

Dynamics of Winner-Take-All Competition in Recurrent Neural Networks With Lateral Inhibition

Zhi-Hong Mao and Steve G. Massaquoi

Abstract—This paper studies the behavior of recurrent neural networks with lateral inhibition. Such network architecture is important in biological neural systems. General conditions determining the existence, number, and stability of network equilibria are derived. The manner in which these features depend upon steepness of neuronal activation functions and the strength of lateral inhibition is demonstrated for a broad range of nondecreasing activation functions including the discontinuous threshold function which represents the infinite gain limit. For uniform lateral inhibitory networks, the lateral inhibition is shown to sharpen neuron output patterns by increasing separation of suprathreshold activity levels of competing neurons. This results in the tendency of one neuron's output to dominate those of the others which can afford a "winner-take-all" (WTA) mechanism. Importantly, multiple stable equilibria may exist and shifts in inputs levels may yield network state transitions that exhibit hysteresis. A limitation of using lateral inhibition to implement WTA is further demonstrated. The possible significance of these identified network dynamics to physiology and pathophysiology of the striatum (particularly in Parkinsonian rest tremor) is discussed.

Index Terms—Discontinuous neuron activations, equilibrium, lateral inhibition, striatum, winner-take-all (WTA).

I. INTRODUCTION

WINNER-TAKE-ALL (WTA) via lateral inhibition is an important mechanism for many fundamental computational abilities of animal neural systems. Since the finding of lateral inhibition in the eye of *Limulus* [1], lateral inhibition has been discovered in many neural circuits, such as those in vertebrate somatosensory cortex [2], auditory cortex [3], visual system [4], hippocampus [5], and basal ganglia [6]. In sensory systems, the process of lateral inhibition improves signal resolution via a simple competitive or WTA mechanism in local neural networks [2]; in some cortical areas, the WTA competition among excitatory neurons with delayed inhibition from interneurons has been suggested to play a key role in the generation of certain natural rhythms such as the 4–7-Hz theta rhythm

in hippocampus [7]; and in the basal ganglia, WTA has been proposed to be the underlying mechanism for the focused selection of competing motor programs [6], [8]. Therefore, as a common functional feature of neural systems, WTA mechanisms deserve further investigation.

Considerable effort has already been made to explain how lateral inhibition can lead to WTA competition among neurons. Coultrip *et al.* [7] simulated and analyzed physiological interactions among excitatory and inhibitory neurons in a modeled network architecture of hippocampal field CA1. They demonstrated the generation of a simple WTA mechanism, which allows only the most strongly activated cell in a group to respond with spiking activity. Ermentrout [9] studied the complex dynamics in WTA neural networks, and showed that as the inhibition slows down, the WTA networks may exhibit oscillatory behaviors. In the aforementioned two insightful studies, however, the network architectures were relatively simple: A layer of excitatory neurons coupled with a single inhibitory interneuron were considered. Hahnloser [10] provided both quantitative analysis and simulations, showing that global inhibition may give rise to multistable WTA mechanism in a recurrent network of neurons. Again, this paper was restricted to single, global inhibition and, in addition, Hahnloser considered for each neuron only linear activation function above threshold. Fukai and Tanaka [11] considered a neural network with uniform lateral inhibition and self-inhibition. They found that the strength of lateral inhibition relative to that of self-inhibition is crucial for determining the steady states of the network. Different ratios between the strengths of lateral inhibition and self-inhibition may lead to either WTA or winners-share-all behaviors. Fukai and Tanaka's work provided profound mathematical basis for understanding neural selection mechanisms; however, their analysis was subject to a specific choice of activation function, i.e., Lotka–Volterra equation [11] for neuronal firing activity. Xie *et al.* [12] extended the grouping of potential winners in the WTA networks beyond single neuron or uniformly arranged groups of neurons. They showed that competition between arbitrary groups of neurons can be realized by organizing lateral inhibition in networks. However, as the authors acknowledged, the activation function considered in their paper was linear threshold function, which fails to characterize the saturation of neuronal response to large input.

Not restricted to neural systems, other efficient engineering realizations of WTA were also proposed, e.g., the WTA cellular neural networks [13]–[15], K-WTA, [17], Maxnet [18], [19], columnar competitive model [20], and networks with presynaptic shunting inhibition [21], just to name a few. Many of these realizations are enlightened by ideas from neural systems, but since they are more application-oriented, some of them may introduce modifications or improvements that are no longer biologically plausible.

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This paper focuses on the analysis of the recurrent neural networks with lateral inhibition, a biologically plausible architecture for WTA competition. Emphasis is given to the study on the characteristics of this basic architecture rather than on the design of more advanced engineering structures. However, results obtained here may be extended to other WTA implementations originated from the network architecture with lateral inhibition. Particularly, this paper derives conditions for the networks with lateral inhibition to present WTA competition among neurons. The underlying mechanism of WTA is illustrated in terms of augmented separation of suprathreshold activities of competing neurons. In addition to WTA, other characteristics of the networks are discussed including the effect of hysteresis and the number and stability of the network equilibria. A limitation of using lateral inhibition to implement WTA is also demonstrated in the sense that the reliability and resolution of WTA may exert conflicting requirements on the strength of lateral inhibition. Then, the results obtained from theoretical analysis are applied to investigate the mechanism of selection and switching in the striatal networks of the basal ganglia under both normal and pathophysiological conditions.

In this paper, a broad range of neuronal activation functions are considered, including the discontinuous threshold function, which models the activity of neurons with infinite gain in limiting situations. In those limiting situations, the networks fail to satisfy conventional results for the existence of solutions to differential equations, and, thus, a generalized concept of solution, Filippov solution, is introduced to describe the network dynamics. In the proof of state convergence and stability for discontinuous threshold function, this paper does not follow the Lyapunov indirect method, but uses the differential inequalities and comparison theorem (see Appendix I) to compute bounds that confine the state trajectories of the networks.

II. EQUATIONS FOR DYNAMICS OF NEURONAL NETWORKS WITH LATERAL INHIBITION

Consider a recurrent network of n neurons with lateral inhibition. Denote x_i the postsynaptic membrane potential and y_i the firing rate of neuron i , $i = 1, \dots, n$. Let d_i be the input (or sum of inputs if there are more than one inputs) to neuron i from the outside of the n -neuron network, and $v_i > 0$ be the synaptic strength of the lateral inhibitory connection from neuron i to neuron k for any $k \neq i$. Here, we assume that the inhibitory connections originating from the same neuron take the same strength, and we do not consider the case of self-inhibition, where a neuron forms inhibitory connection from its output to its own input. Then, the dynamics of the neural network can be modeled by

$$\tau \frac{dx_i}{dt} = -x_i - \sum_{k \neq i} v_k y_k + d_i \quad (1)$$

$$y_i = f_i(x_i) \quad (2)$$

where i takes $1, \dots, n$, τ is a time constant, and $f_i(\cdot)$ is a non-negative activation function characterizing the relation between the membrane potential and firing rate of neuron i . In matrix-vector form, denote $x = [x_1, \dots, x_n]^T$, $y = [y_1, \dots, y_n]^T$, $d = [d_1, \dots, d_n]^T$, and $V = [v_{ik}]_{n \times n}$ with $v_{ii} = 0$ and

$v_{ik} = v_k$ for $i \neq k$. Then, (1) can be written in a compact form as

$$\tau \frac{dx}{dt} = -x - Vy + d. \quad (3)$$

An equilibrium of (1) and (2) is a solution to $-x - Vy + d = 0$, i.e.,

$$x_i = d_i - \sum_{k \neq i} v_k f_k(x_k), \quad i = 1, \dots, n. \quad (4)$$

An equilibrium x^* has the property that whenever the state of the system starts at x^* it will remain at x^* for all future time. Due to the nonnegativity of $f_i(\cdot)$, (4) implies

$$x_i^* \leq d_i, \quad i = 1, \dots, n. \quad (5)$$

An equilibrium x^* is *stable* if, for each $\epsilon > 0$, there is $\delta > 0$ such that

$$\|x(0) - x^*\| < \delta \Rightarrow \|x(t) - x^*\| < \epsilon, \quad \text{for any } t \geq 0$$

where $\|x\|$ can be any norm, but usually we use the Euclidean norm $\|x\| = (x_1^2 + \dots + x_n^2)^{1/2} = (x^T x)^{1/2}$. An equilibrium x^* is *asymptotically stable* if it is stable and δ can be chosen such that

$$\|x(0) - x^*\| < \delta \Rightarrow \lim_{t \rightarrow \infty} \|x(t) - x^*\| = 0.$$

The equilibrium x^* is *globally asymptotically stable* if it is stable and $x(t)$ approaches x^* as $t \rightarrow \infty$ for any $x(0)$.

III. EXISTENCE, UNIQUENESS, AND STABILITY OF EQUILIBRIUM

This section presents some general properties of the equilibria of (1) and (2). Without further declaration, in this section, the neuronal activation function $f_i(\cdot)$ can be any function satisfying Condition 1.

Condition 1: The neuronal activation $f_i(u)$, where $i = 1, \dots, n$, is continuous and nonnegative for any $u \in (-\infty, +\infty)$. Furthermore, $f_i(u)$ has continuous first derivative, and $\dot{f}_i(u)$ is nonnegative for any $u \in (-\infty, +\infty)$.

A. Existence of Equilibrium

Proposition 1: The network of (1) and (2) has at least one equilibrium.

Proof: Denote $h_i(x) = d_i - \sum_{k \neq i} v_k f_k(x_k)$ and $h(x) = [h_1(x), \dots, h_n(x)]^T$. Consider a compact convex set $D = [d_1 - \sum_{k \neq 1} v_k f_k(d_k), d_1] \times \dots \times [d_n - \sum_{k \neq n} v_k f_k(d_k), d_n]$. For any $x \in D$, $h_i(x)$ is no greater than d_i due to $f_k(x_k) \geq 0$ for any k , and $h_i(x)$ is no less than $d_i - \sum_{k \neq i} v_k f_k(d_k)$ due to $f_k(x_k) \leq f_k(d_k)$ for any k (this is because $f_k(\cdot)$ is monotone nondecreasing and $x_k \leq d_k$). Therefore, $h(x) \in D$ for any $x \in D$. According to Brouwer fixed point theorem [22], $x = h(x)$ has a fixed point in D , which implies that the network of (1) and (2) has at least one equilibrium. ■

It can be seen from the proof that Proposition 1 holds for any activation functions that are continuous, nonnegative, and monotone nondecreasing, not just restricted to the activation functions described in Condition 1.

B. Isolated Equilibria and Uniqueness of Equilibrium

Except for assertion of equilibrium existence, Proposition 1 does not give any further information about the equilibrium or equilibria of (1) and (2). In the following, Propositions 2 and 3 address more detailed properties of the system equilibria. Before showing those propositions, we first present an intermediate result, which will be used in the proofs of the two propositions.

Lemma 1: For

$$A = \begin{bmatrix} 1 & a_2 & \cdots & a_{n-1} & a_n \\ a_1 & 1 & \cdots & a_{n-1} & a_n \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 & a_2 & \cdots & 1 & a_n \\ a_1 & a_2 & \cdots & a_{n-1} & 1 \end{bmatrix}$$

where $n \geq 2$, the determinant of A equals

$$\det A = \prod_{k=1}^n (1 - a_k) + \sum_{i=1}^n a_i \prod_{k \neq i} (1 - a_k). \quad (6)$$

Proof: It can be easily verified that (6) holds for $n = 2$ and $n = 3$. In the following, we consider $n \geq 4$.

