

Sufficient Conditions for Oscillations in Competitive Linear-Threshold Brain Networks

Michael McCreesh Tommaso Menara Jorge Cortés

Abstract—Oscillatory activity is highly prevalent in the brain. Oscillations with specific characteristics are associated with a variety of healthy and diseased brain functions. This paper considers two mesoscale brain network models described by linear-threshold and threshold-linear dynamics and takes on the analytical characterization of the emergence of oscillations. The synaptic connectivity is described by an arbitrary network interconnection topology that allows for self-excitatory nodes. We provide a structural characterization for the existence of stable node sets that support asymptotically stable equilibria and identify sufficient conditions for oscillatory behavior in competitive linear-threshold and threshold-linear dynamics. Simulations illustrate our results.

Index Terms—oscillations, competitive brain networks, linear-threshold and threshold-linear dynamics

I. INTRODUCTION

The presence of oscillations in neural activity motivates the study of the dynamical mechanisms behind their emergence. We consider brain networks composed of nodes, each representing a population of neurons with similar firing rate. We consider two dynamical models that describe the evolution of the aggregate firing rates and derive structural and input conditions that give rise to oscillations. The first model, called *linear-threshold network* (LTN), has dynamics

$$\tau \dot{\mathbf{x}} = -\mathbf{x} + [\mathbf{W}\mathbf{x} + \mathbf{u}]_0^{\mathbf{m}}, \quad (1)$$

where $[\cdot]_0^{\mathbf{m}} = \max\{\mathbf{0}, \min\{\cdot, \mathbf{m}\}\}$ (operations are performed elementwise). Here, \mathbf{x}_i represents the firing rate of a neuronal population represented by node $i \in \{1, \dots, N\}$, the synaptic weight matrix \mathbf{W} defines the connectivity between populations of neurons, and \mathbf{u} is an input to the system. The vector \mathbf{m} defines an upper bound on the firing rate. The second model, called *threshold-linear network* (TLN) has dynamics

$$\tau \dot{\mathbf{x}} = -\mathbf{x} + [\mathbf{W}\mathbf{x} + \mathbf{u}]_+, \quad (2)$$

where $[\cdot]_+ = \max\{\mathbf{0}, \cdot\}$. We note that if $\mathbf{m} = \infty \mathbf{1}$, the two dynamics are the same. The parameter τ is a biological constant that defines the timescale of the network. In this work, we assume that the populations of neurons have similar timescales and take $\tau = 1$.

Literature Review: Oscillatory behavior is one of the most commonly observed phenomena in the brain, appearing in both healthy and pathological states. Within healthy activity, oscillations are linked to phenomena such as cognition [1]

and consciousness [2], while also appearing in pathological behavior such as epileptic seizures and Parkinson’s disease [3]. Linear-threshold and threshold-linear models have been used extensively to model a variety of phenomena in the brain, ranging from the retinal behavior of a crab [4], to memory [5], and epilepsy [6], [7]. These are mesoscale models where the naturally decaying neural firing rate of a node is influenced by the firing rates of neighboring nodes and potentially additional background inputs. These dynamics employ piecewise-affine nonlinearities, which generalize sigmoidal nonlinearities [8], and are consistent with empirical descriptions of neural physiology. Further, these dynamics are rich enough to generate key properties such as mono- and multi-stability, limit cycles, and chaotic behavior, see e.g., [7], [9], and include the celebrated Wilson-Cowan model [10], [11] as a particular case. Of particular relevance here are works that relate network structure with dynamical properties of the model, such as stability [12], [13] and oscillations [14], [15]. Model expressivity and chaotic behavior are believed to be directly related, suggesting a small region, referred to as the *edge of chaos* [16], where the transition from stability to instability and the emergence of oscillations play a key role. It is in this region where the computational capacities of the dynamics are maximized for neural learning algorithms [17].

Within the study of oscillatory behavior of these dynamics, the literature is largely divided based upon network structure. Two of the main structures are excitatory-inhibitory networks and competitive networks (in the latter, all interneuronal interactions are inhibitory). While oscillatory behavior in excitatory-inhibitory networks has been studied extensively [15], [18], [19] using both threshold-linear and linear-threshold dynamics, for competitive networks the literature is largely restricted to threshold-linear dynamics. The works [9], [20] provide both analytic and graph-theoretic conditions for oscillations in a general competitive network governed by threshold-linear dynamics. The works [21], [22], [23] study combinatorial threshold-linear networks, a specific form of competitive networks, and provide conditions related to the existence of dynamic attractors, including limit cycles, and both quasi-periodic and chaotic attractors. These studies explicitly rule out node self-excitation and restrict their attention to all-to-all connectivity structures. This is a major difference with respect to the present manuscript, where we allow for self-excitation and consider arbitrary network structures.

Statement of Contributions: We study brain network neural-mass models described by linear-threshold and threshold-linear dynamics. Our first contribution pertains to the existence of asymptotically stable equilibria that have non-zero activity on

This work was partially supported by ONR Award N00014-18-1-2828. The authors are with the Department of Mechanical and Aerospace Engineering, University of California, San Diego, {mmccreesh, tmenara, cortes}@ucsd.edu

only a given subset of nodes in the network for a general linear-threshold dynamics. We provide a characterization of this in terms of the network structure. We build on this result in our second contribution, which characterizes the emergence of oscillatory behavior in competitive linear-threshold and threshold-linear dynamics. We provide sufficient conditions on the synaptic structure and the input that ensure the network does not have stable equilibria (a fact we use as a proxy for the existence of oscillations). Our contributions expand on the state of the art because of the consideration of arbitrary network connectivity patterns and the treatment of linear-threshold dynamics.

II. PROBLEM FORMULATION

In firing-rate models¹ such as linear-threshold or threshold-linear networks, the network structure determined by the synaptic weight matrix \mathbf{W} is classified based upon the properties of the interneuron connections. An interneuron connection is *excitatory* if the corresponding element in the synaptic weight matrix is positive, and is *inhibitory* if the entry is negative. The diagonal elements in the synaptic weight matrix represent the impact a node's activity has on itself, which we refer to as *self-excitatory* if the matrix value is positive, and *self-inhibitory* if the matrix value is negative. A particular class of networks to which we pay attention are *competitive* networks, which represent inhibition-based competition between brain regions, a widely-observed phenomenon [24].

Definition 2.1 (Competitive Network): Consider a linear-threshold (resp., threshold-linear) network defined by \mathbf{W} . The network is competitive if \mathbf{W} is a Z-matrix (i.e., all interneuron connections are inhibitory) and the nodes are either self-excitatory or not self-connected ($w_{ii} \geq 0$ for all i).

This definition generalizes the standard definition of competitive network, e.g., [20], which requires all diagonal elements to be zero. As oscillations in the brain are widely associated with inhibition [25], our goal is to determine conditions under which oscillations arise in competitive brain networks.

