# Selective Recruitment in Hierarchical Complex Dynamical Networks with Linear-Threshold Rate Dynamics

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Abstract-Understanding how the complex network dynamics of the brain support cognition constitutes one of the most challenging and impactful problems ahead of systems and control theory. In this paper, we study the problem of selective recruitment, namely, the simultaneous selective inhibition of activity in one subnetwork and top-down recruitment of another by a cognitively-higher level subnetwork, using the class of linear-threshold rate (LTR) models. We first use singular perturbation theory to provide a theoretical framework for selective recruitment in a bilayer hierarchical LTR network using both feedback and feedforward control. We then generalize this framework to arbitrary number of layers and provide conditions on the joint structure of subnetworks that guarantee simultaneous selective inhibition and top-down recruitment at all layers. We finally illustrate an application of this framework in a biologically-inspired scenario where simultaneous stabilization and control of a lower level excitatory subnetwork is achieved through proper oscillatory activity in a higher level inhibitory subnetwork.

# I. INTRODUCTION

The human brain is constantly under the influx of sensory inputs, and is responsible for integrating and interpreting them while generating appropriate decisions and actions. This activity involves vast and precise communications across the brain, broadly occurring along canonical pathways in two main directions: bottom-up and top-down. Bottom-up communication is responsible for transmission of sensory information from primary sensory areas to cognitively-higher level association areas, which in turn integrate it and make decisions that are then communicated in the top-down direction. Top-down communication is itself responsible for two parallel functions: the recruitment of the subnetworks whose activity is relevant to the present task and the inhibition of other task-irrelevant subnetworks. This hierarchical selective recruitment is critical in enabling the brain to extract useful information from a myriad of distractions that surround us and compete for our limited attention. This work seeks to develop a theoretical understanding of this vital aspect of the brain function in terms of its network structure and dynamics.

This hierarchical structure of the brain is not only implied by the direction in which sensory information and decisions flow, but also by the separation of time-scales between these areas: internal dynamics of each subnetwork grows slower as we move up the hierarchy. Although this hierarchy of time-scales has long been known to neuroscience and subject of extensive experimental and computational studies, a theoretical formulation of it is still missing. Here, we use the well-studied family of LTR models and tools and concepts from systems and control theory to fill in this gap and provide a theoretical framework of selective recruitment in hierarchical brain networks.

# Literature review

The hierarchical organization of the central nervous system (CNS) has long been recognized [1], [2] and studied from various viewpoints. These include a hierarchy of time-scales [3]–[8] (where nodes are grouped into layers according to the time-scale of their dynamics), topological hierarchies [9]–[12] (where nodes are assigned to layers based on their position on bottom-up and top-down pathways), hierarchical clustering [13]–[16] (where nodes only constitute the leafs of a clustering tree), and hierarchical oscillations [17] (where layers correspond to nested oscillatory frequency bands). Here, we particularly focus on the first two aspects.

The seminal work [9] uses the laminar structure of the cortex to distinguish between bottom-up and top-down connections and constructed a comprehensive hierarchical model of (visual) cortex accordingly, inspiring and forming the basis for many subsequent studies. In [3] and [4], a bilayer model with time-scale separation between layers is proposed for motor control and verified through simulations. Experimental evidence for such separation of time-scales is provided in [5], where data from six studies are aggregated and used to show a time-scale gradient as one moves from primary visual and somatosensory areas to the prefrontal cortex. The same gradient is shown more comprehensively using LTR models in [6]. This work further uses the intriguing concept of continuous hierarchies [10], [12] whereby the layer of each node can vary continuously according to its intrinsic time-scale, therefore removing the rigidity and arbitrariness of node assignment in classical hierarchical structures. While these works use the exponential decay rate of the autocorrelation function of each node's firing rate to infer its time-scale, [7] uses the length of the largest time window over which the responses to successive stimuli interfere. Nevertheless, despite the vastness of the literature on hierarchical organization of CNS, we are not aware of any theoretical analysis of the underlying assumptions and network properties that allow for such hierarchical organization.

Here, we use the well-studied class of LTR models and therefore rely on existing results on the dynamical properties of LTR networks when considered autonomously (outside of hierarchies) [18]–[20]. Our previous work [20] provides a thorough description of the stability and stabilizability

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properties of a single-layer LTR network, forming the basis for the present study. This work, however, only formulates the selective inhibition of task-irrelevant subnetworks within a selective recruitment scenario and does not address the topdown recruitment aspect of it. Finally, our work here also relies on established areas of dynamical systems and control such as switched linear and affine systems, see e.g., [21]– [23], and singular perturbation theory, see e.g., [24]–[27].

## Statement of contributions

The present work extends the state-of-the-art theory of LTR networks in three ways. First, we provide a comprehensive framework for selective recruitment in bilayer LTR networks. To this end, we integrate selective inhibition and the theory of singular perturbations for non-smooth dynamics in order to derive conditions on the network structure that guarantee the simultaneous inhibition of the task-irrelevant part of the lower level subnetwork and the stability of the task-relevant part of it towards the desired trajectory set forth for it by the higher-level subnetwork. Next, given the multilayer organization of brain networks, we extend this theory to a hierarchical LTR network with an arbitrary number of time-scale-separated layers. Here, we prove that the subnetwork equilibrium maps at all layers of the hierarchy are continuous and piecewise affine (and therefore globally Lipschitz) and derive a novel condition on the joint structure of the subnetworks in order to guarantee the global exponential stability of the task-relevant part of each subnetwork towards a unique equilibrium. Finally, we extend the existing selective inhibition schemes to incorporate both feedforward and feedback inhibition concurrently. This generalization is critical as the feedforward and feedback inhibition schemes (operating at very slow and fast time-scales, respectively) are complementary and their combination allows for a spectrum of time-scales for selective inhibition. Due to space constraints, proofs are omitted here and available in [28].

