupling. We prove that sequential spiking along the chain with precise timings is the unique global attractor in a wide parameter regime of the excitation and inhibition; furthermore, in the same parameter regime, the spike propagation selects a single chain if multiple chains compete. The analytical results are confirmed numerically with the simplifications removed and noise added.

Many models of biological and physical systems including heart cells, fireflies, earthquakes, and neural networks belong to a broad class of models consisting of systems of pulse-coupled oscillators [9–11]; our simplified neural network model fits into this class as well. Our analytical analysis should add insights into the relationship between the structure of coupling and the dynamics, a key for understanding these diverse systems. Sequential spiking in chains of pulse-coupled oscillating single neurons has been investigated before [12–14] and it has been shown that spike sequences are stable in generic inhibition-dominant networks [15]. However, these works do not show that the dynamics of a given network is attracted to a unique spike sequence attractor regardless of the initial conditions. A unique attractor is robust against perturbations and noise since the basin of attraction is large. This is an important characteristic if the pattern drives a single motor action such as a song syllable [3,4]. Our analysis establishes that the spike propagation in chain networks in the driven-chain regime is a unique stable attractor to which the dynamics converges from all initial conditions.

The dynamics of the neurons in the simplified model is as follows:

$$\tau \frac{dV_j(t)}{dt} = E_R + I - V_j(t) + I_s, \tag{1}$$

where $I_s$ is the synaptic current and is given by

$$I_s = \sum_{n=1}^{\infty} \{-G_E^{j,s_n} V_j(t) + G_I[E_I - V_j(t)]\} \tau \delta(t - t_n). \tag{2}$$

Here $\tau$ is the membrane time constant; $V_j(t)$ is the membrane potential of neuron $j$; $E_R$ and $E_I$ are the resting membrane potential and the reversal potential of the inhibitory synapse, respectively (the reversal potential of the excitatory synapse is 0); $I$ is the constant external input; $G_E^{j,i}$ is the excitatory conductance from neuron $i$ to neuron $j$, which is $G_E > 0$ if $j = i+1$ is the neuron next to neuron $i$ down the chain and 0 otherwise; $G_I > 0$ is the global inhibitory conductance be-

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tween all neurons; $s_n$ is the index of the $n$th spiking neuron in the network; and $t_n$ is the spike time of neuron $s_n$. All conductances are scaled with the leak conductance of the neuron. A neuron spikes when the membrane potential reaches a threshold $\Theta$. After a spike, the membrane potential is reset to the reset potential $V_R$ and all neurons are excited or inhibited immediately. There are three restrictions: (1) $E_I < E_R, V_R, V_j(t) < \Theta < 0$; (2) only one neuron can spike at a time and neurons do not spike immediately after receiving an excitation, which leads to $G_I > G_E\Theta/(E_I-\Theta)$ (see [15]); (3) $I$ is strong enough to make an isolated neuron spike.

In between two consecutive spikes in the network, neurons are uncoupled and their membrane potentials increase due to the external inputs. Since the neuron properties and external drives are homogeneous, the neuron with the highest membrane potential after the last spike will spike first, winning the "race-to-spike." The spike is transmitted to all neurons via the global inhibition, reducing their membrane potentials; it is also delivered to the neuron next to the spiked neuron down the chain via the excitatory connection, increasing its membrane potential and counteracting the inhibition. The spiked neuron's membrane potential is reset and further reduced by the inhibition. After the spike, the race-to-spike resumes.