The notion of neural oscillation we consider here goes beyond periodic trajectories to also include chaotic behavior, as chaotic trajectories are of significant interest in computational neuroscience [26]. Formally, we say a trajectory $\mathbf{x}(t)$ of the LTN (1) or TLN (2) dynamics is oscillatory if it does not converge asymptotically to an equilibrium. Throughout the paper, we use the lack of stable equilibria (LoSE) as a proxy for the existence of oscillations. This is because this criterion is widely applicable, whereas analytic tools for directly studying oscillations (such as Poincaré-Bendixson theory [27]) are limited to 2-dimensional systems or ones whose behavior can

be confined to two dimensions. For the LTN dynamics, this proxy has been shown to be tight [15]. We formalize the problem considered as follows.

Problem statement: Consider a competitive LTN (resp. TLN) with synaptic weight matrix \mathbf{W} . Determine conditions on the structure of \mathbf{W} and the input vector \mathbf{u} such that the network has no stable equilibria.

III. STABLE EQUILIBRIA IN LTN AND TLN NETWORKS

This section studies the conditions for the existence of stable equilibria in a general network topology as a precursor to our focus in Section IV on the study of oscillations in competitive networks. Given the dynamics of LTN (1) and TLN (2) networks, it is clear that the location and stability of the equilibria depend upon the specific input. This brings up two important observations when characterizing them: (i) stability statements could be made for all possible inputs, several inputs, or just one input. Here, we focus on the latter; (ii) rather than the specific location of the equilibria, we focus on its support. This means that we consider equivalence classes of equilibria, as the same set of nodes could correspond to many different actual equilibria. The following definition makes this precise for TLN networks.

Definition 3.1: (Stable Node Set in TLN [9]): Consider a network governed by the threshold-linear dynamics (2). A non-empty subset of nodes $\sigma \subseteq \{1, \dots, N\}$ is *stable* if there exists an asymptotically stable equilibrium point \mathbf{x}^* such that $\text{supp}(\mathbf{x}^*) = \sigma$ for at least one input $\mathbf{u} \in \mathbb{R}^n$.

For LTN dynamics, since they are guaranteed to have bounded trajectories, this definition becomes trivial: for any subset σ , there always exists an input $\mathbf{u} \in \mathbb{R}^n$ such that the point $(\mathbf{0}, \mathbf{m}_\sigma)$ is an asymptotically stable equilibrium point (since, for \mathbf{u} with \mathbf{u}_σ large enough and $\mathbf{u}_{\bar{\sigma}}$ small enough, the dynamics reduces to $\dot{\mathbf{x}}_\sigma = -\mathbf{x}_\sigma + \mathbf{m}_\sigma$ and $\dot{\mathbf{x}}_{\bar{\sigma}} = -\mathbf{x}_{\bar{\sigma}}$). In order to extend our treatment of stable node sets for LTN networks, we first consider the support of a bounded vector.

Definition 3.2: (Support of a Bounded Vector): Let $\mathbf{x} \in [\mathbf{0}, \mathbf{m}] \subset \mathbb{R}^n$, with $\mathbf{m} \in \mathbb{R}_{>0}^n$. The support of \mathbf{x} is the set $\sigma = (\sigma_{\mathbf{m}}, \sigma_{\bar{\mathbf{m}}}) \subseteq \{1, \dots, N\}$, where $\mathbf{x}_i = \mathbf{m}_i$ for all $i \in \sigma_{\mathbf{m}}$, $\mathbf{x}_i \in (0, \mathbf{m}_i)$ for all $i \in \sigma_{\bar{\mathbf{m}}}$ and $\mathbf{x}_i = 0$ for all $i \in \bar{\sigma}$.

The synaptic weight matrix can be block-partitioned according to the the support σ as

$$\mathbf{W} = \begin{bmatrix} \mathbf{W}_{\bar{\sigma}} & \mathbf{W}_{\bar{\sigma}\sigma_{\mathbf{m}}} & \mathbf{W}_{\bar{\sigma}\sigma_{\bar{\mathbf{m}}}} \\ \mathbf{W}_{\sigma_{\mathbf{m}}\bar{\sigma}} & \mathbf{W}_{\sigma_{\mathbf{m}}\sigma_{\mathbf{m}}} & \mathbf{W}_{\sigma_{\mathbf{m}}\sigma_{\bar{\mathbf{m}}}} \\ \mathbf{W}_{\sigma_{\bar{\mathbf{m}}}\bar{\sigma}} & \mathbf{W}_{\sigma_{\bar{\mathbf{m}}}\sigma_{\mathbf{m}}} & \mathbf{W}_{\sigma_{\bar{\mathbf{m}}}\sigma_{\bar{\mathbf{m}}}} \end{bmatrix}, \quad (3)$$

where $(\bar{\sigma}, \sigma_{\mathbf{m}}, \sigma_{\bar{\mathbf{m}}}) = \{1, \dots, N\}$. Next, we have the following notion of stability of node sets in LTN networks.

Definition 3.3: (Non-trivially Stable Node Set in LTN Dynamics): Consider a network defined by the linear-threshold dynamics (1). A non-empty subset of nodes $\sigma = (\sigma_{\mathbf{m}}, \sigma_{\bar{\mathbf{m}}}) \subseteq \{1, \dots, N\}$ is *non-trivially stable* if there exists an asymptotically stable equilibrium point \mathbf{x}^* for the dynamics with $\text{supp}(\mathbf{x}^*) = \sigma = (\sigma_{\mathbf{m}}, \sigma_{\bar{\mathbf{m}}})$ for at least one input $\mathbf{u} \in \mathbb{R}^n$ and either $\sigma_{\bar{\mathbf{m}}} \neq \emptyset$ or there exists $i \in \sigma_{\mathbf{m}}$ such that $(\mathbf{W}\mathbf{x}^* + \mathbf{u})_i = \mathbf{m}_i$.

The key part of Definition 3.3 is that existence of the stable equilibrium cannot be guaranteed solely on the basis of forced saturation by the input. By requiring that either: one of the non-zero components in the equilibrium point is not saturated

¹We use the following notation. We let $\mathbb{R}, \mathbb{R}^n, \mathbb{R}^{n \times m}$, denote reals, real-valued vectors and real-valued matrices, resp. Vectors and matrices are identified by bold-faced letters. For vectors $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$, $\mathbf{x} \leq \mathbf{y}$ is the component-wise comparison (analogously with $<, >, \geq$). We use a similar notation for matrices. For a vector \mathbf{x} and set of indices $\alpha \subseteq \{1, \dots, N\}$ we denote by \mathbf{x}_α the vector composed of the elements of \mathbf{x} by the indices in α . For a set of indices $\alpha \subseteq \{1, \dots, N\}$, we denote by $\bar{\alpha}$ the complement of α , that is $\{1, \dots, N\} \setminus \alpha$. For a vector $\mathbf{x} \in \mathbb{R}^n$ we refer to the set of non-zero components as the support of \mathbf{x} , and denote it by $\text{supp}(\mathbf{x})$. For a matrix \mathbf{W} and two sets of indices, α_1, α_2 we let $\mathbf{W}_{\alpha_1\alpha_2}$ the submatrix defined by the rows indexed α_1 and columns indexed by α_2 . If $\alpha_1 = \alpha_2 = \alpha$ we will denote this principal submatrix by \mathbf{W}_α . The identity matrix of dimension n is \mathbf{I}_n . $\mathbf{0}_n$ and $\mathbf{1}_n$ denote the n -vector of zeros and the n -vector of ones, resp. When clear from the context, we omit the dimensional subindex for the identity or zero matrices.