# Notation

We use  $\mathbb{R}$ ,  $\mathbb{R}_{\geq 0}$ ,  $\mathbb{R}_{\leq 0}$ , and  $\mathbb{R}_{>0}$  to denote the set of reals, nonnegative reals, nonpositive reals, and positive reals, respectively.  $\mathbf{1}_n$ ,  $\mathbf{0}_n$ ,  $\mathbf{0}_{m \times n}$ , 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. The subscripts are omitted when clear from the context. When a vector  $\mathbf{x}$  or matrix  $\mathbf{A}$  are block-partitioned,  $\mathbf{x}_i$  and  $\mathbf{A}_{ij}$  refer to the *i*th block of  $\mathbf{x}$  and (i, j)th block of  $\mathbf{A}$ , respectively. Given  $\mathbf{A} \in \mathbb{R}^{n \times n}$ , its element-wise absolute value and spectral radius are  $|\mathbf{A}|$  and  $\rho(\mathbf{A})$ , respectively.  $\|\cdot\|$  denotes vector 2-norm. For a vector  $\boldsymbol{\sigma}$ , diag( $\boldsymbol{\sigma}$ ) denotes the diagonal matrix with the elements of  $\boldsymbol{\sigma}$  on its diagonal. For any  $x \in \mathbb{R}$ ,  $[x]^+ \triangleq \max\{0, x\}$ . Similarly,  $[\mathbf{x}]^+ \in \mathbb{R}^n_{\geq 0}$  and  $[\mathbf{A}]^+ \in \mathbb{R}^{n \times n}_{\geq 0}$  are defined entrywise for a vector  $\mathbf{x}$  and matrix  $\mathbf{A}$ .

## **II. PROBLEM STATEMENT**

In this work, we use the family of LTR models to study the dynamics of hierarchical networks in the brain. The interested reader is referred to [29, Ch 7], [20, §II] for an explanation of how they arise as dynamical rate models of cortical circuits. A single LTR network is described by

$$\tau \dot{\mathbf{x}}(t) = -\mathbf{x}(t) + [\mathbf{W}\mathbf{x}(t) + \mathbf{d}(t)]^+, \quad t \ge 0.$$
(1)

Here,  $\mathbf{x} \in \mathbb{R}_{\geq 0}^n$  is the collection of the states of all the network nodes, where each node *i* corresponds to a population of neurons with similar activity patterns and  $x_i(t)$  is the average firing rate of these neurons at time *t*. Note that  $\mathbb{R}_{\geq 0}^n$ is invariant under (1), and hence these rates always remain nonnegative. The matrix  $\mathbf{W} \in \mathbb{R}^{n \times n}$  encodes the aggregate synaptic efficacy between any pair of nodes and  $\mathbf{d}(t) \in \mathbb{R}^n$ captures external inputs and potentially nonzero activation thresholds. Finally,  $\tau$  is the time constant of the network and plays a pivotal role in our subsequent analysis.

Interestingly, key dynamical properties of the model (1) with constant external inputs (i.e.,  $\mathbf{d}(t) \equiv \mathbf{d}$ ), such as existence and uniqueness of equilibria, asymptotic stability, and boundedness of solutions, can be accurately characterized in terms of the network structure  $\mathbf{W}$  [20, §IV]. When these conditions are not satisfied, one can resort to a time-varying external input to ensure them. To explain this, assume we seek to stabilize the network towards a unique equilibrium and consider the decomposition of  $\mathbf{d}(t)$  as

$$\mathbf{d}(t) = \mathbf{B}\mathbf{u}(t) + \tilde{\mathbf{d}}.$$
 (2)

where  $\mathbf{u}(t) \in \mathbb{R}^m$  ensures stabilization while  $\tilde{\mathbf{d}} \in \mathbb{R}^n$  determines the network equilibrium. Let  $r \leq n$  be the number of nodes that (directly) receive  $\mathbf{u}(t)$ , and consider the partition of  $\mathbf{W}$  and  $\mathbf{B}$  accordingly<sup>1</sup>,

$$\mathbf{B} = \begin{bmatrix} \mathbf{B}_1 \\ \mathbf{0} \end{bmatrix}, \qquad \mathbf{W} = \begin{bmatrix} \mathbf{W}_{11} & \mathbf{W}_{12} \\ \mathbf{W}_{21} & \mathbf{W}_{22} \end{bmatrix}, \qquad (3)$$

where  $\mathbf{B}_1 \in \mathbb{R}^{r \times m}$  has nonzero rows and  $\mathbf{W}_{11} \in \mathbb{R}^{r \times r}$ . Interestingly, using either constant feedforward  $\mathbf{u}(t) \equiv \bar{\mathbf{u}}$  or linear feedback  $\mathbf{u}(t) = \mathbf{K}\mathbf{x}(t)$  control, any of the aforementioned key dynamical properties (including global asymptotic stability) can be achieved for the overall network  $\mathbf{W}$  *if and only if* the corresponding property is already satisfied by the not-directly controlled subnetwork  $\mathbf{W}_{22}$  [20,  $\S$ V].

In this paper, we are interested in extending this framework to explain selective recruitment in a hierarchical structure. The core idea is to extend (2) to a more general decomposition of the form

$$\mathbf{d}(t) = \mathbf{B}\mathbf{u}(t) + \mathbf{d}(t),\tag{4}$$

and use  $\mathbf{u}(t)$  for selective inhibition of the r task-irrelevant nodes (similar to above) but now use the time-varying  $\tilde{\mathbf{d}}(t)$  for top-down recruitment of the n-r task-relevant nodes. This scheme has then to be replicated at all the layers of the hierarchy, as follows.