This process can be expressed mathematically with the pseudo-spike-time mapping, as shown in [15]. Equation (1) can be integrated in between two consecutive spikes of the network; the jumps of the membrane potentials right after a spike can be computed by integrating over the $\delta$ functions [15]. A key to the race-to-spike is the time for an isolated neuron to spike starting from a membrane potential $V$, which is captured with the pseudo-spike-time factor (PSTF) as

$$\Gamma(V) \equiv (E_R + I - V)/(E_R + I - \Theta). \tag{3}$$

An uncoupled neuron will spike after a time $\tau \ln \Gamma(V)$. By integrating Eq. (1), the membrane potentials of all neurons right after the $n$th spike, denoted as $V_j^{(n)+}$, can be mapped into those right after the next spike, $V_j^{(n+1)+}$. Equivalently, this mapping can be expressed in terms the PSTF's right after the spikes. Denote the PSTF of neuron $j$ right after the $n$th spike as $\Gamma_j^{(n)+} \equiv \Gamma(V_j^{(n)+})$. The neuron that wins the race-to-spike, whose ID is $s_{n+1}$, has the smallest PSTF, or

$$s_{n+1} = \arg\min_j \Gamma_j^{(n)+}. \tag{4}$$

The mapping for the chain network is

$$\Gamma_j^{(n+1)+} = \begin{cases} \varepsilon_I \Gamma_R + \psi_I & \text{if } j = s_{n+1}, \\ \varepsilon_{EI}\Gamma_j^{(n)+}/\Gamma_{s_{n+1}}^{(n)+} + \psi_{EI} & \text{if } j = s_{n+1}+1, \\ \varepsilon_I \Gamma_j^{(n)+}/\Gamma_{s_{n+1}}^{(n)+} + \psi_I & \text{otherwise}. \end{cases} \tag{5}$$

Here $\varepsilon_I = e^{-G_I}$; $\varepsilon_{EI} = e^{-G_I - G_E}$; $\psi_I = (1-\varepsilon_I)\Gamma_I$; $\psi_{EI} = (1-\varepsilon_{EI})\Gamma(E_{EI})$, where $E_{EI} = E_I G_I/(G_E+G_I)$ and $\Gamma_R = \Gamma(V_R)$. The three cases of $j$ correspond to the spiked neuron, the excited neuron, and the inhibited neuron.

A solution of the mapping is spike propagation along the chain, i.e., $s_{n+m} = s_n + m$. It is a translation invariant solution obtained by setting in Eq. (5) $\Gamma_{s_n+1}^{(n)+} = \Gamma_{s_n+2}^{(n+1)+}$ (the PSTF's of the excited neurons) and $\Gamma_j^{(n)+} = \Gamma_j^{(n+1)+}$ if $j > s_n + 2$ (the PSTF's of purely inhibited neurons). Neurons spike at precise times. The stability of this solution can be easily shown using the results in [15]. We now aim to prove that the spike propagation is the unique global attractor in a wide parameter regime.

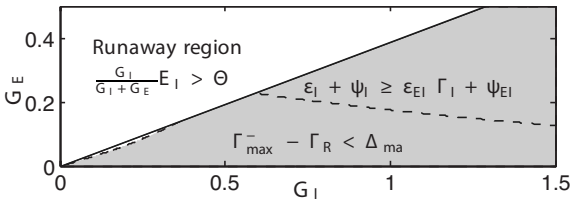


FIG. 1. Phase diagram of spike propagation in an infinitely long chain in the simplified model. In the gray region, spike propagation is the unique spike sequence attractor. The upper right region above the dashed line, computed from Eq. (6), is where the number of the transient spikes is 1. The lower left dashed line is computed from Eq. (7). Parameters: $E_R = -70$ mV, $E_I = -75$ mV, $V_R = -64$ mV, $\Theta = -54$ mV, $\tau = 40$ ms.

A simple case is when both the excitation and inhibition are strong. Right after the first spike in the network, the membrane potential of the neuron next to the spiked neuron, which receives excitation in addition to the inhibition, is higher than those of all other neurons, which receive only inhibition, regardless of their membrane potentials right before the spike. In other words, $\Gamma_{s_1+1}^{(2)+} < \Gamma_j^{(2)+}$ for all $j \neq s_1+1$. Therefore the excited neuron spikes next, i.e., $s_2 = s_1 + 1$. This establishes the spike propagation from any initial condition after the first spike in the network. The precise condition for this case is

$$\varepsilon_I + \psi_I \geq \varepsilon_{EI}\Gamma_I + \psi_{EI}, \tag{6}$$

where $\Gamma_I \equiv \Gamma(E_I)$. The PSTF's approach the translation invariant solution exponentially with the number of spikes. This regime, in which both $G_E$ and $G_I$ are large, is shown in Fig. 1.

