ABSTRACT

Non-random connectivity has been repeatedly reported in cortical networks, yet underlying connection principles of these patterns remain elusive. Proposing an abstract geometric network model reflecting stereotypical axonal and dendritic morphology of local cortical layer 5 networks, we here investigate in how far anisotropy in connectivity can constitute such an underlying connectivity rule. Using a combination of analytical considerations and numerical analysis, we find that while standard network measures and pair connectivity remain unaffected, higher order connectivity is strongly influenced by anisotropy, in many cases reflecting patterns found in local cortical circuits. Presenting an abstract network model featuring connectivity principles beyond distance-dependency, the results shown here not only make a strong case for morphology-induced rules as underlying connection principles of non-random patterns, but may provide another step towards a network archetype greatly improving upon the standard random model.

1 INTRODUCTION

Brain network connectivity, the description of links between the brain's computational units, lies at the heart of many theories trying to explain the exceptionally diverse and robust functionality of the brain. As an essential component in the investigation of the emergence of its unique cognitive abilities, brain connectivity is often associated with memory and the remarkable performance in various perception tasks. Connectivity is, in its essence, intimately tied to mathematical concepts. Relying heavily on a graph theoretical framework for the analysis and discussion of network connectivity, this aspect of brain research is an exciting and highly relevant example of applied mathematics.

In the field of theoretical and computational neuroscience neural network models are studied as of brain networks. Studies interested in the dynamical aspect for example investigate . The standard model for such simulations is that of random graph (Brunel 2000). However, results over the last years show that local cortical circuits display highly non-random connectivity features (Song et al. 2005; Perin et al. 2011). It is unclear how to incorporate such as underlying remain yet to be identified. unclear how to incorporate. Important to identify underlying rules.

The search underlying principles has since (Klinshov et al. 2014). In an effort to contribute to this discussion, we here investigate anisotropy in connectivity. Motivated from observations of stereotypical morphology, the may not only provide but further can be a first step towards network models. Making sure that, the hope is not only to contribute but to help network model.

1.1 OVERVIEW

Following the introduction and this outline, a short overview of the biological terms frequently appearing throughout this text is given as reference at the end of this chapter. The central mathematical objects in this study, various directed graph models, are then introduced and discussed in detail in Chapter **??**. Building on these concepts, Chapter **??** introduces the anisotropic network model as the main object of investigation in this thesis. Next to an in-depth motivation of the anisotropic connectivity concept, the chapter also introduces the rewiring of networks and a measure for anisotropy, laying the groundwork for the analysis of structural features in anisotropic networks in Chapter **??**. First investigating standard network attributes like degree distributions and small-world measures, analysis of higher order connectivity in the latter part of the chapter reveals the highly interesting emerging patterns in anisotropic networks. Closing the structural analysis with a critical discussion of the obtained results, an outlook in Chapter 2 .

1.2 BIOLOGY OF NEURAL NETWORKS

The fundamental computational units in brain networks are neurons, electrically excitable cellular elements that process and transmit information by a cell type dependent regime of electrical and chemical signals. Neurons are linked through synapses, forming together an expansive, interconnected network of different neuron types, dividing into functionally and anatomically distinct areas. The number of neurons in the average human brain is estimated at about 86 billion, connected by 10^{14} - 5×10^{15} synapses (Herculano-Houzel 2009; Drachman 2005). Among the different brain areas studied, the multilayered cerebral cortex stands out as a region of particular interest with many studies analyzing its structural and dynamical features.

The principal excitatory neuron type in cortical networks are pyramidal cells. Connection between those neurons are mainly of chemical nature, in the synaptic contacts between cells the release and consequent reception of neurotransmitters transmits electrical signals. While cortical networks are considered sparse, pyramidal cells typically receive tens of thousands excitatory and several thousand inhibitory inputs, making up for an overall connectivity of about 10% in local networks (Spruston 2009). Such synaptic contacts are inherently asymmetric; signals travel from the cell body of a neuron along the axon to be transmitted at a synapse contacting the dendritic tree of the post-synaptic neuron. Morphology of axon and dendrite are characteristically different; it is this difference that is taken up in this study and serves as a basis for the network model introduced in Chapter **??**.

To enable we introduce For Brain networks . They are well presented by the mathematical object of a directed graph, which will be discussed in detail in the following chapter.

2

OUTLOOK: DYNAMICAL ASPECTS

So far the focus of this study lay in uncovering how anisotropy affects structural aspects of geometric neural networks. Finding that higher order connectivity is indeed strongly influenced by anisotropy, the question arises if and how anisotropy affects dynamical aspects as well. As we studies repeatedly the first question is bound to be answered positively. In this chapter, as an outlook, we show how anisotropy can concretely affect network dynamics.

For this

In a network of N neurons, let f be the fraction of excitatory neurons,

$$f := \frac{N_E}{N_E + N_I},$$

if N_E and N_I are the number of neurons respectively. Balanced network.

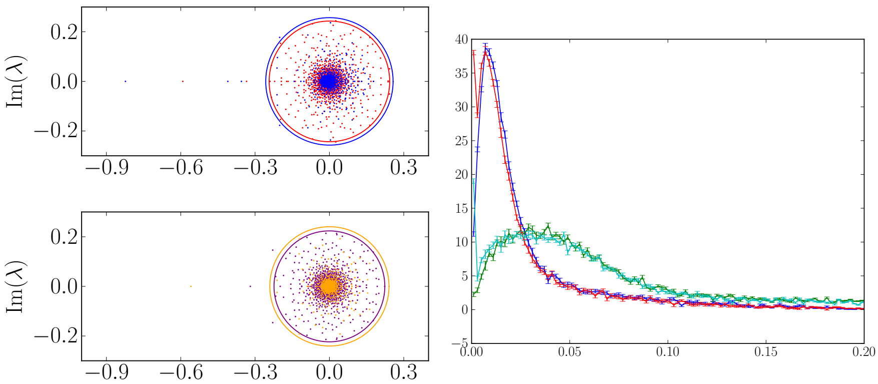

Figure 2.1: High edge counts are overrepresented in networks with anisotropy Normalized difference between number of edges in clusters of 6, 8 and 12 randomly selected neurons in anisotropic networks and rewired networks shows an overrepresentation of high edge counts in networks with anisotropy in connectivity. Errorbars SEM. (`76cc6fa0`, smtcite987992b0, `54329cf4`)