Formally, we consider a hierarchical network composed of N layers, evolving at distinct time-scales, where each layer is only directly connected to the layers immediately below and above it (Figure 1). The *i*'th layer,  $i \in \{1, ..., N\}$ , consists

<sup>&</sup>lt;sup>1</sup>This can always be done by (re-)labeling the r directly controlled nodes as  $1, \ldots, r$ , so that the n - r last entries of **B** are 0.



Fig. 1: The inter-layer connectivity structure of the N-layer hierarchical network. Each layer is only directly connected to the layers below and above it. Longer-range connections between non-successive layers do exist in biological neuronal networks, but are weaker than those between successive layers, and are not considered here for simplicity.

of a subnetwork described by the LTR dynamics<sup>2</sup>

$$\tau_{i} \dot{\mathbf{x}}^{i}(t) = -\mathbf{x}^{i}(t) + [\mathbf{W}^{i,i} \mathbf{x}^{i}(t) + \mathbf{W}^{i,i-1} \mathbf{x}^{i-1}(t)$$
(5)  
+  $\mathbf{W}^{i,i+1} \mathbf{x}^{i+1}(t) + \mathbf{B}^{i} \mathbf{u}^{i}(t) + \mathbf{c}^{i}]^{+},$ 

with state vector  $\mathbf{x}^i \in \mathbb{R}^{n_i}$ , stabilizing control  $\mathbf{u}^i \in \mathbb{R}^{m_i}$ , control matrix

$$\mathbf{B}^{i} = \begin{bmatrix} \mathbf{B}_{1}^{i} \\ \mathbf{0} \end{bmatrix}, \qquad \mathbf{B}_{1}^{i} \in \mathbb{R}_{\leq 0}^{r_{i} \times m_{i}}, \tag{6}$$

constant background activity  $\mathbf{c}^i \in \mathbb{R}^{n_i}$ , and time constant  $\tau_i > 0$ . The remaining matrices have appropriate dimensions and are partitioned in accordance with (6). By convention,  $\mathbf{W}^{1,0} = \mathbf{0}$ ,  $\mathbf{W}^{N,N+1} = \mathbf{0}$ , and  $r_1 = 0$  (so  $\mathbf{B}^1 = \mathbf{0}$  and the first subnetwork has no inhibited part). For  $i = \{1, \ldots, N-1\}$ , let  $\epsilon_i \triangleq \frac{\tau_{i+1}}{\tau_i}$  and define  $\boldsymbol{\epsilon} \triangleq (\epsilon_1, \ldots, \epsilon_{N-1})$ . We are now ready to formulate the problem of interest as follows.

**Problem 1.** (Selective recruitment in hierarchical LTR networks). Consider the hierarchical neuronal network described above. Assuming  $\epsilon \ll 1$ , derive conditions on the joint structure of the subnetworks and inter-layer interactions that guarantee, for each subnetwork, the simultaneous selective inhibition of one (task-irrelevant) set of nodes and the top-down recruitment of the remaining (task-relevant) nodes so that their state tracks a trajectory determined by the corresponding higher-level subnetwork.

**Remark II.1.** (*The role of bottom-up communication*). In actual neuronal networks, bottom-up communications are used for a variety of purposes. The framework above incorporates two of their main functions: the transmission of lower-level (mainly sensory) information to the higher-level subnetwork (that will in turn affect the higher-level dynamics) and the informing of the higher-level subnetwork about the current activity level of the lower-level one so that proper feedback inhibition can be applied.

#### **III. SELECTIVE RECRUITMENT IN BILAYER NETWORKS**

In this section we consider a simplified version of Problem 1 with only two layers, where the lower level network is governed by LTR dynamics of the form (1) and the dynamics of the higher level network is kept arbitrary. This setup allows us to study the key ingredients of selective recruitment in the absence of the extra complications that arise from multilayer architectures. Section IV builds on the insights obtained here to generalize this framework to the multilayer case.

For any  $\mathbf{W} \in \mathbb{R}^{n \times n}$ , define  $h : \mathbb{R}^n \rightrightarrows \mathbb{R}^n_{>0}$  by

$$h(\mathbf{d}) = h_{\mathbf{W}}(\mathbf{d}) \triangleq \{ \mathbf{x} \in \mathbb{R}^{n}_{\geq 0} \mid \mathbf{x} = [\mathbf{W}\mathbf{x} + \mathbf{d}]_{+} \}, \quad (7)$$

which is the set of the equilibria of the LTR dynamics (1) under a constant input d. One can show [20] that h has the piecewise-affine form

$$h(\mathbf{d}) = (\mathbf{I} - \boldsymbol{\Sigma} \mathbf{W})^{-1} \boldsymbol{\Sigma} \mathbf{d}, \ \forall \mathbf{d} \text{ s.t. } (2\boldsymbol{\Sigma} - \mathbf{I})(\mathbf{I} - \mathbf{W} \boldsymbol{\Sigma}) \mathbf{d} \ge 0, \\ \forall \boldsymbol{\Sigma} = \operatorname{diag}(\boldsymbol{\sigma}), \boldsymbol{\sigma} \in \{0, 1\}^{n}.$$
(8)

The existence and uniqueness of equilibria of (1) precisely corresponds to h being single-valued on  $\mathbb{R}^n$ , in which case we let  $h : \mathbb{R}^n \to \mathbb{R}^n_{\geq 0}$  be an ordinary function. To present the main result of this section, we first need a definition<sup>3</sup>.

**Definition III.1.** (Monotone boundedness). The LTR dynamics (1) is monotonically bounded if for any  $\bar{\mathbf{d}} \in \mathbb{R}^n$ there exists  $\nu(\bar{\mathbf{d}})$  such that  $\mathbf{x}(t) \leq \nu(\bar{\mathbf{d}}), \forall t$  if  $\mathbf{d}(t) \leq \bar{\mathbf{d}}, \forall t.\Box$ 

The main result of this section is as follows.