A larger regime, in which it could take more than one transient spike to establish spike propagation, is given by

$$\Gamma^-_{\max} - \Gamma_R < \Delta_{ma}. \tag{7}$$

Here $\Gamma^-_{\max}$ is the upper limit of the PSTF right before each spike and $\Delta_{ma} = (\varepsilon_I + \psi_I - \varepsilon_{EI} - \psi_{EI})/\varepsilon_{EI}$. The proof of this statement is given in Appendix A. To find $\Gamma^-_{\max}$, we define the PSTF right before the $n$th spike as $\Gamma_j^{(n)-} \equiv \Gamma(V_j^{(n)-})$, where $V_j^{(n)-}$ is the membrane potential of neuron $j$ right before the $n$th spike. Iterating $\Gamma_j^{(n+1)-} \leq \max\{(\varepsilon_I\Gamma_R + \psi_I)/\Gamma_{s_{n+1}}^{(n)+}, [\varepsilon_I\Gamma_j^{(n)-} + \psi_I]/\Gamma_{s_{n+1}}^{(n)+}\} < \max\{(\varepsilon_I\Gamma_R + \psi_I)/(\varepsilon_{EI} + \psi_{EI}), [\varepsilon_I\Gamma_j^{(n)-} + \psi_I]/(\varepsilon_{EI} + \psi_{EI})\}$ with an initial condition $\Gamma_j^{(1)-} < \Gamma_I$ and taking $n \to \infty$, we find a reasonable estimate of $\Gamma^-_{\max}$ as $\max[(\varepsilon_I\Gamma_R + \psi_I)/(\varepsilon_{EI} + \psi_{EI}), \psi_I/(\varepsilon_{EI} + \psi_{EI} - \varepsilon_I)]$. With this and Eq. (7), we find the regime in the $G_I - G_E$ space in which the spike propagation along the chain is the unique stable spike sequence attractor, as shown in Fig. 1. The condition covers most area of the permitted region on $G_I - G_E$ space, except a very narrow area below the boundary of permitted region. The remaining part is not yet explored.