($\sigma_{\mathbf{m}} \neq \emptyset$); or, if it is at the saturation value, it is not over-saturated ($(\mathbf{W}\mathbf{x}^* + \mathbf{u})_i = \mathbf{m}_i$), it guarantees that the equilibrium is dependent on the structure of the network and the dynamic behavior, rather than the input. This definition, when applied to a TLN network reduces to Definition 3.1.

We next give a condition for the existence of non-trivially stable equilibria. The proof is provided in the Appendix.

Theorem 3.4: (Existence of Non-trivially Stable Node Set): Consider a network defined by either LTN or TLN dynamics with synaptic weight matrix \mathbf{W} and upper bound \mathbf{m} . A subset of nodes $\sigma = (\sigma_{\mathbf{m}}, \sigma_{\mathbf{m}})$ is non-trivially stable with associated equilibrium \mathbf{x}^* , with $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ for all $i \in \sigma_{\mathbf{m}}$ and $\mathbf{x}_i^* = \mathbf{m}_i$ for all $i \in \sigma_{\mathbf{m}}$ if and only if the matrix $(-\mathbf{I} + \mathbf{W})_{\sigma_{\mathbf{m}}}$ is stable.

The characterization in Theorem 3.4 for the existence of a stable equilibrium for an arbitrary node set under LTN and TLN dynamics is useful for identifying and building networks that possess such equilibria. Conversely, it can also be used for the opposite purpose: identify and build networks that do not. The latter is aligned with seeing the LoSE as a proxy for the existence of oscillatory or chaotic behavior. As such, in the ensuing discussion we focus on identifying conditions on the network structure and the input that ensure that the characterization of Theorem 3.4 is *not* satisfied.

IV. OSCILLATIONS IN COMPETITIVE NETWORKS

In this section, we focus on competitive networks and provide conditions on the structure of the synaptic weight matrix \mathbf{W} and the input \mathbf{u} such that a competitive linear-threshold or threshold-linear network lacks stable equilibria, thus satisfying our criteria for enabling oscillations. We tackle the problem of LoSE by classifying equilibria by their support: equilibria supported on two or more nodes in the interior of $[\mathbf{0}, \mathbf{m}]$; equilibria supported on a single node; and equilibria with components lying on the boundary \mathbf{m} . We then provide conditions such that all equilibria in each class is not stable.

Theorem 4.1: (Oscillations in Competitive Networks with LTN Dynamics): Consider a network defined by the LTN dynamics (1) with synaptic weight matrix \mathbf{W} , upper bound \mathbf{m} , and constant input $\mathbf{u} \in \mathbb{R}^n$. Let \mathbf{W} be a Z-matrix with at least two diagonal elements, indexed i_1, i_2 , such that $w_{i_k i_k} < 1$ and $2| -1 + w_{i_k i_k} | > \rho(-\mathbf{I} + \mathbf{W})$, for $k \in \{1, 2\}$. The following statements hold:

- 1) There are no stable equilibria \mathbf{x}^* with $|\text{supp}(\mathbf{x}^*)| \geq 2$ and $\mathbf{x}_i^* \in (\mathbf{0}, \mathbf{m})$ for all $i \in \text{supp}(\mathbf{x}^*)$ if all 2×2 principal submatrices of $-\mathbf{I} + \mathbf{W}$ are unstable;
- 2) There are no equilibria \mathbf{x}^* with $|\text{supp}(\mathbf{x}^*)| = 1$ and
 - $\mathbf{x}_i^* = \mathbf{m}_i$ if, for each $i \in \{1, \dots, N\}$, there exists k such that $\mathbf{u}_k > -w_{ki} \mathbf{m}_i$;
 - $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ if, for each $i \in \{1, \dots, N\}$ with $w_{ii} \neq 1$, there exists k such that $\text{sign}(\mathbf{u}_i) \frac{\mathbf{u}_k}{\mathbf{u}_i} > -\text{sign}(\mathbf{u}_i) \frac{w_{ki}}{w_{ii} - 1}$ and for each $i \in \{1, \dots, N\}$ with $w_{ii} = 1$ either $\mathbf{u}_i \neq 0$ or $\exists k \neq i$ such that $\mathbf{u}_k > -w_{ki} \mathbf{m}_i$;
- 3) Consider a node set $\sigma = (\sigma_{\mathbf{m}}, \sigma_{\mathbf{m}})$ with $|\sigma| \geq 2$ and $|\sigma_{\mathbf{m}}| \geq 1$. The following hold:
 - If $|\sigma_{\mathbf{m}}| \geq 2$, then there do not exist any stable equilibria \mathbf{x}^* with support σ if all 2×2 principal submatrices of $(-\mathbf{I} + \mathbf{W})_{\sigma_{\mathbf{m}}}$ are unstable;

- If $|\sigma| = |\sigma_{\mathbf{m}}| \geq 2$, then there do not exist any equilibria \mathbf{x}^* with support σ^* if there exists $i \in \sigma_{\mathbf{m}}$ such that $\mathbf{u}_i < \mathbf{m}_i - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j$;
- If $\sigma_{\mathbf{m}} = \{i\}$, then there do not exist any equilibria \mathbf{x}^* with support σ if \mathbf{u} is such that one or more of the following conditions hold:

a) There exists $i \in \sigma_{\mathbf{m}}$ such that:

- i) If $w_{ii} < 1$, then $\mathbf{u}_i \notin (-\sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j, \mathbf{m}_i(1 - w_{ii}) - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j)$, or
- ii) If $w_{ii} > 1$, then $\mathbf{u}_i \notin (\mathbf{m}_i(1 - w_{ii}) - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j, -\sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j)$, or
- iii) If $w_{ii} = 1$, then $\mathbf{u}_i \neq -\sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j$.

b) There exists $k \in \sigma_{\mathbf{m}}$ such that if $w_{ii} \neq 1$

$$\mathbf{u}_k < \mathbf{m}_k - \sum_{j \in \sigma_{\mathbf{m}}} w_{kj} \mathbf{m}_j - \left(\frac{w_{ki}}{1 - w_{ii}} \right) \left(\sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j + \mathbf{u}_i \right),$$

or if $w_{ii} = 1$

$$\mathbf{u}_k \leq \mathbf{m}_k - \sum_{j \in \sigma_{\mathbf{m}}} w_{kj} \mathbf{m}_j.$$

c) There exists $l \in \bar{\sigma}$ such that if $w_{ii} \neq 1$

$$\mathbf{u}_l > -\sum_{j \in \sigma_{\mathbf{m}}} w_{lj} \mathbf{m}_j - \left(\frac{w_{li}}{1 - w_{ii}} \right) \left(\sum_{j \in \sigma_{\mathbf{m}}} w_{ij} \mathbf{m}_j + \mathbf{u}_i \right),$$

or if $w_{ii} = 1$, $\mathbf{u}_l \geq -\sum_{j \in \sigma_{\mathbf{m}}} w_{lj} \mathbf{m}_j - w_{li} \mathbf{m}_i$.

