

Structural Characterization of Oscillations in Brain Networks with Rate Dynamics

Erfan Nozari^a Robert Planas^b Jorge Cortés^c

^a*Department of Mechanical Engineering, Department of Electrical and Computer Engineering, and Department of Bioengineering, University of California, Riverside, erfan.nozari@ucr.edu.*

^b*Department of Mechanical and Aerospace Engineering, University of California, Irvine, planasr@uci.edu.*

^c*Department of Mechanical and Aerospace Engineering, University of California, San Diego, cortes@ucsd.edu.*

Abstract

Among the versatile forms of dynamical patterns of activity exhibited by the brain, oscillations are one of the most salient and extensively studied, yet are still far from being well understood. In this paper, we provide various structural characterizations of the existence of oscillatory behavior in neural networks using a classical neural mass model of mesoscale brain activity called linear-threshold dynamics. Exploiting the switched-affine nature of this dynamics, we obtain various necessary and/or sufficient conditions on the network structure and its external input for the existence of oscillations in (i) two-dimensional excitatory-inhibitory networks (E-I pairs), (ii) networks with one inhibitory but arbitrary number of excitatory nodes, (iii) purely inhibitory networks with an arbitrary number of nodes, and (iv) networks of E-I pairs. Throughout our treatment, and given the arbitrary dimensionality of the considered dynamics, we rely on the lack of stable equilibria as a system-based proxy for the existence of oscillations, and provide extensive numerical results to support its tight relationship with the more standard, signal-based definition of oscillations in computational neuroscience.

1 Introduction

Oscillations are among some of the first forms of neuronal activity to be discovered in the human brain, thanks particularly to the invention of electroencephalogram (EEG) nearly a century ago [3]. Thanks to their conceptual simplicity, prominence, and unmistakable correlation with various neurocognitive processes, oscillations have since been the subject of significant research from experimental and computational perspectives in neuroscience [10, 13, 20, 31, 46, 61]. Nevertheless, the precise mechanisms by which oscillations are generated are still not understood. In this work, we seek to shed light on this challenging problem using an analytical, system-theoretic approach and the linear-threshold mean-field model of neuronal dynamics. Our results constitute some of the first rigorous characterizations of the existence of oscillations in these networks, spanning various network architectures from simple, two-dimensional networks to arbitrarily complex interconnections of them.

Literature Review: Oscillations have been the subject of extensive research in the neuroscience literature, see, e.g. [10, 13, 20, 31, 46, 61], often from solely experimental and/or numerical perspectives. In comparison, *analytical characterizations* of oscillations have remained far behind, even though they can enable a more precise understanding of the role that different network components and their interconnections have in the appearance of oscillations, with potential implications

for the study of abnormal behavior (e.g., epilepsy, Parkinson), information transmission, medical interventions, and beyond. Among analytical studies, the Wilson-Cowan model [64] has played a special role owing to its minimal architecture and richness of non-trivial dynamics at the same time. Nevertheless, analytical characterization of structural conditions giving rise to oscillations even in the Wilson-Cowan model has not moved beyond partial results [2, 4, 39, 45], mainly due to the intractability of the sigmoidal nonlinearity in the standard model. This has motivated the study of variants of the sigmoidal activation function, such as linear-threshold models. Analytical results have been developed in [11] for the Wilson-Cowan model with bounded linear-threshold activation functions, but only under a number of unrealistic assumptions (notably, the violation of Dale’s law, excluding interaction terms inside the nonlinear activation functions, and a chain network topology). Similar to neural mass models with sigmoidal nonlinearities, models with linear-threshold activation functions¹ also exhibit rich nonlinear phenomena including multistability, limit cycles, chaos, and bifurcations, see e.g., [12, 40]. Our previous work [43, 44] studies selective recruitment in linear-threshold networks, characterizing the existence and uniqueness of equilibria and asymptotic stability, and developing feedforward/feedback policies for stabilization of said equilibria in hierarchical multi-layer architectures. More recently, [42] provides sufficient and necessary conditions for the existence of oscillations in two-dimensional excitatory-inhibitory networks and their networked excitatory-coupled interconnection. Among other contributions, the present work

* A preliminary version of this paper appeared at the 2019 American Control Conference as [42]. During the preparation of the bulk of this work, E. Nozari and R. Planas were affiliated with the University of California, San Diego.

¹ not to be confused with binary networks subject to linear integration and thresholding, such as the Hopfield network [25].

extends this characterization to the existence of oscillations in excitatory-inhibitory networks with arbitrary number of excitatory nodes, fully inhibitory networks with arbitrary number of nodes, and networks of two-dimensional oscillators with more realistic, excitatory-to-all inter-oscillator connections.

Oscillations have also been studied extensively using bifurcation theory (particularly the Hopf bifurcation), see e.g., [5, 19, 23, 30, 45, 51, 53, 62] and references therein. However, a fundamental limitation of these works, and a major difference with the approach here, is the univariate nature of the former. In other words, bifurcation analysis is often conducted by fixing all (of the numerous) network parameters and studying the effect of varying one or two parameters at a time. In contrast, our global analysis provides a complete characterization of the set of all parameters that give rise to oscillations, a set whose boundaries consist of bifurcation points. Significant research has been conducted, in the controls and neuroscience communities alike, to characterize oscillatory dynamics using models of phase oscillators, the most notable of which being the Kuramoto model, see [6, 38] and references therein. However, while the Kuramoto model has the advantage of having a smaller (half) state dimension, it is only a valid approximation to the Wilson-Cowan model in the *weakly coupled* regime [26, 52], where interconnected oscillators primarily affect each other's phase dynamics and their amplitude dynamics can be neglected. Moving beyond the weakly connected regime, amplitude dynamics, particularly saturations and phase-amplitude coupling [27, 45], become critical [18] and more complex models, such as the full Wilson-Cowan model are required.

Statement of Contributions: Our main contributions are four-fold, and consist of conditions on the structure of linear-threshold networks and their inputs that are necessary and/or sufficient to guarantee the lack of stable equilibria (LoSE). Since conditions for the existence of limit cycles in systems with higher than two dimensions are unknown in general, we use LoSE (which constitutes the main condition in the Poincaré-Bendixson theory for existence of limit cycles in planar systems) as a proxy for the existence of oscillations. First, motivated by the higher abundance and versatility of excitatory neurons in the mammalian cortex, we provide a necessary and sufficient condition for LoSE in networks with a single inhibitory but arbitrary excitatory nodes. We also describe two important consequences of this result, including a simple, intuitive, and exact characterization of limit cycles in the Wilson-Cowan model with linear-threshold nonlinearity, as well as the fact that purely excitatory networks always have stable equilibria. Second, purely inhibitory networks have long been known to be able to generate oscillations, and are often believed to play a central role in cortical oscillations in the brain. Our second contribution consists of an extensive study of LoSE in such networks, where we provide structural necessary conditions on the synaptic connectivity matrix for LoSE for arbitrary inhibitory networks and a full characterization of LoSE for those with pairwise unstable connectivity matrices. For the latter case, we provide a graph-theoretic interpretation for the existence of inputs that induce oscillations in terms of the presence of special cycles we term *valid* in the complete graph whose weights are defined in terms of the synaptic weight matrix. Next, we study oscillations in networks of multiple brain regions, each modeled by a simple Wilson-Cowan oscillator. Our third contribution consists of exact, necessary and sufficient conditions for LoSE in such networks, when they are coupled either only through

their excitatory nodes or via both excitatory-to-excitatory and excitatory-to-inhibitory connections. Finally, we provide extensive numerical evidence that LoSE is indeed a near necessary and sufficient system-based proxy for the existence of oscillations, where the latter is often defined based on the power spectral density of the system's trajectories. Together, our results provide the first rigorous characterization of the existence of oscillations in linear-threshold networks with several different classes of network architectures, along with the introduction of a novel proxy for oscillatory systems, whose relevance is of independent interest for the study of arbitrary dynamical systems.

2 Problem Formulation

Consider ² a neuronal network composed of a large number of neurons that communicate via sequences of spikes. Grouping together neurons with similar firing rates, under standard assumptions (see, e.g., [15, Ch 7]), the mean-field dynamics of the network can be described by the linear-threshold model

$$\tau \dot{\mathbf{x}}(t) = -\mathbf{x}(t) + [\mathbf{W}\mathbf{x}(t) + \mathbf{u}]_{\mathbf{0}}^{\mathbf{m}}, \quad \mathbf{x}(0) \in [\mathbf{0}, \mathbf{m}], \quad (1)$$

where $\mathbf{x} \in \mathbb{R}^N$ is the state vector with x_i denoting the average firing rate of the i 'th neuronal population, $\mathbf{W} \in \mathbb{R}^{N \times N}$ is the matrix of average synaptic connectivities, $\mathbf{u} \in \mathbb{R}^N$ is the vector of average external (background) inputs to the populations, $\mathbf{m} \in \mathbb{R}_{\geq 0}^N$ is the vector of average maximum firing rates, and $\tau > 0$ is the network time constant. Note that all solutions are bounded as $[\mathbf{0}, \mathbf{m}]$ is invariant under (1).

Our previous work [43] characterized the existence and uniqueness of equilibria and asymptotic stability for a variant of (1) with unbounded activation function ($\mathbf{m} = \infty \cdot \mathbf{1}_N$), and these results are readily extensible to arbitrary finite \mathbf{m} . However, the existence of oscillations in linear-threshold dynamics is not as well understood. Further, brain networks often contain interconnections of multiple coupled oscillators, and our understanding is even smaller about the oscillatory behavior of interconnections of (1). Our goal is to characterize the relationship between network structure and the oscillatory behavior observed in linear-threshold dynamics modeling brain networks.

² Throughout the paper, we employ the following notation. \mathbb{R} , $\mathbb{R}_{>0}$, and $\mathbb{R}_{\geq 0}$ denote the set of reals, positive reals, and nonnegative reals, respectively. Bold-faced letters are used for vectors and matrices. $\mathbf{1}_n$, $\mathbf{0}_n$, $\mathbf{0}_{m \times n}$, and \mathbf{I}_n stand for the n -vector of all ones, the n -vector of all zeros, the m -by- n zero matrix, and the identity n -by- n matrix (we omit the subscripts when clear from the context). Given a vector \mathbf{x} , $x_i = (\mathbf{x})_i$ is its i th component. Likewise, A_{ij} refers to the (i, j) th entry of a matrix \mathbf{A} . For block-partitioned \mathbf{x} , \mathbf{x}_i refers to the i th block of \mathbf{x} . For a vector $\boldsymbol{\sigma}' \in \{0, s\}^n$ and an index $i \in \{1, \dots, n\}$, we say $i \in \boldsymbol{\sigma}'$ if $\sigma'_i = s$ and $i \notin \boldsymbol{\sigma}'$ if $\sigma'_i = 0$. Further, for a (row/column) vector \mathbf{x} , $\mathbf{x}_{\boldsymbol{\sigma}'}$ is its subvector composed of x_i , $i \in \boldsymbol{\sigma}'$ and for a matrix \mathbf{a} , $\mathbf{a}_{i\boldsymbol{\sigma}'}$ is a row vector composed of a_{ij} , $j \in \boldsymbol{\sigma}'$. Likewise, $\mathbf{a}_{i:}$ is the i 'th row of \mathbf{a} and $\mathbf{a}_{:, \boldsymbol{\sigma}'}$ is the submatrix of its columns in $\boldsymbol{\sigma}'$. For $x \in \mathbb{R}$, $[x]^+ = \max\{x, 0\}$ and $[x]_0^m = \min\{\max\{x, 0\}, m\}$, which is extended entry-wise to $[\mathbf{x}]^+$ and $[\mathbf{x}]_0^{\mathbf{m}}$. Given a vector $\mathbf{m} \in \mathbb{R}_{\geq 0}^n$, $[\mathbf{0}, \mathbf{m}] = \prod_{i=1}^n [0, m_i]$. For a set S , $|S|$ and S^c denotes its cardinality and complement. In block representation of vectors and matrices, we use compact notations $[\mathbf{A}, \mathbf{B}]$, $[\mathbf{A}; \mathbf{B}]$, and $\text{diag}(\mathbf{A}, \mathbf{B})$ for horizontal, vertical, and diagonal concatenation and \star for arbitrary blocks. For $a, b \in \mathbb{R}$, $\mathcal{U}(a, b)$ denotes the uniform distribution over $[a, b]$. Finally, we let \mathbb{P} denote the set of P-matrices (a matrix is a P-matrix if all the principal minors are positive).

Problem 1 We seek to answer the following questions for the bounded linear-threshold network dynamics (1):

- (i) What are neural oscillations? That is, what is an objective definition of oscillatory signals and oscillatory systems?
- (ii) What network structures give rise to oscillations?
- (iii) What are the structural conditions for the existence of oscillations in networked interconnections of multiple oscillatory networks?

Following common practice in computational neuroscience [9, 17], we here adopt a broad notion of oscillations that includes both periodic oscillations (limit cycles) and chaotic ones. In the latter case, a chaotic behavior is oscillatory if its state trajectories are near-periodic, as captured by next³.

Definition 2.1 (Oscillation). A state trajectory $\mathbf{x}(t), t \geq 0$ of (1) is oscillatory if

- (i) its power spectrum contains distinct and pronounced resonance peaks; and
- (ii) it does not asymptotically converge to a constant limit. \square

Two remarks about Definition 2.1 are in order. First, property (i) is qualitative and fuzzy in nature, as is the notion of *oscillation*. Different measures can be used to quantify this property, such as the *regularity index* χ_{reg} , cf. Appendix A. Second, the property (ii) is included in the definition of an oscillation to limit our focus to sustained (a.k.a. persistent) oscillations and not transient ones. It is important to note that both types of oscillations are observed in neuronal dynamics (see, e.g., [10, 35, 48, 55] for sustained and [33, 60] for transient), albeit with potentially different underlying dynamical generators. Our focus here is on the former category in light of the vast literature on attractor dynamics in biological neuronal networks [29, 34, 37, 58], while the latter remains an avenue for future research.

The analytical tools in the study of oscillations are generally limited to 2-dimensional systems (cf. the Poincaré-Bendixson theory [47, Ch 3]) or higher-dimensional systems that are essentially confined to 2-dimensional manifolds (see, e.g., [22, 50]). Thus, throughout the paper, we use *lack of stable equilibria (LoSE) as a proxy for oscillations*. In fact, this condition constitutes the main requirement in the Poincaré-Bendixson theory for existence of limit cycles. In Appendix A, we show numerically that this proxy is a tight characterization of oscillatory dynamics for the model (1).