The condition of spike propagation in an infinitely long

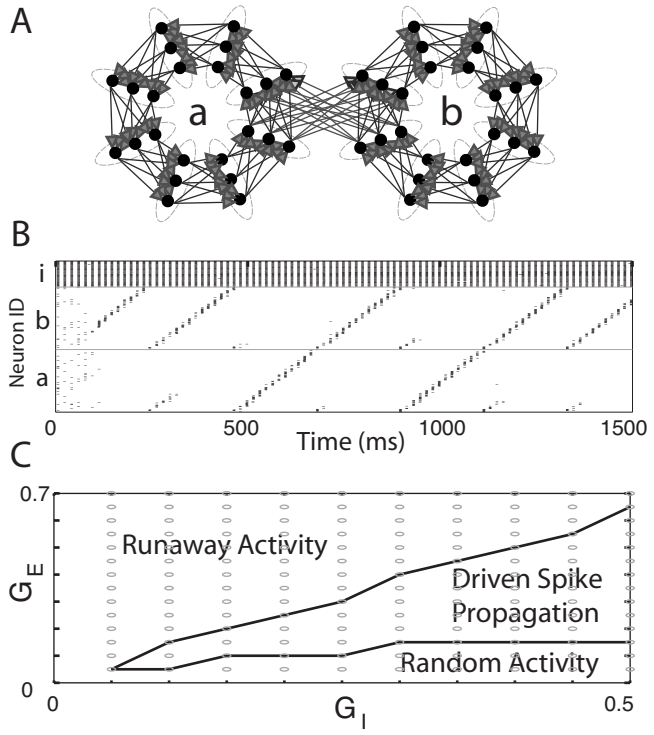


FIG. 2. (a) Schematic diagram of the network. Arrows indicate excitatory connections. Inhibitory neurons are not shown. (b) Spike activity of neurons in the chains (a,b) and the inhibitory neurons (i). Here $G_E$=0.1, $G_I$=0.2, $I$=100 mV. All other parameters are the same as in Fig. 1. (c) Phase diagram constructed based on simulations with $G_I$ and $G_E$ at the grid points.

chain, Eqs. (6) and (7), also guarantees a winner-take-all propagation of spikes when the excitatory connections form multiple infinitely long chains coupled only through the global inhibition. The mutual inhibition between the chains drives the activity into a single chain propagation after some transient spikes. The selection of the winning chain is determined by the initial condition. This can be proved with the same technique as for showing that spike propagation must be established in a single chain; the details are in Appendix B. A simple way of understanding this is to think of the multiple chains as parts of an infinitely long chain; the winner-take-all selection is related to the fact that it is impossible to stably propagate spikes simultaneously in multiple regions of the single chain.

To show that the analytical results are valid in realistic settings with noise and without the simplifications, we simulate a network consisting of 2400 excitatory neurons and 1000 inhibitory neurons. The excitatory neurons are connected into two chain networks consisting of groups of 60 neurons linked into a branched loop pattern [Fig. 2(a)]. A neuron connects to all neurons in the next group with conductance $G_E$. The global feedback inhibition is setup by connecting an excitatory neuron to an inhibitory neuron with a probability 0.5 and conductance randomly selected from 0 to 0.1, and connecting an inhibitory neuron to an excitatory neuron with a probability 0.5 and conductance randomly selected from 0 to $G_I$. The excitatory neurons are modeled as leaky integrate-and-fire neurons described by Eq. (1), except that the synaptic current is no longer pulse coupled but has dynamics: $I_s=-g_E(t)V_j(t)+g_I(t)[E_I-V_i(t)]$. The synaptic conductance $g_E(t)$ on an excitatory neuron obeys a kick-and-decay dynamics: in between spikes it follows $\tau_E dg_E(t)/dt=-g_E(t)$, where $\tau_E$=5 ms is the synaptic time constant; when an excitatory spike arrives, $g_E(t)\rightarrow g_E(t)+G_E$. The inhibitory conductance $g_I(t)$ on an excitatory neuron and the excitatory conductance on an inhibitory neuron are similarly modeled with the synaptic time constants being 5 ms and 1 ms, respectively. Noisy fluctuations of membrane potentials are induced by subjecting the neurons to random spikes such that the inhibitory neurons spontaneously spike with an average frequency of 1 Hz and the membrane potentials of the excitatory neurons fluctuate with a standard deviation of about 2 mV.

In Fig. 2(b), we show a typical run of the dynamics for the case of $G_E$=0.1 and $G_I$=0.2. After a short period of transient spikes, spike propagation spontaneously emerges in one of the chains. The excitatory neurons in the same group spike synchronously; so do the inhibitory neurons. When the activity arrives at the branching points, neurons in both chains are excited. After short transients, spike propagation continues on one randomly selected chain, exhibiting the winner-take-all behavior. The working parameter regime, as shown in Fig. 2(c), is similar to that of the simplified model (Fig. 1), except when the excitation is small, which makes the spike propagation easily disrupted by the random spikes of the inhibitory neurons. We have tested that the synfire activity is not supported in the regime due to the strong inhibition. Indeed, the synfire activity in our networks requires fine tuning of the parameters and is prone to runaway excitation or propagation extinction.