**Theorem III.2.** (Selective recruitment in bilayer hierarchical networks). Consider the multilayer dynamics (5) where N = 2,  $n_1 = n_2 - r_2$ ,  $\mathbf{W}^{2,1} = [\mathbf{0}_{n_1 \times r_2} \mathbf{I}_{n_1}]^T$ ,  $\mathbf{c}^2 = \mathbf{0}$ , and  $\mathbf{x}^1(t)$  is generated by some arbitrary dynamics

$$\tau_1 \dot{\mathbf{x}}^1(t) = \gamma(\mathbf{x}^1(t), \mathbf{x}^2(t), t).$$
(9)

Let  $h_2 = h_{\mathbf{W}_{22}^{2,2}}$  as in (7). If

- (i)  $\gamma$  is measurable in t, locally bounded, and locally Lipschitz in  $(\mathbf{x}^1, \mathbf{x}^2)$  uniformly in t;
- (ii) (9) has bounded solutions uniformly in  $\mathbf{x}^2(t)$ ;
- (*iii*)  $m_2 \ge r_2$ ;
- (iv)  $\mathbf{W}_{22}^{2,2}$  is such that  $\tau \dot{\mathbf{x}}_2^2 = -\mathbf{x}_2^2 + [\mathbf{W}_{22}^{2,2}\mathbf{x}_2^2 + \mathbf{x}^1]^+$  is GES towards a unique equilibrium for any constant  $\mathbf{x}^1$ ;

then there exists  $\mathbf{K}^2 \in \mathbb{R}^{m_2 \times n_2}$  such that by using the feedback control  $\mathbf{u}^2(t) = \mathbf{K}^2 \mathbf{x}^2(t)$ ,

$$\lim_{\epsilon_1 \to 0} \sup_{t \in [\underline{t}, \overline{t}]} \left\| \mathbf{x}^2(t) - \left( \mathbf{0}_{r_2}, h_2(\mathbf{x}^1(t)) \right) \right\| = 0, \tag{10}$$

for any  $0 < \underline{t} < \overline{t} < \infty$ . Further, if the dynamics of  $\mathbf{x}^2$  is monotonically bounded, there also exists a feedforward control  $\mathbf{u}^2(t) \equiv \overline{\mathbf{u}}^2$  such that (10) holds for any  $0 < t < \overline{t} < \infty$ .

**Remark III.3.** (Validity of the assumptions of Theorem III.2.). Assumption (i) is merely technical and is not

<sup>&</sup>lt;sup>2</sup>Here,  $\mathbf{W}^{i,i-1}\mathbf{x}^{i-1}(t) + \mathbf{W}^{i,i+1}\mathbf{x}^{i+1}(t) + \mathbf{c}^{i}$  plays the role of  $\tilde{\mathbf{d}}(t)$  in (4) at each layer *i*.

 $<sup>^{3}</sup>$ Note that the state of real biological neuronal networks is uniformly bounded due to the refractory period of its neurons, implying monotone boundedness.

a restriction in practice. In particular, this assumption is satisfied when using an LTR model for (9). Likewise, assumption (*ii*) is always satisfied in reality, as the state of all biological neuronal networks are bounded by the inverse of the refractory period of their neurons. Even in theory, this assumption can be relaxed to only the boundedness of the reduced-order model in the case of feedback inhibition (cf. Theorem IV.3). Assumption (*iii*) requires that there exist sufficiently many inhibitory control channels to suppress the activity of the first r nodes of the lower-level subnetwork. The most critical requirement is assumption (*iv*), which is not only sufficient but also necessary for inhibitory stabilization (cf. [20] for conditions on  $\mathbf{W}_{22}^{2,2}$  that ensure this assumption as well as its necessity for inhibitory stabilization).

The main conclusion of Theorem III.2 is the Tikhonovtype singular perturbation statement given in (10). According to (10), for any  $\theta > 0$ ,

$$|\mathbf{x}^{2}(t) - (\mathbf{0}_{r_{2}}, h_{2}(\mathbf{x}^{1}(t)))| \le \theta \mathbf{1}_{n_{2}}, \qquad \forall t \in [\underline{t}, \overline{t}], \quad (11)$$

provided that  $\frac{\tau_2}{\tau_1}$  is sufficiently small, i.e., the higher-level dynamics is sufficiently slower than the lower-level one. As discussed in the introduction, this time-scale separation is characteristic of biological neuronal networks.

An important observation regarding (11) is that the equilibrium map  $h_2$  does not have a closed-form expression, so the reference trajectory  $h_2(\mathbf{x}^1(t))$  of the lower-level network is only implicitly known for any given  $\mathbf{x}^1(t)$ . However, if a desired trajectory  $\boldsymbol{\xi}_2^2(t) \in \mathbb{R}_{\geq 0}^{n_2-r_2}$  for  $\mathbf{x}_2^2$  is known a priori, one can specify the appropriate  $\gamma$  such that  $h_2(\mathbf{x}^1(t)) = \boldsymbol{\xi}_2^2(t)$ . To see this, let the dynamics of  $\boldsymbol{\xi}_2^2(t)$  be given by

$$\tau_1 \dot{\boldsymbol{\xi}}_2^2(t) = \gamma_{\boldsymbol{\xi}}(\boldsymbol{\xi}_2^2(t), t).$$

Then, choosing  $\mathbf{d}_2^1(t) = (\mathbf{I} - \mathbf{W}_{22}^{2,2})\boldsymbol{\xi}_2^2(t)$ , yields

$$[\mathbf{W}_{22}^{2,2}\boldsymbol{\xi}_{2}^{2}(t) + \mathbf{x}^{1}(t)]^{+} = [\boldsymbol{\xi}_{2}^{2}(t)]^{+} = \boldsymbol{\xi}_{2}^{2}(t).$$

which, according to (7), implies  $\boldsymbol{\xi}_2^2(t) = h_2(\mathbf{x}^1(t))$ .