To study the equilibria of (1), we use its representation as a switched affine system [32, 36]. It is straightforward to show [43] that \mathbb{R}^N can be decomposed into 3^N switching regions $\{\Omega_{\sigma}\}_{\sigma \in \{0, \ell, s\}^N}$ defined by

$$\mathbf{x} \in \Omega_{\sigma} \Leftrightarrow \begin{cases} (\mathbf{W}\mathbf{x} + \mathbf{u})_i \in (-\infty, 0]; & \forall i \text{ s.t. } \sigma_i = 0, \\ (\mathbf{W}\mathbf{x} + \mathbf{u})_i \in [0, m_i]; & \forall i \text{ s.t. } \sigma_i = \ell, \\ (\mathbf{W}\mathbf{x} + \mathbf{u})_i \in [m_i, \infty); & \forall i \text{ s.t. } \sigma_i = s, \end{cases}$$

where 0, ℓ , and s denote a node in *inactive*, *active*, and *saturated* state, respectively. Thus, (1) can be rewritten in the switched affine form

$$\tau \dot{\mathbf{x}} = (-\mathbf{I} + \Sigma^{\ell} \mathbf{W})\mathbf{x} + \Sigma^{\ell} \mathbf{u} + \Sigma^s \mathbf{m}, \quad \forall \mathbf{x} \in \Omega_{\sigma}, \quad (2)$$

³ Note the similarity (relaxing the need for perfect periodicity) as well as the difference (requiring near-periodicity here) of this definition with the *Yakubovich self-sustained oscillations* [49, 57].

where for any $\sigma \in \{0, \ell, s\}^N$, $\Sigma^{\ell} \in \mathbb{R}^{N \times N}$ and $\Sigma^s \in \mathbb{R}^{N \times N}$ are diagonal matrices with entries

$$\Sigma_{ii}^{\ell} = \begin{cases} 1 & \text{if } \sigma_i = \ell, \\ 0 & \text{if } \sigma_i = 0, s, \end{cases} \quad \Sigma_{ii}^s = \begin{cases} 1 & \text{if } \sigma_i = s, \\ 0 & \text{if } \sigma_i = 0, \ell. \end{cases}$$

Each Ω_{σ} then has a corresponding *equilibrium candidate*

$$\mathbf{x}_{\sigma}^* = (\mathbf{I} - \Sigma^{\ell} \mathbf{W})^{-1}(\Sigma^{\ell} \mathbf{u} + \Sigma^s \mathbf{m}), \quad (3)$$

and the equilibria of (1) consist of all equilibrium candidates \mathbf{x}_{σ}^* that belong to their respective switching regions. Note, in particular, that while the position of the equilibrium candidates depend on all four of \mathbf{W} , \mathbf{u} , \mathbf{m} , and σ , their stability is a sole function of \mathbf{W} and σ .

To summarize, the main goal of the paper is to develop understanding of the role that network structure plays in the emergence (or lack of thereof) of oscillations in linear-threshold networks. These biologically-grounded dynamical models describe the behavior of aggregate populations of neurons at a mesoscale level in the brain. Because of the arbitrary dimensionality of the state space considered here, developing such quantitative understanding is challenging. This is why we have structured the presentation of the results with various (and increasingly more complex) architectures. In Section 3, we start our development with simple, 2-dimensional networks with one excitatory and one inhibitory nodes. Subsequently, we generalize this case to networks with arbitrary number of excitatory (but still one inhibitory) nodes, cf. Section 3.1, and separately study networks that are purely inhibitory, Section 3.2. Finally, Section 4 studies arbitrarily large networks of 2-dimensional networks. The network architectures that we study respect an important property of mammalian cortical networks, known as Dale's law [15, 64], according to which each node has either an excitatory or inhibitory effect on other nodes, but not both. This means that each column of \mathbf{W} is either nonnegative or nonpositive, a condition that we follow throughout the paper.

3 Oscillations in Single Networks

We analyze the dynamics (1) and derive conditions on the network $(\mathbf{W}, \mathbf{u}, \mathbf{m})$ giving rise to oscillatory behavior.

3.1 Excitatory-Inhibitory Networks

The reciprocal interactions between excitatory and inhibitory populations of cortical neurons have long been known to be a major contributor to cortical oscillations [31]. Arguably, the simplest scenario with only one excitatory and one inhibitory populations (each abstracted to one network node) has been the most popular in theoretical neuroscience [14]. Interestingly, this coincides with the fact that LoSE is, under mild conditions, necessary and sufficient for the existence of almost globally (excluding trajectories starting at an unstable equilibrium) asymptotically stable limit cycles when $N = 2$. This two-dimensional case, hereafter called an *E-I pair*, is the celebrated Wilson-Cowan model used in computational neuroscience for decades [2, 4, 39, 45, 64]. Unlike the standard model with sigmoidal activation functions, however, the next result shows that a complete characterization of limit cycles can be obtained for Wilson-Cowan models with bounded linear-threshold nonlinearities.

Theorem 3.1 (Limit cycles in E-I pairs). Consider the dynamics (1) with $N = 2$ and

$$\mathbf{W} = \begin{bmatrix} a & -b \\ c & -d \end{bmatrix}, \quad a, b, c, d \geq 0.$$

All network trajectories (except those starting at an unstable equilibrium, if any) converge to a limit cycle if and only if

$$d + 2 < a, \quad (4a)$$

$$(a - 1)(d + 1) < bc, \quad (4b)$$

$$(a - 1)m_1 < bm_2, \quad (4c)$$

$$0 < u_1 < bm_2 - (a - 1)m_1, \quad (4d)$$

$$0 < (d + 1)u_1 - bu_2 < [bc - (a - 1)(d + 1)]m_1. \quad (4e)$$

PROOF. By [54, Thm 4.1], all the trajectories (except those starting at unstable equilibria, if any) converge to a limit cycle if and only if the network does not have any stable equilibria. This is, nevertheless, not a special case of Theorem 3.3 as we here do not presume (4a) but rather show its necessity together with (4b)-(4e).

If $a < 1$, then all the regions $\Omega_{\sigma}, \sigma \in \{0, \ell, s\}^2$ are stable, ensuring the existence of a stable equilibrium (since the existence of an equilibrium is always guaranteed by Brouwer Fixed-Point Theorem [7]). Thus, assume $a \geq 1$. Then, as shown in the proof of Theorem 3.3, the trivially stable regions $(\sigma', j), \sigma' \in \{0, s\}, j \in \{0, \ell, s\}$ do not contain their equilibrium candidates iff $u \in Y^c$. One can readily show

$$Y = \left\{ (u_1, u_2) \mid u_1 \leq \max \left\{ 0, \min \left\{ bm_2, \frac{b}{d+1}u_2 \right\} \right\} \text{ or } u_1 \geq -(a-1)m_1 + \min \left\{ bm_2, \max \left\{ 0, \frac{b(u_2 + cm_1)}{d+1} \right\} \right\} \right\}.$$

Therefore, $u \in Y^c$ if and only if

$$u_1 > 0, \quad (5a)$$

$$u_1 < bm_2 - (a - 1)m_1, \quad (5b)$$

$$u_1 > \min \left\{ bm_2, \frac{b}{d+1}u_2 \right\}, \quad (5c)$$

$$u_1 < -(a - 1)m_1 + \max \left\{ 0, \frac{b(u_2 + cm_1)}{d+1} \right\}. \quad (5d)$$

Next, we characterize when the conditions (5) are *feasible*, i.e., when there exists u_1 satisfying them (and hence Y^c is non-empty). In fact, for (5) to be feasible, it is necessary and sufficient that

$$(5a) \text{ and } (5b) : bm_2 - (a - 1)m_1 > 0, \quad (6a)$$

$$(5a) \text{ and } (5d) : u_2 > -\frac{bc - (a - 1)(d + 1)}{b}m_1, \quad (6b)$$

$$(5b) \text{ and } (5c) : u_2 < \frac{d + 1}{b}(bm_2 - (a - 1)m_1), \quad (6c)$$

$$(5c) \text{ and } (5d) : bc > (a - 1)(d + 1). \quad (6d)$$

Conditions (6a) and (6d) are the same as (4c) and (4b), respectively. Furthermore, under (6), (5) simplifies to (4d) and (4e), which in turn ensure (6b) and (6c). In conclusion, $u \in Y^c$ if and only if (4b)-(4e) hold.

What remains to study are the regions $(\ell, 0)$, (ℓ, s) , and (ℓ, ℓ) . The first two are not stable since $a \geq 1$. Also, though not needed, they do not include their equilibrium candidates due to (4d). On the other hand, for $\sigma = (\ell, \ell)$,

$$\mathbf{x}_{\sigma}^* = \frac{1}{bc - (a - 1)(d + 1)} \begin{bmatrix} (d + 1)u_1 - bu_2 \\ cu_1 - (a - 1)u_2 \end{bmatrix} = \mathbf{W}\mathbf{x}_{\sigma}^* + \mathbf{u}.$$

The first component of $\mathbf{W}\mathbf{x}_{\sigma}^* + \mathbf{u}$ clearly belongs to $[0, m_1]$ by (4b) and (4e). For its second component, we have⁴

$$(4b), (4e) \Rightarrow cu_1 > (a - 1)u_2,$$

$$(4d), (4e) \Rightarrow u_2 > \frac{c}{a - 1}u_1 - \frac{bc - (a - 1)(d + 1)}{a - 1}m_2,$$

ensuring that $\sigma = (\ell, \ell)$ always contains its equilibrium candidate. Therefore, this region must be unstable which, under (4b), happens if and only if $a > d + 2$. \square

Remark 3.2 (Connections with experimental observations in the neuroscientific literature). While existing *quantitative* measurements of synaptic weight relationships that give rise to oscillations in biological neural networks are extremely few, if any, particularly at the mean-field scale of analysis most relevant to our study, the bounds in Theorem 3.1 do resonate with some of the known *qualitative* properties of oscillations in cortical networks. For instance, similar to our conditions (4a) restricting the balance between excitation and inhibition and (4b) requiring strong reciprocal excitatory-inhibitory interconnections, [21] states that “Gamma oscillations emerge from the synchronized firing of interconnected excitatory glutamatergic and primarily inhibitory fast-spiking GABAergic PV+ interneurons, and its power (i.e., amplitude) is modulated by the E/I balance at distinct synaptic sites in the circuit and the intrinsic excitable properties of the neurons” and [59] that “Generation of synchronized neural activity in neocortical circuits is dependent on negative feedback inhibition of pyramidal cells by GABA (γ -aminobutyric acid)-ergic [inhibitory] interneurons that express the Ca²⁺-binding protein parvalbumin”. Even more specifically, it is mentioned in [21] that “A prominent hypothesis for SCZ [schizophrenia] pathophysiology posits that NMDARs on PV+ neurons [excitatory to inhibitory synaptic weights, c in our Theorem 3.1] are hypofunctional, thus resulting in lowered GABAergic signaling, overstimulation of excitatory neurons, and a consequent loss of gamma wave oscillations” which is in line with the lower bound on c in (4b). However, even such qualitative parallels become hard to draw when it comes to less characterized quantities such as the maximal firing rates of different cell types (m_1 and m_2 in Theorem 3.1) or network structures more detailed than a simple E-I pair, further highlighting the importance of theoretical studies that can move beyond experimental limitations. \square

The simplicity of the two-dimensional E-I model in Theorem 3.1, while having led to its long-standing popularity in computational neuroscience, comes at the price of limited flexibility to model the complex dynamics of the brain. In the rest of this paper, therefore, we extend the above analysis to more

⁴ In the proof we only consider the scenario where $a > 1$ since $(\mathbf{W}\mathbf{x}_{\sigma}^* + \mathbf{u})_2 \in [0, m_2]$ trivially if $a = 1$.

complex scenarios, beginning with the following analysis of higher-dimensional excitatory-inhibitory networks.

Inhibitory neurons constitute about 20% of neurons in the cortex and have broader (less specific) interconnection and activity patterns than excitatory neurons. Therefore, we focus on networks with a single inhibitory node and arbitrary number of excitatory nodes. Let $N = n + 1$, $n \geq 1$, and consider

$$\mathbf{W} = \begin{bmatrix} \mathbf{a} & -\mathbf{b} \\ \mathbf{c} & -d \end{bmatrix}, \quad \mathbf{u} = \begin{bmatrix} \mathbf{u}_e \\ u_{n+1} \end{bmatrix}, \quad \mathbf{m} = \begin{bmatrix} \mathbf{m}_e \\ m_{n+1} \end{bmatrix}, \quad (7)$$

where $\mathbf{a} \in \mathbb{R}_{\geq 0}^{n \times n}$, $\mathbf{b} \in \mathbb{R}_{\geq 0}^{n \times 1}$, $\mathbf{c} \in \mathbb{R}_{\geq 0}^{1 \times n}$, $d \in \mathbb{R}_{\geq 0}$. Note that this class of networks includes, as a special case, the well-known 2-dimensional Wilson-Cowan model ($n = 1$) extensively used in the computational neuroscience [16]. We are ready to give our first result on LoSE for (1), (7).

Theorem 3.3 (Networks with a single inhibitory node). Consider the dynamics (1), (7) and assume that

$$a_{ii} > d + 2 \quad \forall i \in \{1, \dots, n\}. \quad (8)$$

Then, the network does not have any stable equilibria iff $\mathbf{u} \in \mathbb{R}^{n+1} \setminus Y$, where

$$Y = \bigcup_{\sigma' \in \{0, s\}^n} \left[\bigcap_{i \in \sigma'} (Y_{\sigma', s, i} \cup (Y_{\sigma', 0, i} \cap Y_{\sigma', \ell, i})) \cap \bigcap_{i \notin \sigma'} (Y_{\sigma', 0, i} \cup (Y_{\sigma', s, i} \cap Y_{\sigma', \ell, i})) \right],$$

$$Y_{\sigma', j, i} = \begin{cases} \{\mathbf{u} \mid u_i \geq y_{\sigma', j, i}\}; & \text{if } i \in \sigma' \\ \{\mathbf{u} \mid u_i \leq y_{\sigma', j, i}\}; & \text{if } i \notin \sigma' \end{cases} \quad \forall j \in \{0, \ell, s\},$$

$y_{\sigma', 0, i} = -(\mathbf{a}_{i\sigma'} - \mathbf{I}_{i\sigma'})\mathbf{m}_{\sigma'}$, $y_{\sigma', s, i} = y_{\sigma', 0, i} + b_i m_{n+1}$, and $y_{\sigma', \ell, i} = y_{\sigma', 0, i} + \frac{b_i(u_{n+1} + \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'})}{d+1}$ for $\sigma' \in \{0, s\}^n$ and $i \in \{1, \dots, n\}$.