To prove this statement, the following result guaranteeing LoSE supported on multiple nodes is useful.

Lemma 4.2: (Conditions for Unstable Equilibria Supported on Multiple Nodes): Consider a network defined by the LTN dynamics (1) with a Z-matrix \mathbf{W} . If all 2×2 principal submatrices of $-\mathbf{I} + \mathbf{W}$ are unstable and there exist i_1, i_2 with $w_{i_k i_k} < 1$ and $2| -1 + w_{i_k i_k} | > \rho(-\mathbf{I} + \mathbf{W})$ for $k \in \{1, 2\}$, then the network has no stable equilibria supported on more than one node in the interior of $[\mathbf{0}, \mathbf{m}]$.

This result is a generalization of [9, Corollary 4.4] to the case of synaptic weight matrices with non-zero elements in the diagonal. The proof is given in the appendix. We are now ready to prove Theorem 4.1.

Proof of Theorem 4.1: We proceed by deriving conditions so that each classification of equilibria by their support contains no stable equilibria.

Statement 1): It directly follows from Lemma 4.2: if all 2×2 principal submatrices of $-\mathbf{I} + \mathbf{W}$ are unstable², then there exist no stable equilibria supported on more than two nodes in the interior of $[\mathbf{0}, \mathbf{m}]$.

Statement 2): Without loss of generality, assume \mathbf{x}^* is a potential equilibrium point supported only on node i . Then the equilibrium equations are $\mathbf{x}_i^* = [w_{ii} \mathbf{x}_i^* + \mathbf{u}_i]_0^{\mathbf{m}_i}$ and $0 = [w_{ki} \mathbf{x}_i^* + \mathbf{u}_k]_0^{\mathbf{m}_k}$, for all $k \neq i$. These conditions are satisfied iff $w_{ki} \mathbf{x}_i^* + \mathbf{u}_k \leq 0$ for all $k \neq i$. There are three possible cases for the remaining equation:

- $w_{ii} \mathbf{x}_i^* + \mathbf{u}_i \geq \mathbf{m}_i$, which implies $\mathbf{x}_i^* = \mathbf{m}_i$;
- $w_{ii} \mathbf{x}_i^* + \mathbf{u}_i \in (\mathbf{0}, \mathbf{m}_i)$, which implies $\mathbf{x}_i^* = \frac{\mathbf{u}_i}{1 - w_{ii}}$ unless $w_{ii} = 1$, in which case $\mathbf{u}_i = 0$ and \mathbf{x}_i^* can take any value within the interval;
- $w_{ii} \mathbf{x}_i^* + \mathbf{u}_i \leq 0$, which implies $\mathbf{x}_i^* = 0$, contradicting the assumption that \mathbf{x}^* is supported on node i .

²Lemma 1.1 provides detailed expressions for this condition to hold.

Therefore, we need to consider only the first two cases. For the case in which $\mathbf{x}_i^* = \mathbf{m}_i$, \mathbf{x}^* is an equilibrium iff, for all $k \neq i$, it holds that $w_{ki}\mathbf{m}_i + \mathbf{u}_k \leq 0$. As such there is no equilibrium supported on a single node at the boundary if for all $i \in \{1, \dots, N\}$ there exists $k \neq i$ such that $\mathbf{u}_k > -w_{ki}\mathbf{m}_i$. For the case where $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$, first consider when $w_{ii} = 1$. In this case, \mathbf{x}^* is an equilibrium for any $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ iff $\mathbf{u}_i = 0$ and $w_{ki}\mathbf{x}_i^* + \mathbf{u}_k \leq 0$ for all $k \neq i$. Rearranging these conditions, we get that there is no equilibrium supported on a single node $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ if either $\mathbf{u}_i \neq 0$ or there exists $k \neq i$ such that $\mathbf{u}_k > -w_{ki}\mathbf{m}_i$. If $w_{ii} \neq 1$, \mathbf{x}^* is an equilibrium iff for all $k \neq i$

$$w_{ki} \left(\frac{\mathbf{u}_i}{1 - w_{ii}} \right) + \mathbf{u}_k \leq 0.$$

Rearranging this expression, we get that there is no equilibrium supported on a single node with $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ if, for each $i \in \{1, \dots, N\}$ with $w_{ii} \neq 1$, there exists $k \neq i$ such that

$$\text{sign}(\mathbf{u}_i) \frac{\mathbf{u}_k}{\mathbf{u}_i} > -\text{sign}(\mathbf{u}_i) \frac{w_{ki}}{1 - w_{ii}}.$$

Statement 3): Equilibria supported on two or more nodes, with at least one taking values on the boundary \mathbf{m} , come in the following three cases based upon the structure of the node set $\sigma = (\sigma_{\mathbf{m}}, \sigma_{\bar{\mathbf{m}}})$: a) $|\sigma_{\mathbf{m}}| \geq 1, |\sigma_{\bar{\mathbf{m}}}| \geq 2$; b) $|\sigma| = |\sigma_{\mathbf{m}}| \geq 2$; c) $|\sigma_{\mathbf{m}}| \geq 1$ and $|\sigma_{\bar{\mathbf{m}}}| = 1$. Consequently,

a) If $|\sigma_{\bar{\mathbf{m}}}| \geq 2$, these are equilibria supported on two or more nodes in the interior of $[\mathbf{0}, \mathbf{m}]$. By Lemma 4.2, if all 2×2 principal submatrices of $(-\mathbf{I} + \mathbf{W})$ are unstable, no such equilibrium is stable.

b) If $|\sigma| = |\sigma_{\mathbf{m}}| \geq 2$, then a point \mathbf{x}^* with support σ is an equilibrium if and only if $\mathbf{m}_i \leq \sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{x}_j^* + \mathbf{u}_i$ for all $i \in \sigma_{\mathbf{m}}$. Rearranging, we have that there is no equilibrium with this structure if there exists $i \in \sigma_{\mathbf{m}}$ such that $\mathbf{u}_i < \mathbf{m}_i - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j$;

c) If $|\sigma_{\bar{\mathbf{m}}}| = 1$ and $|\sigma_{\mathbf{m}}| \geq 1$, let \mathbf{x}^* be a candidate point with node i supported on $(0, \mathbf{m}_i)$ and let us identify the interval of inputs \mathbf{u} that would actually make \mathbf{x}^* an equilibrium. For \mathbf{x}^* to be an equilibrium, the following must hold:

$$\mathbf{x}_i^* = \sum_{j \in \sigma} w_{ij}\mathbf{x}_j^* + \mathbf{u}_i, \quad (4a)$$

$$\mathbf{m}_k \leq \sum_{j \in \sigma} w_{kj}\mathbf{x}_j^* + \mathbf{u}_k, \quad \forall k \in \sigma_{\mathbf{m}}, \quad (4b)$$

$$0 \geq \sum_{j \in \sigma} w_{lj}\mathbf{x}_j^* + \mathbf{u}_l, \quad \forall l \in \bar{\sigma}. \quad (4c)$$

From (4a), we get

$$(1 - w_{ii})\mathbf{x}_i^* = \sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j + \mathbf{u}_i. \quad (5)$$

To enforce $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$, the input \mathbf{u}_i must satisfy:

- If $w_{ii} < 1$, then $\mathbf{u}_i \in (-\sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j, \mathbf{m}_i(1 - w_{ii}) - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j)$;
- If $w_{ii} > 1$, then $\mathbf{u}_i \in (\mathbf{m}_i(1 - w_{ii}) - \sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j, -\sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j)$;
- If $w_{ii} = 1$, then $\mathbf{u}_i = -\sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j$.