Subtracting the first row from the other rows of A , we get a new matrix

$$A_1 = \begin{bmatrix} 1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ a_1 - 1 & 1 - a_2 & 0 & \cdots & 0 & 0 \\ a_1 - 1 & 0 & 1 - a_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 - 1 & 0 & 0 & \cdots & 1 - a_{n-1} & 0 \\ a_1 - 1 & 0 & 0 & \cdots & 0 & 1 - a_n \end{bmatrix}.$$

According to the property of the determinant of a matrix [23], $\det A$ equals $\det A_1$. Further using the Laplace expansion by minors along the first row of A_1 [23], we have equation shown at the bottom of the page.

For each determinant except the first one in that equation, we use the Laplace expansion by minors along the first column of the determinant. Then, we have

$$\begin{aligned} \det A &= \prod_{k=2}^n (1 - a_k) + (-1)a_2(a_1 - 1) \prod_{k=3}^n (1 - a_k) \\ &\quad + \sum_{i=3}^{n-1} (-1)^{1+i} a_i (-1)^{1+i-1} (a_1 - 1) \\ &\quad \times \prod_{k=2}^{i-1} (1 - a_k) \prod_{k=i+1}^n (1 - a_k) \\ &\quad + (-1)^{1+n} a_n (-1)^{1+n-1} (a_1 - 1) \prod_{k=2}^{n-1} (1 - a_k) \\ &= \prod_{k=2}^n (1 - a_k) + \sum_{i=2}^n a_i \prod_{k \neq i} (1 - a_k) \\ &= \prod_{k=1}^n (1 - a_k) + \sum_{i=1}^n a_i \prod_{k \neq i} (1 - a_k). \end{aligned}$$

Proposition 2: Let x^* be an equilibrium of (1) and (2). If

$$\prod_{k=1}^n [1 - v_k \dot{f}_k(x_k^*)] + \sum_{i=1}^n v_i \dot{f}_i(x_i^*) \prod_{k \neq i} [1 - v_k \dot{f}_k(x_k^*)] \neq 0 \quad (7)$$

then x^* is an isolated equilibrium.

Proof: Since $\dot{f}_i(x_i)$ is continuous for any $i = 1, \dots, n$, (7) implies that there exists an $\epsilon > 0$ and an open set $S(x^*, \epsilon) \equiv \{x \mid |x_i - x_i^*| < \epsilon \text{ for any } i = 1, \dots, n\}$ such that $\prod_{k=1}^n [1 - v_k \dot{f}_k(x_k)] + \sum_{i=1}^n v_i \dot{f}_i(x_i) \prod_{k \neq i} [1 - v_k \dot{f}_k(x_k)]$ is not equal to 0 for any $x \in S(x^*, \epsilon)$.

Next, we prove that x^* is the only equilibrium in $S(x^*, \epsilon)$. Assume that there exists another equilibrium $x' \in S(x^*, \epsilon)$. Apparently, x' satisfies $x'_i = d_i - \sum_{k \neq i} v_k f_k(x'_k)$ for any $i =$

$$\begin{aligned} \det A = \det A_1 &= (-1)^{1+1} \begin{vmatrix} 1 - a_2 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & 1 - a_n \end{vmatrix} + (-1)^{1+2} a_2 \begin{vmatrix} a_1 - 1 & 0 & \cdots & 0 \\ a_1 - 1 & 1 - a_3 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ a_1 - 1 & 0 & \cdots & 1 - a_n \end{vmatrix} \\ &\quad + \sum_{i=3}^{n-1} (-1)^{1+i} a_i \cdot \begin{vmatrix} a_1 - 1 & 1 - a_2 & \cdots & 0 & 0 \\ a_1 - 1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 - 1 & 0 & \cdots & 0 & 1 - a_{i-1} \\ a_1 - 1 & 0 & \cdots & 0 & 0 \\ a_1 - 1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 - 1 & 0 & \cdots & 0 & 0 \end{vmatrix} \\ &\quad + (-1)^{1+n} a_n \begin{vmatrix} a_1 - 1 & 1 - a_2 & \cdots & 0 & 0 \\ a_1 - 1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 - 1 & 0 & \cdots & 0 & 1 - a_{n-1} \\ a_1 - 1 & 0 & \cdots & 0 & 0 \end{vmatrix}. \end{aligned}$$

$1, \dots, n$. Let $u = x' - x^*$, and substitute $x' = x^* + u$ into the aforementioned equilibrium equation for x' : $x_i^* + u_i = d_i - \sum_{k \neq i} v_k f_k(x_k^* + u_k)$. According to the mean value theorem [22] and the fact that \dot{f} is continuous, there exist $\eta_i, i = 1, \dots, n$, such that $f_i(x_i^* + u_i) = f_i(x_i^*) + \dot{f}_i(x_i^* + \eta_i u_i) u_i$ where $0 \leq \eta_i \leq 1$. Therefore, we have $x_i^* + u_i = d_i - \sum_{k \neq i} v_k [f_k(x_k^*) + \dot{f}_k(x_k^* + \eta_k u_k) u_k]$, which becomes $u_i = -\sum_{k \neq i} v_k \dot{f}_k(x_k^* + \eta_k u_k) u_k, i = 1, \dots, n$. Denote $a_i = v_i \dot{f}_i(x_i^* + \eta_i u_i)$, and write the previous equations in matrix form $Au = 0$ where

$$A = \begin{bmatrix} 1 & a_2 & \cdots & a_{n-1} & a_n \\ a_1 & 1 & \cdots & a_{n-1} & a_n \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ a_1 & a_2 & \cdots & 1 & a_n \\ a_1 & a_2 & \cdots & a_{n-1} & 1 \end{bmatrix}.$$

Since $x' = x^* + u \in S(x^*, \epsilon)$ and $0 \leq \eta_i \leq 1$ for any $i = 1, \dots, n$, we have $(x_1^* + \eta_1 u_1, \dots, x_n^* + \eta_n u_n)^T \in S(x^*, \epsilon)$. Thus, $\prod_{k=1}^n (1 - a_k) + \sum_{i=1}^n a_i \prod_{k \neq i} (1 - a_k) \neq 0$. According to Lemma 1, $\det A$ is not equal to 0. Hence, $Au = 0$ has only one solution, i.e., $u = 0$, which implies $x' = x^*$. There is only one equilibrium in the open set $S(x^*, \epsilon)$ containing x^* . In other words, x^* is an isolated equilibrium. ■

Corollary 1: Let x^* be an equilibrium of (1) and (2). If

$$v_i \dot{f}_i(x_i^*) < 1, \quad \text{for any } i = 1, \dots, n \quad (8)$$

or

$$v_i \dot{f}_i(x_i^*) > 1, \quad \text{for any } i = 1, \dots, n \quad (9)$$

then x^* is an isolated equilibrium.

Proof: We only need to show that (8) or (9) implies (7). If (8) is satisfied (note that $v_i \dot{f}_i(x_i^*)$ is also nonnegative for any $i = 1, \dots, n$), then we have $\prod_{k=1}^n [1 - v_k \dot{f}_k(x_k^*)] + \sum_{i=1}^n v_i \dot{f}_i(x_i^*) \prod_{k \neq i} [1 - v_k \dot{f}_k(x_k^*)] > 0$, so (7) is satisfied.

If (9) is satisfied, then $v_i \dot{f}_i(x_i^*) / (1 - v_i \dot{f}_i(x_i^*))$ is less than -1 for any $i = 1, \dots, n$. Hence

$$1 + \frac{v_1 \dot{f}_1(x_1^*)}{1 - v_1 \dot{f}_1(x_1^*)} + \cdots + \frac{v_n \dot{f}_n(x_n^*)}{1 - v_n \dot{f}_n(x_n^*)} < 0$$

and thus

$$\begin{aligned} & \prod_{k=1}^n [1 - v_k \dot{f}_k(x_k^*)] + \sum_{i=1}^n v_i \dot{f}_i(x_i^*) \prod_{k \neq i} [1 - v_k \dot{f}_k(x_k^*)] \\ &= \left\{ \prod_{k=1}^n [1 - v_k \dot{f}_k(x_k^*)] \right\} \\ & \times \left(1 + \frac{v_1 \dot{f}_1(x_1^*)}{1 - v_1 \dot{f}_1(x_1^*)} + \cdots + \frac{v_n \dot{f}_n(x_n^*)}{1 - v_n \dot{f}_n(x_n^*)} \right) \neq 0. \end{aligned}$$

Inequality (7) is also satisfied. ■

Proposition 3: The network of (1) and (2) has only one equilibrium if there exists M_i such that $\dot{f}_i(x_i) \leq M_i$ for any x_i and

$$v_i M_i < 1 \quad (10)$$

for any $i = 1, \dots, n$.

Proof: Let x^* be an equilibrium, and assume that there exists another equilibrium x' . Then, following similar steps as in the proof of Proposition 2, we may prove $x' = x^*$. ■

Proposition 3, as well as Proposition 5 in Section III-C, presents a sufficient condition of uniqueness of equilibrium for the network of (1) and (2). To demonstrate how conservative this condition is, consider a simple scenario where v_i equals v and M_i equals M for $i = 1, \dots, n$, and see what the existing results from general recurrent (Hopfield) network theory can offer us concerning the uniqueness of equilibrium. Using the results presented in [24] and [25], for example, it can be derived that the network of (1) and (2) has only one equilibrium if

$$(n-1)vM < 1. \quad (11)$$

This condition is the same as what we can get by using the contract mapping theorem [22]. As a comparison, Proposition 3 gives the following condition:

$$vM < 1$$

which is much less conservative than (11) for large n .

It is further demonstrated in Fig. 1 that the uniqueness conclusion of Proposition 3 may not hold when (10) is relaxed to include equality. Fig. 1 shows an example of a two-neuron network with an infinite number of stable equilibria. In the network, the neuronal activation functions $f_1(\cdot)$ and $f_2(\cdot)$ equal $f(\cdot)$, and $f(\cdot)$ is a smoothed linear threshold function [see Fig. 1(a)]

$$f(u) = \begin{cases} 1/(1 + e^{-4u}), & \text{if } u \leq 0 \\ u + \frac{1}{2}, & \text{if } u > 0 \end{cases}.$$

Note that $\dot{f}(u)$ equals 1 for any $u \geq 0$. The lateral inhibitory connections between the two neurons are symmetric, i.e., $v_1 = v_2 \equiv v$, and v is set to 1. Thus, $v \max \dot{f}(u)$ equals 1. The network inputs are $d_1 = d_2 = 1$. Fig. 1(b) presents several trajectories, each of which shows how the dynamics of the two-neuron network evolves from a specific initial state. It can be seen that the network state trajectories, starting from various initial states, converge to a line segment between (0, 0.5) and (0.5, 0). Any point on that line segment is an equilibrium, which is stable but not asymptotically stable. Let x^* be an equilibrium on the line segment between (0, 0.5) and (0.5, 0). Obviously, x^* is not an isolated equilibrium, since there is an infinite number of equilibria in any neighborhood of x^* no matter how small the neighborhood is. It can be seen that $v \dot{f}(x_1^*) = v \dot{f}(x_2^*) = 1$, which fails to satisfy (7), so Proposition 2 does not apply. This example further demonstrates that the conditions presented in Proposition 3 (and Proposition 5—see Section III-C) cannot be relaxed: The right side of (10) cannot be relaxed to any number greater than 1, and (10) cannot even be relaxed to include equality.

