1

## STRUCTURAL ASPECTS

Subjecting the anisotropic network model to a critical examination of its structural features, we identify prevalent patterns of connectivity and relate theoretical and computational results to findings from experiments in the rat's cortex.

## 1.1 COMMON NEIGHBOR RULE

In their study, Perin et al. follow their report of increased edge counts in neuron clusters with the observation of a "common neighbor rule": Relying once again on their data in the rat's somatsensory cortex, Perin et al. find that not only do neuron pairs with a high number of common neighbor count appear significantly more often than expected, but also that such pairs display a higher probability of being connected. In fact, the relationship between pair connectivity and number of common neighbors appears to be linear. Perin et al. also report that this effect is most pronounced when only considering common in-neighbors, that is other neurons that are projecting to both neurons in the pair.

Here we also investigate our networks for the existence of such a common neighbor relationship. Simultaneously recording connection probabilities and the number of common neighbors between pairs of neurons, we find inherent dependencies between the two quantities in all network types (Figure 1.1).

common neighbor rule as underlying principle?

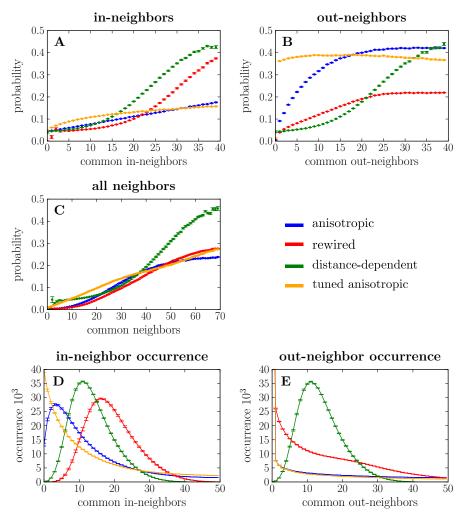


Figure 1.1: Distance-independent overrepresentation of reciprocal connections (something)

Analyzing the results, we immediately note the sharp difference between in- and out-neighbors in their effect on connection probabilities in anisotropic networks, as well as in rewired networks. Only in distance-dependent networks it appears that in- and out-neighbors can be considered equivalent in their influence on connection probabilities (Figure 1.1 A-B). Furthermore, while the distribution of the number of common neighbors is consistent in distance-dependent networks, the other network types display a characteristic distribution of common out-neighbors (Figure 1.1 D-E). While the latter observation clearly also relates to the differences in out-degree distributions found in Section ??, finding differences between common inputs and outputs in neuron pairs is consistent with the observations of Perin et al., who report a significant difference in effect of the common neighbor rule. In trying to model the inherently asymmetric axonal-dendritic connections between pyramidal cells in cortical circuits with the anisotropic networks, finding such disparity is not only expected but gives the model

further validity as an approach to obtain network connectivity going beyond the distance-dependent archetype, which here fails to produce diverging connectivity statistics for in- and outputs.

Both for in- and out-neighbors, we find characteristic curves describing their influence on connection probabilities. The in-neighbor profiles split into two categories: While networks with anisotropy in connectivity (blue, orange) display a constant increase, distance-dependent network types (red, green) show a sigmoidal shared input-connection probability curve (Figure 1.1 A). We thus find a strong influence of anisotropy on the shared input relationship, inducing a common neighbor rule characteristically different from isotropic, distance-dependent networks.

anisotropy induces characteristic common neighbor rule

Does this anisotropy-induced rule reflect the findings in cortical networks? Perin et al. report a linear common neighbor relationship, finding a stronger effect when considering only in-neighbors. Imposing the common neighbor rule on in silico networks reflecting a distancedependency as determined in vivo, Perin et al. were then able to reproduce the observed overrepresentation of high edge counts in neuron clusters, identifying the common neighbor effect as an underlying connection principle inducing increased high edge counts in clusters comparable to the profiles shown in ??. Showing not only the presence of such an edge count overrepresentation in anisotropic networks, but also finding that only networks featuring anisotropy display an approximately linear relationship between common inputs and connection probability, we identify anisotropy in connectivity as a candidate for an underlying connection principle motivated from neuronal morphology, to induce a common neighbor rule, that may be at the heart of many of the nonrandom connectivity statistics observed in local cortical networks.

anisotropy as underlying connection principle!

Extending the analysis of shared inputs in the different network types, we further observe that anisotropy affects the number of common inneighbors typically observed itself (Figure 1.1 D). We specifically find that increases anisotropy in connectivity induces an increased variance in the distribution of common inputs of a random neuron pair Figure 1.2). Such increased variance may provide an important advantage in the processing of information, allowing a heightened functional specificity in the network, where many neurons do not share many common inputs, enabling a high variety of functionality, and where few neuron pairs have a high number of shared inputs, strengthening their correlation and thus their capacity to relay related information.

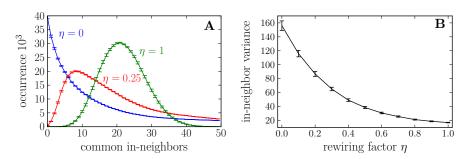


Figure 1.2: Anisotropy increases variance of common input distribution Recording common in-neighbor counts for random neuron pairs in tuned anisotropic networks and their rewired versions reveals increased variance in networks with a high degree of anisotropy. A) Common in-neighbor distribution for original tuned anisotropic networks ( $\eta = 0$ , blue) and rewired versions with 1/4 of all edges rewired ( $\eta = 0.25$ , red) and completely rewired ( $\eta = 1$ , green). (5841710e) B) Variance of the common in-neighbor distributions declines with increasing rewiring factor  $\eta$ ; highest variance is found in networks with the highest degree of anisotropy ( $\eta = 0$ ). Errorbars SEM. (ffcefe9b)