

## STRUCTURAL ASPECTS

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## 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. Per-  
nice2011, 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<sup>1</sup> 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,



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  $n \in \{4, 5, \dots, 16\}$  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

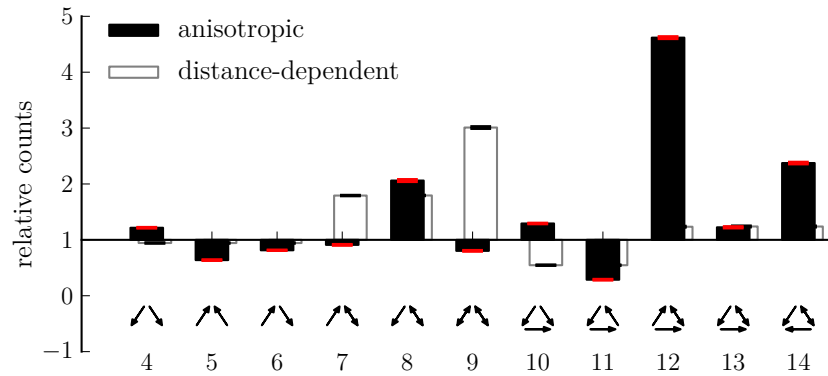
$$\begin{aligned} \mathbf{P}(X = 4) &= 3p_s^2 p_u & \mathbf{P}(X = 9) &= 3p_r^2 p_u & \mathbf{P}(X = 13) &= 6p_s^2 p_r \\ \mathbf{P}(X = 5) &= 3p_s^2 p_u & \mathbf{P}(X = 10) &= 6p_s^3 & \mathbf{P}(X = 14) &= 3p_s^2 p_r \\ \mathbf{P}(X = 6) &= 6p_s^2 p_u & \mathbf{P}(X = 11) &= 2p_s^3 & \mathbf{P}(X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

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*

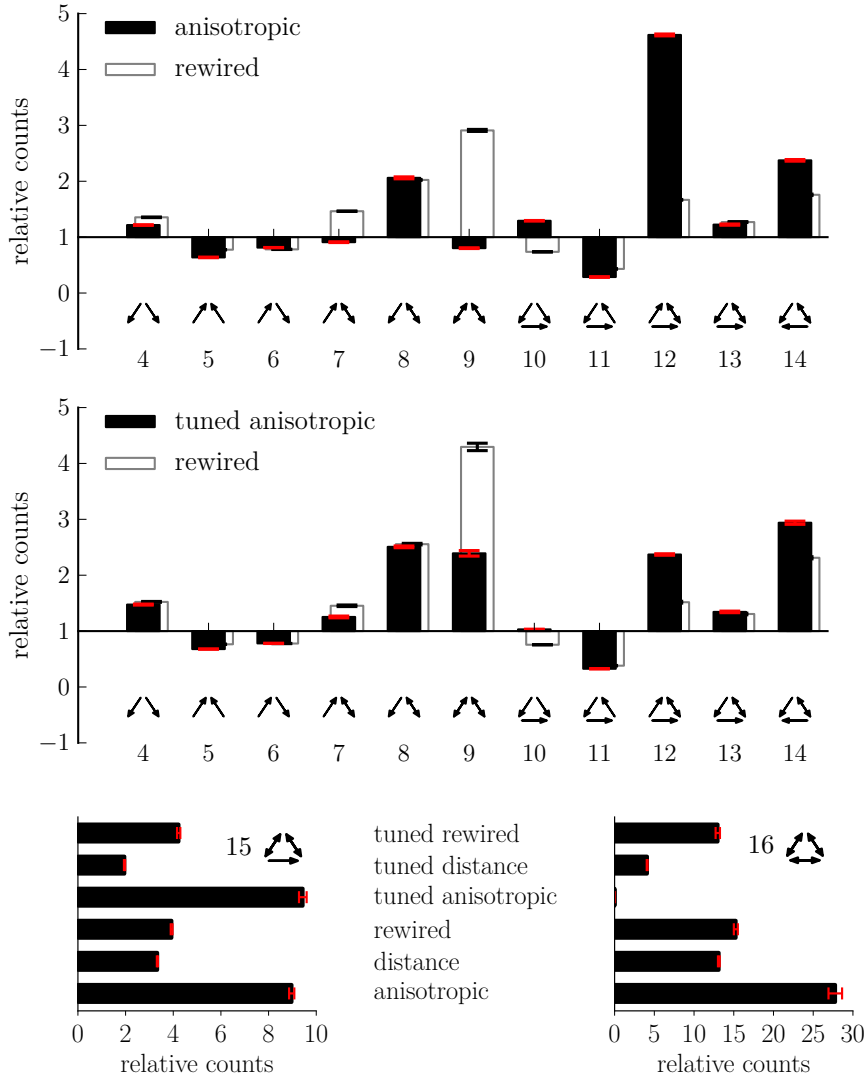
<sup>1</sup> There are 16 simple directed with 3 nodes. Three of those graphs are unconnected (cf. Davis 1953, N. J. A. Sloane. The On-Line Encyclopedia of Integer Sequences, <http://oeis.org>. Sequence A000273).

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)

This . Perin et al. (2011) confirm the overrepresentation of motifs 4, 10, 12 and 14. In anisotropic networks we find increased counts of motifs 4, 8, 10, 12, 13 and 14. However, comparison with motif counts in distance-dependent networks shows that only the increased occurrence of motif 4, 10, 12 and 14



**Figure 1.2: 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 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 (4,11) it does not accurately reflect observed for other motifs (8).

, however not in motif 4. Additionally, anisotropy in connectivity causes for large in motifs . Motif 9 is significantly underrepresented in anisotropic networks, also reflecting the findings of Song et al. Overrep of 8 not reported, here consistent through network types.