# IV. SELECTIVE RECRUITMENT IN MULTILAYER NETWORKS

In this section, we address the general scenario stated in Problem 1 involving an *N*-layer hierarchical structure of subnetworks with LTR dynamics. Given the model (5), let

$$\begin{split} h_{2}^{i}: \mathbf{c}_{2}^{i} \rightrightarrows \{\mathbf{x}_{2}^{i} \mid \mathbf{x}_{2}^{i} = [\mathbf{W}_{22}^{i,i+1} h_{2}^{i+1} (\mathbf{W}_{22}^{i+1,i} \mathbf{x}_{2}^{i} + \mathbf{c}_{2}^{i+1}) \\ &+ \mathbf{W}_{22}^{i,2} \mathbf{x}_{2}^{i} + \mathbf{c}_{2}^{i}]^{+} \}, \ i = 2, \dots, N - 1, \end{split}$$

be the recursive definition of the (set-valued) equilibria map of subnetwork *i*, with  $h_2^N = h_{\mathbf{W}_{22}^{N,N}}$  as in (7). The maps  $\{h_2^i\}_{i=2}^N$  play a central role in the multiple-time scale dynamics of (5). Therefore, we next characterize their piecewise affinity and global Lipschitzness properties. These results play a key role in our forthcoming developments.

Lemma IV.1. (Piecewise affinity of equilibrium maps is preserved along the layers of a hierarchical LTR network).

Let  $h : \mathbb{R}^n \to \mathbb{R}^n$  be a piecewise affine function of the form

$$h(\mathbf{c}) = \mathbf{F}_{\lambda}\mathbf{c} + \mathbf{f}_{\lambda}, \qquad \forall \mathbf{c} \in \Psi_{\lambda} \triangleq \{\mathbf{c} \mid \mathbf{G}_{\lambda}\mathbf{c} + \mathbf{g}_{\lambda} \ge \mathbf{0}\}, \\ \forall \lambda \in \Lambda,$$

where  $\Lambda$  is a finite index set and  $\bigcup_{\lambda \in \Lambda} \Psi_{\lambda} = \mathbb{R}^{n}$ . Given three matrices  $\mathbf{W}^{\ell}, \ell = 1, 2, 3$  and a vector  $\bar{\mathbf{c}}$ , assume

$$\mathbf{x} = [\mathbf{W}^1 \mathbf{x} + \mathbf{W}^2 h(\mathbf{W}^3 \mathbf{x} + \bar{\mathbf{c}}) + \mathbf{c}']^+, \qquad (12)$$

is known to have a unique solution  $\mathbf{x} \in \mathbb{R}^{n'}$  for all  $\mathbf{c}' \in \mathbb{R}^{n'}$ and let  $h'(\mathbf{c}')$  be this unique solution. Then, there exists a finite index set  $\Lambda'$  and  $\{(\mathbf{F}'_{\lambda'}, \mathbf{f}'_{\lambda'}, \mathbf{G}'_{\lambda'}, \mathbf{g}'_{\lambda'})\}_{\lambda' \in \Lambda'}$  such that

$$\begin{split} h'(\mathbf{c}') &= \mathbf{F}'_{\lambda'}\mathbf{c}' + \mathbf{f}'_{\lambda'}, \quad \forall \mathbf{c}' \in \Psi'_{\lambda'} \triangleq \{\mathbf{c}' \mid \mathbf{G}'_{\lambda'}\mathbf{c}' + \mathbf{g}'_{\lambda'} \geq \mathbf{0}\} \\ &\quad \forall \lambda' \in \Lambda', \end{split}$$

and  $\bigcup_{\lambda' \in \Lambda'} \Psi'_{\lambda'} = \mathbb{R}^{n'}$ .

Note that an important special case of Lemma IV.1 is when  $W^2 = 0$ , in which case h' becomes the standard equilibrium map (7) of the LTR dynamics.

**Lemma IV.2.** (*Piecewise affine equilibrium maps are glob*ally Lipschitz). Let  $h : \mathbb{R}^n \to \mathbb{R}^n$  be a piecewise affine function of the form

$$h(\mathbf{c}) = \mathbf{F}_{\lambda}\mathbf{c} + \mathbf{f}_{\lambda}, \qquad \forall \mathbf{c} \in \Psi_{\lambda} \triangleq \{\mathbf{c} \mid \mathbf{G}_{\lambda}\mathbf{c} + \mathbf{g}_{\lambda} \ge \mathbf{0}\}, \\ \forall \lambda \in \Lambda,$$

where  $\Lambda$  is a finite index set and  $\bigcup_{\lambda \in \Lambda} \Psi_{\lambda} = \mathbb{R}^n$ . Then, h is globally Lipschitz.

We are now ready to generalize Theorem III.2 to an *N*-layer architecture while relaxing several of its simplifying assumptions in favor of generality.