PROOF. The proof consists of two steps: first, we determine the list of $\Omega_{\sigma'}$ that are stable and second, we ensure that they do not contain their equilibrium candidates iff $\mathbf{u} \in \mathbb{R}^{n+1} \setminus Y$.

Step 1: The switching regions can be naturally decomposed into two groups: those in which at least one of the excitatory nodes is active and those in which all the excitatory nodes are either inactive or saturated. We next show that these correspond to unstable and stable switching regions, respectively. Consider any $\sigma' \in \{0, \ell, s\}^n$ and let $L = \{i \in \{1, \dots, n\} \mid \sigma_i = \ell\}$ (note that L is independent of σ_{n+1}). Let $r = |L|$, and let Π be the permutation matrix such that $\Pi\sigma' = (\mathbf{0}_{n-r}, \ell, \dots, \ell, \sigma_{n+1})'$. Let $\Sigma \in \mathbb{R}^{N \times N}$ be a diagonal matrix with entries $\Sigma_{ii} = 1$ if $\sigma_i \in \{\ell, s\}$ and $\Sigma_{ii} = 0$ otherwise. The coefficient matrix $-\mathbf{I} + \Sigma\mathbf{W}$ in the region $\Omega_{\sigma'}$ then satisfies $\Pi(-\mathbf{I} + \Sigma\mathbf{W})\Pi^T = [-\mathbf{I}_{n-r}, \mathbf{0}; \star, \mathbf{P}]$, where $\mathbf{P} = [-\mathbf{I}_r + \mathbf{a}_L, \star; \star, -1 - \Sigma_{n+1, n+1}d]$, \mathbf{a}_L is the principal submatrix of \mathbf{a} composed of its rows and columns in L , and $\Sigma_{n+1, n+1}$ is the bottom-right element of Σ . Thus, the eigenvalues of $-\mathbf{I} + \Sigma\mathbf{W}$ consist of (-1) with multiplicity $n - r$ and the eigenvalues of \mathbf{P} . Therefore,

- if $r > 0$, $\Omega_{\sigma'}$ is unstable since $\text{tr}(\mathbf{P}) = \sum_{i \in L} (a_{ii} - 1) - 1 - \Sigma_{n+1, n+1}d \geq \sum_{i \in L} (a_{ii} - 1) - 1 - d \stackrel{(8)}{>} 0$;
- if $r = 0$, $\Omega_{\sigma'}$ is stable since $P = -1 - \Sigma_{n+1, n+1}d < 0$.

Step 2: According to Step 1, we only need to ensure that regions $\Omega_{\sigma'}$ with $r = 0$ do not contain their equilibrium candidates⁵. These regions have the form

$$\sigma = (\sigma', j), \quad \sigma' \in \{0, s\}^n, \quad j \in \{0, \ell, s\}.$$

We consider three cases based on the value of j .

- (i) $j = 0$: It is straightforward to verify that

$$\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} = \begin{bmatrix} \mathbf{a}_{\cdot, \sigma'}\mathbf{m}_{\sigma'} + \mathbf{u}_e \\ \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'} + u_{n+1} \end{bmatrix},$$

and that $\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} \in \Omega_{\sigma'}$ if and only if $\mathbf{u} \in \bigcap_{i=1}^{n+1} Y_{\sigma', 0, i}$ where $Y_{\sigma', 0, n+1} = \{\mathbf{u} \mid u_{n+1} \leq -\mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'}\}$.

- (ii) $j = s$: similarly, it follows that

$$\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} = \begin{bmatrix} \mathbf{a}_{\cdot, \sigma'}\mathbf{m}_{\sigma'} - \mathbf{b}m_{n+1} + \mathbf{u}_e \\ \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'} - dm_{n+1} + u_{n+1} \end{bmatrix},$$

and $\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} \in \Omega_{\sigma'} \Leftrightarrow \mathbf{u} \in \bigcap_{i=1}^{n+1} Y_{\sigma', s, i}$ where $Y_{\sigma', s, n+1} = \{\mathbf{u} \mid u_{n+1} \geq (d+1)m_{n+1} - \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'}\}$.

- (iii) $j = \ell$: it also follows similarly that

$$(d+1)\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} = \begin{bmatrix} (\mathbf{a}_{\cdot, \sigma'}(d+1) - \mathbf{b}\mathbf{c}_{\sigma'})\mathbf{m}_{\sigma'} - \mathbf{b}u_{n+1} + (d+1)\mathbf{u}_e \\ \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'} + u_{n+1} \end{bmatrix},$$

and $\mathbf{W}\mathbf{x}_{\sigma'}^* + \mathbf{u} \in \Omega_{\sigma'} \Leftrightarrow \mathbf{u} \in \bigcap_{i=1}^{n+1} Y_{\sigma', \ell, i}$ where $Y_{\sigma', \ell, n+1} = \{\mathbf{u} \mid -\mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'} \leq u_{n+1} \leq (d+1)m_{n+1} - \mathbf{c}_{\sigma'}\mathbf{m}_{\sigma'}\}$.

Therefore, for no stable region to contain its equilibrium candidate it is necessary and sufficient that

$$\mathbf{u} \in \mathbb{R}^{n+1} \setminus \bar{Y}, \quad \bar{Y} = \bigcup_{\sigma' \in \{0, s\}^n} \bigcup_{j \in \{0, \ell, s\}} \bigcap_{i=1}^{n+1} Y_{\sigma', j, i}. \quad (9)$$

It only remains to show $\bar{Y} = Y$. For $\sigma' \in \{0, s\}^n$, let

$$\bar{Y}_{\sigma'} = \bigcup_{j \in \{0, \ell, s\}} \bigcap_{i=1}^{n+1} Y_{\sigma', j, i}. \quad (10)$$

Then, we have $\bar{Y}_{\sigma'}^c = \bigcap_{j \in \{0, \ell, s\}} \bigcup_{i=1}^{n+1} Y_{\sigma', j, i}^c = \bigcap_{j=1}^5 (A_j^c \cup B_j^c)$, where (in what follows, $^\circ$ denotes the interior of a set)

$$A_1 = \bigcap_{i=1}^n Y_{\sigma', 0, i}, \quad B_1 = Y_{\sigma', 0, n+1}^\circ,$$

⁵ Note that if an equilibrium lies at the boundary of a stable switching region, it still attracts (at least half of) nearby trajectories: if all the switching regions sharing an equilibrium are stable, their coefficient matrices $\{-\mathbf{I} + \Sigma\mathbf{W}\} \subseteq \{-\mathbf{I}, [-\mathbf{I}, \mathbf{0}; \mathbf{c}, -1-d]\}$ hence share a common quadratic Lyapunov function. If an equilibrium is also shared with an unstable switching region, it is not difficult to show that the switching hyperplane between the stable and unstable regions coincides with the slow eigenspace of the coefficient matrices $\{-\mathbf{I} + \Sigma\mathbf{W}\}$ of the stable regions, ensuring that the equilibrium attracts all trajectories initiating in the stable side.

$$\begin{aligned}
A_2 &= A_1, & B_2 &= Y_{\sigma',0,n+1} \cap Y_{\sigma',\ell,n+1}, \\
A_3 &= \bigcap_{i=1}^n Y_{\sigma',\ell,i}, & B_3 &= Y_{\sigma',\ell,n+1}^\circ, \\
A_4 &= A_3, & B_4 &= Y_{\sigma',\ell,n+1} \cap Y_{\sigma',s,n+1}, \\
A_5 &= \bigcap_{i=1}^n Y_{\sigma',s,i}, & B_5 &= Y_{\sigma',s,n+1}^\circ.
\end{aligned}$$

Since the sets $\{B_j\}_{j=1}^5$ partition \mathbb{R}^{n+1} , it follows that $\bar{Y}_{\sigma'}^c = \bigcup_{j=1}^5 (A_j^c \cap B_j)$, or

$$\begin{aligned}
\bar{Y}_{\sigma'}^c &= \bigcup_{j \in \{0,\ell,s\}} \left(\left(\bigcup_{i=1}^n Y_{\sigma',j,i}^c \right) \cap Y_{\sigma',j,n+1} \right) \\
&= \bigcup_{i=1}^n \bigcup_{j \in \{0,\ell,s\}} (Y_{\sigma',j,i}^c \cap Y_{\sigma',j,n+1}). \quad (11)
\end{aligned}$$

For any $i \in \sigma'$, we have

$$\begin{aligned}
\bar{Y}_{\sigma',i}^c &\triangleq \bigcup_{j \in \{0,\ell,s\}} (Y_{\sigma',j,i}^c \cap Y_{\sigma',j,n+1}) \\
&\stackrel{(a)}{=} \bigcup_{j \in \{0,\ell,s\}} [(Y_{\sigma',j,i}^c \cap Y_{\sigma',j,n+1}) \cup (Y_{\sigma',0,i}^c \cap Y_{\sigma',j,n+1})] \\
&\stackrel{(b)}{=} \bigcup_{j \in \{0,\ell,s\}} (Y_{\sigma',j,i}^c \cap Y_{\sigma',j,n+1}) \cup Y_{\sigma',0,i}^c \\
&= Y_{\sigma',0,i}^c \cup (Y_{\sigma',\ell,i}^c \cap Y_{\sigma',\ell,n+1}) \cup (Y_{\sigma',s,i}^c \cap Y_{\sigma',s,n+1}) \\
&\stackrel{(c)}{=} Y_{\sigma',0,i}^c \cup (Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,n+1}) \cup (Y_{\sigma',s,i}^c \cap Y_{\sigma',s,n+1}) \\
&\stackrel{(d)}{=} Y_{\sigma',0,i}^c \cup (Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,n+1} \cap Y_{\sigma',s,i}^c) \\
&\quad \cup (Y_{\sigma',s,i}^c \cap Y_{\sigma',s,n+1} \cap Y_{\sigma',\ell,i}^c) \\
&= Y_{\sigma',0,i}^c \cup (Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,i}^c) \\
&\stackrel{(d)}{=} (Y_{\sigma',0,i}^c \cup Y_{\sigma',\ell,i}^c) \cap Y_{\sigma',s,i}^c, \quad (12)
\end{aligned}$$

where (a) is because $Y_{\sigma',0,i}^c \cap Y_{\sigma',j,n+1} \subseteq Y_{\sigma',j,i}^c \cap Y_{\sigma',j,n+1}$ for both $j = \ell$ and $j = s$ (and is trivial for $j = 0$), (b) is because $\{Y_{\sigma',j,n+1}\}_{j \in \{0,\ell,s\}}$ cover \mathbb{R}^{n+1} , (c) is because $Y_{\sigma',\ell,i}^c \cap Y_{\sigma',\ell,n+1} \subseteq Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,n+1}$ and

$$(Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,n+1}) \setminus (Y_{\sigma',\ell,i}^c \cap Y_{\sigma',\ell,n+1}) \subseteq Y_{\sigma',0,i}^c,$$

(d) is because $Y_{\sigma',\ell,i}^c \cap Y_{\sigma',s,n+1} \subseteq Y_{\sigma',s,i}^c$ and $Y_{\sigma',s,i}^c \cap Y_{\sigma',s,n+1} \subseteq Y_{\sigma',\ell,i}^c$, and (e) is because $Y_{\sigma',0,i}^c \subseteq Y_{\sigma',s,i}^c$. By a parallel argument, it can be shown that for any $i \notin \sigma'$,

$$\bar{Y}_{\sigma',i}^c = (Y_{\sigma',s,i}^c \cup Y_{\sigma',\ell,i}^c) \cap Y_{\sigma',0,i}^c. \quad (13)$$

Therefore, (9)-(13) gives $\bar{Y} = Y$, completing the proof. \square

While the description of Y in Theorem 3.3 may seem complex, it has a simple interpretation. Consider a fixed value for u_{n+1} . Then, each of the sets $(Y_{\sigma',s,i} \cup (Y_{\sigma',0,i} \cap Y_{\sigma',\ell,i}))$ or $(Y_{\sigma',0,i} \cup (Y_{\sigma',s,i} \cap Y_{\sigma',\ell,i}))$ in the definition of Y are a half space of the form $\{u_i \geq y\}$ or $\{u_i \leq y\}$ (depending on whether $i \in \sigma'$ or not) that drive x_i to saturation or inactivity, respectively. Therefore, the cross section of Y for this fixed value of u_{n+1} is composed of 2^n closed orthants, each unbounded towards a different direction in \mathbb{R}^n . Figure 1 shows an example of this for $n = 2$. The union of these orthants (the shaded area in Figure 1) characterizes the region where the network has at least one stable equilibrium.

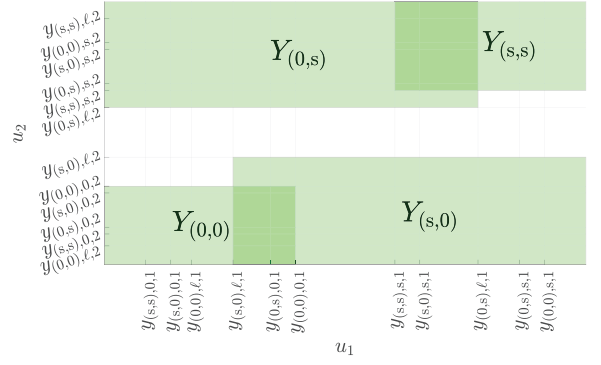


Fig. 1. Illustration of the region Y in Theorem 3.3 for an example network with $n = 2$. The four shaded quadrants represent the cross section of $Y_{\sigma'}, \sigma' \in \{0,s\}^2$ at $u_3 = -5$, so the white area is where the network lacks any stable equilibria. Network parameters are $\mathbf{a} = [8.5, 1, 1, 5]$, $\mathbf{b} = [5, 7]$, $\mathbf{c} = [4, 5]$, $d = 1$, $\mathbf{m} = [2, 3, 6]$.

Nevertheless, the set Y^c may in general be non-convex, unbounded, and disconnected. The complex nature of this set is consistent with the fact that as we are trying to emulate the complex behavior of brain networks. The assumption (8) in Theorem 3.3 is closely aligned with the biology of real brain networks. For the trajectories to oscillate, one needs the exciting parts of the network to impose a greater effect than its inhibitory counterparts since, otherwise, the whole system could be forced into an inactive state where no oscillations can occur. The next result gives simpler and easier-to-interpret, but more conservative, conditions.

