1

STRUCTURAL ASPECTS

1.1 MOTIFS

In this chapter we analyze the strucarl. The term motif referes to... . Studies of Song et al. (2005) and Perin et al. (2011) show stuff. Pernice2011, Sporns , Zhao2011.

Here we investigate the occurrence of three-neuron patterns in anisotropic networks. Song et al. (2005) reported a characteristic, highly non-random motif distribution of pyramidal cells in the rat's visual cortex (layer 5), a result later confirmed by Perin et al. (2011) in their experiment in the rat's somatosensory cortex (layer 5).

There are 13[1] three-neuron motifs that represent non-isomorphic, connected simple directed graphs. In reference to Song et al.'s result, the patterns are labeled 4 to 16,

4 5 6 7 8 9 10 11 12 13 14 15 16.

Let X be a random variable that maps three random vertices $v_1 \neq v_2 \neq v_3$ in a graph G to the $n \in \{4, 5, \ldots, 16\}$ labeling the isomorphism class of their spanned subgraph in G as above if the subgraph is connected, and let X map to $n = 0$ otherwise.

A first idea of how to compute the distribution of X is by inferring the probabilities of motif occurrence from the two-neuron connection probabilities from Section **??**. In anisotropic networks we found that the probabilities of occurrence are

$$\begin{aligned} p_u &= 0.791336 && \text{for unconnected pairs,} \\ p_s &= 0.184151 && \text{for single connections and} \\ p_r &= 0.024513 && \text{for reciprocal connections.} \end{aligned}$$

From these we may, for example, calculate the probability of occurrence for motif 8,

$$\mathbf{P}(X = 8) = 6\, p_u p_s p_r,$$

where the factor 6 is determined by the number of different *labeled* graphs belonging to the isomorphism class. The distribution of X for the remaining motifs is given by

$$\begin{array}{lll} \mathbf{P}(X = 4) = 3p_s^2 p_u & \mathbf{P}(X = \;\;9) = 3p_r^2 p_u & \mathbf{P}(X = 13) = 6p_s^2 p_r \\ \mathbf{P}(X = 5) = 3p_s^2 p_u & \mathbf{P}(X = 10) = 6p_s^3 & \mathbf{P}(X = 14) = 3p_s^2 p_r \\ \mathbf{P}(X = 6) = 6p_s^2 p_u & \mathbf{P}(X = 11) = 2p_s^3 & \mathbf{P}(X = 15) = 6p_s p_r^2 \\ \mathbf{P}(X = 7) = 6p_s p_u p_r & \mathbf{P}(X = 12) = 3p_s^2 p_r & \mathbf{P}(X = 16) = p_r^3. \end{array}$$

Does this distribution accurately reflect the occurrences of three-neuron motifs in anisotropic or even distance-dependent networks? Here we take the distribution determined from the two-neuron probabilities as

distribution from neuron-pairs as reference

1 There are 16 simple directed with 3 nodes. Three of those graphs are unconnected (cf. Davis 1953, N. J. A. Sloane. The On-Line Encyclopedia of Integer Sequences, http://oeis.org. Sequence A000273).

a reference to analyze occurrences of three-neuron motifs in our sets of sample graphs. Counting the occurrences of patterns in we find that there are significant over- and underrepresentations in anisotropic as well as distance-dependent networks, relative to our expectation (Figure 1.1). We find, for example, that in anisotropic graphs pattern 12 occurs almost 5 times as often as we would have expected from the two-neuron probabilities, whereas the counts for pattern 11 only make up less than 30% of the occurrences expected.

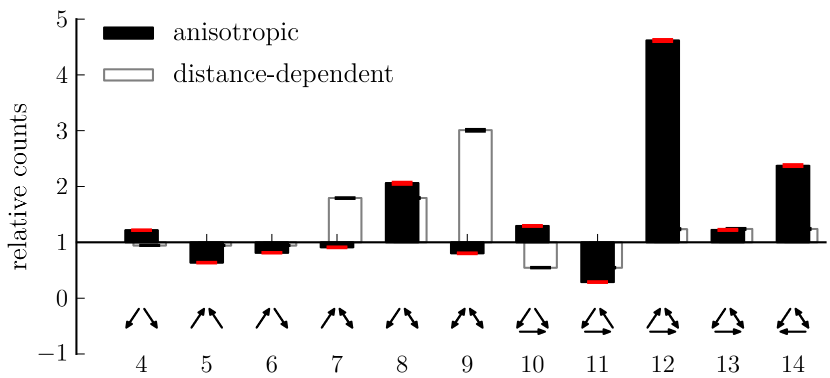

Figure 1.1: Relative occurrence of three-neuron patterns Extracting the counts of three-node motifs in anisotropic (filled bars) and distance-dependent networks (unfilled bars), the quotient of the obtained count with the number of occurrences expected from the two-neuron connection probabilities in the networks (cf. Section **??**) shows the over- and underrepresentation of specific motifs in the network (red and black errorbars are SEM). In anisotropic networks pattern 12, for example, appears around five times more often than we would expect from the occurrence two-neuron connections. The relative counts for anisotropic networks resemble the findings of Song et al. (2005) and differ significantly from the counts in distance-dependent networks, implying that anisotropy has a strong influence on the relative occurrence of three-neuron patterns. (`4839ce41`)