**Theorem IV.3.** (Selective recruitment in multilayer hierarchical networks). Consider the dynamics (5), (6). If<sup>4</sup>

(i) The reduced-order model (ROM)

$$\tau_1 \dot{\mathbf{x}}_2^1 = -\bar{\mathbf{x}}_2^1 + [\mathbf{W}_{22}^{1,1} \bar{\mathbf{x}}_2^1 + \mathbf{W}_{22}^{1,2} h_2^2 (\mathbf{W}_{22}^{2,1} \bar{\mathbf{x}}_2^1 + \mathbf{c}_2^2) + \mathbf{c}_2^1]^+,$$

of the first subnetwork has bounded solutions;

(*ii*) For all 
$$i = 2, ..., N$$
,

$$\begin{aligned} \tau_i \dot{\mathbf{x}}_2^i(t) &= -\mathbf{x}_2^i(t) + [\mathbf{W}_{22}^{i,i} \mathbf{x}_2^i(t) \\ &+ \mathbf{W}_2^{i,i+1} h_2^{i+1} (\mathbf{W}_{22}^{i+1,i} \mathbf{x}_2^i(t) + \mathbf{c}_2^{i+1}) + \mathbf{c}_2^i]^+, \end{aligned}$$

is GES towards a unique equilibrium for any  $\mathbf{c}_2^{i+1}$  and any  $\mathbf{c}_2^i$ ;

then there exists  $\mathbf{K}^i \in \mathbb{R}^{m_i \times n_i}$  and  $\bar{\mathbf{u}}^i : \mathbb{R}_{\geq 0} \to \mathbb{R}^{m_i}_{\geq 0}, i \in \{2, \ldots, N\}$  such that using the feedback-feedforward control

$$\mathbf{u}^{i}(t) = \mathbf{K}^{i} \mathbf{x}^{i}(t) + \bar{\mathbf{u}}^{i}(t), \qquad i \in \{2, \dots, N\},$$
(13)

we have, for any  $0 < \underline{t} < \overline{t} < \infty$ ,

$$\lim_{\epsilon \to \mathbf{0}} \sup_{t \in [\underline{t}, \underline{t}]} \| \mathbf{x}_1^i(t) \| = \mathbf{0}, \qquad \forall i \in \{2, \dots, N\},$$
(14a)

<sup>4</sup>Recall that  $\mathbf{x}^1 \equiv \mathbf{x}_2^1$  since  $r_1 = 0$ .

$$\lim_{\boldsymbol{\epsilon} \to \mathbf{0}} \sup_{t \in [0,\bar{t}]} \|\mathbf{x}_2^1(t) - \bar{\mathbf{x}}_2^1(t)\| = 0,$$
(14b)

$$\lim_{\epsilon \to \mathbf{0}} \sup_{t \in [\underline{t}, \overline{t}]} \|\mathbf{x}_2^2(t) - h_2^2(\mathbf{W}_{22}^{2, 1}\mathbf{x}_2^1(t) + \mathbf{c}_2^2)\| = 0,$$
(14c)

 $\lim_{\epsilon \to \mathbf{0}} \sup_{t \in [t,\bar{t}]} \lVert \mathbf{x}_{2}^{N}(t) - h_{2}^{N}(\mathbf{W}_{22}^{N,N-1}\mathbf{x}_{2}^{N-1}(t) + \mathbf{c}_{2}^{N}) \rVert = 0.$ (14d)

Unlike Theorem III.2, (13) uses a combination of feedback and feedforward inhibition. While using only feedforward or feedback inhibition has the advantage of simpler implementation, their combination results in more flexibility and less conservativeness: in pure feedforward inhibition, countering local excitations requires monotone boundedness and a sufficiently large  $\bar{\mathbf{u}}$  that provides inhibition under the worst-case scenario, a goal that is achieved more efficiently using feedback. On the other hand, pure feedback inhibition needs to dynamically cancel local excitations at all times and is also unable to counter the effects of constant background excitation, limitations that are easily addressed when combined with feedforward inhibition.

Similar to Remark III.3, assumption *(ii)* of Theorem IV.3 is its only critical requirement, which is both necessary and sufficient for selective inhibition. The next result relates this condition to the joint structure of the subnetworks, serving as a vital step in the practical utilization of Theorem IV.3.

**Theorem IV.4.** (Sufficient condition for existence and uniqueness of equilibria and GES in multilayer LTR networks). Let  $h : \mathbb{R}^n \to \mathbb{R}^n$  be a piecewise affine function of the form

$$h(\mathbf{c}) = \mathbf{F}_{\lambda}\mathbf{c} + \mathbf{f}_{\lambda}, \qquad \forall \mathbf{c} \in \Psi_{\lambda} \triangleq \{\mathbf{c} \mid \mathbf{G}_{\lambda}\mathbf{c} + \mathbf{g}_{\lambda} \ge \mathbf{0}\}, \\ \forall \lambda \in \Lambda, \tag{15}$$

where  $\Lambda$  is a finite index set and  $\bigcup_{\lambda \in \Lambda} \Psi_{\lambda} = \mathbb{R}^{n}$ . Further, let  $\bar{\mathbf{F}} \triangleq \max_{\lambda \in \Lambda} |\mathbf{F}_{\lambda}|$  be the matrix whose elements are the maximum of the corresponding elements from  $\{|\mathbf{F}_{\lambda}|\}_{\lambda \in \Lambda}$ and  $\mathbf{W}^{\ell}, \ell = 1, 2, 3$  be arbitrary matrices. If  $\rho(|\mathbf{W}^{1}| + |\mathbf{W}^{2}|\bar{\mathbf{F}}|\mathbf{W}^{3}|) < 1$ , then the LTR dynamics

$$\tau \dot{\mathbf{x}}(t) = -\mathbf{x}(t) + [\mathbf{W}^1 \mathbf{x}(t) + \mathbf{W}^2 h(\mathbf{W}^3 \mathbf{x}(t) + \bar{\mathbf{c}}) + \mathbf{c}]^+,$$

is GES towards a unique equilibrium for all  $\bar{\mathbf{c}}$  and  $\mathbf{c}$ .