C. Stability of Equilibrium

Proposition 4: Let x^* be an equilibrium of (1) and (2). If $v_i \dot{f}_i(x_i^*) < 1$ for any $i = 1, \dots, n$, then x^* is an asymptotically stable equilibrium.

Proof: Given x , denote $u = x - x^*$ and $u_i = x_i - x_i^*$ for $i = 1, \dots, n$. Furthermore, denote $g_i(u_i) = f_i(x_i) - f_i(x_i^*) = f_i(x_i^* + u_i) - f_i(x_i^*)$ and

$$M_v = \frac{1}{2} + \frac{\max_i \{v_i \dot{f}_i(x_i^*)\}}{2}.$$

Apparently, M_v is strictly greater than $v_i \dot{f}_i(x_i^*)$ for any $i = 1, \dots, n$ and strictly less than 1, since $v_i \dot{f}_i(x_i^*)$ is less than 1.

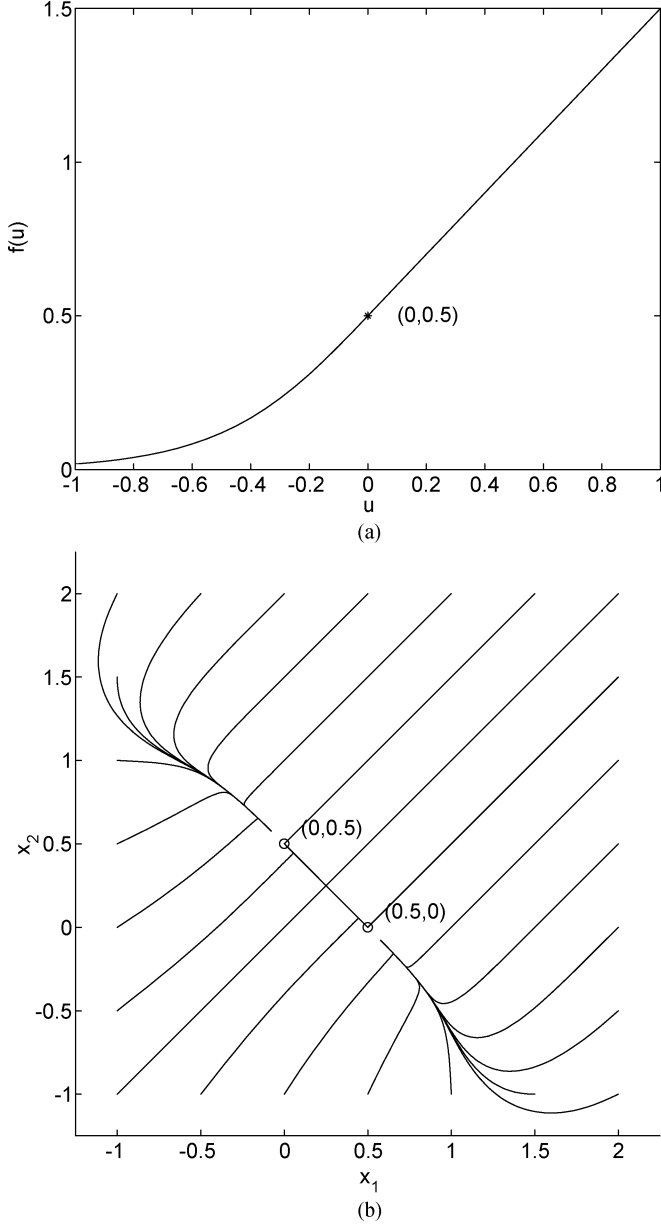


Fig. 1. (a) Smoothed linear threshold function as neuronal activation function. (b) Dynamics of a two-neuron network, which has an infinite number of stable (but not asymptotically stable) equilibria. Any point on the line segment between $(0, 0.5)$ and $(0.5, 0)$ is an equilibrium.

Because $\dot{f}_i(x_i)$ is continuous and M_v is strictly greater than $\max\{v_i \dot{f}_i(x_i^*)\}$, there exists an $\epsilon > 0$ and a domain containing x^* , $S(x^*, \epsilon) \equiv \{x \mid |x_i - x_i^*| < \epsilon, \text{ for any } i = 1, \dots, n\}$, such that $v_i \dot{f}_i(x_i)$ is less than M_v for any $x \in S(x^*, \epsilon)$ and for any $i = 1, \dots, n$. Correspondingly, denote $D = \{u \mid u + x^* \in S(x^*, \epsilon)\}$. Therefore

$$v_i \dot{g}_i(u_i) < M_v, \quad \text{for any } u \in D. \quad (12)$$

We use a Lure-type Lyapunov function [24], [26]

$$V(u) = \frac{1}{2} \sum_{i=1}^n c u_i^2 + \sum_{i=1}^n \int_0^{u_i} v_i g_i(s) ds \quad (13)$$

where c is a positive constant satisfying

$$c < \frac{4}{n}(1 - M_v). \quad (14)$$

Obviously, $V(0)$ equals 0 and $V(u)$ is greater than 0 for any $u \in D$ except for $u = 0$.

In the following, we want to show $dV/dt < 0$ for any $u \in D$ and $u \neq 0$. If this is true, then we can claim that $u = 0$, i.e., $x = x^*$, is asymptotically stable, according to [26, Th. 3.1, p. 100].

Let us first calculate $\tau(du_i/dt)$. $\tau(du_i/dt) = \tau(dx_i/dt) = -x_i - \sum_{k \neq i} v_k f_k(x_k) + d_i = -x_i^* - u_i - \sum_{k \neq i} v_k [f_k(x_k^*) + g_k(u_k)] + d_i = -u_i - \sum_{k \neq i} v_k g_k(u_k)$. Then, we have

$$\begin{aligned} \tau \frac{dV}{dt} &= \sum_{i=1}^n c u_i \left(\tau \frac{du_i}{dt} \right) + \sum_{i=1}^n v_i g_i(u_i) \left(\tau \frac{du_i}{dt} \right) \\ &= \sum_{i=1}^n [c u_i + v_i g_i(u_i)] \left(\tau \frac{du_i}{dt} \right) \\ &= \sum_{i=1}^n [c u_i + v_i g_i(u_i)] \left[-u_i - \sum_{k \neq i} v_k g_k(u_k) \right] \\ &= \sum_{i=1}^n [c u_i + v_i g_i(u_i)] \\ &\quad \times \left\{ -[u_i - v_i g_i(u_i)] - \sum_{k=1}^n v_k g_k(u_k) \right\} \\ &= - \sum_{i=1}^n [c u_i + v_i g_i(u_i)] [u_i - v_i g_i(u_i)] \\ &\quad - \sum_{i=1}^n [c u_i + v_i g_i(u_i)] \sum_{k=1}^n v_k g_k(u_k). \end{aligned}$$

Note that

$$\begin{aligned} &\sum_{i=1}^n [c u_i + v_i g_i(u_i)] \sum_{k=1}^n v_k g_k(u_k) \\ &= \sum_{i=1}^n c u_i \sum_{k=1}^n v_k g_k(u_k) + \left[\sum_{k=1}^n v_k g_k(u_k) \right]^2 \\ &= \sum_{i=1}^n \left\{ c u_i \sum_{k=1}^n v_k g_k(u_k) + \frac{1}{n} \left[\sum_{k=1}^n v_k g_k(u_k) \right]^2 \right\} \\ &= \sum_{i=1}^n \left\{ \frac{c^2 n}{4} u_i^2 + c u_i \left[\sum_{k=1}^n v_k g_k(u_k) \right] \right. \\ &\quad \left. + \frac{1}{n} \left[\sum_{k=1}^n v_k g_k(u_k) \right]^2 \right\} - \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &= \sum_{i=1}^n \left\{ \frac{c \sqrt{n}}{2} u_i + \frac{1}{\sqrt{n}} \left[\sum_{k=1}^n v_k g_k(u_k) \right] \right\}^2 - \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &\geq - \sum_{i=1}^n \frac{c^2 n}{4} u_i^2. \end{aligned}$$

Therefore

$$\tau \frac{dV}{dt} \leq - \sum_{i=1}^n [c u_i + v_i g_i(u_i)] [u_i - v_i g_i(u_i)] + \sum_{i=1}^n \frac{c^2 n}{4} u_i^2.$$

According to (12) and the definition of M_v , for any $u \in D$, we have the following: 1) $0 \leq v_i g_i(u_i) \leq M_v u_i$ when $u_i > 0$ and 2) $M_v u_i \leq v_i g_i(u_i) \leq 0$ when $u_i < 0$. Since $M_v < 1$, we have $0 \leq v_i g_i(u_i) < u_i$ for $u_i > 0$ and $u_i < v_i g_i(u_i) \leq 0$ for $u_i < 0$. Thus, $v_i g_i(u_i)[u_i - v_i g_i(u_i)]$ is no less than 0 for any $u \in D$. Therefore

$$\begin{aligned} \tau \frac{dV}{dt} &\leq - \sum_{i=1}^n [cu_i + v_i g_i(u_i)] [u_i - v_i g_i(u_i)] + \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &= - \sum_{i=1}^n cu_i [u_i - v_i g_i(u_i)] \\ &\quad - \sum_{i=1}^n v_i g_i(u_i) [u_i - v_i g_i(u_i)] + \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &\leq - \sum_{i=1}^n cu_i [u_i - v_i g_i(u_i)] + \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &\leq - \sum_{i=1}^n cu_i (u_i - M_v u_i) + \sum_{i=1}^n \frac{c^2 n}{4} u_i^2 \\ &= - \sum_{i=1}^n \left[c(1 - M_v) - \frac{c^2 n}{4} \right] u_i^2. \end{aligned}$$

According to (14), $c(1 - M_v) - (c^2 n/4)$ is strictly greater than 0, so dV/dt is strictly negative for any $u \in D$ except for $u = 0$. ■

Proposition 5: If there exists M_i such that $\dot{f}_i(x_i) \leq M_i$ for any x_i and $v_i M_i < 1$ for any $i = 1, \dots, n$, then the network of (1) and (2) has a unique equilibrium, which is globally asymptotically stable.

Proof: The proof follows similar steps as in the proof of Proposition 4. ■

Proposition 5 can be extended to more general activation functions. We may relax the constraint of “differentiable $f_i(u)$ with nonnegative $\dot{f}_i(u)$ ” in Condition 1 to that $f_i(u)$ is globally Lipschitz continuous, i.e.,

$$0 \leq \frac{f_i(u_1) - f_i(u_2)}{u_1 - u_2} \leq M_i \quad (15)$$

for any two different u_1, u_2 . Then, using the Lure-type Lyapunov function as constructed in the proof of Proposition 4, we may prove that if M_i in (15) is constrained by $v_i M_i < 1$ for any $i = 1, \dots, n$, the network of (1) and (2) has a unique equilibrium, which is globally asymptotically stable.

IV. WTA COMPETITION

In the study of WTA competition, we want to be “fair” with each individual neuron: We assume that the network is symmetric for each neuron, i.e., all neurons have the same activation function and same synaptic strength of lateral inhibitory connection between neurons. Specifically, let $f_i(\cdot) = f(\cdot)$ and $v_i = v$ for $i = 1, \dots, n$. Then, (1) becomes

$$\tau \frac{dx_i}{dt} = -x_i - \sum_{k \neq i} v f(x_k) + d_i, \quad i = 1, \dots, n. \quad (16)$$

A. Order-Preserving Equilibrium

An equilibrium of (16), x^* , is said to be *order-preserving with respect to the network inputs*, if x_i^* is less than x_j^* whenever d_i is less than d_j , where $i, j \in \{1, \dots, n\}$.