Corollary 3.4 (Simpler conditions for networks with a single inhibitory node). Consider the same assumptions as in Theorem 3.3. Then, for the network not to have any stable equilibria, it is necessary that

$$-\mathbf{cm}_e < u_{n+1} < (d+1)m_{n+1}, \quad (14)$$

and sufficient that either

$$0 \leq u_{n+1} \leq (d+1)m_{n+1} - \mathbf{cm}_e, \quad (15a)$$

$$\exists i_0 \text{ s.t. } (a_{i_0 i_0} - 1)(d+1) < b_{i_0} c_{i_0}, \quad (15b)$$

$$\frac{b_{i_0} u_{n+1}}{d+1} < u_{i_0} < \frac{b_{i_0} (u_{n+1} + c_{i_0} m_{i_0})}{d+1} - (a_{i_0 i_0} - 1)m_{i_0}, \quad (15c)$$

$$u_i < \frac{b_i u_{n+1} - [(\mathbf{a}_{i,:} - \mathbf{I}_{i,:})(d+1) - b_i \mathbf{c}]^+ \mathbf{m}_e}{d+1}, \forall i \neq i_0, \quad (15d)$$

or

$$(d+1)m_{n+1} - \min_i (c_i m_i) \leq u_{n+1} \leq (d+1)m_{n+1}, \quad (16a)$$

$$\exists i_0 \text{ s.t. } (a_{i_0 i_0} - 1)m_{i_0} < b_{i_0} m_{n+1}, \quad (16b)$$

$$0 < u_{i_0} < b_{i_0} m_{n+1} - (a_{i_0 i_0} - 1)m_{i_0}, \quad (16c)$$

$$u_i < b_i m_{n+1} - (\mathbf{a}_{i,:} - \mathbf{I}_{i,:}) \mathbf{m}_e, \quad \forall i \neq i_0. \quad (16d)$$

PROOF. First, we prove the sufficiency of the conditions in (15), by showing that any \mathbf{u} satisfying all the conditions in (15) will not belong to Y as defined in Theorem 3.3. Note that the expression for Y can be greatly simplified if we can restrict \mathbf{u} such that for all $\sigma' \in \{0,s\}^n$,

$$\begin{aligned}
Y_{\sigma',s,i} \cup (Y_{\sigma',0,i} \cap Y_{\sigma',\ell,i}) &= Y_{\sigma',\ell,i} & \forall i \in \sigma', \\
Y_{\sigma',0,i} \cup (Y_{\sigma',s,i} \cap Y_{\sigma',\ell,i}) &= Y_{\sigma',\ell,i} & \forall i \notin \sigma' \quad (17)
\end{aligned}$$

Given the definition of the sets $Y_{\sigma',j,i}$, we can see that this holds if for all $\sigma' \in \{0, s\}^n$,

$$-\mathbf{c}_{\sigma'} \mathbf{m}_{\sigma'} \leq u_{n+1} \leq (d+1)m_{n+1} - \mathbf{c}_{\sigma'} \mathbf{m}_{\sigma'}, \quad (18)$$

which gives (15a) since $\max_{\sigma'} -\mathbf{c}_{\sigma'} \mathbf{m}_{\sigma'} = 0$ and $\min_{\sigma'} -\mathbf{c}_{\sigma'} \mathbf{m}_{\sigma'} = -\mathbf{c}_e$.

Given (17), \mathbf{u} will not be in Y if and only if for any $\sigma' \in \{0, s\}^n$, there exists an i such that

$$u_i < \frac{b_i}{d+1} u_{n+1} + \frac{b_i \mathbf{c}_{\sigma'} - (\mathbf{a}_{i\sigma'} - \mathbf{I}_{i\sigma'})(d+1)}{d+1} \mathbf{m}_{\sigma'}, \quad (19a)$$

if $i \in \sigma'$, or

$$u_i > \frac{b_i}{d+1} u_{n+1} + \frac{b_i \mathbf{c}_{\sigma'} - (\mathbf{a}_{i\sigma'} - \mathbf{I}_{i\sigma'})(d+1)}{d+1} \mathbf{m}_{\sigma'}, \quad (19b)$$

if $i \notin \sigma'$. Note that these are 2^n sets of inequalities, where at least one inequality needs to be satisfied from each set using only the n variables u_1, \dots, u_n . This provides us with a choice of which inequality from each set we choose to enforce, with any choice imposing 2^n upper/lower bounds on u_1, \dots, u_n . Here, care should be taken to ensure the resulting system of inequalities is feasible. For any variable u_i , as long as the inequalities imposed on it are all either lower bounds or upper bounds, a feasible u_i exists. However, any lower and upper bounds imposed on the same u_i must be ensured to be collectively feasible, in turn putting additional restrictions on \mathbf{W} and \mathbf{m} . With this background in mind, we obtain an explicit yet minimally restrictive set of sufficient conditions as follows.

Assume that (15b) holds. Then, we impose the i 'th inequality corresponding to $\sigma' = \mathbf{0}$ and $\sigma'_i = (0, 0, \dots, s, \dots, 0)$ where the s is in the i 'th position. The result will be (15c), which is feasible by (15b). For any other $\sigma' \neq \mathbf{0}, \sigma'_i$, we only impose some (or all) of the upper bound inequalities in (19a) for $j \neq i$, which will always be feasible without any further restrictions on \mathbf{W} and \mathbf{m} . This leads to potentially multiple upper bounds for each $j \neq i$, but all of them are greater than the bound in (15b) and are thus satisfied if (15b) is. This completes the proof of the sufficiency of (15).

Second, we prove the sufficiency of the conditions in (16) following a similar construction. Here, instead of (17), we restrict \mathbf{u} such that for all $\sigma' \neq \mathbf{0}$,

$$Y_{\sigma',s,i} \cup (Y_{\sigma',0,i} \cap Y_{\sigma',\ell,i}) = Y_{\sigma',s,i} \quad \forall i \in \{1, \dots, n\}, \quad (20)$$

and for $\sigma' = \mathbf{0}$,

$$Y_{\sigma',s,i} \cup (Y_{\sigma',0,i} \cap Y_{\sigma',\ell,i}) = Y_{\sigma',0,i} \quad \forall i \in \{1, \dots, n\}. \quad (21)$$

Similar to (18), these will hold if $-\mathbf{c}_{\sigma'} \mathbf{m}_{\sigma'} + (d+1)m_{n+1} \leq u_{n+1} \leq (d+1)m_{n+1}$, for all $\sigma' \neq \mathbf{0}$, which is equivalent to (16a). Then, similar to the proof of (15), we assume that there exists at least one i for which (16b) holds, and enforce the i 'th inequality for $\sigma' = \mathbf{0}$ and $\sigma' = \sigma'_i$. These together impose (16c) on u_i , whose feasibility requires (16b). For any other σ' , we enforce the j 'th inequality(s) for some (or all) $j \in \sigma', j \neq i$, which requires $u_j < -(\mathbf{a}_{j\sigma'} - \mathbf{I}_{j\sigma'}) \mathbf{m}_{\sigma'} + b_j m_{n+1}$ and satisfied if the stronger condition (16d) holds.

Finally, we prove the necessity of (14) by contradiction. Assume, first, that $u_{n+1} \geq (d+1)m_{n+1}$. This implies that (20)

holds for all $\sigma' \in \{0, s\}^n$ and all i . We can then make a sequential argument as follows. Starting from $\sigma' = \mathbf{0}$, we would need at least one i such that $u_i > b_i m_{n+1}$. This i can then never satisfy $u_i < b_i m_{n+1} - (\mathbf{a}_{i\sigma'} - \mathbf{I}_{i\sigma'}) \mathbf{m}_{\sigma'}$ for any σ' , which means that \mathbf{u} cannot belong to any $Y_{\sigma',s,i}^c$ where $i \in \sigma'$. To simplify the discussion and without loss of generality, assume we have chosen $i = 1$. Then, \mathbf{u} cannot belong to any $Y_{\sigma',s,1}^c$ for any $\sigma' = (s, *, \dots, *)$. Therefore, for $\sigma' = (s, 0, \dots, 0)$, we need at least one $i \geq 2$ such that $u_i > b_i m_{n+1} - a_{i1} m_1$. Again, for simplicity and without loss of generality, assume $i = 2$. Then, \mathbf{u} cannot belong to any $Y_{\sigma',s,2}^c$ for any $\sigma' = (s, s, *, \dots, *)$. Continuing this argument, we will ultimately have to impose lower bounds on all the elements of \mathbf{u}_e , which prevent \mathbf{u} from belonging to $Y_{\sigma',s,i}^c$ for $\sigma' = (s, s, \dots, s)$ and any i , ensuring the existence of a stable equilibrium by Theorem 3.3, which is a contradiction. An analogous argument shows that $u_{n+1} \leq -\mathbf{c}_e$ also leads to a contradiction. \square

Note the parallelism between (4) and (15)-(16). In fact, conditions (15b), (15c)-(15d), (16b), and (16c)-(16d) are generalizations of (4b), (4e), (4c), and (4d), respectively. Further, Corollary 3.4 has itself a further consequence with great neuroscientific value, as given next.

Corollary 3.5 (Fully excitatory networks). *Given the dynamics (1), if \mathbf{W} is fully excitatory (all entries are non-negative), then the network has at least one stable equilibrium.*

PROOF. A fully excitatory network corresponds to (1), (7) with a sufficiently negative u_{n+1} that drives the inhibitory node into negative saturation, effectively removing it from the network. This happens if, for all t , $\mathbf{c}\mathbf{x}_e(t) - d\mathbf{x}_{n+1}(t) + u_{n+1} < 0 \Leftrightarrow u_{n+1} < -\mathbf{c}\mathbf{x}_e(t) \Leftrightarrow u_{n+1} < -\mathbf{c}_e$, which, by Corollary 3.4, implies at least one stable equilibrium exists. \square

This result can also be established using the theory of monotone systems [1, 24]. Corollary 3.5 provides a simple and rigorous explanation for the well-known necessity of inhibitory nodes in brain oscillations [63]. On the other hand, the computational neuroscience literature has long shown the possibility of oscillatory activity in *purely inhibitory* networks [31], an important class of networks that we treat next.

3.2 Inhibitory Networks

Our focus here is on linear-threshold network models (1) where only inhibitory nodes are present. Consequently,

$$\mathbf{W} = \begin{bmatrix} -d_{1,1} & -d_{1,2} & \dots & -d_{1,N} \\ -d_{2,1} & -d_{2,2} & \dots & -d_{2,N} \\ \vdots & \ddots & \dots & \vdots \\ -d_{N,1} & -d_{N,2} & \dots & -d_{N,N} \end{bmatrix}$$

with $d_{i,j} \geq 0$ for all i, j .

3.2.1 Necessary Conditions for LoSE

We start by identifying a necessary condition for the lack of stable equilibria of fully inhibitory networks.

Theorem 3.6 (Necessary condition for oscillatory behavior in fully inhibitory networks). *If a fully inhibitory network does not have any stable equilibria, then $\mathbf{I} - \mathbf{W} \notin \mathbb{P}$.*

PROOF. We argue the counter positive: if $\mathbf{I} - \mathbf{W} \in \mathbb{P}$, then a stable equilibrium point exists. The fact that an equilibrium exists for any $\mathbf{u} \in \mathbb{R}^N$ is a direct consequence of [43, Theorem IV.1]. To show it is stable, let us consider any switching region Ω_σ containing the equilibrium. Over this region, the dynamics is described by $-\mathbf{I} + \Sigma \mathbf{W}$. Let r be the cardinality of the set of nodes in active state and let Π be a permutation matrix such that $\Pi\sigma = (\sigma_1, \dots, \sigma_{n-r}, \ell, \dots, \ell)$, where $\sigma_i \in \{0, s\}$. Then,

$$\Pi(-\mathbf{I} + \Sigma \mathbf{W})\Pi^T = \begin{bmatrix} -\mathbf{I} & 0 \\ * & \mathbf{P} \end{bmatrix}, \quad (22)$$

for some matrix \mathbf{P} . The eigenvalues of the system are therefore -1 , with multiplicity $n-r$, and the eigenvalues of \mathbf{P} . Note that \mathbf{P} is a principal submatrix of the matrix $-\mathbf{I} + \mathbf{W}$. Since any principal submatrix of a P -matrix is also a P -matrix, we deduce $-\mathbf{P}$ is a P -matrix too. In addition, since \mathbf{W} corresponds to a fully inhibitory network, $-\mathbf{P}$ is a sign-symmetric matrix, meaning that $(-\mathbf{P}(I, J))(-\mathbf{P}(I, J)) \geq 0$ for all $I, J \subset \{1, \dots, n\}$ such that $|I| = |J|$. By [56, Theorem 1], a sign-symmetric P -matrix is positive stable (if a matrix \mathbf{A} is positive stable, then $-\mathbf{A}$ is stable in the traditional Lyapunov sense, so all the eigenvalues of $-\mathbf{A}$ have negative real parts). Consequently, the eigenvalues of \mathbf{P} fall in the negative complex quadrant and the equilibrium is stable. \square

Theorem 3.6 provides a necessary condition based on the intrinsic properties of the network connectivity. The next result provides an alternative, much simpler necessary condition based on the number of nodes. This result can also be derived using the theory of monotone systems [1, 24], but we here present an independent proof that is instructive in the context of our methodology.

Proposition 3.7 (2-node fully inhibitory networks always have a stable equilibrium). *A fully inhibitory network with only two nodes always has a stable equilibrium.*

PROOF. We divide the proof in two cases depending on whether $(d_{1,1} + 1)(d_{2,2} + 1) - d_{1,2}d_{2,1}$ is (i) greater than 0 or (ii) less than or equal to 0. In case (i), the fact that the network is fully inhibitory results in all the principal minors of $\mathbf{I} - \mathbf{W}$ being greater than zero, and hence $\mathbf{I} - \mathbf{W} \in \mathbb{P}$. By Theorem 3.6, a stable equilibrium point exists.

In case (ii), we look at the equilibrium candidates. Note that only one switching region has a non-stable equilibrium candidate (the one where both nodes are found in active state), while all the other switching regions have stable equilibrium candidates. Hence, proving the existence of multiple equilibrium points in the system is enough to prove the stability of it. By Brouwer Fixed-Point Theorem [7], an equilibrium point exists. Then, since (ii) implies that $\mathbf{I} - \mathbf{W} \notin \mathbb{P}$, we use [43, Theorem VI.1] to conclude that the equilibrium is not unique. As, at least, two equilibrium points exist, one necessarily corresponds to a stable equilibrium candidate. \square

3.2.2 Sufficient Conditions for LoSE

In the following, we derive sufficient conditions for LoSE by investigating the instability properties of the equilibrium candidate of each switching region. In our study, we focus on the following class of network structures.