Theorem IV.4 applies to each layer of (5) separately. When put together, assumption *(ii)* of Theorem IV.3 is satisfied if

$$\begin{split} \rho \left( |\mathbf{W}_{22}^{2,2}| + |\mathbf{W}_{22}^{2,3}|\bar{F}_2^3|\mathbf{W}_{22}^{3,3}| \right) < 1, \\ &\vdots \\ \rho \left( |\mathbf{W}_{22}^{N-1,N-1}| + |\mathbf{W}_{22}^{N-1,N}|\bar{F}_2^N|\mathbf{W}_{22}^{N,N-1}| \right) < 1, \\ \rho \left( |\mathbf{W}_{22}^{N,N}| \right) < 1, \end{split}$$

where  $\bar{F}_2^i$ , i = 3, ..., N is the matrix described in Theorem IV.4 corresponding to  $h_2^i$ , and the affine form (15) of  $h_2^i$  is computed recursively using Lemma IV.1.



Fig. 2: The network structure (left) and trajectories (right) of the two-time scale network in (16). The red pyramids and blue circles depict excitatory and inhibitory nodes, respectively, and the trajectory colors on the right correspond to node colors on the left.

# V. SIMULATIONS

In this section, we provide an illustrative example of the selective recruitment framework developed above in a biologically-inspired bilayer hierarchical structure. Consider the dynamics (5) with N = 2, a 3-dimensional excitatory subnetwork at the lower level, and a 3-dimensional inhibitory subnetwork at the higher level. Let

$$\mathbf{W}^{1,1} = \begin{bmatrix} 0 & -0.8 & -1.7 \\ -1 & 0 & -0.5 \\ -0.7 & -1.8 & 0 \end{bmatrix}, \quad \mathbf{c}^{1} = \begin{bmatrix} 11 \\ 10 \\ 10 \end{bmatrix}, \\ \mathbf{W}^{2,2} = \begin{bmatrix} 0 & 0.9 & 1.2 \\ 0.7 & 0 & 1 \\ 0.8 & 0.2 & 0 \end{bmatrix}, \quad \mathbf{B}^{2} = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \quad \mathbf{c}^{2} = \begin{bmatrix} 2 \\ 3.5 \\ 2.5 \end{bmatrix}, \\ \mathbf{W}^{1,2} = \mathbf{0}, \quad \mathbf{W}^{2,1} = -\mathbf{I}, \quad u^{2} = -5.$$
(16)

It is straightforward to verify that this example satisfies all the assumptions of Theorem III.2. Therefore, we expect the actual  $\mathbf{x}^2$ -trajectory to be close to the *desired*  $\mathbf{x}^2$ -trajectory  $(0, h_2^2(\mathbf{x}^1(t))$  provided that  $\epsilon_1 \ll 1$ . Figure 2 shows the trajectories of this system for  $\epsilon_1 = 0.1$  together with a schematic of the interconnections. With this separation of time scales,  $\mathbf{x}^2(t)$  and  $(0, h_2^2(\mathbf{x}^1(t)))$  are almost identical and not (visually) distinguishable.

It is easy to see that the complete  $\mathbf{x}^2$ -subsystem is unstable by itself. However, when  $x_1^2$  is inhibited, the remaining  $x_2^2$  $x_3^2$  subnetwork becomes GES. Therefore, the higher-lever inhibitory network (which is oscillatory itself) has selectively inhibited  $x_1^2$  while simultaneously recruiting (by inducing an oscillation in) the  $x_2^2$ - $x_3^2$  part.<sup>5</sup> Note that although  $x_1^2$  is not effectively used here, it can be replaced by  $x_2^2$  or  $x_3^2$  at other times. In other words, while the full  $\mathbf{x}^2$ -dynamics is unstable, any two-node part of it is GES. Therefore, different "tasks" can be accomplished at different times through the selective inhibition of one of  $\{x_1^2, x_2^2, x_3^2\}$  and top-down recruitment of the other two. Generalizing this to larger networks results in more flexible selective recruitment of different subsets of nodes at different times, as observed in nature.

<sup>&</sup>lt;sup>5</sup>Coherent oscillatory activity has been widely shown to be involved in transfer of information between cortical circuits, see, e.g., [30]–[32].

## VI. CONCLUSIONS AND FUTURE WORK

We have proposed a model-based framework for understanding selective recruitment in multilayer hierarchical networks inspired by the dynamical behavior of the brain. Accordingly, we have modeled the dynamics of the layers by LTR networks. Our results provide conditions on the network structure and the inter-layer communications that guarantee selective recruitment, in the sense that each subnetwork inhibits activity in one (task-irrelevant) part and controls the trajectory of the other (task-relevant) part of the subnetwork at the level below it. Our framework requires that each recruited subnetwork be asymptotically stable towards a fixedpoint attractor, which then moves along a desired trajectory set by the subnetwork above. Future work will extend this framework to cases where the recruited subnetworks can be asymptotically stable towards more complex attractors, such as limit cycles and chaotic attractors. We are also interested in pursuing the data-driven validation of our results and modeling framework as well as their generalization to more general dynamical models, including bounded LTR models.

