Non-random connectivity comes in pairs

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Abstract

Overrepresentation of bidirectional connections in local cortical networks has been repeatedly reported and is in the focus of the ongoing discussion of non-random connectivity. Here we show in a brief mathematical analysis that in a network in which connection probabilities are symmetric in pairs, $P_{ij} = P_{ji}$, the occurrence of bidirectional connections and non-random structures are inherently linked; an overabundance of reciprocally connected pairs emerges necessarily when the network structure deviates from a random network in any form.

Introduction

Increasing evidence implies that cortical microcircuitry is highly structured [1, 2]. The relative occurrence of bidirectionally connected pairs has been of particular interest and connectivity of layer 5 pyramidal neurons in the rat visual cortex [1] and somatosensory cortex [3, 2] was shown to have a significantly stronger reciprocity than expected. However, the exact relationship between non-random network structure and the relative occurrence of bidirectionally connected neuron pairs has not been explained.

Results

Define a **random network model** in which node-to-node connection probabilities themselves follow a random distribution; some pairs of neurons have a higher chance to be connected than others.

Consider a random network model of N neurons in which a connection from node i to node j exists with probability P_{ij}. Here, the P_{ij}, with $i, j = 1, \ldots, N$ and $i \neq j$, are identically distributed random variables in $[0, 1]$, yielding a probability of connection for each ordered pair of nodes in the network.

Example: Network in which connection probability is either high or low, depending on whether the target neuron share the same feature (e.g. orientation tuning) or not.

The overall connection probability μ, that is the chance to have a connection from a random node i to another node j, is

$$\mu = \mathbf{E}(P_{ij}). \tag{1}$$

For example, if the P_{ij} have a probability density function f with essential support in $[0, 1]$, we can compute the connection fraction as

$$\mu = \int_0^1 x f(x)\, dx. \tag{2}$$

The probability for a random pair of nodes i and j to be connected reciprocally is then

$$P_{\text{rec}} = \mathbf{E}(P_{ij}P_{ji}). \tag{3}$$

The relative occurrence ϱ of these reciprocally connected pairs within the network compares P_{rec} with the occurrence of bidirectionally connected pairs in an Erdős-Rényi graph, in which each unidirectional connection is equally likely to occur with probability μ. Formally,

$$\varrho = \frac{P_{\text{rec}}}{\mu^2} = \frac{\mathbf{E}\left(P_{ij}P_{ji}\right)}{\mathbf{E}\left(P_{ij}\right)^2}. \tag{4}$$

If connection probabilities are **symmetric in pairs**, $P_{ij} = P_{ji}$, then

$$\varrho = \frac{\mathbf{E}(P_{ij}^2)}{\mathbf{E}\left(P_{ij}\right)^2}. \tag{5}$$

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Since $x \mapsto x^2$ is a strictly convex function, **Jensen's inequality** [4] yields

$$\mathbf{E}(P_{ij}^2) \geq \mathbf{E}(P_{ij})^2. \tag{6}$$

Equality holds in (6) if and only if P_{ij} is a constant. Thus *any* non-degenerate distribution of connection probabilities *necessarily* induces an overrepresentation of bidirectional connections in the network, $\varrho > 1$.

Summary: In a network where some pairs are more likely connected than others, the count of expected reciprocally connected pairs is strictly underestimated by the statistics of an Erdős-Rényi graph with same overall connection probability $\mathbf{E}(P_{ij}) = \mu$.

Two-point distribution

Consider P_{ij} to follow the discrete **two-point distribution**, where

$$\mathbf{Prob}(P_{ij} = x) = p \quad \text{and} \quad \mathbf{Prob}(P_{ij} = y) = 1 - p. \tag{7}$$