Proposition 6: If $f(\cdot)$ is continuous, nonnegative, and monotone nondecreasing, then the network of (16) always has an equilibrium x^* that is order-preserving with respect to the network inputs.

Proof: Without loss of generality, let $d_1 \leq \dots \leq d_n$. Denote $h_i(x) = d_i - \sum_{k \neq i} v f(x_k)$ and $h(x) = [h_1(x), \dots, h_n(x)]^T$. Consider a compact convex set $D = \{x | d_i - \sum_{k \neq i} v f(d_k) \leq x_i \leq d_i, i = 1, \dots, n, \text{ and } x_1 \leq \dots \leq x_n\}$. Similar to the proof of Proposition 1, it can be shown that for any $x \in D$, $h_i(x)$ is no greater than d_i and no less than $d_i - \sum_{k \neq i} v f(d_k)$. Furthermore, for any $i < j$ (and, thus, $d_i \leq d_j$), we have $h_i(x) - h_j(x) = d_i - d_j + v f(x_i) - v f(x_j) \leq 0$, because $d_i \leq d_j$ and $f(x_i) \leq f(x_j)$ (since f is monotone nondecreasing and x_i is no greater than x_j due to $i < j$ and $x \in D$). Therefore, $h(x) \in D$ for any $x \in D$. According to Brouwer fixed point theorem [22], $x = h(x)$ has a fixed point in D , which implies that (16) has at least one equilibrium, say x^* , such that $x_1^* \leq \dots \leq x_n^*$.

For any $d_i < d_j$, we have $x_i^* \leq x_j^*$ and, thus, $f(x_i^*) \leq f(x_j^*)$. Therefore, $x_i^* - x_j^* = d_i - d_j + v f(x_i^*) - v f(x_j^*) \leq d_i - d_j < 0$, so x_i^* is strictly less than x_j^* . Hence, we proved that x^* is order-preserving with respect to the network inputs. ■

It is apparent from Proposition 6 that if the network of (16) has only one equilibrium, this equilibrium has to be order-preserving with respect to the network inputs.

B. Increased Differences Between Neuronal Activities

Proposition 7: Let x^* be an order-preserving equilibrium of (16). If $f(\cdot)$ is strictly monotone increasing, then, for any $d_i < d_j$, we have

$$x_j^* - x_i^* > d_j - d_i > 0 \quad (17)$$

i.e., expressed in another form

$$d_i - x_i^* > d_j - x_j^* \geq 0. \quad (18)$$

Proof: Since x^* is an order-preserving equilibrium, we have $x_i^* < x_j^*$ for any $d_i < d_j$ and, thus, $f(x_i^*) < f(x_j^*)$ because $f(\cdot)$ is strictly monotone increasing. Therefore, $x_j^* - x_i^* = d_j - d_i + v f(x_j^*) - v f(x_i^*) > d_j - d_i$; so, we get (17). Expressing this inequality in another form, we have $d_i - x_i^* > d_j - x_j^*$. Inequality (5) guarantees $d_j - x_j^* \geq 0$. Then, we get (18). ■

The significance of Proposition 7 is that it reveals the underlying mechanism of WTA competition in a recurrent network with lateral inhibition. Inequality (17) shows the expansion of neuronal postsynaptic membrane potentials in the presence of lateral inhibition: The lateral inhibition between every pair of neurons plays a role of increasing the differences between neuronal potentials at any order-preserving equilibrium (without the lateral inhibition, x_i^* equals d_i for any i and, thus, $x_j^* - x_i^* = d_j - d_i$). Inequality (18) shows the asymmetric effect of lateral inhibition: Although the lateral inhibition decreases the postsynaptic membrane potential of each neuron, such effect

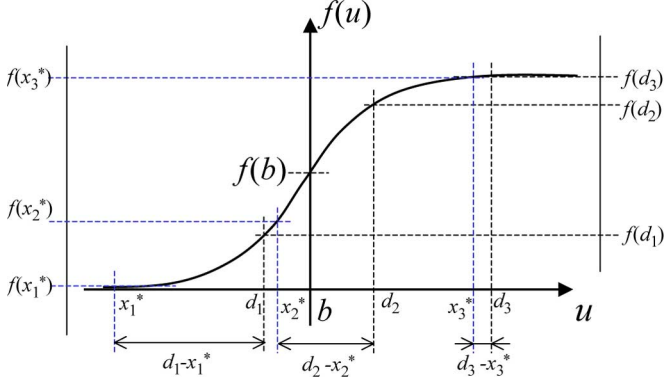


Fig. 2. Distribution of the network inputs versus individual elements of an order-preserving equilibrium x^* . If $d_i < d_j$, then $d_i - x_i^* > d_j - x_j^*$.

is not symmetric; at an order-preserving equilibrium, the potential of a neuron with larger input is decreased less than that of a neuron with smaller input. This is demonstrated in Fig. 2.

For our particular interest in the WTA networks, we now restrict our attention to a family of sigmoidal activation functions, with which the networks may implement WTA computation effectively. The activation function $f(u)$ considered in the following satisfies Condition 2.

Condition 2: The neuronal activation $f(u)$ is continuous, nonnegative, and strictly monotone increasing; $\dot{f}(u)$ is continuous; $\dot{f}(u)$ is monotone decreasing on $[b, \infty)$ and monotone increasing on $(-\infty, b]$ —this implies that $\dot{f}(u)$ achieves its maximum at $u = b$ and that $f(u)$ is concave on the right side of $u = b$ and convex on the left side of $u = b$.

In the aforementioned condition, b is called the *bias* or membrane potential *threshold* of a neuron. Neuron i is said to be *active* at time t if $x_i(t) > b$ and *inactive* if $x_i(t) \leq b$.

Proposition 8: Consider a network of (16) with neuronal activation function satisfying Condition 2. Let d_i and d_j be two inputs such that $b < d_i < d_j$, and let x^* be an order-preserving equilibrium of (16). If neurons i and j are both active at x^* , i.e., $b < x_i^* < x_j^*$, then, there must be

$$v\dot{f}(d_j) < 1 \quad (19)$$

$$x_j^* - x_i^* \geq \frac{d_j - d_i}{1 - v\dot{f}(d_j)} \quad (20)$$

and

$$f(x_j^*) - f(x_i^*) \geq f(d_j) - f(d_i) + \frac{v\dot{f}(d_j)\dot{f}(d_i)}{1 - v\dot{f}(d_j)}(d_j - d_i). \quad (21)$$

Proof: First, prove (19) and (20). Since $\dot{f}(\cdot)$ is continuous, we have

$$\begin{aligned} x_j^* - x_i^* &= d_j - d_i + v f(x_j^*) - v f(x_i^*) \\ &= d_j - d_i + v \dot{f}(\xi) (x_j^* - x_i^*) \end{aligned} \quad (22)$$

where $\xi \in [x_i^*, x_j^*] \subset (b, d_j]$, according to the mean value theorem [22]. Hence, $\dot{f}(\xi) \geq \dot{f}(d_j)$ ($\dot{f}(\cdot)$ is monotone decreasing on $[b, \infty)$). Because $x_i^* < x_j^*$ and $d_i < d_j$, there must be $v\dot{f}(\xi) < 1$; otherwise, we may derive $x_j^* - x_i^* \geq d_j - d_i + x_j^* - x_i^*$ and, thus, $d_j \leq d_i$, causing contradiction. Therefore, we have

$v\dot{f}(d_j) \leq v\dot{f}(\xi) < 1$, which leads to (19). Following (22), we further have

$$x_j^* - x_i^* = \frac{d_j - d_i}{1 - v\dot{f}(\xi)} \geq \frac{d_j - d_i}{1 - v\dot{f}(d_j)}$$

which leads to (20).

Next, prove (21). According to (20), the fact that $b < x_i^* < x_j^* \leq d_j$, and that $f(\cdot)$ is strictly monotone increasing and $\dot{f}(\cdot)$ is monotone decreasing on $[b, \infty)$, we have

$$\begin{aligned} f(x_j^*) - f(x_i^*) &\geq f(d_j) - f(d_j - (x_j^* - x_i^*)) \\ &\geq f(d_j) - f\left(d_j - \frac{d_j - d_i}{1 - v\dot{f}(d_j)}\right) \\ &= f(d_j) - f\left(d_i - \frac{v\dot{f}(d_j)(d_j - d_i)}{1 - v\dot{f}(d_j)}\right) \\ &\geq f(d_j) - f(d_i) + \dot{f}(d_i) \frac{v\dot{f}(d_j)(d_j - d_i)}{1 - v\dot{f}(d_j)} \\ &= f(d_j) - f(d_i) + \frac{v\dot{f}(d_j)\dot{f}(d_i)}{1 - v\dot{f}(d_j)}(d_j - d_i) \end{aligned}$$

completing the proof. \blacksquare

Proposition 8 indicates that the lateral inhibition increases both the differences between postsynaptic membrane potentials and the differences between outputs of active neurons at an order-preserving equilibrium. Fig. 3 presents an example showing the outcome of competition among neurons in a nine-neuron network under different strength of lateral inhibition v . The neuronal activation function is a logistic function

$$f(u) = \frac{1}{1 + e^{-\frac{u-b}{a}}} \quad (23)$$

where b is a translation factor and a is a dilation factor. With appropriate choice of v , the network may present WTA competition among neurons such that there can be at most a single neuron active at the equilibrium.

Corollary 2: Consider a network of (16) with neuronal activation function satisfying Condition 2. Let d_j and d_i be the largest and second largest inputs, respectively, with $b < d_i < d_j$, and x^* an order-preserving equilibrium of (16). If

$$v\dot{f}(d_j) \geq 1 \quad (24)$$

or if

$$v\dot{f}(d_j) < 1 \quad \text{and} \quad d_j - b < \frac{d_j - d_i}{1 - v\dot{f}(d_j)} \quad (25)$$

then the network has at most one active neuron at x^* .

Proof: The proof directly follows Proposition 8. \blacksquare

Corollary 2 presents some sufficient conditions for the network to have at most a single neuron active at the equilibrium. It can be seen that these single-winner conditions become very conservative when the networks have steep neuronal activation functions (i.e., with large gain or $\dot{f}(b)$). To obtain a deeper understanding of situations involving steep activation functions, we consider in Section V a limiting situation where the neuronal activation functions have infinite gain. This special case provides us with a more detailed picture of WTA competition.