First suppose $w_{ii} \neq 1$, and considering (4b), by rearranging and substituting (5), we get

$$\mathbf{u}_k \geq \mathbf{m}_k - \sum_{j \in \sigma_{\mathbf{m}}} w_{kj}\mathbf{m}_j - \left(\frac{w_{ki}}{1 - w_{ii}} \right) \left(\sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j + \mathbf{u}_i \right),$$

must be satisfied for all $k \in \sigma_{\mathbf{m}}$ in order for \mathbf{x}^* to be an equilibrium. Similarly, from (4c),

$$\mathbf{u}_l \leq - \sum_{j \in \sigma_{\mathbf{m}}} w_{lj}\mathbf{m}_j - \left(\frac{w_{li}}{1 - w_{ii}} \right) \left(\sum_{j \in \sigma_{\mathbf{m}}} w_{ij}\mathbf{m}_j + \mathbf{u}_i \right),$$

must be satisfied for all $l \in \bar{\sigma}$ for \mathbf{x}^* to be an equilibrium. If instead $w_{ii} = 1$, by considering (4b) and noting from (5) that all $\mathbf{x}_i^* \in (0, \mathbf{m}_i)$ are possible equilibrium values, we get that there exists an equilibrium iff $\mathbf{u}_k > \mathbf{m}_k - \sum_{j \in \sigma_{\mathbf{m}}} w_{kj}\mathbf{m}_j$ is satisfied for all $k \in \sigma_{\mathbf{m}}$. In the same fashion, from (4c), there exists an equilibrium iff $\mathbf{u}_l < -\sum_{j \in \sigma_{\mathbf{m}}} w_{lj}\mathbf{m}_j - w_{li}\mathbf{m}_i$ holds for all $l \in \bar{\sigma}$. Taking the complement of this set of conditions on the input provides the conditions on equilibria for the case $|\sigma_{\bar{\mathbf{m}}}| = 1$ and $|\sigma_{\mathbf{m}}| \geq 1$ given in the statement. ■

Theorem 4.1 is noteworthy in that it provides quantitative conditions for the existence of oscillations in competitive LTNs. These conditions depend both on the network structure and the inputs, which has physiological relevance in two ways. First, the structural conditions, in particular the pairwise instability of the nodes, show that a small portion can pull the network into a stable equilibrium rather than exhibiting oscillatory behavior. This aligns with observations [28] made of brain injuries, where a small injury can lead to significant behavioral changes. Second, the requirements on the inputs show that only the right ones lead to the emergence of oscillatory behavior for a given network structure. Given that inputs could come from other brain regions or external sources, this illustrates that the behavior of a brain network is highly dependent on its connections with other parts of the nervous system. Further, the dependence on the input opens the door to exciting design possibilities related to the robustness (or lack thereof) of oscillatory behavior: as an example, for a given input (resp. network structure), one might consider how to modify the network structure (resp. input) such that oscillatory behavior is maintained, gained, or lost.

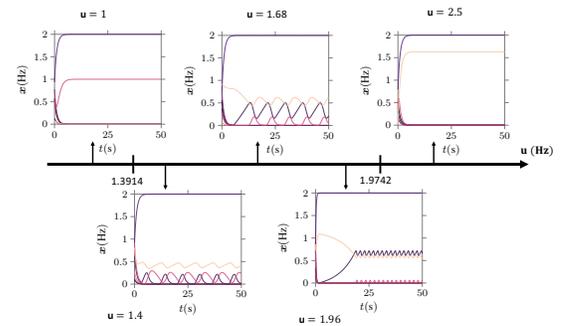


Fig. 1: Oscillatory behavior of a 7-node competitive network with LTN dynamics subject to homogeneous inputs $\mathbf{u} = u\mathbf{1}_7$. According to Theorem 4.1, oscillations are possible in the input range $u \in (1.3914, 1.9742)$, while outside it, there exists a stable equilibrium. The panels vary based upon the system input and illustrate how the behavior changes. In panels with $u = 1$ and $u = 2.5$, the input lies outside of the oscillatory range and the dynamics settles to an equilibrium. In the other panels, the same three nodes exhibit oscillations while the remaining ones either settle to zero or saturate (albeit not shown here, heterogeneous inputs can make different set of nodes oscillate). The varying input values lead to settling into significantly different limit cycles.

Remark 4.3: (Oscillations in Competitive Networks with TLN Dynamics): The result in Theorem 4.1 is also applicable to threshold-linear networks by taking $\mathbf{m} = \infty\mathbf{1}$. In this case, some of the conditions can be discarded right away since

no equilibria exist with components on an upper threshold: specifically, conditions 3), along with the first component of the condition 2) can be discarded as they become trivially satisfied. This gives rise to a generalization to arbitrary networks of [9, Theorem 2.2], which only considers the all-to-all case, with no self-loops, and positive inputs. •

We believe the assumption in Theorem 4.1 requiring at least two diagonal elements to be small enough is not necessary. In simulations, we have found that oscillatory behavior still arises without enforcing this constraint.

Example 4.4: (Oscillations in a Seven-Node Competitive network with LTN dynamics): We consider a competitive LTN dynamics with $n = 7$ nodes that exhibits oscillatory behavior, as per the conditions identified in Theorem 4.1, and illustrate the impact of the inputs on network behavior. While Theorem 4.1 permits arbitrary inputs, in this example we consider only homogeneous inputs of the form $\mathbf{u} = u\mathbf{1}_7$. The synaptic weight matrix \mathbf{W} is as follows:

$$\mathbf{W} = \begin{bmatrix} 0 & -0.349 & -0.055 & -0.434 & -0.745 & -0.053 & -0.381 \\ -2.907 & 0 & -0.338 & 0 & -0.376 & -0.556 & -0.558 \\ -18.07 & -2.981 & 0 & -0.764 & -0.043 & -0.823 & -0.807 \\ -0.696 & -0.03 & -0.01 & 1.435 & -0.166 & -0.331 & -0.179 \\ -1.425 & -2.664 & -23.347 & -0.20 & 0 & -0.353 & -0.958 \\ -18.83 & -1.866 & -1.255 & -0.517 & -2.887 & 0 & -0.06 \\ -2.643 & -1.84 & -1.325 & -0.138 & -1.064 & -16.64 & 0 \end{bmatrix}$$

With such inputs, and according to Theorem 4.1, oscillations are possible when the network is subject to inputs in the interval $u \in (1.3914, 1.9742)$. Figure 1 illustrates the network behavior with different inputs, three inside the range and two outside. For those inside, the same three nodes fall into limit cycles and one node saturates, but the relative values of the limit cycles vary significantly. For inputs outside the interval, the dynamics settles to a stable equilibrium. •

V. CONCLUSIONS

We have studied linear-threshold and threshold-linear dynamics inspired by firing-rate models of neuron populations in the brain. We have provided conditions characterizing the existence of a stable equilibrium supported on an arbitrary subset of nodes for linear-threshold networks. Using LoSE as a proxy for the presence of oscillations, we have characterized the emergence of oscillatory behavior in both linear-threshold and threshold-linear competitive networks, where all interneuron connections are inhibitory. Specifically, we have provided conditions on the structure of the network and the inputs such that the networks do not have stable equilibria. Future work will further explore the physiological interpretation of the conditions along with possible additional requirements to be biologically plausible. We will also study dynamic attractors in linear-threshold competitive networks, analyze the robustness of oscillatory behavior to neuron addition and removal and its connection with neurogenesis in brain networks.