Definition 3.8 (Pairwise unstable connectivity matrix). *\mathbf{W} is a pairwise unstable connectivity matrix if the system matrix $-\mathbf{I} + \Sigma \mathbf{W}$ corresponding to each switching region involving only two nodes in active state is unstable.*

The definition is valid for arbitrary (i.e., not necessarily inhibitory) networks. For inhibitory networks, it is equivalent to asking each principal minor $M_{i,j}$ of order two of $-\mathbf{I} + \mathbf{W}$ to be negative, $M_{i,j} < 0$, which can only be achieved if $d_{i,j} > 0$ when $i \neq j$. Interestingly, this property allows us to establish conclusions about the instability of the switching regions that involve more than two nodes in active state.

Theorem 3.9 (Instability of networks with pairwise unstable connectivity matrices). *Let \mathbf{W} be a pairwise unstable connectivity matrix. Then, the system matrix $-\mathbf{I} + \Sigma \mathbf{W}$ corresponding to each switching region Ω_σ involving more than two nodes in active state is unstable.*

PROOF. Let Ω_σ be a switching region involving more than two nodes in active state and consider its corresponding system matrix $-\mathbf{I} + \Sigma \mathbf{W}$. Using the same decomposition as in (22), the system eigenvalues are -1 with multiplicity $N-r$ and the eigenvalues of the $r \times r$ -matrix \mathbf{P} . For the latter, consider the characteristic polynomial of \mathbf{P} , $\text{Char}(\mathbf{P} - \lambda \mathbf{I}) = (-1)^r \lambda^r + (-1)^{r-1} K_{r-1} \lambda^{r-1} + \dots + (-1) K_1 \lambda + K_0$, where K_k represents the sum of all the principal minors of order $r-k$. In particular, since $r > 2$, $K_{r-2} = \sum_{i \neq j \text{ with } \sigma_i, \sigma_j = \ell} M_{i,j}$. Since \mathbf{W}

is pairwise unstable, we deduce $K_{r-2} < 0$ and, consequently, $\text{sign}((-1)^r) \neq \text{sign}((-1)^{r-2} K_{r-2})$. Given that the characteristic polynomial has a sign change in its coefficients, using the Routh-Hurwitz criteria [28] we deduce that there exists a root λ of the characteristic polynomial with $\text{Re}(\lambda) > 0$, as claimed. \square

The implication of Theorem 3.9 is that the analysis of LoSE for networks with pairwise unstable connectivity matrices can be reduced to the study of those switching regions where only up to one node is in active state. This is what we do in our next result.

Proposition 3.10 (Characterization of LoSE in networks with pairwise unstable connectivity matrices). *Let $(\mathbf{W}, \mathbf{u}, \mathbf{m})$ be a fully inhibitory network with a pairwise unstable connectivity matrix. Define*

$$\begin{aligned} \mathbb{T}_0 &= \{\mathbf{u} \mid \exists i \in \{1, \dots, N\} \text{ s.t. } u_i > 0\}, \\ \mathbb{T}_i &= \{\mathbf{u} \mid \bigvee_{i \neq j \in \{1, \dots, n\}} (u_j > \frac{d_{j,i}}{d_{i,i} + 1} u_i)\}, \end{aligned}$$

for $i \in \{1, \dots, N\}$, and let $\mathbb{T} = \bigcap_{i \in \{0, \dots, n\}} \mathbb{T}_i$. If $\mathbf{u} \in C = [0, (d_{1,1} + 1)m_1] \times \dots \times [0, (d_{N,N} + 1)m_N] \neq \emptyset$, then LoSE holds iff $\mathbf{u} \in \mathbb{T}$.

PROOF. From Theorem 3.9, the equilibrium candidate of any switching region with more than one node in active state is unstable. In addition, one can show that no switching region with a node in positive saturation can contain its corresponding equilibrium candidate. This is because the dynamics for such node, say k , would take the form

$$\tau \dot{x}_k = -x_k + \left[- \sum_{i \neq k} d_{k,i} x_i - d_{k,k} m_k + u_k \right]_0^{m_k}.$$

Since $\mathbf{u} \in C$, we deduce $u_k < (d_{k,k} + 1)m_k$, and so $-d_{k,k}m_k + u_k < m_k$. Consequently, the node always goes out of positive saturation. Similarly, for the switching region where all nodes are in negative saturation, the fact that the equilibrium candidate falls outside it is a consequence of $\mathbf{u} \in \mathbb{T}_0$. Finally, for the switching region where node $i \in \{1, \dots, N\}$ is in active state and all others are in negative saturation, its corresponding equilibrium candidate falls outside it iff $\mathbf{u} \in \mathbb{T}_i$. \square

The assumption that $\mathbf{u} \in C$ in Proposition 3.10 means that the input has a low magnitude, avoiding positive saturation of the nodes in key switching regions. We can relate this assumption to actual brain networks by observing that these networks are not designed to process a range of inputs that would drive them directly to a saturated state, but rather that allow the oscillatory behavior to take place. Thus, although restrictive from a mathematical standpoint, the assumption is biologically consistent and helps successfully capture important existent behavior in real brain networks.

Given Proposition 3.10, we next focus on understanding the conditions on the network connectivity matrix ensuring that \mathbb{T} is nonempty. We first note that such conditions must involve at least three nodes. This is because if only two nodes, say i and j , are considered then, by the pairwise instability assumption, $\frac{d_{j,i}}{d_{i,i}+1} < \frac{d_{j,j}+1}{d_{i,j}}$, and therefore if $u_j > \frac{d_{j,i}}{d_{i,i}+1}u_i$ then $u_i < \frac{d_{i,j}}{d_{j,j}+1}u_j$, and vice versa. To find then conditions involving three or more nodes, we re-interpret the inequalities that define $\mathbb{T}_{-0} := \bigcap_{i \in \{1, \dots, N\}} \mathbb{T}_i$ using graph-theoretic concepts. Consider the weighted complete graph with vertex set $\{1, \dots, N\}$, edge set $\{1, \dots, N\} \times \{1, \dots, N\} \setminus \{(i, i) \mid i \in \{1, \dots, N\}\}$ (i.e., self-loops are excluded), and weight matrix

$$\mathbf{F} = \begin{bmatrix} 0 & \frac{d_{1,1}+1}{d_{2,1}} & \frac{d_{1,1}+1}{d_{3,1}} & \dots & \frac{d_{1,1}+1}{d_{N,1}} \\ \frac{d_{2,2}+1}{d_{1,2}} & 0 & \frac{d_{2,2}+1}{d_{3,2}} & \dots & \frac{d_{2,2}+1}{d_{N,2}} \\ \frac{d_{3,3}+1}{d_{1,3}} & \frac{d_{3,3}+1}{d_{2,3}} & 0 & \dots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{d_{N,N}+1}{d_{1,N}} & \frac{d_{N,N}+1}{d_{2,N}} & \frac{d_{3,3}+1}{d_{N,3}} & \dots & 0 \end{bmatrix}.$$

In this definition, edge (i, j) corresponds to the inequality $u_j \frac{d_{i,i}+1}{d_{j,i}} > u_i$. In this way, the row i of \mathbf{F} corresponds to the set of inequalities that define the set \mathbb{T}_i . To find conditions such that \mathbb{T}_{-0} is not empty, it is necessary and sufficient that there exists a path that involves every node and corresponds to a feasible sequence of inequalities. Note that \mathbb{T}_i is not empty when some inequality holds, meaning that node i has an outgoing edge. Then, for \mathbb{T}_{-0} to be non empty, every node needs to have an outgoing edge. This is only possible if a cycle exists, restricting all those u_i involved in it. For those i not involved in the cycle, there always exists a sufficiently small value of u_i that ensures \mathbb{T}_i , and consequently \mathbb{T}_{-0} , is not empty.

Given these observations, we consider the collection of cycles of length 3 or more of the graph defined above. This collection represents all the ways the inequalities involved in the definition of the set \mathbb{T}_{-0} can be satisfied while remaining compatible with the pairwise instability condition. For each cycle $G_c = (V_c, E_c)$, consider the connectivity matrix \mathbf{F}_c , of dimension $|V_c|$, that results from having the edges inherit their weights from the full adjacency matrix \mathbf{F} . The matrix \mathbf{F}_c has one non-zero element per row and column. Consequently, for

the cycle defined by G_c , we have successfully reduced the feasibility problem of the inequalities to the problem of finding \mathbf{v} such that $\mathbf{F}_c \mathbf{v} > \mathbf{v}$ holds componentwise. If \mathbf{v} exists, then the inequalities defined by G_c are feasible, and the set \mathbb{T}_{-0} is not empty. Moreover, if the resulting \mathbf{v} has some positive component, then the set \mathbb{T} is not empty.

Theorem 3.11 (Sufficient condition for LoSE in fully inhibitory networks with pairwise unstable connectivity matrix). *Let \mathbf{W} be fully inhibitory and a pairwise unstable connectivity matrix. If there is cycle whose adjacency matrix satisfies $\rho(\mathbf{F}_c) > 1$, then there exists \mathbf{u} for which LoSE holds.*

PROOF. Let G_c be a cycle whose adjacency matrix \mathbf{F}_c satisfies $\rho(\mathbf{F}_c) > 1$. Since G_c is strongly connected, \mathbf{F}_c is irreducible. Using the Perron-Frobenius theorem for irreducible matrices [8, Theorem 1.11], we deduce that $\rho(\mathbf{F}_c)$ is an eigenvalue of \mathbf{F}_c and has an eigenvector \mathbf{v} with positive components. Since $\rho(\mathbf{F}_c) > 1$, $\mathbf{F}_c \mathbf{v} = \rho(\mathbf{F}_c) \mathbf{v} > \mathbf{v}$ element-wise. We can use this eigenvector to construct \mathbf{u} belonging to \mathbb{T} and C as follows. Let $\lambda \in (0, \min_{i \in V_c} \frac{(d_{i,i}+1)m_i \|\mathbf{v}\|}{v_i})$. Then, for every i in the cycle, let $u_i = \frac{v_i}{\|\mathbf{v}\|} \lambda$. Since $\mathbf{F}_c \mathbf{v} > \mathbf{v}$, we have $\mathbf{u} \in \mathbb{T}_i$ for every i in the cycle. Moreover, by definition, $u_i \leq m_i(d_{i,i}+1)$. Since the components of \mathbf{v} are all positive, so are the ones of \mathbf{u} . For those nodes j that do not belong to the cycle, we can find values that satisfy the inequalities by setting $u_j = 0$. Since the entries u_i are positive for all the nodes i in the cycle, the vector \mathbf{u} so constructed belongs to \mathbb{T} and C , and LoSE follows from Proposition 3.10. \square

We refer to the cycle in Theorem 3.11 as *valid*. The next result guarantees the necessity of the existence of a valid cycle when the input is restricted to have small values.

Corollary 3.12 (Necessary condition for LoSE in fully inhibitory networks with pairwise unstable connectivity matrix with small inputs). *Let \mathbf{W} be fully inhibitory and a pairwise unstable connectivity matrix. If \mathbf{u} is restricted to C , a valid cycle exists iff there is \mathbf{u} for which LoSE holds.*

PROOF. The implication from left to right follows from Theorem 3.11. To show the other implication, by Proposition 3.10, we only need to prove that, when $\mathbf{u} \in C$, the existence of a valid cycle is necessary for \mathbb{T} to be not empty. We reason by contradiction, i.e., assume there does not exist any valid cycle but $\mathbb{T} \neq \emptyset$. Let $\mathbf{u} \in C \cap \mathbb{T}$. As $\mathbf{u} \in \mathbb{T}$, there exists a feasible sequence of inequalities. Let G_c be the corresponding cycle, say of t nodes i_1, \dots, i_t , encoding this sequence,

$$u_{i_1} < u_{i_2} \frac{d_{i_1,i_1}+1}{d_{i_2,i_1}}, \dots, u_{i_t} < u_{i_1} \frac{d_{i_t,i_t}+1}{d_{i_1,i_t}}$$

holds, which implies $\frac{d_{i_1,i_1}+1}{d_{i_2,i_1}} \frac{d_{i_2,i_2}+1}{d_{i_3,i_2}} \dots \frac{d_{i_t,i_t}+1}{d_{i_1,i_t}} > 1$. Due to the structure of the adjacency matrix \mathbf{F}_c of the cycle, this means that $\det(\mathbf{F}_c) > 1$, and hence $\rho(\mathbf{F}_c) > 1$, implying that the cycle is valid, which is a contradiction.

The graph-theoretical approach to characterize LoSE in inhibitory networks with pairwise unstable connectivity matrices can also be used to derive conditions on how the system oscillations occur.

Theorem 3.13 (Node outside valid cycle does not oscillate). *Consider a fully inhibitory network with pairwise unstable connectivity matrix and let i be one of its nodes. There*

exists $\mathbf{u} \in C$ that provides lack of stable equilibria for which the node i does not oscillate, i.e. is always found in the same saturated state, if and only if the node i does not belong to the valid cycle associated to \mathbf{u} .

PROOF. We prove the implication from left to right (the other one can be reasoned analogously). As the node i does not oscillate, then it must be in positive or negative saturation. As $\mathbf{u} \in C$, $u_i < (d_{i,i} + 1)m_i$, then it must be in negative saturation, because the node cannot remain in positive saturation state. If a node is in negative saturation, then it does not contribute to the oscillations of the other nodes, meaning that it is effectively as considering a new network with $N - 1$ nodes. For this network to oscillate for \mathbf{u}_{-i} , it is necessary that there exists a valid cycle (which will not include node i). \square

4 Oscillations in Networks of Networks

Here, we build on the results of Section 3 to study the oscillatory behavior of a network of oscillators, each itself represented by a linear-threshold network. Motivated by the experimental and computational evidence in brain networks, we are interested in the phenomena of synchronization and phase-amplitude coupling. Consider n oscillators, each modeled by an E-I pair, connected over a network with adjacency matrix $\mathbf{A} \in \mathbb{R}_{\geq 0}^{n \times n}$ via their excitatory nodes [41]. Since \mathbf{A} captures inter-oscillator connections, its diagonal entries are zero. The dynamics of the resulting network of networks is

$$\mathbf{T}\dot{\mathbf{x}} = -\mathbf{x} + [\mathbf{W}\mathbf{x} + \mathbf{u}]_0^{\mathbf{m}}, \quad (23a)$$

where $\mathbf{x} = [\mathbf{x}_1, \dots, \mathbf{x}_n]$, $\mathbf{x}_i = [x_{i,1}, x_{i,2}]$, \mathbf{u} and \mathbf{m} have similar decompositions, $\mathbf{T} = \text{diag}(\tau_1, \tau_1, \tau_2, \tau_2, \dots, \tau_n, \tau_n)$, and

$$\mathbf{W} = \text{diag}(\mathbf{W}_1, \dots, \mathbf{W}_n) + \mathbf{A} \otimes \mathbf{E}, \quad \mathbf{E} = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}, \quad (23b)$$

$$\mathbf{W}_i = \begin{bmatrix} a_i & -b_i \\ c_i & -d_i \end{bmatrix}, \quad A_{ii} = 0, \quad i \in \{1, \dots, n\}, \quad (23c)$$

and \otimes denotes the Kronecker product. We assume each E-I pair oscillates on its own. The first question we address is whether the pairs maintain oscillatory behavior once inter-connected.