The driven-chain activity is most robust when the connection strengths between the groups are uniform, the external inputs are homogeneous, and the delay in inhibition introduced by the inhibitory neurons is small, since this case is the closest to the simplified model. Increasing disorders in the connection strengths or inhomogeneity of the external inputs or noise levels tends to reduce the parameter regime; nonetheless, spike propagation can be robustly established when both excitation and inhibition are strong. The delay of the inhibition tends to make several nearby groups spike synchronously, especially when the external inputs are large and the inhibition is strong, creating effective neuron groups that are larger than the group size specified in the network connectivity. Delays in spike transmissions can significantly change the dynamics of spiking neural networks [16]. It will be interesting to investigate in detail how the delays and heterogeneity of neuron and network properties affect the driven chain activity.

The winner-take-all propagation when there are multiple chains is robust in the driven-chain regime. In contrast, such a competition in the synfire regimes requires delicate balancing of excitation and inhibition: strong inhibition tends to stop the spike propagation, while weak inhibition cannot suppress simultaneous spike propagations in multiple chains. Although simultaneous propagation can be useful in some settings [17], it is undesirable if the chains encode mutually exclusive action elements such as syllables in birdsong [4]. Connecting the chains in branched patterns [Fig. 2(a)] en-

ables probabilistic selection of a chain for the propagation to continue from a previous chain, which can be a mechanism for variable syllable sequences observed in many songbird species [18].

In conclusion, we have shown that spike propagation is a robust dynamical attractor in chain networks with dominant feedback inhibition. This regime is distinctive from the synfire regime and permits a robust winner-take-all propagation when there are multiple chains competing through the inhibition.

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## APPENDIX A

Here we prove that Eq. (7) is a sufficient condition for the spike propagation along the chain to establish within a finite number of transient spikes from all initial conditions.

Four lemmas are useful.

*Lemma 1*. If $\Gamma_i^{(n)-}-\Gamma_j^{(n)-}<\Delta_{ma}$, and neuron $i$ receives excitation but neuron $j$ does not, then $\Gamma_i^{(n)+}<\Gamma_j^{(n)+}$. The proof is straightforward. The lemma describes a sufficient condition for the excited neuron to have a priority to spike over a purely inhibited neuron.

*Lemma 2*. If right before the $n$th spike $\Gamma_i^{(n)-}-\Gamma_j^{(n)-}<\Delta_{ma}$ and, for the next $m$ spikes, neuron $j$ receives only inhibition and both neurons do not spike, then $\Gamma_i^{(n+m)-}-\Gamma_j^{(n+m)-}<\Delta_{ma}$.

*Proof*. Case 1: Both neurons are only inhibited. According to Eq. (5), $\Gamma_i^{(n+1)-}-\Gamma_j^{(n+1)-}=\frac{\varepsilon_I}{\Gamma_{s_{n+1}}^{(n)+}}(\Gamma_i^{(n)-}-\Gamma_j^{(n)-})$. Since $\Gamma_{s_{n+1}}^{(n)+}\geq\varepsilon_{EI}\Gamma_{s_{n+1}}^{(n)-}+\psi_{EI}>\varepsilon_{EI}+\psi_{EI}$, we have $0<\varepsilon_I/\Gamma_{s_{n+1}}^{(n)+}<\rho$, where $\rho\equiv\varepsilon_I/(\varepsilon_{EI}+\psi_{EI})<1$. Therefore $\Gamma_i^{(n+1)-}-\Gamma_j^{(n+1)-}<\rho\Delta_{ma}<\Delta_{ma}$. Iteration leads to $\Gamma_i^{(n+m)-}-\Gamma_j^{(n+m)-}<\rho^m\Delta_{ma}<\Delta_{ma}$. Case 2: Neuron $i$ is excited any number of times during the period. The excitations only lower the PSTF of neuron $i$ compared to case 1. Hence the statement of the lemma holds.