REFERENCES

- [1] L. M. Ward, "Synchronous neural oscillations and cognitive processes," *Trends in Cognitive Sciences*, vol. 7, no. 12, pp. 553–559, 2003.
- [2] A. Engel and P. Fries, "Neuronal oscillations, coherence, and consciousness," in *The Neurology of Consciousness*, pp. 49–60, Elsevier, 2016.
- [3] E. J. Müller, S. J. van Albada, J. W. Kim, and P. A. Robinson, "Unified neural field theory of brain dynamics underlying oscillations in parkinson's disease and generalized epilepsies," *Journal of theoretical biology*, vol. 428, pp. 132–146, 2017.
- [4] F. Ratliff and H. K. Hartline, *Studies on Excitation and Inhibition in the Retina*. Rockefeller University Press, 1974.
- [5] Z. Yi, L. Zhang, J. Yu, and K. K. Tan, "Permitted and forbidden sets in discrete-time linear threshold recurrent neural networks," *IEEE Transactions on Neural Networks*, vol. 20, no. 6, pp. 952–963, 2009.
- [6] T. Arakaki, S. Mahon, S. Champier, A. Leblois, and D. Hansel, "The role of striatal feedforward inhibition in the maintenance of absence seizures," *Journal of Neuroscience*, vol. 36, no. 37, pp. 9618–9632, 2016.
- [7] F. Celi, A. Allibhoy, F. Pasqualetti, and J. Cortés, "Linear-threshold dynamics for the study of epileptic events," *IEEE Control Systems Letters*, vol. 5, no. 4, pp. 1405–1410, 2021.
- [8] P. Dayan and L. F. Abbott, *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. Computational Neuroscience, Cambridge, MA: MIT Press, 2001.
- [9] K. Morrison, A. Degeratu, V. Itskov, and C. Curto, "Diversity of emergent dynamics in competitive threshold-linear networks: a preliminary report," *arXiv preprint arXiv:1605.04463*, 2016.
- [10] H. R. Wilson and J. D. Cowan, "Excitatory and inhibitory interactions in localized populations of model neurons," *Biophysical Journal*, vol. 12, no. 1, pp. 1–24, 1972.
- [11] A. Destexhe and T. J. Sejnowski, "The Wilson-Cowan model, 36 years later," *Biological Cybernetics*, vol. 101, no. 1, pp. 1–2, 2009.
- [12] H. Zhang, Z. Wang, and D. Liu, "A comprehensive review of stability analysis of continuous-time recurrent neural networks," *IEEE Transactions on Neural Networks and Learning Systems*, vol. 25, no. 7, pp. 1229–1262, 2014.
- [13] E. Nozari and J. Cortés, "Hierarchical selective recruitment in linear-threshold brain networks. Part I: Intra-layer dynamics and selective inhibition," *IEEE Transactions on Automatic Control*, vol. 66, no. 3, pp. 949–964, 2021.
- [14] S. Campbell and D. Wang, "Synchronization and desynchronization in a network of locally coupled Wilson-Cowan oscillators," *IEEE Transactions on Neural Networks*, vol. 7, no. 3, pp. 541–554, 1996.
- [15] E. Nozari, R. Planas, and J. Cortés, "Structural characterization of oscillations in brain networks with rate dynamics," *Automatica*, vol. 146, p. 110653, 2022.
- [16] J. M. Beggs, *The Cortex and the Critical Point: Understanding the Power of Emergence*. Cambridge, MA: MIT Press, 2022.
- [17] R. Legenstein and W. Maass, "Edge of chaos and prediction of computational performance for neural circuit models," *Neural Networks*, vol. 20, no. 3, pp. 323–334, 2007.
- [18] A. Allibhoy, F. Celi, F. Pasqualetti, and J. Cortés, "Optimal network interventions to control the spreading of oscillations," *IEEE Open Journal of Control Systems*, vol. 1, pp. 141–151, 2022.
- [19] A. Bel, R. Cobiaga, W. Reartes, and H. G. Rotstein, "Periodic solutions in threshold-linear networks and their entrainment," *SIAM Journal on Applied Dynamical Systems*, vol. 20, no. 3, pp. 1177–1208, 2021.
- [20] C. Curto, J. Geneson, and K. Morrison, "Fixed points of competitive threshold-linear networks," *Neural Computation*, vol. 31, no. 1, pp. 94–155, 2019.
- [21] C. Parmelee, J. Alvarez, C. Curto, and K. Morrison, "Sequential attractors in combinatorial threshold-linear networks," *SIAM Journal on Applied Dynamical Systems*, vol. 21, no. 2, pp. 1597–1630, 2022.
- [22] C. Parmelee, S. Moore, K. Morrison, and C. Curto, "Core motifs predict dynamic attractors in combinatorial threshold-linear networks," *PLoS one*, vol. 17, no. 3, p. e0264456, 2022.
- [23] K. Morrison and C. Curto, "Predicting neural network dynamics via graphical analysis," in *Algebraic and Combinatorial Computational Biology*, Elsevier, 2018.
- [24] A. M. C. Kelly, L. Q. Uddin, B. B. Biswal, F. X. Castellanos, and M. P. Milham, "Competition between functional brain networks mediates behavioral variability," *Neuroimage*, vol. 39, no. 1, pp. 527–537, 2008.
- [25] D. Dupret, B. Pleydell-Bouverie, and J. Csicsvari, "Inhibitory interneurons and network oscillations," *Proceedings of the National Academy of Sciences*, vol. 105, no. 47, pp. 18079–18080, 2008.
- [26] T. Donoghue, M. Haller, E. J. Peterson, P. Varma, P. Sebastian, R. Gao, T. Noto, A. H. Lara, J. D. Wallis, R. T. Knight, A. Shestyuk, and B. Voytek, "Parameterizing neural power spectra into periodic and aperiodic components," *Nature Neuroscience*, vol. 23, no. 12, pp. 1655–1665, 2020.
- [27] L. Perko, *Differential Equations and Dynamical Systems*, vol. 7 of *Texts in Applied Mathematics*. New York: Springer, 3rd ed., 2000.
- [28] B. G. Windham, B. Deere, M. E. Griswold, W. Wang, D. C. Bezerra, D. Shibata, K. Butler, D. Knopman, R. F. Gottesman, G. Heiss, et al., "Small brain lesions and incident stroke and mortality: a cohort study," *Annals of internal medicine*, vol. 163, no. 1, pp. 22–31, 2015.
- [29] C. Curto, A. Degeratu, and V. Itskov, "Flexible memory networks," *Bulletin of Mathematical Biology*, vol. 74, no. 3, pp. 590–614, 2012.
- [30] R. A. Horn and C. R. Johnson, *Matrix Analysis*. Cambridge University Press, 2012.