Theorem 4.1 (Excitatory-to-excitatory-coupled networks). *Consider the dynamics (23) and assume that each \mathbf{W}_i satisfies the conditions of Theorem 3.1. Then, the overall network does not have any stable equilibria if and only if*

$$\sum_{j=1}^N A_{ij} m_{j,1} < \bar{u}_{i,1} - u_{i,1}, \quad (24)$$

$$\bar{u}_{i,1} \triangleq b_i \min \left\{ m_{i,2}, \frac{u_{i,2} + c_i m_{i,1}}{d_i + 1} \right\} - (a_i - 1)m_{i,1},$$

holds for at least one $i \in \{1, \dots, n\}$. Moreover, the state of any E-I pair for which (24) holds may not converge to a fixed value (except for trivial solutions at unstable equilibria, if any) irrespective of the validity of (24) for other pairs.

PROOF. Consider an arbitrary $\sigma \in \{0, \ell, s\}^{2n}$ and let $L \subseteq \{1, \dots, n\}$, $|L| = r$ be the set of pairs whose respective switching region from σ is unstable (i.e., $\sigma_i = (\ell, j)$, $j \in \{0, \ell, s\}$, $i \in L$). Let $\Pi = \bar{\Pi} \otimes \mathbf{I}_2$ be the permutation matrix that permutes the pairs such that these r

pairs are placed first. Then, $\Pi(-\mathbf{I} + \Sigma\mathbf{W})\Pi^T = [\mathbf{R}, \star; \mathbf{0}, \mathbf{N}]$ where $\mathbf{R} = -\mathbf{I} + \Sigma_L(\text{diag}(\{\mathbf{W}_i\}_{i \in L}) + \mathbf{A}_L \otimes \mathbf{E})$, $\mathbf{N} = -\mathbf{I} + \Sigma_{L^c} \text{diag}(\{\mathbf{W}_i\}_{i \in L^c})$, and Σ_L is the $2r \times 2r$ principal submatrix of Σ consisting of rows and columns corresponding to the pairs in L . \mathbf{A}_L and Σ_{L^c} are defined similarly. Therefore, the eigenvalues of $-\mathbf{I} + \Sigma\mathbf{W}$ consist of those of \mathbf{R} and \mathbf{N} .

\mathbf{N} has $n - r$ eigenvalues equal to -1 and $n - r$ eigenvalues that equal $-1 - d_i$ or -1 , depending on whether $\sigma_{i,2} = \ell$ or not for each $i \in L^c$. On the other hand, if $r > 0$, then

$$\begin{aligned} \text{tr}(\mathbf{R}) &= \text{tr}(-\mathbf{I} + \Sigma_L \text{diag}(\{\mathbf{W}_i\}_{i \in L})) \\ &\geq \text{tr}(-\mathbf{I} + \text{diag}(\{\mathbf{W}_i\}_{i \in L})) = \sum_{i=1}^r a_i - d_i - 2 > 0. \end{aligned}$$

Thus, any switching region Ω_σ is stable if and only if $\sigma_{i,1} \neq \ell$ for all $i \in \{1, \dots, n\}$. To prove the sufficiency of (24), consider any stable Ω_σ . Then, if (24) holds for even one i ,

$$u_{i,1} + \sum_{j=1}^n A_{ij}(\mathbf{x}_\sigma^*)_{j,1} \leq u_{i,1} + \sum_{j=1}^n A_{ij} m_{j,1} \stackrel{(24)}{<} \bar{u}_{i,1},$$

ensuring $\mathbf{x}_\sigma^* \notin \Omega_\sigma$ (by Theorem 3.1) and the sufficiency of (24). Regarding the last statement of the theorem, note that for \mathbf{x}_i to converge to a fixed value, $\sum_j A_{ij} \mathbf{x}_{j,1}(t)$ must either also converge to a fixed value or be greater than or equal to $\bar{u}_{i,1} - u_{i,1}$ for sufficiently large t , both contradicting (24).

To prove the necessity of (24), assume that it does not hold for any i or, in other words, at least one of

$$u_{i,1} + \sum_{j=1}^N A_{ij} m_{j,1} > b_i m_{i,2} - (a_i - 1)m_{i,1}, \quad (25a)$$

$$u_{i,1} + \sum_{j=1}^N A_{ij} m_{j,1} > \frac{b_i(u_{i,2} + c_i m_{i,1})}{d_i + 1} - (a_i - 1)m_{i,1}, \quad (25b)$$

holds for all $i \in \{1, \dots, n\}$. Now, define $\sigma \in \{0, \ell, s\}^n$ by

$$\sigma_i = \begin{cases} (s, s) & \text{if } u_{i,2} \geq (d_i + 1)m_{i,2} - c_i m_{i,1}, \\ (s, \ell) & \text{if } u_{i,2} < (d_i + 1)m_{i,2} - c_i m_{i,1}. \end{cases}$$

Note that (25b) implies (25a) if $u_{i,2} \geq (d_i + 1)m_{i,2} - c_i m_{i,1}$ and (25a) implies (25b) otherwise. Given that all the excitatory nodes are at saturation in σ , it is not difficult to show that Ω_σ (which is stable, by the reasoning above) contains its equilibrium, showing the necessity of (24). \square

The assumptions of Theorem 4.1 are consistent with the observation that long-range connections between different brain regions are almost exclusively excitatory. Nevertheless, it is possible that these excitatory connections target both excitatory and inhibitory populations in the receiving region. Therefore, a more realistic scenario is where the inter-network coupling consists of both excitatory-to-excitatory and excitatory-to-inhibitory connections. This generality, however, comes at the price that condition (24) becomes only sufficient.

Theorem 4.2 (Excitatory-to-all-coupled networks). *Consider the dynamics (1) with*

$$\mathbf{W} = \text{diag}(\mathbf{W}_1, \dots, \mathbf{W}_N) + \mathbf{A}^e \otimes \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix} + \mathbf{A}^i \otimes \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix},$$

where $\mathbf{A}^e, \mathbf{A}^i \in \mathbb{R}_{\geq 0}^{N \times N}$, $\text{diag}(\mathbf{A}^e) = \text{diag}(\mathbf{A}^i) = \mathbf{0}$,

$$\mathbf{W}_i = \begin{bmatrix} a_i & -b_i \\ c_i & -d_i \end{bmatrix}, \quad a_i, b_i, c_i, d_i > 0, \quad \forall i \in \{1, \dots, N\},$$

and each \mathbf{W}_i satisfies the conditions of Theorem 3.1. Then, this system does not have any stable equilibria if

$$\sum_{j=1}^N A_{ij}^e m_{j,1} < b_i m_{i,2} - (a_i - 1) m_{i,1} - u_{i,1} \quad (26a)$$

$$\sum_{j=1}^N [(d_i + 1) A_{ij}^e - b_i A_{ij}^i]^+ m_{j,1} < (b_i c_i - (a_i - 1)(d_i + 1)) m_{i,1} - (d_i + 1) u_{i,1} + b_i u_{i,2} \quad (26b)$$

$$\sum_{j=1}^N [b_i A_{ij}^i - (d_i + 1) A_{ij}^e]^+ m_{j,1} < (d_i + 1) u_{i,1} - b_i u_{i,2} \quad (26c)$$

all hold for at least one $i \in \{1, \dots, N\}$.

PROOF. Consider $\sigma \in \{0, \ell, s\}^{2N}$ and let $0 \leq n \leq N$ be the number of pairs whose respective switching region from σ is unstable (i.e., $(\ell, 0)$, (ℓ, ℓ) , (ℓ, s)). Without loss of generality, let them be the first n pairs. Then,

$$-\mathbf{I} + \Sigma \mathbf{W} = \Pi \begin{bmatrix} \mathbf{B}_1 & \star & \star \\ \mathbf{0} & \mathbf{B}_2 & \star \\ \mathbf{0} & \mathbf{0} & -\mathbf{I} \end{bmatrix} \Pi^T,$$

where $\mathbf{B}_1 = -\mathbf{I} - \Sigma_{n+1:N}^i \text{diag}(d_{n+1}, \dots, d_N)$ and $\mathbf{B}_2 = -\mathbf{I} + \Sigma_{1:n}(\text{diag}(\mathbf{W}_1, \dots, \mathbf{W}_n) + \mathbf{A}_{1:n} \otimes \text{diag}(1, 0))$, and Π is a permutation matrix to separate the excitatory and inhibitory nodes of the stable pairs. Therefore, similar to Theorem 4.1, $\sigma \in \{0, \ell, s\}^{2N}$ is stable if and only if all its N subindices are stable. Assume this is the case and (26) holds (at least) for $i \in \{1, \dots, N\}$. Then, from (26a), $u_{i,1} + \sum_{j=1}^N A_{ij}^e \mathbf{x}_{j,1}^* < b_i m_{i,2} - (a_i - 1) m_{i,1}$, and from (26b)-(26c),

$$0 < (d_i + 1) \left(u_{i,1} + \sum_{j=1}^N A_{ij}^e \mathbf{x}_{j,1}^* \right) - b_i \left(u_{i,2} + \sum_{j=1}^N A_{ij}^i \mathbf{x}_{j,1}^* \right) < (b_i c_i - (a_i - 1)(d_i + 1)) m_{i,1},$$

ensuring that $\mathbf{x}_\sigma^* \notin \Omega_\sigma$. \square

Unlike Theorem 4.1, the condition of Theorem 4.2 is not necessary. The reason is that even if (26) is violated for all i , they need not be violated with the same excitatory saturation patterns (i.e., vectors in $\{0, s\}^N$ showing whether the excitatory node of each pair is in negative or positive saturation) while in Theorem 4.1, if (24) is violated for any node, it would be with the excitatory saturation pattern of (s, \dots, s) (possibly among others). This ensures the existence of at least one stable $\sigma \in \{0, \ell, s\}^{2N}$ (whose excitatory elements are all s) that contains its equilibrium candidate. On the other hand, when (26) is violated for each i , it may be with one or more excitatory activation patterns none of which may be shared among all the pairs. Therefore, the necessary and sufficient

condition for lack of stable equilibria in this case is that the intersection of the sets of excitatory activation patterns of all pairs is empty, with the convention that this set is empty for any pair for which (26) holds.

5 Conclusions and Future Work

We have studied nonlinear networked dynamical systems with bounded linear-threshold activation functions and different classes of architectures interconnecting excitatory and inhibitory nodes. Given the arbitrary dimensionality of these networks, and motivated by the Poincare-Bendixson theorem, we have relied on the lack of stable equilibria (LoSE) as a system-based proxy for the commonly used signal-based definitions of oscillatory dynamics. Our main contributions are various necessary and/or sufficient conditions on the structure of linear-threshold networks for LoSE. In particular, we considered three classes of network architectures motivated by different aspects of mammalian cortical architecture: networks with multiple excitatory and one inhibitory nodes, purely inhibitory networks, and arbitrary networks of two-dimensional excitatory-inhibitory subnetworks. Among the important avenues for future work, we highlight the extension of our results to include conduction delays, the robustness analysis to process noise, and the characterization of phase-phase and phase-amplitude coupling.

Appendix A Lack of Stable Equilibria as a Proxy for Oscillations

Throughout the paper, we employ LoSE as a proxy for oscillations, as defined in Definition 2.1. Here we provide numerical evidence that, at least for systems with linear-threshold dynamics, this proxy is tight. The evidence is structured along three directions. First, we perform a Monte Carlo sampling of a 10-node linear-threshold network and show the strong overlap between networks that satisfy Definition 2.1 and those without stable equilibria. Second, for the same sampled set, we perform a similar comparison *locally* around the boundaries of the LoSE parameter set, and show that the transition from oscillating to non-oscillating and the transition from LoSE to presence of stable equilibria are tightly related. Third, we exploit the analytical characterizations in Section 4 to show not only the tightness of LoSE as a binary measure of the existence of oscillations, but also the relationship between the distance of a network to the appearance of stable equilibria and the strength of its oscillations.

To numerically measure the existence and strength of oscillations, we construct an *oscillation index* directly based on Definition 2.1. First, we define a *regularity index* to quantify Definition 2.1(i), i.e., the existence of distinct and pronounced resonance peaks in the power spectrum of a state trajectory. After mean-centering all state trajectories $x_i(t)$, we let $X_i(f)$ be the Fourier transform of $x_i(t)$, and $f_i = \arg \max_f |X_i(f)|$. The regularity index is defined as

$$\chi_{\text{reg}} = \max_{i=1, \dots, n} \chi_{\text{reg}, i},$$

$$\chi_{\text{reg}, i} = \frac{|X_i(f_i)|}{\max\{|X_i((1 - \epsilon)f_i)|, |X_i((1 + \epsilon)f_i)|\}} \in [1, \infty),$$

where $\epsilon \in (0, 1)$. For each i , a value of $\chi_{\text{reg}, i} = 1$ indicates a flat power spectrum (lack of oscillations) whereas $\chi_{\text{reg}, i} \rightarrow \infty$ indicates a Dirac delta at f_i (periodic oscillations). Clearly, the regularity of oscillations lies on a continuum, with more

regularity (less chaotic behavior) as $\chi_{\text{reg},i}$ grows. We then take the maximum of $\chi_{\text{reg},i}$ to obtain a regularity index of the collection of state trajectories $\mathbf{x}(t)$.

Second, we quantify Definition 2.1(ii) (lack of a constant asymptotic limit) simply by the steady state peak to peak amplitude of the oscillating trajectories, normalized by its maximum value possible, and maximized over all trajectories,

$$\chi_{\text{pp}} = \max_{i=1,\dots,n} \frac{\limsup_{t \rightarrow \infty} x_i(t) - \liminf_{t \rightarrow \infty} x_i(t)}{m_i}$$

The larger χ_{pp} , the stronger the oscillations in (at least one channel of) $\mathbf{x}(t)$, regardless of how regular or chaotic they are. Inclusion of this second metric is critical in distinguishing between oscillations that are extremely regular but almost vanishing in magnitude (and hence devoid of any practical significance), and oscillations with significant amplitudes.