anisotropy strongly affects 3-motif occurrence

Comparing the relative counts for motifs in anisotropic graphs with those in comparable distance-dependent networks, we identify a strong influence of anisotropy in connectivity on three-neuron motif occurrence (Figure 1.1). In their experiments, Song et al. and Perin et al. find an overrepresentation of motifs 4, 10, 12 and 14. In anisotropic networks increased counts of motifs 4, 8, 10, 12, 13 and 14 were recorded. However, motifs 8 and 13 are overrepresented in distance-dependent networks as well, leaving the reported motifs 4, 10, 12 and 14 as motifs that are overrepresented due to anisotropy. To analyze this effect closer, we also compare three-neuron counts before and after rewiring in anisotropic networks (Figure 1.2).

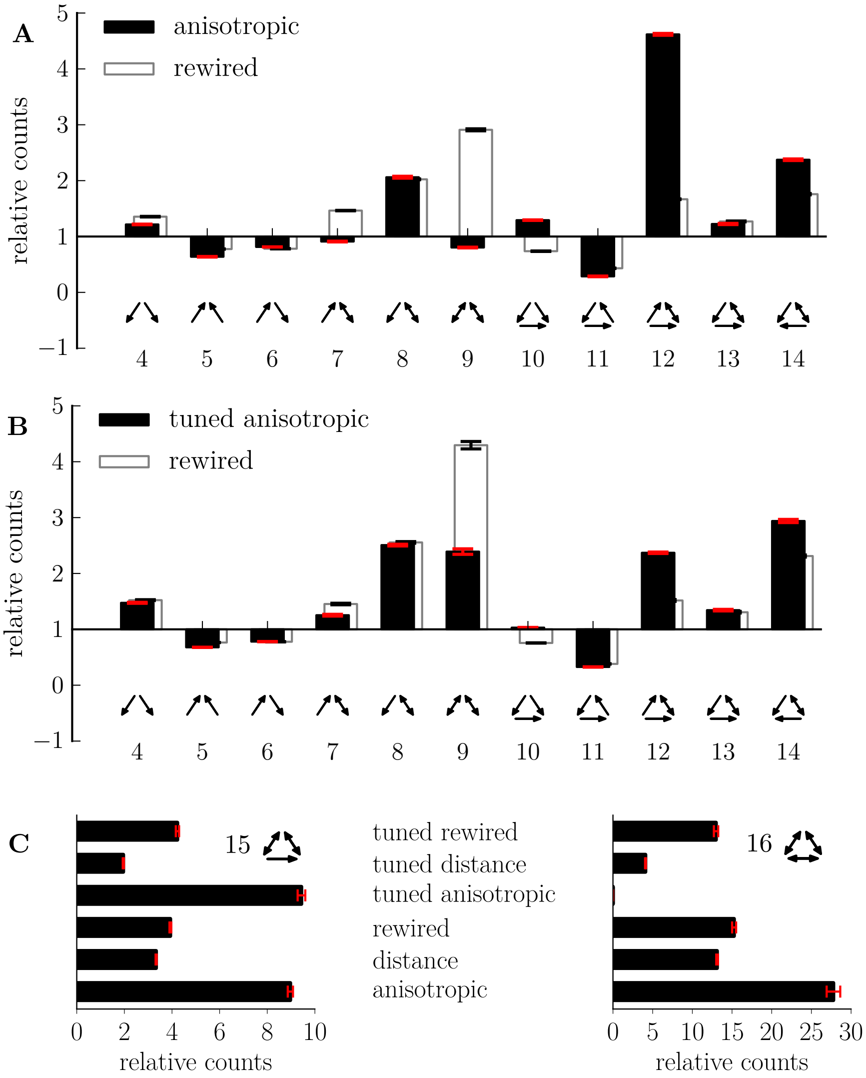

Figure 1.2: Three-neuron motif occurrence in different network types A) Comparing counts in anisotropic sample graphs with their rewired counterparts. **B)** Three-neuron motifs occurrence in tuned anisotropic networks (cf. Section **??**) with their rewired counterparts. For this two-neuron connection probabilities were extracted as in Section **??** and motif probabilities were calculated analogously to anisotropic networks. **C)** (`4839ce41`)

Here we find that .

Anisotropy in connectivity induces increased occurrence of motifs 10, 12, 14 and 15 in the network. It has strong influence the counts of motif 16. While over- and underrepresentation observed in local cortical circuits can be indirectly linked to anisotropy for some motifs (4,9) it does not accurately reflect observed counts for other motifs (8).