We derive an expression for the relative occurrence of reciprocal pairs ϱ as

$$\varrho = \frac{x + y}{\mu} - \frac{xy}{\mu^2}. \tag{8}$$

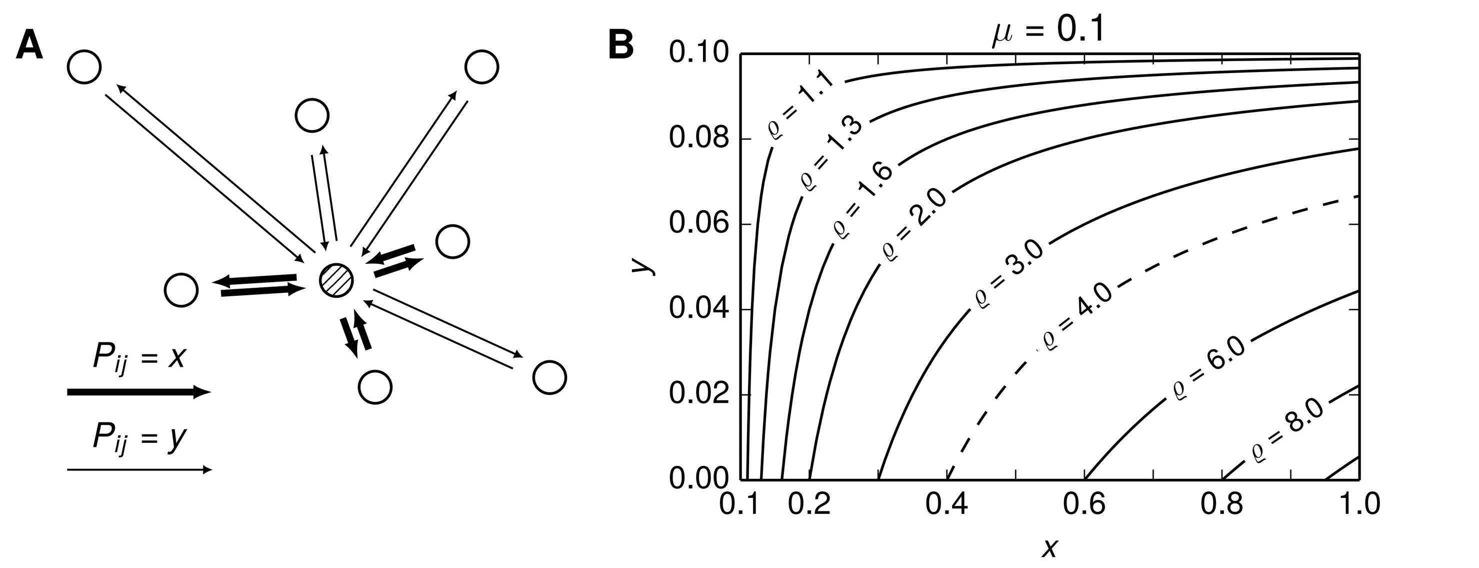

Figure 1: A Sketch of a network with connection probabilities x and y **B** For $\mu = 0.1$ fixed, different pairings of x and y can induce high values of the relative occurrence of bidirectionally connected pairs ϱ. Dashed line marks an overrepresentation of $\varrho = 4$ as observed for layer 5 pyramidal neurons in the rat visual cortex [1].

Truncated gamma distribution

Consider the P_{ij} to follow the continuous **truncated gamma distribution**, which is given by the density function f^T as

$$f^T_{\alpha,\beta}(x) = \begin{cases} K_{\alpha,\beta} \frac{1}{\beta^\alpha \Gamma(\alpha)} x^{\alpha-1} e^{-x/\beta} & 0 \leq x \leq 1 \\ 0 & \text{otherwise,} \end{cases} \tag{9}$$

where the normalization factor $K_{\alpha,\beta}$ is the inverse of the cumulative probability that $x \leq 1$ of the untruncated gamma distribution

$$K_{\alpha,\beta} = \left(\int_0^1 \frac{1}{\beta^\alpha \Gamma(\alpha)} x^{\alpha-1} e^{-x/\beta}\, dx \right)^{-1}. \tag{10}$$

When the overall connection probability μ is fixed, only one free parameter remains, and the relative overrepresentation of bidirectional connections ϱ can be approximated as