We combine the regularity and peak to peak indices to obtain the oscillation index,

$$\chi_{\text{osc}} = \chi_{\text{reg}} \cdot \chi_{\text{pp}} \quad (27)$$

Among the various potential ways of combining χ_{reg} and χ_{pp} , this choice acts a *conjunction* of regularity and strength measures, so that a signal is considered oscillatory if it has high regularity *and* strength, as required in Definition 2.1.

A.1 Global Inspection via Monte-Carlo Sampling of Structural Parameters

We start our numerical inspection of the relationship between LoSE and existence of oscillations using a global Monte-Carlo sampling of the parameter space of linear-threshold networks. In general, the distribution of indices χ_{reg} , χ_{pp} , and χ_{osc} depend on the number and excitatory/inhibitory mix of the nodes. However, this dependence is not critical while, at the same time, sweeping over N_E and N_I would be computationally prohibitive for our Monte-Carlo sampling. Therefore, we here generate 20000 random networks using the fixed medium-range values of $N_E = N_I = 5$ and address the role of network size in Section A.3. We use parameter values drawn randomly and independently from the following distributions

$$|w_{ij}| \sim \mathcal{U}(0, B), \quad u_i \sim \mathcal{U}(-B, B), \quad m_i \sim \mathcal{U}(1, B) \\ x_i(0) \sim \mathcal{U}(0, m_i), \quad \forall i, j = 1, \dots, n,$$

where $n = N_E + N_I = 10$ and $B = 10$ is an (arbitrary, but necessary) upper bound on the parameter values. We employ the value of $\tau = 1$ throughout as the timescale only compresses or stretches the trajectories over time. For each random network, we first check whether it possesses any stable equilibria from (3). For networks that lack any stable equilibria, we simulate their trajectories, starting from random initial conditions, over a sufficiently long time horizon⁶ and compute their value of χ_{osc} in (27). For networks that did have (one or more) stable equilibria, we repeat the same but starting from 10 different initial conditions to capture the possibility of the co-existence of oscillatory and equilibrium attractors.

Figure 2 shows the resulting statistics. First, we observe that the lack of stable equilibria is less frequent than their exist-

tence in random networks. Second, the values of χ_{osc} lie on a continuous spectrum, regardless of whether the networks possess or lack stable equilibria. However, the distribution of χ_{osc} is significantly different between the two cases.

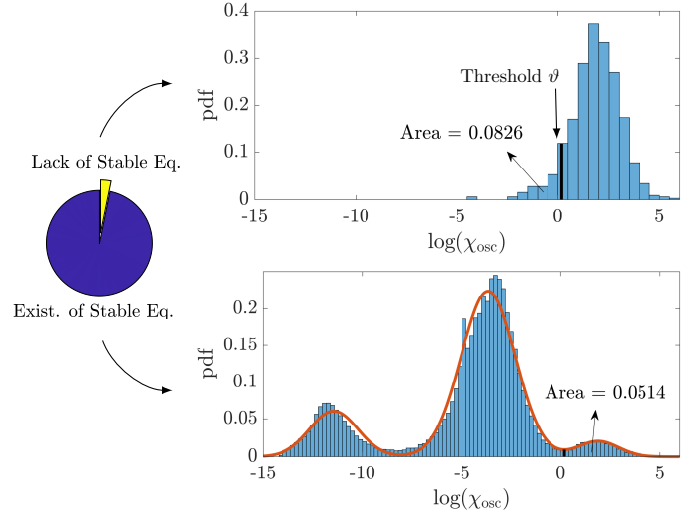


Fig. 2. The statistics of LoSE and χ_{osc} for randomly generated linear-threshold networks via Monte-Carlo sampling of their parameter space, as described in Section A.1. Top right, only about 8% of networks without stable equilibria lack strong oscillations (though the majority still possess weak oscillations). Bottom right, only about 5% of networks with stable equilibria also have strongly oscillatory trajectories (corresponding to rare oscillatory attractors that co-exist with equilibrium attractors).

To quantify this difference, we need to place a threshold on the value of χ_{osc} and binarize the networks into ones that do show oscillatory activity and ones that do not. In order to avoid using arbitrary thresholds, we chose to obtain it from the empirical distribution of χ_{osc} we have just obtained. It can be seen from the bottom-right panel of Figure 2 that the distribution of χ_{osc} for networks with stable equilibria is naturally tri-modal. The three chunks of the distribution correspond, roughly, to strongly oscillating, barely oscillating, and effectively non-oscillating trajectories, respectively. We thus fit a Gaussian mixture model to this distribution and use the trough of the distribution between the center and right modes as the threshold for the existence of oscillations. Let this threshold be called ϑ . To ensure uniformity, ϑ is also used for networks without stable equilibria. Accordingly, we observe that only about 8% of networks *without* stable equilibria lack strong oscillations (though the majority of which still possess weak oscillations) indicating the near-sufficiency of LoSE for existence of oscillations. On the other hand, only about 5% of networks *with* stable equilibria also have strongly oscillatory trajectories (corresponding to rare oscillatory attractors that co-exist with equilibrium attractors, each having their respective regions of attraction) showing the near-necessity of LoSE for exhibiting oscillations.

In conclusion, on a global landscape of the parameter space, LoSE provides an unambiguous and system-based proxy with great analytical utility for the existence of oscillations which closely matches the signal-based definition of oscillations (cf. Definition 2.1) used in computational neuroscience.

⁶ We simulate all network trajectories over $t \in [0, 2000]$ with a time step of 0.01 using MATLAB's `ode45` and use the final 5% of the trajectories for the computation of χ_{reg} and χ_{pp} .

A.2 Local Inspection via Linear Sweeping of Structural Parameters

In this section, we assess the consistency of LoSE as a proxy for oscillations on a local basis. Our basic idea is the following: given a pair of networks, one which displays strong oscillations and another that displays none, consider the convex combination of their parameters $(\mathbf{W}, \mathbf{m}, \mathbf{u})$. As we traverse the resulting convex set, the strong oscillations present on one extreme eventually disappear into the non-oscillatory behavior of the other extreme. Given our discussion above, the value of the convex parameter where this transition occurs can be determined in two different ways: either through LoSE or through the oscillatory metric χ_{osc} . The extent to which the two ways coincide offers a measure of the *local* consistency of LoSE as a proxy for oscillations.

We carry out this vision by randomly selecting 500 pairs of networks out of the 20000 generated in Section A.1 as follows. The first network of each pair is uniformly randomly selected among the strongly oscillating networks of the top-right panel of Figure 2 (those to the right of the black vertical line) that also lack stable equilibria, while the second network of each pair is uniformly randomly selected from the almost non-oscillating networks of the bottom-right panel of Figure 2 (those belonging to the left-most bump in the distribution) that have some stable equilibria as well. Letting $(\mathbf{W}_1, \mathbf{m}_1, \mathbf{u}_1)$ and $(\mathbf{W}_2, \mathbf{m}_2, \mathbf{u}_2)$ denote the parameters of these networks, we then linearly sweep between the two to obtain networks with parameters $\mathbf{W} = (1 - \alpha)\mathbf{W}_1 + \alpha\mathbf{W}_2$, $\mathbf{m} = (1 - \alpha)\mathbf{m}_1 + \alpha\mathbf{m}_2$, $\mathbf{u} = (1 - \alpha)\mathbf{u}_1 + \alpha\mathbf{u}_2$, $\alpha \in [0, 1]$,

and compute LoSE and χ_{osc} for each intermediate network. Given the fact that the set of networks with LoSE is not convex, we only retain the cases for which only one switching in LoSE occurred between the end points as we sweep (due to the complexity of estimating the switching point in χ_{osc} , as discussed next). The value of α at which LoSE switches (i.e., a stable equilibrium point appeared) is defined as α_{LoSE}^* . Similarly, the value of α at which $\log(\chi_{\text{osc}})$ crosses the threshold ϑ is defined as $\alpha_{\chi_{\text{osc}}}^*$. Due to the noisy nature of χ_{osc} estimation (see, e.g., Figure 3(b-d)), the numerical (or even visual) detection of this threshold crossing is often not straightforward. Here, we define $\alpha_{\chi_{\text{osc}}}^*$ as the first time (while increasing α from 0 to 1) that the average of 3 consecutive χ_{osc} values is above ϑ and the average of the following 3 χ_{osc} values falls below ϑ .

The resulting comparison of α_{LoSE}^* and $\alpha_{\chi_{\text{osc}}}^*$ for the 500 random pairs of networks (except those having more than one switch in LoSE, as noted above) is shown in Figure 3(a). Details of three sample scenarios are also shown in Figure 3(b-d), with the corresponding points marked in Figure 3(a). Even though not all the points lie on the $\alpha_{\chi_{\text{osc}}}^* = \alpha_{\text{LoSE}}^*$ line, they are often very close to it, indicating a strong consistency between the detection of oscillations using LoSE and χ_{osc} .

In addition to the closeness of the majority of the points to the $\alpha_{\chi_{\text{osc}}}^* = \alpha_{\text{LoSE}}^*$ line, also notable from Figure 3(a) is the fact that the majority of the points lying away from this line lie above it, a situation exemplified in Figure 3(c). This corresponds to scenarios where the creation of the stable equilibrium point at α_{LoSE}^* does not immediately nullify the ongoing oscillatory attractor, but the two coexist with distinct regions of attraction for some range of α values. The points lying below the $\alpha_{\chi_{\text{osc}}}^* = \alpha_{\text{LoSE}}^*$ line, however, often indicate a complexity with the detection of $\alpha_{\chi_{\text{osc}}}^*$. An example of this can be seen in Figure 3(d), where $\alpha_{\chi_{\text{osc}}}^*$ is detected as the first

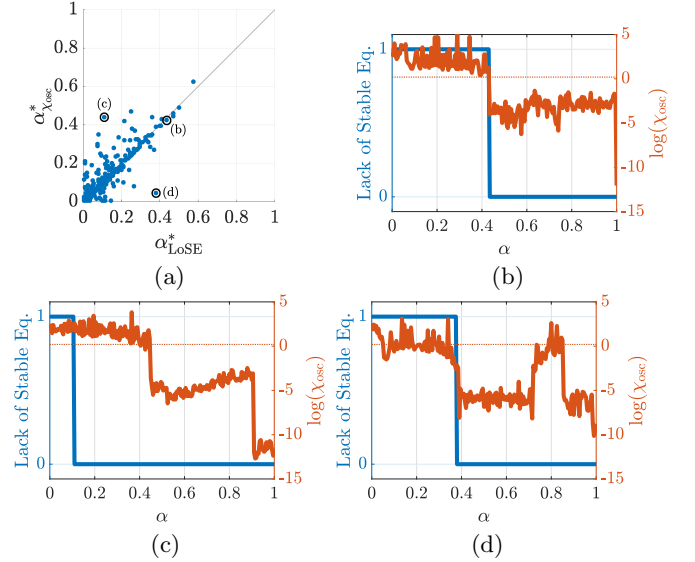


Fig. 3. The consistency of LoSE (as a proxy for oscillations) and χ_{osc} (as a “ground truth” measure of oscillations) when locally sweeping between network parameters that give rise to oscillations and those that do not. **(a)** The value of α at which LoSE switches vs. the value of α at which $\log(\chi_{\text{osc}})$ crosses the threshold ϑ . Note the gathering of the majority of the points around the $\alpha_{\chi_{\text{osc}}}^* = \alpha_{\text{LoSE}}^*$ line. **(b-d)** Sample plots of LoSE (left vertical axis) and $\log(\chi_{\text{osc}})$ (right vertical axis) as a function of α for three sample cases denoted in panel (a). The red horizontal dotted line indicate the oscillation threshold ϑ . Panel (b) illustrates a common mid-point scenario where $\alpha_{\chi_{\text{osc}}}^* \simeq \alpha_{\text{LoSE}}^*$ while (c) and (d) illustrate two extreme conditions.

threshold crossing, much sooner (smaller) than α_{LoSE}^* , even though a meaningful drop in χ_{osc} is also clearly visible near α_{LoSE}^* . Note, also, that $\alpha_{\chi_{\text{osc}}}^* < \alpha_{\text{LoSE}}^*$ indicates a range of α values for which neither a stable equilibrium point nor a strong oscillation exists. Since an attractor must nevertheless exist, it can either be a highly chaotic one (small χ_{reg}) or an oscillatory one with very small amplitude (small χ_{pp}), neither of which we found to be common in networks of size $n \simeq 10$.

A.3 Global Inspection in Networks of E-I Pairs

In Sections A.1 and A.2, we have inspected general excitatory-inhibitory networks with arbitrary connection patterns between the nodes. Here, we inspect the networks of E-I pairs studied in Section 4. These networks not only constitute an important special case from a computational neuroscience standpoint, but they also lend themselves to theoretical characterizations such as that in Theorem 4.1. Here, we inspect the quality of LoSE as a proxy for oscillations using the theoretical condition in (24). To this end, we construct random networks according to

$$\begin{aligned} d_i &\sim \mathcal{U}(0, d_{\text{max}}), & a_i &\sim \mathcal{U}(a_{\text{min}}, a_{\text{max}}), & a_{\text{min}} &> d_{\text{max}} + 2, \\ b_i &= c_i \sim \mathcal{U}(b_{\text{min}}, b_{\text{max}}), & b_{\text{min}} &> \sqrt{(a_{\text{max}} - 1)(d_{\text{max}} + 1)}, \\ m_{j,i} &\sim \mathcal{U}(m_{j,\text{min}}, m_{j,\text{max}}), & m_{2,\text{min}} &> \frac{a_{\text{max}} - 1}{b_{\text{min}}} m_{1,\text{max}}, \\ \tau_i &\sim \mathcal{U}(\tau_{\text{min}}, \tau_{\text{max}}), & \text{i.i.d. } \forall j = 1, 2, i \in \{1, \dots, n\}, \end{aligned} \quad (28)$$

all satisfying (4a)-(4c). The values of $u_{i,1}$ and $u_{i,2}$ are chosen at the center of their respective ranges in (4d)-(4e) so that the E-I pairs oscillate at their maximum amplitude before interconnection. For \mathbf{A} , we first generate a random $\mathbf{G} \in \mathbb{R}_{\geq 0}^{n \times n}$ with zero diagonal and set $\mathbf{A} = \eta \mathbf{A}$, $\mathbf{A} = \text{diag}(\bar{\mathbf{u}}_1 -$

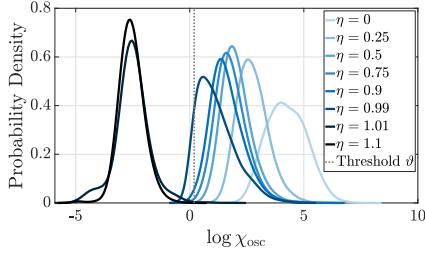


Fig. 4. Strength and regularity of oscillations as a function of inter-oscillator connection strength (η). The probability density function of $\log \chi_{\text{osc}}$ is plotted for $n = 10$ and varying η . Each distribution is based on 1000 random networks (28) with $d_{\text{max}} = 1$, $a_{\text{min}} = 3.5$, $a_{\text{max}} = 5$, $b_{\text{min}} = \sqrt{8} + 0.5$, $b_{\text{max}} = \sqrt{8} + 2$, $m_{1,\text{min}} = 1$, $m_{1,\text{max}} = 2$, $m_{2,\text{min}} = 8/b_{\text{min}} + 0.5$, $m_{2,\text{max}} = 8/b_{\text{min}} + 2$, $\tau_{\text{min}} = 1$, $\tau_{\text{max}} = 10$.