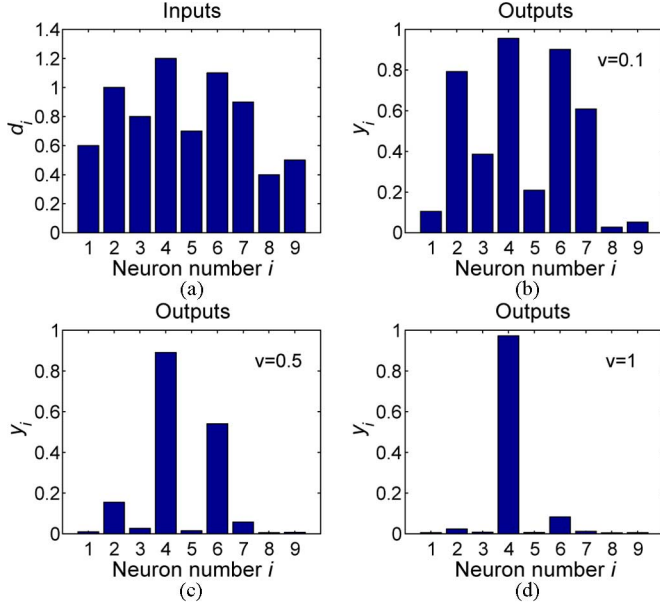


Fig. 3. WTA(s) competition in a network with lateral inhibition. The network has nine neurons, with logistic function (23) as neuronal activation function, where $a = 1/8$ and $b = 0.5$. The initial state is $x(0) = 0$. (a) Network inputs $d = [0.6, 1.0, 0.8, 1.2, 0.7, 1.1, 0.9, 0.4, 0.5]^T$. (b) Four active neurons (neurons 2, 4, 6, and 7) at the equilibrium when $v = 0.1$. (c) Two active neurons (neurons 4 and 6) at the equilibrium when $v = 0.5$. (d) Single winner, i.e., neuron 4 as the single active neuron, at the equilibrium when $v = 1$.

V. DYNAMICS OF WTA IN A LIMITING SITUATION

This section investigates the WTA competition under a limiting situation where neurons have discontinuous activation functions. We are primarily interested in the situations with activation functions that possess high-slope nonlinearities. However, rather than studying the case that the slope is high but of finite value, we choose to model the network here as a system of differential equations with discontinuous right-hand side (with infinite gain). Analyzing the ideal discontinuous case has several advantages [27]–[29]. For example, as pointed out by Forti and Nistri [28], “such analysis is usually able to give a clear picture of the salient features of motion, such as the presence of sliding modes, i.e., the possibility that trajectories be confined for some time intervals on discontinuity surfaces.”

The discontinuous neuronal activation function considered in this section is of the following form:

$$\sigma(u - b) = \begin{cases} 1, & \text{if } u > b \\ 0, & \text{if } u \leq b \end{cases} \quad (26)$$

where b represents the bias or threshold of a neuron. Let $v_i = v$ for $i = 1, \dots, n$. Then, the network of (1) and (2) becomes

$$\tau \frac{dx_i}{dt} = -x_i - v \sum_{k \neq i} y_k + d_i \quad (27)$$

$$y_i = \sigma(x_i - b) \quad (28)$$

where $i = 1, \dots, n$. This system fails to satisfy conventional results for the existence of solutions to differential equations. A generalization of the concept of solution is thus required.

A. Filippov Solutions

Filippov [30] developed a solution concept for differential equations whose right-hand sides were only required to be Lebesgue measurable in the state and time variables. Consider the vector differential equation in the form

$$\frac{dx}{dt} = f(x, t) \quad (29)$$

where $f : R^n \times R \rightarrow R^n$ is measurable and essentially locally bounded. A vector function $x(t)$, defined on the interval $[t_0, t_1]$, is called a *Filippov solution* of (29) if it is absolutely continuous and if, for almost all $t \in [t_0, t_1]$, the vector $dx(t)/dt$ belongs to $K[f](x, t)$, which is defined as the smallest convex closed set containing the limiting values of vector field $f(\cdot)$ in progressively smaller neighborhoods of $x(t)$ in the space of x except for a set of measure zero [30] (see Appendix I for a precise expression of $K[f](x, t)$ in mathematical notation). In Filippov’s definition, sets of measure zero are discarded. This technical detail allows solutions to be defined at points even where the vector field itself is not defined, such as at the interface of two regions in a piecewise-defined vector field. In the case of continuous right-hand side of differential equations, $K[f](x, t)$ contains a single point coinciding with $f(x, t)$ when $f(x, t)$ is continuous. Thus, for this case, the solution of (29) in the sense of Filippov is the same as the solution in the ordinary sense.

Existence of Filippov solutions of (27) and (28) is guaranteed by the existence theorem [30]. In the rest of this section, any trajectories of $x(t)$ of (27) and (28) are meant to be Filippov solutions of (27) and (28). A vector x^* is said to be an *equilibrium* of (27) and (28) if $x(t) = x^*$ is a Filippov solution of the system. Considering a system subject to (29), an equilibrium x^* is a vector satisfying $0 \in K[f](x^*, t)$. Note that this definition is consistent with the previous definition of equilibrium in the situation where $f(x, t)$ is continuous.

B. WTA in a Limiting Situation

We show that lateral inhibition among neurons can lead to WTA competition in the network: Only a single neuron is active in the network at an equilibrium. Denote $d_{\max} = \max\{d_1, \dots, d_n\}$.

Proposition 9: Let $x(t)$ be a state trajectory of (27) and (28) originating from $x(0)$. Then, for any $i = 1, \dots, n$, $\lim_{t \rightarrow \infty} x_i(t)$ is no greater than d_i . In other words, for any $\epsilon > 0$, there exists a $T_i \geq 0$ such that $x_i(t) < d_i + \epsilon$ for any $t > T_i$. Furthermore, T_i can be chosen as

$$T_i = \begin{cases} 0, & \text{if } x_i(0) \leq d_i + \epsilon \\ \tau \ln \left(\frac{x_i(0) - d_i}{\epsilon} \right), & \text{if } x_i(0) > d_i + \epsilon. \end{cases} \quad (30)$$

Proof: Since $v \sum_k \sigma(x_k - b)$ is no less than 0 for any x , we have $M_x\{-x_i + d_i - v \sum_k \sigma(x_k - b)\} \leq M_x\{-x_i + d_i\} = -x_i + d_i$, where $M_x\{\cdot\}$ is defined in Appendix I. For $x(t)$ is a Filippov solution of (27) and (28), $x(t)$ should satisfy (36) (see Appendix I): $\tau(dx_i(t)/dt)$ is no greater than $M_x\{-x_i + d_i - v \sum_k \sigma(x_k - b)\} \leq -x_i + d_i$ for (at least) almost all t . According to the comparison theorem (see Appendix I), $x_i(t) \leq$

$(x_i(0) - d_i)e^{-(t/\tau)} + d_i$. It can be seen from this inequality and from (30) that $x_i(t)$ is less than $d_i + \epsilon$ for any $t > T_i$. ■

The tangent vector of the state trajectory $dx(t)/dt$ does not necessarily satisfy (27) and (28) for almost all t , so we cannot derive inequalities directly from (27) and (28); rather than that, we use (36) (Appendix I) to estimate bounds for dx/dt .

Corollary 3: If $d_{\max} < b$, the network of (27) and (28) has only one equilibrium x^* with $x_i^* = d_i$ for all i , and at the equilibrium all neurons output 0. Furthermore, the equilibrium x^* is globally asymptotically stable.

Proof: We show that $x(t)$ converges to x^* no matter where $x(t)$ originates; following this, it has to be true that x^* is the only equilibrium of the system. For $d_{\max} < b$, according to Proposition 9, there exists a $T \geq 0$ (T takes 0 when $x(0) \in \{x|x_i < b, i = 1, \dots, n\}$) such that, for any $t \geq T$, $x(t)$ belongs to $\{x|x_i < b, i = 1, \dots, n\}$, which is an open set. In this open set, $x(t)$ is a solution of the following differential equations with continuous right-hand sides: $\tau(dx_i(t)/dt) = -x_i(t) + d_i$ for $i = 1, \dots, n$. Consequently, $x_i(t) = (x_i(T) - d_i)e^{-(t-T)/\tau} + d_i$ for any $t \geq T$, and further $\lim_{t \rightarrow \infty} x_i(t) = d_i$ and $\lim_{t \rightarrow \infty} x(t) = x^*$. Due to the convergence of $x(t)$ to x^* no matter where $x(t)$ originates and due to the exponential convergence of $x(t)$ toward x^* whenever $x(t)$ originates in $\{x|x_i < b, i = 1, \dots, n\}$ —an open set containing x^* —the equilibrium x^* has to be globally asymptotically stable. It is obvious that at the equilibrium all neurons output 0. ■

Proposition 10: Assume that q is a nonnegative integer and q and v satisfy $qv > d_{\max} - b$. Let $x(t)$ be a state trajectory of (27) and (28) originating from $x(0)$. Denote $F = \{x | \sum_i \sigma(x_i - b) \leq q\}$ and $F^c = \{x | \sum_i \sigma(x_i - b) \geq q + 1\}$. Then, for any $x(0) \in F$, $x(t)$ remains in F for any $t > 0$; for any $x(0) \in F^c$, $x(t)$ will converge to F such that $x(t)$ belongs to F for any $t > T$, where

$$T = \max \left\{ \tau \ln \frac{x_i(0) + qv - d_i}{b + qv - d_i} | x_i(0) > b \right\}. \quad (31)$$

Proof: See Appendix II. ■

Consider two special cases of Proposition 10: $q = 0$ and $q = 1$. In the former case, $d_{\max} < b$, Proposition 10 tells us: If $y_i(0) = 0$ for all i , then $y_i(t)$ will keep being 0 for any $t > 0$; if $y_i(0) = 1$ for some i , then all neurons will be quiet (outputting 0) after a time interval no greater than $T = \max\{\tau \ln(x_i(0) - d_i/b - d_i) | x_i(0) > b\}$. In the latter case, $v > d_{\max} - b$, Proposition 10 states that there is at most one neuron active (outputting 1) in the network for any $t > T$, where T equals 0 if initially there is at most one active neuron in the network and T equals $\max\{\tau \ln(x_i(0) + v - d_i/b + v - d_i) | x_i(0) > b\}$ otherwise.

Proposition 11: Let v be strictly greater than $d_{\max} - b$, the set $I = \{i | d_i > b\} = \{i_1, \dots, i_p\}$ be nonempty, and d_j be strictly less than b for $j \notin I$. Then, the network of (27) and (28) has the following properties.

- The system has exactly p stable equilibria $x^{(1)}, \dots, x^{(p)}$, where $x^{(k)}$ ($k = 1, \dots, p$) is determined by $x_{i_k}^{(k)} = d_{i_k}$ and $x_j^{(k)} = d_j - v$ for $j \neq i_k$; at the equilibrium $x^{(k)}$, only the i_k th neuron outputs 1 and other neurons output 0.
- If $p = 1$, any trajectory of $x(t)$ will converge to the equilibrium $x^{(1)}$ no matter where $x(0)$ is located.

- If $p \geq 2$, any trajectory of $x(t)$ will converge to one of the stable equilibria $x^{(k)}$, $k = 1, \dots, p$, or converge to and reach the following set within a finite time:

$$U = \bigcup_{r_1, r_2 \in I, r_1 \neq r_2} \{x | x_{r_1} = b, x_{r_2} = b, x_j \leq b \text{ for } j \neq r_1, r_2\} \quad (32)$$

furthermore, there is no stable equilibrium on U in the sense that some infinitely small perturbation can cause $x(t)$ on U to leave U and converge to one of $x^{(k)}$, $k = 1, \dots, p$.

