Statistical Dynamics of Balanced Cortical Circuits

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Cortical networks are strongly and densely connected with individual neurons receiving thousands of excitatory synaptic projections even though only tens of inputs are needed to drive spiking. This notion seems at first inconsistent with the sparse, irregular neural activity observed in cortical recordings. How do cortical networks maintain low spiking rates in the presence of strong positive feedback? How can nearby neurons share a significant proportion of their inputs yet produce irregular and asynchronous spiking activity? The balanced network modeling paradigm offers parsimonious answers to these questions. In balanced network models, strong recurrent excitation is stabilized by strong recurrent inhibition, creating a push-pull dynamic that combines with random connectivity and chaotic network dynamics to produce sparse, irregular spiking activity similar to that observed in experimental recordings [vVS96]. The notion that inhibition balances excitation in cortical networks is supported by numerous experimental studies and a disruption of excitatory-inhibitory balance is associated with some diseases of the nervous system.

The majority of balanced network studies assume a homogeneous network structure in which connection probability depends only on cell type (excitatory or inhibitory), but anatomical and electrophysiological studies reveal that connection probability depends on distance in physical space and, in sensory systems, tuning space. As a consequence, previous models fail to capture several salient features of cortical network dynamics. On the other hand, mathematical analysis of spatially extended neuronal networks typically requires the solution of nonlinear integral equations that are only tractable in simple cases and only quantitatively accurate for networks of simplified binary neuron models [Bre12].

We extend the theory of balanced networks to spatially extended network topologies. We show that, in the balanced network state, the typically nonlinear fixed point problem associated with spatially extended neural fields is reduced to a more tractable system of linear integral equations in the thermodynamic limit. Moreover, spiking statistics in the balanced state are mathematically tractable for a large class of neuron models including the popular AdEx model.

Our earlier work explored the spatial profile of firing rates in balanced networks with isotropic, distance-dependent connections [RD14]. We extend this theory to networks with arbitrary spatial structure and express the firing rate profiles using a novel "balanced network expansion." We then use linear response theory to analyze the stability of the balanced state. We discover spatiotemporal pattern forming instabilities that depend on the full spectrum of neurons' linear response functions and therefore cannot be captured by the simpler firing rate models often used to study spatially extended network dynamics. Finally, we extend our analysis to derive closed form expressions for the spatiotemporal profile of pairwise spike train correlations in balanced networks. We find that the asynchronous state described in [RdLRB+10] is escaped under certain spatial topologies, potentially resolving an ongoing debate over the magnitude of spike train correlations in cortex [EBK+10, CK11]. We compare our theoretical results to in vivo data to explore the mechanisms responsible for shaping the spatiotemporal profile of correlations in primate visual cortex [SK08]. In summary, we utilize the widely reported balance of excitation and inhibition in cortical networks to build a promising new theoretical framework for studying the spatial profile of firing rates, correlated variability and pattern forming dynamics in recurrently connected networks of biologically realistic neuron models.

References

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