$\mathbf{u}_1 \mathbf{G} [\text{diag}(\mathbf{G} \mathbf{1}_n) \text{diag}(\mathbf{m}_1)]^{-1}$. \mathbf{A} then satisfies (24) for all $i \in \{1, \dots, n\}$ iff $\eta \in [0, 1)$.

Figure 4 shows the distribution of $\log \chi_{\text{osc}}$ for random networks of $n = 10$ oscillators, $\epsilon = 0.1$, and varying interconnection strength η . For disconnected oscillators ($\eta = 0$), each oscillator has a perfectly regular oscillation (by Theorem 3.1) and thus very large χ_{osc} (though finite, due to the finiteness of χ_{reg} , which is in turn due to finite signal length and numerical error). These oscillations lose their regularity and/or strength as we increase the connection strength η towards 1, but still persist up to $\eta = 0.99$, showing the almost sufficiency of (24). Moving beyond $\eta = 1$, almost no oscillations persist even at $\eta = 1.01$ (and less so at $\eta = 1.1$) due to convergence to the stable equilibria ensured by Theorem 4.1. This shows that (24) is also almost necessary for existence of oscillations in the network dynamics (23).

Acknowledgments

The work was supported by NSF Award CMMI-1826065 (EN and JC) and ARO Award W911NF-18-1-0213 (JC). RP's stay at San Diego was funded by the Centro de Formación Interdisciplinaria Superior from Universitat Politècnica de Catalunya.

References

- [1] D. Angeli and E. D. Sontag. Monotone control systems. *IEEE Transactions on Automatic Control*, 48(10):1684–1698, 2003.
- [2] B. Baird. Nonlinear dynamics of pattern formation and pattern recognition in the rabbit olfactory bulb. *Physica D: Nonlinear Phenomena*, 22(1-3):150–175, 1986.
- [3] H. Berger. Über das elektroencephalogramm des menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, 87(1):527–570, Dec 1929.
- [4] R. M. Borisjuk and A. B. Kirillov. Bifurcation analysis of a neural network model. *Biological Cybernetics*, 66(4):319–325, 1992.
- [5] M. Breakspear, J. A. Roberts, J. R. Terry, S. Rodrigues, N. Mahant, and P. A. Robinson. A unifying explanation of primary generalized seizures through nonlinear brain modeling and bifurcation analysis. *Cerebral Cortex*, 16(9):1296–1313, 2006.
- [6] M. Breakspear, S. Heitmann, and A. Daffertshofer. Generative models of cortical oscillations: neurobiological implications of the Kuramoto model. *Frontiers in Human Neuroscience*, 4:190, 2010.
- [7] L. E. J. Brouwer. Über abbildung von mannigfaltigkeiten. *Mathematische Annalen*, 71(1):97–115, 1911.
- [8] F. Bullo, J. Cortés, and S. Martinez. *Distributed Control of Robotic Networks*. Applied Mathematics Series. Princeton University Press, 2009. ISBN 978-0-691-14195-4.

- [9] G. Buzsáki. *Rhythms of the Brain*. Oxford University Press, Oxford, UK, 2006.
- [10] G. Buzsáki and A. Draguhn. Neuronal oscillations in cortical networks. *Science*, 304(5679):1926–1929, 2004.
- [11] S. Campbell and D. Wang. Synchronization and desynchronization in a network of locally coupled Wilson-Cowan oscillators. *IEEE Transactions on Neural Networks*, 7(3):541–554, 1996.
- [12] F. Celi, A. Allibhoy, F. Pasqualetti, and J. Cortés. Linear-threshold dynamics for the study of epileptic events. *IEEE Control Systems Letters*, 5(4):1405–1410, 2021.
- [13] S. R. Cole and B. Voytek. Brain oscillations and the importance of waveform shape. *Trends in Cognitive Sciences*, 21(2):137–149, 2017.
- [14] J. D. Cowan, J. Neuman, and W. van Drongelen. Wilson-Cowan equations for neocortical dynamics. *The Journal of Mathematical Neuroscience*, 6(1):1, 2016.
- [15] P. Dayan and L. F. Abbott. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. Computational Neuroscience. MIT Press, Cambridge, MA, 2001.
- [16] A. Destexhe and T. J. Sejnowski. The Wilson-Cowan model, 36 years later. *Biological Cybernetics*, 101(1):1–2, 2009.
- [17] 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*, 23(12):1655–1665, 2020.
- [18] G. B. Ermentrout and N. Kopell. Oscillator death in systems of coupled neural oscillators. *SIAM Journal on Applied Mathematics*, 50(1):125–146, 1990.
- [19] G. B. Ermentrout and D. H. Terman. *Mathematical Foundations of Neuroscience*, volume 35. Springer, New York, 2010.
- [20] P. Fries. Rhythms for cognition: Communication through coherence. *Neuron*, 88:220–235, 2015.
- [21] R. Gao and P. Penzes. Common mechanisms of excitatory and inhibitory imbalance in schizophrenia and autism spectrum disorders. *Current Molecular Medicine*, 15(2):146–167, 2015.
- [22] W. Grasman. Periodic solutions of autonomous differential equations in higher-dimensional spaces. *The Rocky Mountain Journal of Mathematics*, 7(3):457–466, 1977.
- [23] J. Harris and B. Ermentrout. Bifurcations in the Wilson-Cowan equations with nonsmooth firing rate. *SIAM Journal on Applied Dynamical Systems*, 14(1):43–72, 2015.
- [24] M. W. Hirsch and H. Smith. Monotone dynamical systems. In *Handbook of differential equations: ordinary differential equations*, volume 2, pages 239–357. Elsevier, Oxford, UK, 2006.
- [25] J. J. Hopfield. Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Sciences*, 79(8):2554–2558, 1982.
- [26] F. C. Hoppensteadt and E. M. Izhikevich. *Weakly connected neural networks*, volume 126. Springer Science & Business Media, 2012.
- [27] M. J. Hülsemann, E. Naumann, and B. Rasch. Quantification of phase-amplitude coupling in neuronal oscillations: Comparison of phase-locking value, mean vector length, modulation index, and generalized linear modeling cross-frequency coupling. *Frontiers in Neuroscience*, 13:573, 2019.
- [28] A. Hurwitz. Ueber die bedingungen, unter welchen eine gleichung nur wurzeln mit negativen reellen theilen besitzt. *Mathematische Annalen*, 46(1):273–284, 1895.
- [29] H. K. Inagaki, L. Fontolan, S. Romani, and K. Svoboda. Discrete attractor dynamics underlies persistent activity in the frontal cortex. *Nature*, 566(7743):212–217, 2019.
- [30] E. M. Izhikevich. *Dynamical Systems in Neuroscience*. MIT Press, Cambridge, MA, 2007.
- [31] M. P. Jari and T. J. Sejnowski. Regulating cortical oscillations in an inhibition-stabilized network. *Proceedings of the IEEE*, 102(5):830–842, 2014.
- [32] M. K. J. Johansson. *Piecewise Linear Control Systems: A*

- Computational Approach*. Lecture Notes in Control and Information Sciences. Springer Berlin Heidelberg, 2003.
- [33] S. R. Jones. When brain rhythms aren't 'rhythmic': implications for their mechanisms and meaning. *Current Opinion in Neurobiology*, 40:72–80, 2016.
 - [34] S. Kalitzin, G. Petkov, P. Suffczynski, V. Grigorovsky, B. L. Bardakjian, F. Lopes da Silva, and P. L. Carlen. Epilepsy as a manifestation of a multistate network of oscillatory systems. *Neurobiology of Disease*, 130:104488, 2019.
 - [35] S. T. Kissinger, A. Pak, Y. Tang, S. C. Masmanidis, and A. A. Chubykin. Oscillatory encoding of visual stimulus familiarity. *Journal of Neuroscience*, 38(27):6223–6240, 2018.
 - [36] D. Liberzon. *Switching in Systems and Control*. Systems & Control: Foundations & Applications. Birkhäuser, 2003.
 - [37] M. Mattia, P. Pani, G. Mirabella, S. Costa, P. Del Giudice, and S. Ferraina. Heterogeneous attractor cell assemblies for motor planning in premotor cortex. *Journal of Neuroscience*, 33(27):11155–11168, 2013.
 - [38] T. Menara, G. Baggio, D. S. Bassett, and F. Pasqualetti. Stability conditions for cluster synchronization in networks of heterogeneous Kuramoto oscillators. *IEEE Transactions on Control of Network Systems*, 7(1):302–314, 2020.
 - [39] L. H. A. Monteiro, M. A. Bussab, and J. G. C. Berlinck. Analytical results on a Wilson-Cowan neuronal network modified model. *Journal of Theoretical Biology*, 219(1):83–91, 2002.
 - [40] 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.
 - [41] S. F. Muldoon, F. Pasqualetti, S. Gu, M. Cieslak, S. T. Grafton, J. M. Vettel, and D. S. Bassett. Stimulation-based control of dynamic brain networks. *PLOS Computational Biology*, 12(9):e1005076, 2016.
 - [42] E. Nozari and J. Cortés. Oscillations and coupling in interconnections of two-dimensional brain networks. In *American Control Conference*, pages 193–198, Philadelphia, PA, July 2019.
 - [43] 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*, 66(3):949–964, 2021.
 - [44] E. Nozari and J. Cortés. Hierarchical selective recruitment in linear-threshold brain networks. Part II: Inter-layer dynamics and top-down recruitment. *IEEE Transactions on Automatic Control*, 66(3):965–980, 2021.
 - [45] A. C. E. Onslow, M. W. Jones, and R. Bogacz. A canonical circuit for generating phase-amplitude coupling. *PLOS One*, 9(8):e102591, 2014.
 - [46] L. Papadopoulos, C. W. Lynn, D. Battaglia, and D. S. Bassett. Relations between large-scale brain connectivity and effects of regional stimulation depend on collective dynamical state. *PLOS Computational Biology*, 16(9):1–43, 09 2020.
 - [47] L. Perko. *Differential Equations and Dynamical Systems*, volume 7 of *Texts in Applied Mathematics*. Springer, New York, 3rd edition, 2000.
 - [48] R. Quentin, J. King, E. Sallard, N. Fishman, R. Thompson, E. R. Buch, and L. G. Cohen. Differential brain mechanisms of selection and maintenance of information during working memory. *Journal of Neuroscience*, 39(19):3728–3740, 2019.
 - [49] V. Răşvan. A new dissipativity criterion – towards Yakubovich oscillations. *International Journal on Robust and Nonlinear Control*, 17(5-6):483–495, 2007.
 - [50] L. A. Sanchez. Existence of periodic orbits for high-dimensional autonomous systems. *Journal of Mathematical Analysis and Applications*, 363(2):409–418, 2010.
 - [51] T. Sase, Y. Katori, M. Komuro, and K. Aihara. Bifurcation analysis on phase-amplitude cross-frequency coupling in neural networks with dynamic synapses. *Frontiers in Computational Neuroscience*, 11:18, 2017.
 - [52] H. G. Schuster and P. Wagner. A model for neuronal oscillations in the visual cortex. 1. mean-field theory and derivation of the phase equations. *Biological Cybernetics*, 64(1):77–82, 1990.
 - [53] M. Segneri, H. Bi, S. Olmi, and A. Torcini. Theta-nested gamma oscillations in next generation neural mass models. *Frontiers in Computational Neuroscience*, 14:47, 2020.
 - [54] S. Simic, K. H. Johansson, J. Lygeros, and S. Sastry. Hybrid limit cycles and hybrid Poincaré-Bendixson. In *IFAC World Congress*, 2002.
 - [55] M. Steriade. Grouping of brain rhythms in corticothalamic systems. *Neuroscience*, 137(4):1087–1106, 2006.
 - [56] A. K. Tang, A. Simsek, A. Ozdaglar, and D. Acemoglu. On the stability of p-matrices. *Linear Algebra and its Applications*, 426(1):22–32, 2007.
 - [57] E. A. Tomberg and V. A. Yakubovich. Conditions for auto-oscillations in nonlinear systems. *Siberian Mathematical Journal*, 30(4):641–653, 1989.
 - [58] N. Tort-Colet, C. Capone, M. V. Sanchez-Vives, and M. Mattia. Attractor competition enriches cortical dynamics during awakening from anesthesia. *bioRxiv*, 2019. URL <https://www.biorxiv.org/content/early/2019/01/10/517102>.
 - [59] P. J. Uhlhaas and W. Singer. Abnormal neural oscillations and synchrony in schizophrenia. *Nature Reviews Neuroscience*, 11:100–113, 2010.
 - [60] F. van Ede, A. J. Quinn, M. W. Woolrich, and A. C. Nobre. Neural oscillations: sustained rhythms or transient burst-events? *Trends in Neurosciences*, 41(7):415–417, 2018.
 - [61] X. Wang. Neurophysiological and computational principles of cortical rhythms in cognition. *Physiological Reviews*, 90(3):1195–1268, 2010.
 - [62] J. A. White, T. Budde, and A. R. Kay. A bifurcation analysis of neuronal subthreshold oscillations. *Biophysical Journal*, 69(4):1203–1217, 1995.
 - [63] M. A. Whittington, R. D. Traub, N. Kopell, B. Ermentrout, and E. H. Buhl. Inhibition-based rhythms: experimental and mathematical observations on network dynamics. *International Journal of Psychophysiology*, 38(3):315–336, 2000.
 - [64] H. R. Wilson and J. D. Cowan. Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysical Journal*, 12(1):1–24, 1972.