

## STRUCTURAL ASPECTS

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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 MOTIFS

In obtaining and discussing the previous results, we closely followed the approach described by [Song et al. \(2005\)](#). Here, relying on analytical considerations, we submit these results to a critical analysis and identify potential caveats when dealing with motif distributions in distance-dependent networks.

For this consider for example the motifs 9, 15 and 16 as labeled above. In distance-dependent networks we find that each of the patterns is over-represented, observing that the motifs occur about 3, 3 and 12 times more often than expected from the two-neuron connection probabilities, respectively (??). Thus, in distance-dependent networks, triplets in which two of the pairs are reciprocally connected appear more often than expected, regardless of the connectivity in the third pair. This is surprising, as probabilities for the first two neuron pairs in a triplet should be independent and the probabilities of obtaining a certain connectivity should reflect the product of two-neuron probabilities. The overrepresentation found in these motifs may thus not necessarily be an inherent feature of the network connectivity but rather an artifact of triplet selection.

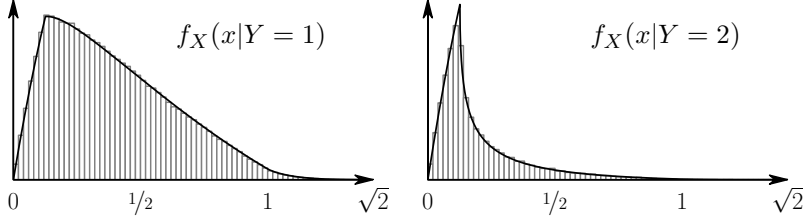
To analyze this further, we compute the relative probabilities of occurrence motifs 9, 15 and 16. Formulated differently, given a triplet with two reciprocally connected pairs, what is probability of connection in the third pair? For this we first find the probability density function of the distance between a random neuron pair, given that we know its connectivity, meaning the existence of either 0, 1 or 2 edges between the neuron. Let  $X$  be the random variable mapping a random neuron pair of neurons to the distance between them and  $Y$  the random variable mapping to the number of edges between the pair. By the relation

$$f_X(x|Y = n) = \frac{f_{X,Y}(x, n)}{\mathbf{P}(Y = n)},$$

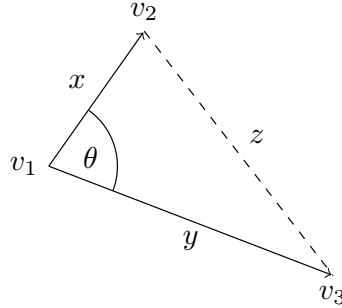
for  $n = 0, 1, 2$ , the probability density function  $f_X$  of the continuous variable  $X$  conditioned on the discrete variable  $Y$ , are then computed as the quotients

$$\begin{aligned} f_X(x|Y = 0) &= \frac{f(x)(1 - C(x))^2}{\int_0^{\sqrt{2}} f(x)(1 - C(x))^2 dx} \\ f_X(x|Y = 1) &= \frac{f(x)2C(x)(1 - C(x))}{\int_0^{\sqrt{2}} f(x)2C(x)(1 - C(x)) dx} \\ f_X(x|Y = 2) &= \frac{f(x)C(x)^2}{\int_0^{\sqrt{2}} f(x)C(x)^2 dx}, \end{aligned} \tag{1.1}$$

where  $f(x)$  is the probability density function of the distance between two random in the unit square the found in Theorem ?? and  $C(x)$  the distance-dependent connectivity from Theorem ?. Values for the denominator in Equation 1.1 have already been determined in Section ?. Evaluating the products in the numerator, we find that the expected probability density function is perfectly match by the distance distributions found in the simulated distance-dependent network model (38c11969):



Consider then a triplet with vertices  $v_1, v_2$  and  $v_3$ , the pairs  $(v_1, v_2)$  and  $(v_1, v_3)$  being reciprocally connected. With the density function  $f_X(x|Y=2)$  we then have a distribution for the distances  $x = d(v_1, v_2)$  and  $y = d(v_1, v_3)$ . In the triangle spanned by the positions of the vertices, the distance  $z = d(v_2, v_3)$  is then determined by the angle  $\theta$  between  $x$  and  $y$ :



By the law of cosines we have the relation

$$z = \sqrt{x^2 + y^2 - 2xy \cos \theta}.$$

Extensively using Lemma ??, we can use this relation to calculate the probability density of  $z$  in the triplet  $(v_1, v_2, v_3)$  from the densities  $f_X(x|Y=2)$  of  $x$  and  $y$ . Here, however it is sufficient to find the expected value of  $z$ . The expected value for  $x$  and  $y$  is

$$r := \mathbf{E}[x] = \mathbf{E}[y] = \int_0^{\sqrt{2}} x f_X(x|Y=2) dx.$$

Finding an expected value of  $z$  is then well known problem of determining the length of a chord between two random points on the circle. From symmetry :

Quotient with expected probabilities from two neuron connections

$$\mathbf{P}(X = 9) = 3p_r^2p_u, \quad \mathbf{P}(X = 15) = 6p_sp_r^2, \quad \mathbf{P}(X = 16) = p_r^3,$$

and have

Thus, while motif 9 and 15 appear in relatively among three-motifs with two reciprocal connections, motif 16 appears four times as often. This result is immediately confirmed by our computational results, finding that triplets with appear 3 in general, and .

The “true” overrepresentation may thus only be present in motif 16, appearing four more times as expected.

How does this affect the results described above? As distant-dependent networks are clearly

However, here we relied on finding impacts of anisotropy on networks, finding only relative. Such an analysis Closely inspecting the results of Song et al., we identify this problem in motifs 4, 10 and 12, each being reported as overrepresented although together making up a two neuron pairs with single connections each, implying a potentially biased selection of neuron triplets.