Proof: See Appendix III. ■

VI. DISCUSSION

A. Limitation of Using Lateral Inhibition to Implement WTA

Resolution of WTA and uniqueness of network equilibrium are two crucial design specifications in the implementation of WTA using a network with lateral inhibition. It is apparent that the network is desired to achieve high output resolution of WTA, i.e., to obtain significant contrast between the “winner” and “losers.” Meanwhile, the network is also desired to possess a unique equilibrium at which the neuron with the largest input is guaranteed to “win” regardless of the system initial conditions. According to Proposition 6, a unique equilibrium implies that the equilibrium is order-preserving with respect to the network inputs. When the network has multiple stable equilibria, however, the neuron with the largest input may not win the competition with other neurons, as shown in Proposition 11 and Fig. 4. Therefore, uniqueness of network equilibrium can be considered as an indication of the reliability of the WTA implementation.

However, the aforementioned two design specifications exert conflicting requirements on the strength of lateral inhibition in the network. As demonstrated in Fig. 3, strong lateral inhibition can improve the contrast between the winner and losers, but at the same time, it may not guarantee the neuron with the largest input to win—it may result in multiple stable equilibria in the network due to the break of (10) in Proposition 3. In comparison, weak lateral inhibition has relatively poor capability to improve WTA resolution, but it may guarantee the uniqueness of network equilibrium and, thus, order-preserved outputs with respect to the network inputs. Therefore, a satisfactory WTA resolution and uniqueness of network equilibrium may not be guaranteed simultaneously.

B. Hysteresis and Schmitt Triggers

In the study of recurrent networks, one of the most interesting problems is the uniqueness of network equilibrium. From practical point of view, if a network possesses a unique equilibrium which in addition is globally asymptotically stable, this network becomes very attractive to optimization problems, since global convergence prevents a network from the risk of being trapped at some local minimum of the energy function [28]. On the other hand, however, networks with multiple stable equilibria are of significant value in applications as well. For example, they have been widely used as associative memories [31]–[33]. Various input patterns can be stored in an associative memory as stable equilibria of the network. Moreover, we show that the recurrent networks with lateral inhibition and possessing multiple stable

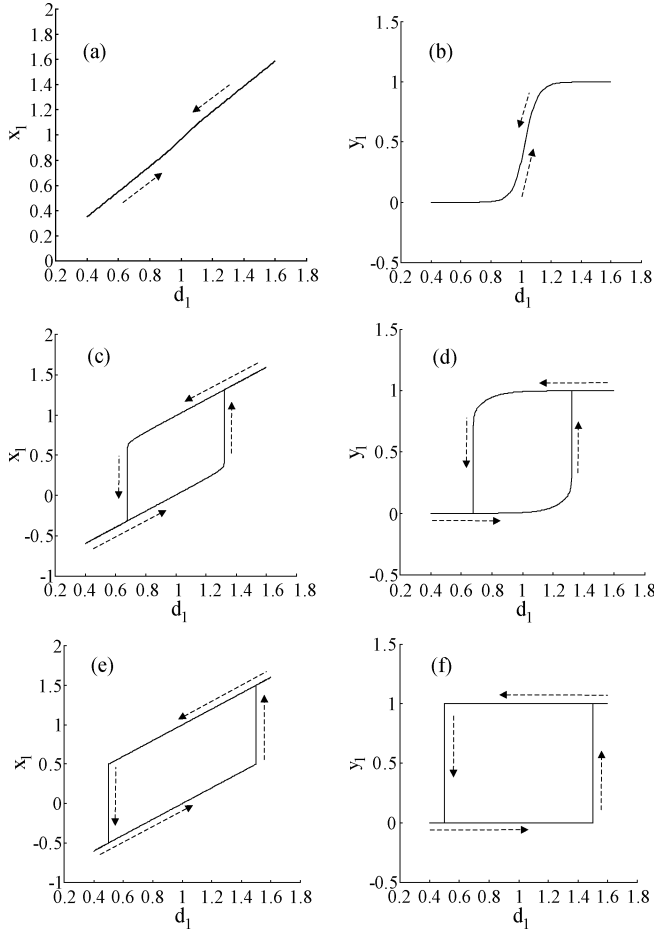


Fig. 4. Hysteresis in two-neuron networks with lateral inhibition. Each pair of pictures in (a)–(b), (c)–(d), or (e)–(f) presents the trajectories (with dashed arrows indicating the directions of motions) of x_1 and y_1 of one neuron as its input d_1 is quasi-statically increased from 0.4 to 1.6 and then decreased from 1.6 to 0.4. The other input is fixed to $d_2 = 1$. The network evolves from $x = 0$ as d_1 starts to increase from 0.4. (a)–(b) Network with single equilibrium does not have the effect of hysteresis. The activation function is of the form of (23); $a = 1/20$, $b = 1$, and $v = 0.1$. (c)–(d) Network with multiple equilibria may have the effect of hysteresis. The activation function is of the form of (23); $a = 1/10$, $b = 0.5$, and $v = 1$. (e)–(f) Network clearly shows hysteresis. The neuronal activation function is of the form of (26); $b = 0.5$ and $v = 1$.

equilibria can exhibit *hysteresis* in the response of output state transition to shift in input state. Such behavior is characteristic of the Schmitt trigger circuit [34] that can be used to guard systems against spurious state switches due to input signal noise.

Fig. 4 presents examples of hysteresis realized by networks with lateral inhibition. Each pair of pictures in Fig. 4(a)–(b), (c)–(d), or (e)–(f), shows the trajectories of quasi-steady state responses x_1 and y_1 of neuron 1, one neuron in a two-neuron network, as the input to neuron 1 d_1 is quasi-statically increased from 0.4 to 1.6 and then decreased from 1.6 to 0.4. The input to the other neuron is fixed to $d_2 = 1$. The lower two pairs of pictures, Fig. 4(c)–(d) and (e)–(f), demonstrate hysteresis while Fig. 4(a)–(b) does not as there is a single equilibrium for any network inputs. This is guaranteed by the fact that in the network of Fig. 4(a)–(b), $v \max_u \dot{f}(u)$ equals $1/2$, which is less than 1. Further simulations (not shown

here) suggest that hysteresis is produced and made more prominent by increasing either the steepness of the neural activation functions $f(\cdot)$ or the strength of lateral inhibition v .

C. Selection Reliability and Efficiency in Striatal Networks

Lateral inhibition has been proposed as a mechanism underlying the neural competition within the basal ganglia [35]–[37] that enables them to select or switch motor programs. Recently, a multiple-input–multiple-output adaptive switching (MIMOAS) model of frontocortical and basal ganglionic interaction was proposed [37], [38], in which cortical inputs to the striatum (an input processing component of the basal ganglia), modeled as a single layer, recurrent lateral inhibitory network, must specify effectively binary control outputs. Because the control outputs are postulated to strongly modulate frontocortical activity, it is important that this system does not suffer spurious fluctuations. Rather, changes in control output should occur only with definitive changes in cortical state. Owing to the Schmitt-trigger-like behavior described previously, striatal output control appears to be quite robust to noise and fluctuations in cortical input signals. Under pathophysiological conditions, the hysteresis effect may no longer persist in the striatal networks, and this could give rise to instability.

We propose that the lack of hysteresis effect (Schmitt-trigger-like behavior) in the striatal networks is a mechanism underlying the classic 4–6-Hz rest tremor seen in Parkinson's disease. Parkinson's disease is a disorder in which a deficiency in the neurotransmitter dopamine results in decreased peak slope of activation functions of striatal neurons (among other effects) [36]. Shallower functions $f(\cdot)$ reduce the hysteresis effect (e.g., Fig. 4), resulting in inappropriate switching in presence of fluctuations in cortical input signals. Consistent with this mechanism is the particular efficacy of dopamine replacement and anticholinergic medications in relieving Parkinsonian tremor—both medications likely steepen the activation function $f(\cdot)$ [36]. Our proposal does not argue explicitly against other proposed mechanisms of Parkinsonian tremor involving the subthalamic nucleus (STN) and external globus pallidus (GPe) [39]. However, our proposal indicates that the STN-GPe instability is not required for Parkinsonian tremor.

Thus, it appears that both physiological and pathophysiological features of the striatal network may be better understood in terms of the analysis presented herein.

VII. CONCLUSION

This paper studied the properties of recurrent neural networks with lateral inhibition. The dynamics of general networks of this type were analyzed in terms of number and stability of the equilibria, including a condition derived for the existence of a globally asymptotically stable equilibrium. This condition depends upon the product of the lateral inhibitory strength and the maximal steepness of the neuronal activation functions. It is less conservative than that for uniqueness of equilibrium in more general Hopfield networks and holds for recurrent lateral inhibitory networks with arbitrary nondecreasing continuous activation functions. For recurrent networks with identical neuronal activation functions and symmetric lateral inhibition, it was shown that an equilibrium must exist that is order-

preserving with respect to the network input. Given this property, conditions are established that guarantee the dominance of activity of a single neuron at an order-preserving equilibrium. This WTA effect results from augmented separation of suprathreshold activities of competing neurons. For networks with discontinuous threshold activation functions, conditions for WTA behavior and a richer characterization of the equilibrium states can be derived using Filippov's analysis. This paper also revealed a limitation of using lateral inhibition in WTA implementation: Two design specifications, resolution of WTA and uniqueness of network equilibrium, may exert conflicting requirements on the strength of lateral inhibition.

Finally, under conditions that give rise to multiple equilibria, transitions between network equilibrium states (and thus outputs) resulting from shifts in inputs may show hysteresis which potentially affords these networks considerable robustness to input noise. This feature may have biological significance in terms of the reliability of striatal function in the basal ganglia.

APPENDIX I FILIPPOV SOLUTIONS

Definition 1 (Filippov [30]): Consider a differential equation

$$\frac{dx}{dt} = f(x, t) \quad (33)$$

where $f : R^n \times R \rightarrow R^n$ is measurable and essentially locally bounded. A vector function $x(\cdot)$ is called a solution of (33) on $[t_0, t_1]$ if $x(\cdot)$ is absolutely continuous on $[t_0, t_1]$ and for almost all $t \in [t_0, t_1]$

$$\frac{dx}{dt} \in K[f](x, t) \equiv \bigcap_{\delta > 0} \bigcap_{\mu N = 0} \overline{\text{conv}} f(B(x, \delta) - N, t) \quad (34)$$

where μ is the Lebesgue measure, $\bigcap_{\mu N = 0}$ denotes the intersection over all sets N of Lebesgue measure zero, $B(x, \delta)$ represents a δ -neighborhood of the point x in the space, $\overline{\text{conv}} E$ denotes the closure of convex hull of a set E (convex hull of E is the smallest convex set containing E), and $f(E)$ is the set of values that the vector function $f(E)$ takes on the set E .

As for the absolutely continuous vector function $x(t)$ to be a Filippov solution of (33), it is necessary and sufficient that, for almost all t and for every vector e , the following inequality hold [30]:

$$\frac{dx}{dt} \cdot e \leq M_x \{f(x, t) \cdot e\} \quad (35)$$

where $M_x \{\phi(x, t)\}$ is defined by $\lim_{\delta \rightarrow 0} \text{ess} \max_{x' \in B(x, \delta)} \{\phi(x', t)\}$, and $\text{ess} \max_{x' \in B} \{\phi(x', t)\}$ denotes the essential upper bound of $\phi(\cdot)$ on set B if we neglect the values of the function $\phi(\cdot)$ on sets of measure zero: $\text{ess} \max_{x' \in B} \phi(x', t) = \inf_{\mu N = 0} \sup_{x' \in B - N} \phi(x', t)$. Especially, if we denote $f(\cdot) = [f_1(\cdot), \dots, f_n(\cdot)]^T$ and set $e = [0, \dots, 0, \pm 1, 0, \dots, 0]^T$ with the i th element of e being ± 1 and other elements being 0, then a Filippov solution $x(t)$ should satisfy

$$\frac{dx_i}{dt} \leq M_x \{f_i(x, t)\} \text{ and } -\frac{dx_i}{dt} \leq M_x \{-f_i(x, t)\}. \quad (36)$$

Condition 3 is required by the Comparison theorem.