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#### REFERENCES

- N. Tinbergen, "The hierarchical organization of nervous mechanisms underlying instinctive behaviour," in *Symposium for the Society for Experimental Biology*, vol. 4, no. 305-312, 1950.
- [2] A. R. Luria, "The functional organization of the brain," *Scientific American*, vol. 222, no. 3, pp. 66–79, 1970.
- [3] S. J. Kiebel, J. Daunizeau, and K. J. Friston, "A hierarchy of timescales and the brain," *PLOS Computational Biology*, vol. 4, no. 11, p. e1000209, 2008.
- [4] Y. Yamashita and J. Tani, "Emergence of functional hierarchy in a multiple timescale neural network model: a humanoid robot experiment," *PLOS Computational Biology*, vol. 4, no. 11, p. e1000220, 2008.
- [5] J. D. Murray, A. Bernacchia, D. J. Freedman, R. Romo, J. D. Wallis, X. Cai, C. Padoa-Schioppa, T. Pasternak, H. Seo, D. Lee, and X. Wang, "A hierarchy of intrinsic timescales across primate cortex," *Nature Neuroscience*, vol. 17, no. 12, p. 1661, 2014.
- [6] R. Chaudhuri, K. Knoblauch, M. Gariel, H. Kennedy, and X. Wang, "A large-scale circuit mechanism for hierarchical dynamical processing in the primate cortex," *Neuron*, vol. 88, no. 2, pp. 419–431, 2015.
- [7] U. Hasson, J. Chen, and C. J. Honey, "Hierarchical process memory: memory as an integral component of information processing," *Trends in Cognitive Sciences*, vol. 19, no. 6, pp. 304–313, 2015.
- [8] M. I. Rabinovich, I. Tristan, and P. Varona, "Hierarchical nonlinear dynamics of human attention," *Neuroscience & Biobehavioral Reviews*, vol. 55, pp. 18–35, 2015.
- [9] D. J. Felleman and D. C. V. Essen, "Distributed hierarchical processing in the primate cerebral cortex," *Cerebral Cortex*, vol. 1, no. 1, pp. 1– 47, 1991.
- [10] A. Krumnack, A. T. Reid, E. Wanke, G. Bezgin, and R. Kötter, "Criteria for optimizing cortical hierarchies with continuous ranges," *Frontiers in Neuroinformatics*, vol. 4, p. 7, 2010.
- [11] G. Zamora-López, C. Zhou, and J. Kurths, "Cortical hubs form a module for multisensory integration on top of the hierarchy of cortical networks," *Frontiers in Neuroinformatics*, vol. 4, p. 1, 2010.

- [12] N. T. Markov, J. Vezoli, P. Chameau, A. Falchier, R. Quilodran, C. Huissoud, C. Lamy, P. Misery, P. Giroud, S. Ullman, P. Barone, C. Dehay, K. Knoblauch, and H. Kennedy, "Anatomy of hierarchy: feedforward and feedback pathways in macaque visual cortex," *Journal of Comparative Neurology*, vol. 522, no. 1, pp. 225–259, 2014.
- [13] D. S. Bassett, E. T. Bullmore, B. A. Verchinski, V. S. Mattay, D. R. Weinberger, and A. Meyer-Lindenberg, "Hierarchical organization of human cortical networks in health and schizophrenia," *Journal of Neuroscience*, vol. 28, no. 37, pp. 9239–9248, 2008.
- [14] D. Meunier, R. Lambiotte, A. Fornito, K. Ersche, and E. T. Bullmore, "Hierarchical modularity in human brain functional networks," *Frontiers in Neuroinformatics*, vol. 3, p. 37, 2009.
- [15] D. Meunier, R. Lambiotte, and E. T. Bullmore, "Modular and hierarchically modular organization of brain networks," *Frontiers in Neuroscience*, vol. 4, p. 200, 2010.
- [16] Z. Zhen, H. Fang, and J. Liu, "The hierarchical brain network for face recognition," *PLOS One*, vol. 8, no. 3, p. e59886, 2013.
- [17] P. Lakatos, A. S. Shah, K. H. Knuth, I. Ulbert, G. Karmos, and C. E. Schroeder, "An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex," *Journal of Neurophysiology*, vol. 94, no. 3, pp. 1904–1911, 2005.
- [18] K. P. Hadeler and D. Kuhn, "Stationary states of the Hartline-Ratliff model," *Biological Cybernetics*, vol. 56, no. 5-6, pp. 411–417, 1987.
- [19] 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.
- [20] E. Nozari and J. Cortés, "Stability analysis of complex networks with linear-threshold rate dynamics," in *American Control Conference*, Milwaukee, WI, May 2018, pp. 191–196.
- [21] H. Lin and P. J. Antsaklis, "Stability and stabilizability of switched linear systems: A survey of recent results," *IEEE Transactions on Automatic Control*, vol. 54, no. 2, pp. 308–322, 2009.
- [22] D. Liberzon, Switching in Systems and Control, ser. Systems & Control: Foundations & Applications. Birkhäuser, 2003.
- [23] M. K. J. Johansson, Piecewise Linear Control Systems: A Computational Approach, ser. Lecture Notes in Control and Information Sciences. Springer Berlin Heidelberg, 2003.
- [24] A. N. Tikhonov, "Systems of differential equations containing small parameters in the derivatives," *Matematicheskii Sbornik*, vol. 73, no. 3, pp. 575–586, 1952.
- [25] P. V. Kokotović, H. K. Khalil, and J. O'Reilly, Eds., Singular Perturbation Methods in Control: Analysis and Design. SIAM, 1999.
- [26] V. Veliov, "A generalization of the Tikhonov theorem for singularly perturbed differential inclusions," *Journal of Dynamical & Control Systems*, vol. 3, no. 3, pp. 291–319, 1997.
- [27] F. Watbled, "On singular perturbations for differential inclusions on the infinite interval," *Journal of Mathematical Analysis and Applications*, vol. 310, no. 2, pp. 362–378, 2005.
- [28] E. Nozari and J. Cortés, "Hierarchical selective recruitment in complex dynamical networks. Part II: Top-down recruitment and multilayer architectures," *IEEE Transactions on Automatic Control*, 2018, submitted.
- [29] P. Dayan and L. F. Abbott, *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*, ser. Computational Neuroscience. Cambridge, MA: MIT Press, 2001.
- [30] P. Fries, "A mechanism for cognitive dynamics: neuronal communication through neuronal coherence," *Trends in Cognitive Sciences*, vol. 9, no. 10, pp. 474–480, 2005.
- [31] T. J. Buschman and E. K. Miller, "Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices," *Science*, vol. 315, no. 5820, pp. 1860–1862, 2007.
- [32] D. Rubino, K. A. Robbins, and N. G. Hatsopoulos, "Propagating waves mediate information transfer in the motor cortex," *Nature Neuroscience*, vol. 9, no. 12, pp. 1549–1557, 2006.