An additional lemma can be derived from the above proof:

*Lemma 3*. If both neurons $i$ and $j$ are inhibited $m$ times from the $n$th to $(n+m-1)$th spikes and they do not spike, the difference between their PSTF's right before the spikes decay according to $|\Gamma_i^{(n+m)-}-\Gamma_j^{(n+m)-}|<\rho^m|\Gamma_i^{(n)-}-\Gamma_j^{(n)-}|<\rho^m(\Gamma_I-1)$. Let $N_1$ be an integer such that $\rho^{N_1}(\Gamma_I-1)<\Delta_{ma}$. After $N_1$ consecutive spikes, the PSTF's of all neurons not spiked and not excited during the span differ by less than $\Delta_{ma}$.

Using lemmas 1 to 3, we can prove the following statement:

*Lemma 4*. Given the condition in Eq. (7), a spiked neuron cannot spike again unless it is excited.

*Proof*. Suppose that neuron $i$ emits the $n$th spike. Its PSTF right after the reset and before the global inhibition is $\Gamma_R$. According to Eq. (7), $\Gamma_j^{(n)-}-\Gamma_R<\Gamma_{\max}^{-}-\Gamma_R<\Delta_{ma}$ for any $j\neq i$. Suppose that neuron $i$ is only inhibited at each of the spikes following the $n$th. Define neuron $k$ as the neuron with the largest index among the neurons that have been excited after the $n$th spike. It is clear that neuron $k$ has never spiked after the $n$th spike. According to lemma 1 and lemma 2, right after it is excited, neuron $k$ has a priority over neuron $i$ to spike. The priority lasts as long as neuron $k$ does not spike and neuron $i$ is not excited. If neuron $k$ spikes, neuron $k+1$ replaces neuron $k$ as the largest index neuron. Therefore neuron $i$ cannot spike again unless excited.

*Theorem*. After a finite number of transient spikes, spike propagation along the chain must be established if Eq. (7) is satisfied.

*Proof*. The following steps lead to the proof. (1) Define $A_n$ as the set of neurons that have spiked but not been excited after their recent spikes up to the $n$th spike. According to lemma 4, the $(n+1)$th spike cannot come from $A_n$. (2) Define $B_n$ as the set of neurons that are not in $A_n$ and not neuron $s_n+1$, which is excited by the $n$th spike. A neuron that is not $s_n+1$ is either in $A_n$ or $B_n$. Note that the neuron $s_{n+1}$, which spikes next, must be either neuron $s_n+1$ or come from $B_n$. (3) If $n$ is large enough, the $(n+1)$th spike cannot come from $B_n$, therefore the excited neuron must spike next, i.e., $s_{n+1}=s_n+1$. The spike propagation is then established.

The statement (3) is proved using the following:

*Lemma 5*. Consider a neuron $j$ in $B_n$ and a purely inhibited neuron $k$ (which is also in $B_n$). The difference between the PSTF's of neuron $k$ and $j$ is upper bounded by an exponential decay, i.e., $\Gamma_k^{(n)+}-\Gamma_j^{(n)+}\leq\rho^n(\Gamma_I-1)$.

*Proof*. We use mathematical induction. For $n=1$, all neurons in $B_1$ are inhibited by the first spiking neuron, hence $\Gamma_k^{(1)+}-\Gamma_j^{(1)+}\leq\rho(\Gamma_I-1)$, following a derivation similar to that of lemma 2. If the equation holds for $n=m$, it also holds for $n=m+1$. A neuron $j$ in $B_{m+1}$ either (a) was in $B_m$ or (b) was excited by the $m$th spike but did not spike next, i.e., $j\neq s_{m+1}$. For any case $\Gamma_j^{(m)+}\geq\min_{i\in B_m}\Gamma_i^{(m)+}$, which is obvious for (a), and is true for (b) because the next spiking neuron, $s_{m+1}$, should come from $B_m$ and $\Gamma_j^{(m)+}>\Gamma_{s_{m+1}}^{(m)+}$. Therefore, $\Gamma_k^{(m)+}-\Gamma_j^{(m)+}\leq\Gamma_k^{(m)+}-\min_{i\in B_m}\Gamma_i^{(m)+}\leq\rho^m(\Gamma_I-1)$. Using this and observing that both neurons $k$ and $j$ are inhibited by the $(m+1)$th spike, we find $\Gamma_k^{(m+1)+}-\Gamma_j^{(m+1)+}\leq\rho^{m+1}(\Gamma_I-1)$.