Condition 3: In an open or closed region Q of the space x, t , the function $f(x, t)$ of (33) is defined almost everywhere in Q , is measurable, and, for any bounded closed domain $D \subset Q$, there exists a summable function $A(t)$ (with well-defined and finite integral of $|A(t)|$ on D) such that almost everywhere in D we have $|f(x, t)| \leq A(t)$.

Consider a single (scalar) equation

$$\frac{dx}{dt} = f(x, t) \quad (37)$$

in a domain Q of the (x, t) -plane. According to [30], if (37) satisfies Condition 3, then among all solutions of this equation passing through an arbitrary fixed point (x_0, t_0) , there is an upper solution $\bar{x}(t)$ such that any solution $x(t)$ passing through this point satisfies the inequality $x(t) \leq \bar{x}(t)$.

Theorem 1 (Comparison Theorem [30]): If (37) and

$$\frac{dx}{dt} = F(x, t) \quad (38)$$

satisfy Condition 3 in a domain Q and $F(x, t) \geq f(x, t)$ almost everywhere in this domain, then any solution $x(t)$ of (37) passing through the point (x_0, t_0) is not greater than the upper solution $\bar{X}(t)$ of (38) through the same point when $t \geq t_0$.

APPENDIX II PROOF OF PROPOSITION 10

The proof has the following two parts.

Part 1) Show that $x(t)$ remains in F for any $t > 0$, given $x(0) \in F$. We prove this by contradiction. Assume that there exists a time $T < \infty$ at which $x(T) \in F^c$. Then, denote $T_0 = \sup\{t | x(t) \in F, 0 \leq t < T\}$, and introduce a notation $K(t) = \{k | x_k(t) > b\}$. Obviously, $\sum_i y_i(t) = |K(t)|$, where $|K(t)|$ denotes the number of elements in $K(t)$. The outline of the proof for Part 1 is to show first $x(T_0) \in F$ and, then, to derive $x_k(T) \leq b$ for some $k \in K(T)$, which causes contradiction to the definition of $K(T)$. First, we show $x(T_0) \in F$. Assume this is not true, i.e., $x(T_0)$ belongs to F^c . Denote $\epsilon = \min\{x_k(T_0) - b | k \in K(T_0)\}$, which is greater than 0, and

$$B(x(T_0), \epsilon) = \{x' | \|x' - x(T_0)\| < \epsilon\}. \quad (39)$$

Since $x(T_0) \in F^c$, we have $\sum_i y_i(T_0) = |K(T_0)| \geq q + 1$. It can be further tested that, for any $k \in K(T_0)$, x_k is greater than b for any $x \in B(x(T_0), \epsilon)$. Hence, for any $x \in B(x(T_0), \epsilon)$, $\sum_i y_i$ is no less than $|K(T_0)| \geq q + 1$, which implies $B(x(T_0), \epsilon) \subset F^c$. Since $B(x(T_0), \epsilon)$ is an open set centered at $x(T_0)$ and $x(t)$ is a continuous function of t , there exists a $\delta > 0$ such that, for any $t \in (T_0 - \delta, T_0 + \delta)$, $x(t)$ belongs to $B(x(T_0), \epsilon) \subset F^c$. However, since $T_0 = \sup\{t | x(t) \in F, 0 \leq t < T\}$, there exists at least one $t_\delta \in (T_0 - \delta, T_0]$ such that $x(t_\delta) \in F$ no matter how small δ is. This leads to contradiction. Therefore, $x(T_0)$ should not belong to F^c , and thus $x(T_0) \in F$ and $T_0 < T$. Next, we derive $x_k(T) \leq b$

for some $k \in K(T)$. For $|K(T_0)| \leq q < q + 1 \leq |K(T)|$, there exists at least one k satisfying $k \in K(T)$ but $k \notin K(T_0)$, i.e., $x_k(T_0) \leq b$, while $x_k(T) > b$. According to the definition of T_0 , $x(t)$ belongs to F^c for any $t \in (T_0, T)$. Thus, for any $t \in (T_0, T)$, there exists a $\epsilon(t) > 0$ such that $x(t)$'s neighborhood $B(x(t), \delta)$ is a subset of F^c whenever $\delta \in (0, \epsilon(t))$ [following the steps similar to the construction of $B(x(T_0), \epsilon)$ in (39)]. As a consequence, for any $x' \in B(x(t), \delta)$, we have $-x'_k + d_k - v \sum_{i \neq k} \sigma(x'_i - b) \leq -x'_k + d_k - v(\sum_i \sigma(x'_i - b) - 1) \leq -x'_k + d_{\max} - qv < -x'_k + b$. Referring to (36), we may derive

$$\begin{aligned} \tau \frac{dx_k(t)}{dt} &\leq M_x \left\{ -x_k + d_k - v \sum_{i \neq k} \sigma(x_i - b) \right\} \\ &\leq M_x \{-x_k + b\} \\ &= -x_k(t) + b. \end{aligned}$$

Further, according to the comparison theorem (Appendix I), we have

$$x_k(t) \leq (x_k(T_0) - b) e^{-\frac{t-T_0}{\tau}} + b \leq b$$

for any $t \in [T_0, T)$. Due to the continuity of $x_k(t)$ at time T , we have $x_k(T) \leq b$, which causes contradiction to $k \in K(T)$ and which completes the proof of Part 1.

Part 2) Show that, given $x(0) \in F^c$, $x(t)$ will converge to F , and will be trapped in F in a time no greater than (31). We prove this by contradiction. Denote $T_f = \inf\{t | x(t) \in F, t \geq 0\}$. Assume

$$T_f > T = \max \left\{ \tau \ln \frac{x_i(0) + qv - d_i}{b + qv - d_i} | x_i(0) > b \right\}.$$

According to the definition of T_f , $x(t)$ remains in F^c for $t < T_f$. Similar to the argument in Part 1, we may derive that, for almost all $t < T_f$, $\tau(dx_i(t)/dt) \leq -x_i(t) + d_i - qv$. Using the comparison theorem again, we have

$$x_i(t) \leq (x_i(0) + qv - d_i) e^{-\frac{t}{\tau}} + d_i - qv$$

for any $t \in [0, T_f)$. Considering those i with $x_i(0) \leq b$, if $x_i(0) + qv - d_i \geq 0$, then $x_i(t) \leq (x_i(0) + qv - d_i) e^{-(0/\tau)} + d_i - qv \leq x_i(0) \leq b$ for any $t \in [0, T_f)$; if $x_i(0) + qv - d_i < 0$, then $x_i(t) < d_i - qv \leq d_{\max} - qv < b$ for any $t \in [0, T_f)$. For those i with $x_i(0) > b$ and for any $t \in [T, T_f) = [\max\{\tau \ln((x_i(0) + qv - d_i)/(b + qv - d_i)) | x_i(0) > b\}, T_f)$

$$\begin{aligned} x_i(t) &\leq (x_i(0) + qv - d_i) e^{-\frac{T}{\tau}} + d_i - qv \\ &\leq (x_i(0) + qv - d_i) e^{-\ln \frac{x_i(0) + qv - d_i}{b + qv - d_i}} + d_i - qv \\ &= b. \end{aligned}$$

Therefore, $x_i(t)$ is no greater than b for any i and any $t \in [T, T_f)$. That is to say, $x(t)$ belongs to F for $t \in [T, T_f)$, which is contrary to that “ $x(t)$ remains in F^c for $t < T_f$.” Hence, the assumption of $T_f > T$ cannot hold, and, thus, we have $T_f = \inf\{t | x(t) \in F, t \geq 0\} \leq T$, which implies $x(t) \in F$ for any $t > T$.

APPENDIX III

PROOF OF PROPOSITION 11

First, we introduce the following notations:

$$\begin{aligned} F &= \left\{ x \mid \sum_k \sigma(x_k - b) \leq 1 \right\} \\ F^c &= \left\{ x \mid \sum_k \sigma(x_k - b) > 1 \right\} \\ F_i &= \{x | x_i > b, x_k \leq b, k \neq i\}, \quad i = 1, \dots, n \\ F_0 &= \{x | x_k \leq b, k = 1, \dots, n\}. \end{aligned}$$

According to the previous definition, $F_r \cap F_s$ is empty for any $r \neq s$ and $r, s \in \{0, 1, \dots, n\}$, and F equals $F_0 \cup F_1 \cup \dots \cup F_n$, i.e., $\{F_r, r = 0, 1, \dots, n\}$ is a partition of F . Further, denote

$$\begin{aligned} F_i^{\text{inner}} &= \{x | x_i > b, x_k < b, k \neq i\}, \quad i = 1, \dots, n \\ F_0^{\text{inner}} &= \{x | x_k < b, k = 1, \dots, n\}. \end{aligned}$$

Obviously, $F_r^{\text{inner}} (r \in \{0, 1, \dots, n\})$ is the largest open set contained in F_r .

The rest of the proof consists of the following four parts.

Part 1) Prove that, no matter where $x(0)$ is located, there exists a time $T \geq 0$ such that, for any $t \geq T$, we have $x(t) \in F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$, where $i_1, \dots, i_p \in I$. According to Proposition 10, there exists a time $T_1 \geq 0$ such that $x(t)$ belongs to F for any $t \geq T_1$. Further, since $d_j < b$ for $j \notin I$, according to Proposition 9, there exists a time T_2 such that, for any $t \geq T_2$ and for any $j \notin I$, we have $x_j(t) < b$ and, thus, $x_j(t) \notin F_j$. Let $T = \max\{T_1, T_2\}$. Then, for any $t \geq T$, $x(t)$ belongs to $F = F_0 \cup F_1 \cup \dots \cup F_n$, but does not belong to F_j for any $j \notin I$. Therefore, $x(t)$ belongs to $F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$ for any $t \geq T$.

The conclusion of Part 1 implies that the network of (27) and (28) does not have any equilibrium outside the set $F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$, and any trajectories of $x(t)$, no matter where it originates, will eventually be trapped in $F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$ within a finite time. Therefore, in the following, we only need to consider the case where $x(t)$ originates in $F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$.