$$\varrho \approx 1 + \frac{1}{\alpha}. \tag{11}$$

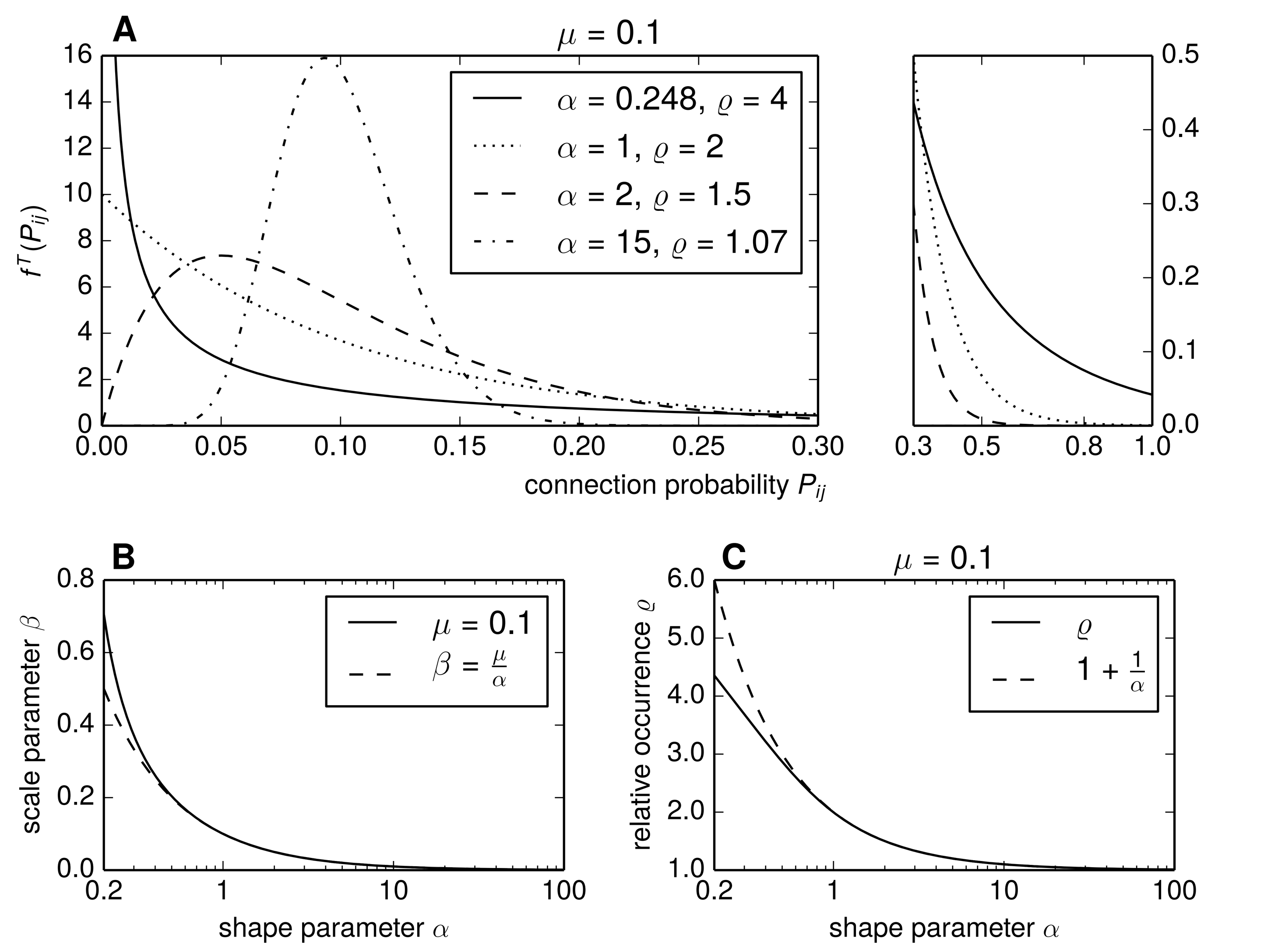

Figure 2: A Probability density functions of the truncated gamma distribution for different shape parameters α and the induced relative overrepresentation ϱ in the network with such distributed connection probabilities P_{ij}. For a given α, the scale parameter β was chosen such that $\mu = 0.1$. **B** Contour of α, β pairings that yield an overall connection probability of $\mu = 0.1$. **C** Relative occurrence ϱ in dependence on α for fixed $\mu = 0.1$. For $\alpha \geq 1$ this relationship is well approximated by $\varrho \approx 1 + \frac{1}{\alpha}$.

Conclusions

- In networks with symmetric connection probabilities in pairs any non-random network structure induces an overrepresentation of bidirectionally connected neuron pairs
- Neuron properties, such as inter-neuron distance, age or orientation preference, that impose a discrete or continuous distribution of connection probabilities, can significantly affect the relative occurrence of reciprocal pairs
- Understanding of local cortical circuits requires a more refined view of non-random network connectivity that goes beyond bidirectional pairs and focuses on the emergence of higher order network structures

References

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