- [31] M. Fiedler and V. Ptak, "On matrices with non-positive off-diagonal elements and positive principal minors," *Czechoslovak Mathematical Journal*, vol. 12, no. 3, pp. 382–400, 1962.
- [32] R. A. Horn and C. R. Johnson, *Topics in Matrix Analysis*. Cambridge University Press, 1991.

APPENDIX

Proof of Theorem 3.4: For TLN dynamics, the result corresponds to [29, Theorem 1.2]. Hence, we focus on LTN dynamics. First suppose that $(-\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}}$ is stable. Let \mathbf{x}_{σ}^* be the vector with support σ such that $\mathbf{x}_{\sigma_{\bar{m}}}^* = \mathbf{m}_{\sigma_{\bar{m}}}$ and $\mathbf{x}_{\sigma_{\bar{m}}}^* = \alpha \mathbf{m}_{\sigma_{\bar{m}}}$, where $\alpha \in (0, 1)$ is arbitrary. Define $\mathbf{u}_{\sigma_{\bar{m}}} = \alpha(\mathbf{I} - \mathbf{W})_{\sigma_{\bar{m}}} \mathbf{m}_{\sigma_{\bar{m}}}$. Choose $\mathbf{u}_{\bar{\sigma}}$ such that $\mathbf{u}_{\bar{\sigma}} < -\mathbf{W}_{\bar{\sigma}\sigma} \mathbf{x}_{\sigma}^*$ and $\mathbf{u}_{\sigma_{\bar{m}}}$ such that $\mathbf{u}_{\sigma_{\bar{m}}} > -\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{m}_{\sigma_{\bar{m}}}$. With this choice of \mathbf{u} , the vector \mathbf{x}_{σ}^* satisfies $(\mathbf{I} - \mathbf{W})_{\sigma} \mathbf{x}_{\sigma}^* = \mathbf{u}_{\sigma}$ and is therefore an equilibrium. We next prove it is stable.

To do so, consider the following change of variables. Define $(\mathbf{q}, \mathbf{y}, \mathbf{z}) = \mathbf{x} - \mathbf{x}^*$, with $\mathbf{q} = (\mathbf{x} - \mathbf{x}^*)_{\bar{\sigma}} \in \mathbb{R}^{|\bar{\sigma}|}$, $\mathbf{y} = (\mathbf{x} - \mathbf{x}^*)_{\sigma_{\bar{m}}} \in \mathbb{R}^{|\sigma_{\bar{m}}|}$ and $\mathbf{z} = (\mathbf{x} - \mathbf{x}^*)_{\sigma_{\bar{m}}} \in \mathbb{R}^{|\sigma_{\bar{m}}|}$. These variables represent the components of the dynamics corresponding to where the equilibrium is equal to 0, are on the boundary \mathbf{m} , and are in the interior of $[\mathbf{0}, \mathbf{m}]$, resp. This change of variables shifts the equilibrium \mathbf{x}^* to the origin, and the system becomes

$$\dot{\mathbf{q}} = -\mathbf{q} + [\mathbf{W}_{\bar{\sigma}\sigma} \mathbf{q} + \mathbf{W}_{\bar{\sigma}\sigma_{\bar{m}}} \mathbf{y} + \mathbf{W}_{\bar{\sigma}\sigma_{\bar{m}}} \mathbf{z} + (\mathbf{W}_{\bar{\sigma}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\bar{\sigma}})]_{\mathbf{0}}^{\mathbf{m}_{\bar{\sigma}}} \quad (6a)$$

$$\dot{\mathbf{y}} = -(\mathbf{y} + \mathbf{m}_{\sigma_{\bar{m}}}) + [\mathbf{W}_{\sigma_{\bar{m}}\bar{\sigma}} \mathbf{q} + \mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{y} + \mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{z} + (\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\sigma_{\bar{m}}})]_{\mathbf{0}}^{\mathbf{m}_{\sigma_{\bar{m}}}} \quad (6b)$$

$$\dot{\mathbf{z}} = -(\mathbf{z} + \mathbf{x}_{\sigma_{\bar{m}}}^*) + [\mathbf{W}_{\sigma_{\bar{m}}\bar{\sigma}} \mathbf{q} + \mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{y} + \mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{z} + (\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\sigma_{\bar{m}}})]_{\mathbf{0}}^{\mathbf{m}_{\sigma_{\bar{m}}}}. \quad (6c)$$

Note that with our choice of \mathbf{u} above, the constant terms satisfy $\mathbf{W}_{\bar{\sigma}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\bar{\sigma}} < \mathbf{0}$, $\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\sigma_{\bar{m}}} > \mathbf{m}_{\sigma_{\bar{m}}}$ and $\mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{x}_{\sigma_{\bar{m}}}^* + \mathbf{u}_{\sigma_{\bar{m}}} \in (\mathbf{0}, \mathbf{m}_{\sigma_{\bar{m}}})$. It follows that in a neighborhood of the origin, the sign of the threshold terms are determined solely by the sign of the constant term. The behavior of the system (6) is determined by the linear system $\frac{d}{dt} [\mathbf{q}, \mathbf{y}, \mathbf{z}] = \mathbf{W} [\mathbf{q}, \mathbf{y}, \mathbf{z}]^T$ where \mathbf{W} takes the form (3), and in particular is lower triangular with diagonal elements $-\mathbf{I}_{\bar{\sigma}}$, $-\mathbf{I}_{\sigma_{\bar{m}}}$ and $(-\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}}$. Then, since $(-\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}}$ is stable, the equilibrium point is stable, and therefore the subset of nodes σ is non-trivially stable.

Now, suppose that $(-\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}}$ is not stable. We reason by contradiction. Assume $\sigma = (\sigma_{\bar{m}}, \sigma_{\bar{m}})$ is a non-trivially stable node set. This means that there exists an input \mathbf{u} such that \mathbf{x}^* is a stable equilibrium point with $\mathbf{W}_{\bar{\sigma}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\bar{\sigma}} \leq \mathbf{0}$, $\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\sigma_{\bar{m}}} \geq \mathbf{m}_{\sigma_{\bar{m}}}$ and $\mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{x}_{\sigma_{\bar{m}}}^* + \mathbf{u}_{\sigma_{\bar{m}}} \in (\mathbf{0}, \mathbf{m}_{\sigma_{\bar{m}}})$. Now, since $\mathbf{W}_{\sigma_{\bar{m}}\sigma} \mathbf{x}_{\sigma}^* + \mathbf{u}_{\sigma_{\bar{m}}} \in (\mathbf{0}, \mathbf{m}_{\sigma_{\bar{m}}})$, in a neighborhood of \mathbf{x}^* , the component of the dynamics \mathbf{z} acts linearly as $\dot{\mathbf{z}} = -(\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}\sigma} \mathbf{z} + \mathbf{W}_{\sigma_{\bar{m}}\bar{\sigma}} \mathbf{q} + \mathbf{W}_{\sigma_{\bar{m}}\sigma_{\bar{m}}} \mathbf{y}$. Since $(-\mathbf{I} + \mathbf{W})_{\sigma_{\bar{m}}}$ is not stable, it then follows that \mathbf{x}^* is not a stable equilibrium, providing a contradiction. This completes the proof. ■