Part 2) Prove that $x(t)$ will converge to the equilibrium $x^{(k)}$ if $x(0) \in F_{i_k} (k = 1, \dots, p)$, and further show that $x^{(k)}$ is asymptotically stable. It is obvious that at the equilibrium $x^{(k)}$ only the i_k th neuron outputs 1 and other neurons output 0. In this part, first consider the case of $x(0) \in F_{i_k}^{\text{inner}} (i_k \in I)$, and show that $x(t)$ remains in $F_{i_k}^{\text{inner}}$ for any $t > 0$. We prove this by contradiction. Assume that there is some time t such that $x(t) \notin F_{i_k}^{\text{inner}}$. Then, denote $T = \inf\{t | x(t) \notin F_{i_k}^{\text{inner}}, t \geq 0\}$. Since $F_{i_k}^{\text{inner}}$ is an open set, it has to be true that $x(T) \notin F_{i_k}^{\text{inner}}$ and $x(t) \in F_{i_k}^{\text{inner}}$ for any $t \in [0, T)$ (proof of this is similar to that of $x(T_0) \in F$ in the proof of Proposition 10). In the open set $F_{i_k}^{\text{inner}}$, $x(t)$, $t \in [0, T)$, is a solution of differential equations with continuous right-hand side: $\tau(dx_{i_k}(t)/dt) = -x_{i_k}(t) + d_{i_k}$ and $\tau(dx_j(t)/dt) =$

$-x_j(t) + d_j - v$ for $j \neq i_k$. Consequently, for any $t \in [0, T]$, $x_{i_k}(t) = (x_{i_k}(0) - d_{i_k})e^{-(t/\tau)} + d_{i_k} \geq \min\{x_{i_k}(0), d_{i_k}\} > b$, and $x_j(t) = (x_j(0) - d_j + v)e^{-(t/\tau)} + d_j - v \leq \max\{x_j(0), d_j - v\} < b$ for $j \neq i_k$. Due to the continuity of $x(t)$ at $t = T$, we have $x_{i_k}(T) \geq \min\{x_{i_k}(0), d_{i_k}\} > b$ and $x_j(T) \leq \max\{x_j(0), d_j - v\} < b$ for $j \neq i_k$, i.e., $x(T) \in F_{i_k}^{\text{inner}}$, which is contrary to our previous assumption. This means that we proved that $x(t)$ remains in $F_{i_k}^{\text{inner}}$ for any $t > 0$, whenever $x(0) \in F_{i_k}^{\text{inner}}$. Next, we show that $x(t)$ converges to $x^{(k)}$ whenever $x(0) \in F_{i_k}^{\text{inner}}$, and $x^{(k)}$ is an asymptotically stable equilibrium. Since $x(t)$ remains in $F_{i_k}^{\text{inner}}$ for $t \geq 0$, as already shown, we have $x_{i_k}(t) = (x_{i_k}(0) - d_{i_k})e^{-(t/\tau)} + d_{i_k}$ and $x_j(t) = (x_j(0) - d_j + v)e^{-(t/\tau)} + d_j - v$ for $j \neq i_k$. It is clear that $\lim_{t \rightarrow \infty} x_{i_k}(t) = d_{i_k}$ and $\lim_{t \rightarrow \infty} x_j(t) = d_j - v$ for $j \neq i_k$. Thus, $\lim_{t \rightarrow \infty} x(t) = x^{(k)}$. Obviously, $x^{(k)}$ is an equilibrium of the system. Due to the exponential convergence of $x(t)$ toward $x^{(k)}$ whenever $x(t)$ originates in $F_{i_k}^{\text{inner}}$, an open set containing $x^{(k)}$, the equilibrium $x^{(k)}$ is asymptotically stable. The rest of Part 2 is to show that $x(t)$ also converges to $x^{(k)}$ when $x(0)$ belongs to F_{i_k} but does not belong to $F_{i_k}^{\text{inner}}$, i.e., $x(0) \in F_{i_k} - F_{i_k}^{\text{inner}}$. Due to the previous paragraph, we only need to show that there exists some $t > 0$ such that $x(t) \in F_{i_k}^{\text{inner}}$. Let $\epsilon = x_{i_k}(0) - b$, which is greater than 0 due to $x(0) \in F_{i_k}$. Consider in the space of x the ϵ -neighborhood of $x(0)$ and $B(x(0), \epsilon)$. According to the definition of ϵ , x_{i_k} is strictly greater than b for any $x \in B(x(0), \epsilon)$. Due to the continuity of $x(t)$, there exists a $\delta > 0$ such that $x(t) \in B(x(0), \epsilon)$ for any $t \in [0, \delta]$. Obviously, $x_{i_k}(\delta) > b$. Note that for any $t \in [0, \delta]$ (which implies $x(t) \in B(x(0), \epsilon)$) and any $j \neq i_k$, $M_x\{-x_j + d_j - v \sum_{r \neq j} \sigma(x_r - b)\} \leq M_x\{-x_j + d_j - v\} = -x_j + d_j - v$ (refer to Appendix I for the definition of $M_x\{\cdot\}$). According to (36), $\tau(dx_j(t)/dt)$ should be no greater than $M_x\{-x_j + d_j - v \sum_{r \neq j} \sigma(x_r - b)\} \leq -x_j + d_j - v$ for almost all $t \in [0, \delta]$. Using the comparison theorem (Appendix I), for any $j \neq i_k$ (which implies $x_j(0) \leq b$) we have $x_j(t) \leq (x_j(0) - d_j + v)e^{-(t/\tau)} + d_j - v$ for any $t \in [0, \delta]$ and, thus, $x_j(\delta) \leq (x_j(0) - d_j + v)e^{-(\delta/\tau)} + d_j - v < \max\{x_j(0), d_j - v\} \leq b$. In summary, we have shown that $x_{i_k}(\delta) > b$ and $x_j(\delta) < b$ for $j \neq i_k$, i.e., $x(\delta) \in F_{i_k}^{\text{inner}}$. Starting from $x(\delta)$, an inner point of $F_{i_k}^{\text{inner}}$, $x(t)$ will converge to $x^{(k)}$ (according to the previous paragraph).

Part 3) Show that $x(t)$ will converge to one of $x^{(k)}$, $k = 1, \dots, p$, or converge to and reach the set U defined by (32) within a finite time, when $x(0) \in F_0$. Since Part 3 is obviously true for the case of $x(0) \in U$, in the following, we only need to consider the case of $x(0) \in F_0 - U$. Note that U is empty for the case of $p = 1$; thus, when $p = 1$, the statement of Part 3 becomes that any trajectory of $x(t)$ will converge to the equilibrium $x^{(1)}$. First, prove that, for

any $x(0) \in F_0^{\text{inner}}$, there exists some t such that $x(t) \notin F_0^{\text{inner}}$. This can be shown by contradiction, following the steps similar to those in the proof of Corollary 3: Assume that $x(t) \in F_0^{\text{inner}}$ for any $t > 0$, and then we may derive that $\lim_{t \rightarrow \infty} x_i(t) = d_i$ for any i , which implies that $d_i \leq b$ for any i and which is contrary to $d_i > b$ for $i \in I$. Then, it makes sense to denote $T_0 = \inf\{t | x(t) \notin F_0^{\text{inner}}, t \geq 0\}$. Because 1) F_0^{inner} is an open set, 2) F_0 is the closure of F_0^{inner} , and 3) $x(t)$ is continuous, $x(T_0)$ should stay on the boundary of F_0 , i.e., $x(T_0) \in F_0 - F_0^{\text{inner}}$. If $x(T_0)$ belongs to U , then we are done. In the following, we only need to consider the case that $x(t)$ starts from a point in $F_0 - F_0^{\text{inner}} - U$. Without loss of generality, assume that $x(t)$ originates in $F_0 - F_0^{\text{inner}} - U$ at time 0, which falls into the following two categories.

Case 3.1) $x_j(0) = b$ for some $j \notin I$. According to Proposition 9, $x_j(t)$ will be strictly less than b for any $j \notin I$ and any $t > 0$. Arbitrarily pick up a $t_0 > 0$, we know from the proof of Part 1 that $x(t_0)$ could only belong to $F_0 \cup F_{i_1} \cup \dots \cup F_{i_p}$. If $x(t_0) \in F_{i_k}$, $i_k \in I$, then $x(t)$ will converge to $x^{(k)}$, according to Part 2. According to the previous arguments in Part 3, if $x(t_0) \in F_0$, then there exists a $T \geq t_0$ ($T = t_0$ when $x(t_0)$ is already on the boundary of F_0) such that $x(T)$ is on the boundary of F_0 with $x_i(T) = b$ for some $i \in I$ and $x_j(T) < b$ for any $j \notin I$. If $x(T)$ belongs to U , then we are done. Therefore, we only need to consider the case that $x_{i_k}(T) = b$ for only one $i_k \in I$ and $x_j(T) < b$ for any $j \neq i_k$. This case will be covered by the argument for Case 3.2.

Case 3.2) $x_{i_k}(0) = b$ for only one $i_k \in I$, and $x_j(0) < b$ for any $j \neq i_k$. Let $\epsilon = \min\{b - x_j(0) | j \neq i_k\}$. Consider the ϵ -neighborhood of $x(0)$, $B(x(0), \epsilon)$. According to the definition of ϵ , x_j is strictly less than b for any $x \in B(x(0), \epsilon)$. Due to the continuity of $x(t)$, there exists a $\delta > 0$ such that $x(t) \in B(x(0), \epsilon)$ for any $t \in [0, \delta]$. Obviously, $x_j(\delta) < b$ for any $j \neq i_k$. Note that for any $t \in [0, \delta]$ ($x(t) \in B(x(0), \epsilon)$), $M_x\{-(-x_{i_k} + d_{i_k} - v \sum_{j \neq i_k} \sigma(x_j - b))\} = -(-x_{i_k} + d_{i_k})$. Denote $z(t) = -x_{i_k}(t)$. According to (36), $-\tau(dx_{i_k}(t)/dt) = \tau(dz(t)/dt)$ should be no greater than $M_x\{-(-x_{i_k} + d_{i_k} - v \sum_{j \neq i_k} \sigma(x_j - b))\} = -(-x_{i_k} + d_{i_k}) = -z - d_{i_k}$ for almost all $t \in [0, \delta]$. Using the comparison theorem (Appendix I), $z(t) \leq (z(0) + d_{i_k})e^{-(t/\tau)} - d_{i_k}$ for any $t \in [0, \delta]$ and, thus, $x_{i_k}(\delta) \geq (x_{i_k}(0) - d_{i_k})e^{-(\delta/\tau)} + d_{i_k} > \min\{x_{i_k}(0), d_{i_k}\} \geq b$. In summary, we have shown that $x_{i_k}(\delta) > b$ and $x_j(\delta) < b$ for $j \neq i_k$, i.e., $x(\delta) \in F_{i_k}^{\text{inner}}$. Starting from $x(\delta)$, $x(t)$ will converge to $x^{(k)}$, according to Part 2.

Part 4) Show that there is no stable equilibrium on U in the sense that, for any $x(0) = x_0 \in U$, some infinitely small perturbations can cause $x(t)$ to deviate from U and converge to a stable equilibrium, which is one of $x^{(k)}$, $k = 1, \dots, p$. For any $x_0 \in U$, consider the following perturbation on the initial value of $x(t)$ starting from x_0 : $x(0) = x_0 + \epsilon e_{i_k}$, where $\epsilon > 0$ and

$e_{i_k} = [0, \dots, 0, 1, 0, \dots, 0]^T$ with the i_k th element of e_{i_k} being 1 and other elements being 0, $i_k \in I$. Under such perturbation, no matter how small ϵ is, we have $x(0) \in F_{i_k}$ and, thus, $x(t)$ converges to $x^{(k)}$, according to Part 2. Therefore, there cannot be any stable equilibrium on U .

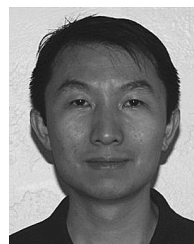
Parts 1–4 imply that the system has exactly p stable equilibria $x^{(1)}, \dots, x^{(p)}$, where $i_1, \dots, i_p \in I$.

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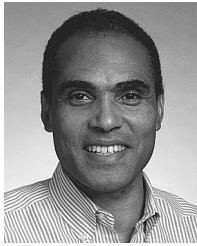
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