Lemma 5 shows that the PSTF of a purely inhibited neuron is vanishingly close to the minimum of the PSTF's of neurons in $B_n$ as $n$ increases. Since the PSTF of the excited neuron is smaller than that of the purely inhibited neuron by a finite value, the excited neuron has a priority to spike to all neurons in $B_n$ for a large enough $n$.

## APPENDIX B

Here we show that the condition given by Eq. (7) also guarantees a winner-take-all propagation of spikes when the excitatory connections form multiple infinitely long chains coupled only through the global inhibition.

Using the same reasoning for the single chain case, it can be shown that spikes must propagate successively in each chain after some transient spikes. We now show that alternating propagation in multiple chains is not possible. It is

sufficient to study the case of two chains since the reasoning applies equally to any number of chains.

Denote the index of the neuron that emitted the $n$th spike as $(c_n,s_n)$, where $c_n=1,2$ is the index of the chain and $s_n$ is the index of the neuron in the chain $c_n$, and the chain that does not contain the $n$th spiked neuron as $\bar{c}_n$. Consider a spike sequence with alternating propagation: $(1,a_1),(1,a_1+1),\ldots,(1,a_2-1)$, $(2,b_1),(2,b_1+1),\ldots,(2,b_2-1),(1,a_2),\ldots$ where $a_1<a_2<\ldots,b_1<b_2<\ldots$. We show that, if $n\geq N_1+1$, then $(c_{n+1},s_{n+1})=(c_n,s_n+1)$, i.e., the spike activity settles to a propagation in chain $c_n$.

To prove the above statement, we use the following:

*Lemma 6*. Consider a purely inhibited neuron $(c,k)$. Then $\Gamma^{(n)+}_{c,k}-\Gamma^{(n)+}_{\bar{c}_n,j}<\rho^n(\Gamma_I-1)$.

*Proof*. The proof is similar to that of lemma 5. For $n=1$, all neurons in branch $\bar{c}_1$ are inhibited by the first spike, hence $\Gamma^{(1)+}_{c,k}-\Gamma^{(1)+}_{\bar{c}_1,j}<\rho(\Gamma_I-1)$. If the lemma holds for $n=m$, it also holds for $n=m+1$. From $\Gamma^{(m)+}_{c,k}-\Gamma^{(m)+}_{\bar{c}_m,j}<\rho^m(\Gamma_I-1)$, we get $\Gamma^{(m)+}_{c,k}-\Gamma^{(m)+}_{\bar{c}_{m+1},j}<\rho^m(\Gamma_I-1)$. This is obvious if $c_{m+1}=c_m$; if $c_{m+1}=\bar{c}_m$, the neuron $(c_{m+1},s_{m+1})$ has smaller PSTF than $\Gamma^{(m)+}_{c_m,j}$ and satisfies $\Gamma^{(m)+}_{c,k}-\Gamma^{(m)+}_{c_{m+1},s_{m+1}}<\rho^m(\Gamma_I-1)$. All neurons in branch $\bar{c}_{m+1}$ are inhibited by the $(m+1)$th spike, hence $\Gamma^{(m+1)+}_{c,k}-\Gamma^{(m+1)+}_{\bar{c}_{m+1},j}<\rho^{m+1}(\Gamma_I-1)$.

According to the lemma, after a finite number of transient spikes, the excited neuron has a priority to spike over all neurons in the other branch because the lower bound of their PSTF's are vanishingly close to that of a purely inhibited neuron. Therefore the alternating spiking pattern cannot last indefinitely.


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