Conditions 1) and 3) in Theorem 4.1 require checking the instability of all 2×2 principal submatrices of a given matrix. Therefore, it is desirable to have a simple condition to check for instability of a 2×2 matrix. The *determinant condition for instability* reads as follows: "given $\mathbf{W} \in \mathbb{R}^{2 \times 2}$, if $\text{Tr}(\mathbf{W}) \leq 0$, \mathbf{W} is unstable if and only if $\det(\mathbf{W}) < 0$; if $\text{Tr}(\mathbf{W}) > 0$, then \mathbf{W} is unstable". The next result details when the determinant condition for instability holds in competitive networks.

Lemma 1.1: (Requirements for Determinant Condition for Instability for Competitive Networks): Let $\mathbf{W} \in \mathbb{R}^{2 \times 2}$ be a Z-matrix. The determinant condition for instability holds for $-\mathbf{I} + \mathbf{W}$ in the following cases:

- 1) If $w_{11} = w_{22} = 0$ and $\frac{1}{|w_{12}|} < |w_{21}|$;
- 2) If one or both of $w_{12}, w_{21} = 0$, then either w_{11} or $w_{22} > 1$;
- 3) If neither of the preceding cases hold and $\text{Tr}(-\mathbf{I} + \mathbf{W}) \leq 0$, then $(-1 + w_{11})(-1 + w_{22}) - w_{12}w_{21} \leq 0$.

The proof follows directly from the equation for the determinant of a 2×2 -matrix. The next result is useful later in our proof of Lemma 4.2.

Lemma 1.2: Let $\mathbf{W} \in \mathbb{R}^{n \times n}$ be a stable Z-matrix with two or more negative diagonal elements $w_{i_1 i_1} < w_{i_2 i_2} < 0$ such that $2|w_{i_k i_k}| > \rho(\mathbf{W})$ for $k \in \{1, 2\}$. Then \mathbf{W} has a stable 2×2 principal submatrix.

Proof: As \mathbf{W} is a Z-matrix, we can write it as $\mathbf{W} = \alpha \mathbf{I} - \mathbf{P}$, where $\alpha = \max_i \{w_{ii}\}$ and \mathbf{P} is a non-negative matrix. Since \mathbf{W} is a stable Z-matrix, $\rho(\mathbf{P}) > \alpha$ and $\rho(\mathbf{W}) = \rho(\mathbf{P}) - \alpha$.

Without loss of generality, assume that the two smallest diagonal elements are $w_{11} < w_{22} < 0$. We then claim the submatrix \mathbf{W}_{12} is stable. We can write this matrix to be

$$\mathbf{W}_{12} = \begin{bmatrix} w_{11} & -\bar{w}_{12} \\ -\bar{w}_{21} & w_{22} \end{bmatrix} = \alpha \mathbf{I} - \mathbf{P}_{12},$$

where $\bar{w}_{12}, \bar{w}_{21} \geq 0$. Since \mathbf{P} is a non-negative matrix, and \mathbf{P}_{12} is a principal submatrix, we have $\rho(\mathbf{P}_{12}) < \rho(\mathbf{P})$ [30, Corollary 8.1.20] and therefore $\rho(\mathbf{W}) > \rho(\mathbf{W}_{12})$. On the other hand, note that since \mathbf{W}_{12} is a Z-matrix, for $\gamma \geq \rho(\mathbf{W}_{12})$, we have $\mathbf{W}_{12} + \gamma \mathbf{I}$ is a M-matrix. Since $2|w_{22}| > \rho(\mathbf{W}_{12})$, the matrix $\mathbf{B}_{12} = \mathbf{W}_{12} + \gamma \mathbf{I}$ with $\gamma = 2|w_{22}|$, given as follows,

$$\mathbf{B}_{12} = \begin{bmatrix} w_{11} + 2|w_{22}| & -\bar{w}_{12} \\ -\bar{w}_{21} & |w_{22}| \end{bmatrix},$$

is a M-matrix. Since $w_{11} < w_{22}$, it follows that $|w_{11}| > w_{11} + 2|w_{22}|$. Therefore the matrix $\tilde{\mathbf{B}}_{12}$ defined by

$$\tilde{\mathbf{B}}_{12} = \begin{bmatrix} |w_{11}| & -\bar{w}_{12} \\ -\bar{w}_{21} & |w_{22}| \end{bmatrix},$$

satisfies $\tilde{\mathbf{B}}_{12} \geq \mathbf{B}_{12}$ and, by [31, Theorem 4.6], is a M-matrix. Then since $\tilde{\mathbf{B}}_{12} \geq \mathbf{W}_{12}$ and the diagonal elements of $\tilde{\mathbf{B}}_{12}$ are equal to the absolute value of the diagonal elements of \mathbf{W}_{12} , by [32, Section 2.5, Problem 34b)], the eigenvalues of \mathbf{W}_{12} satisfy $\lambda(\mathbf{W}_{12}) < -\lambda_{\min}(\tilde{\mathbf{B}}_{12}) < 0$, proving \mathbf{W}_{12} is stable. ■

Proof of Lemma 4.2: We recall from Theorem 3.4 that a subset of nodes $\sigma \subseteq \{1, \dots, N\}$ supports a stable equilibrium in the interior of the range $[\mathbf{0}, \mathbf{m}]$ iff the matrix $(-\mathbf{I} + \mathbf{W})_{\sigma}$ is stable. Since all 2×2 principal submatrices of $-\mathbf{I} + \mathbf{W}$ are unstable, it is immediate that there are no stable equilibria supported on subsets of nodes σ with $|\sigma| = 2$ taking values in the interior of $[\mathbf{0}, \mathbf{m}]$. It remains to be shown that this holds for all subsets of nodes $\sigma \subseteq \{1, \dots, N\}$ with $|\sigma| \geq 3$. We reason by contradiction. Suppose $(-\mathbf{I} + \mathbf{W})_{\sigma}$ is stable. Then, since there exist i_1, i_2 with $w_{i_k i_k} < 1$ and $2|-1 + w_{i_k i_k}| > \rho(-\mathbf{I} + \mathbf{W})$ for $k \in \{1, 2\}$, we can invoke Lemma 1.2 to ensure that $-\mathbf{I} + \mathbf{W}$ has exists a stable 2×2 principal submatrix. This contradicts our assumption that all its 2×2 principal submatrices are unstable, and therefore $(-\mathbf{I} + \mathbf{W})_{\sigma}$ cannot be stable, implying that σ , with $|\sigma| \geq 3$, does not support a stable equilibrium taking values in the interior of $[\mathbf{0}, \mathbf{m}]$. ■