

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 $i, j = 1, \dots, N$ 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

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

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

$$\mu = \int_0^1 x f(x) dx. \quad (2)$$

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

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

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,

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

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

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

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

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

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

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

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

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

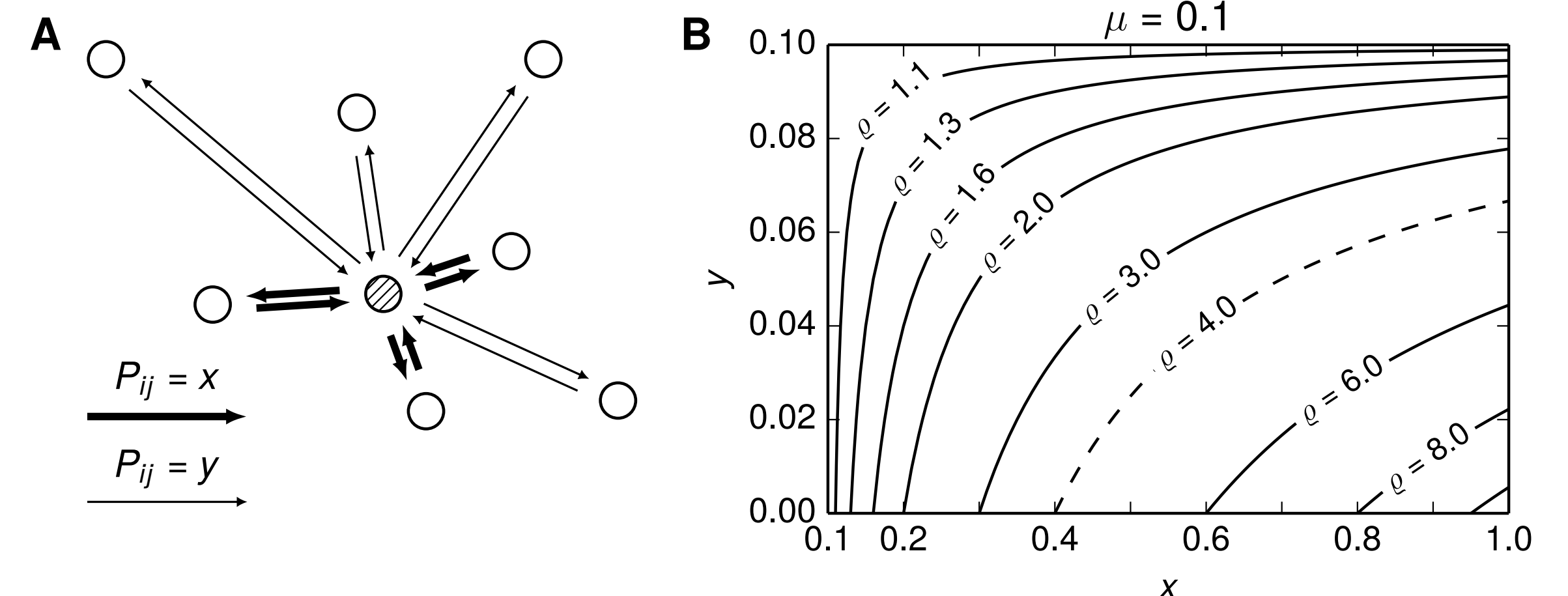


Figure 1: **A** Sketch of a network with connection probabilities x and y **B** For $\mu = 0.1$ fixed, different pairings of x and y can induce high values of the relative occurrence of bidirectionally connected pairs ϱ . Dashed line marks an overrepresentation of $\varrho = 4$ as observed for layer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

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

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

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

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

$$\varrho \approx 1 + \frac{1}{\alpha}. \quad (11)$$

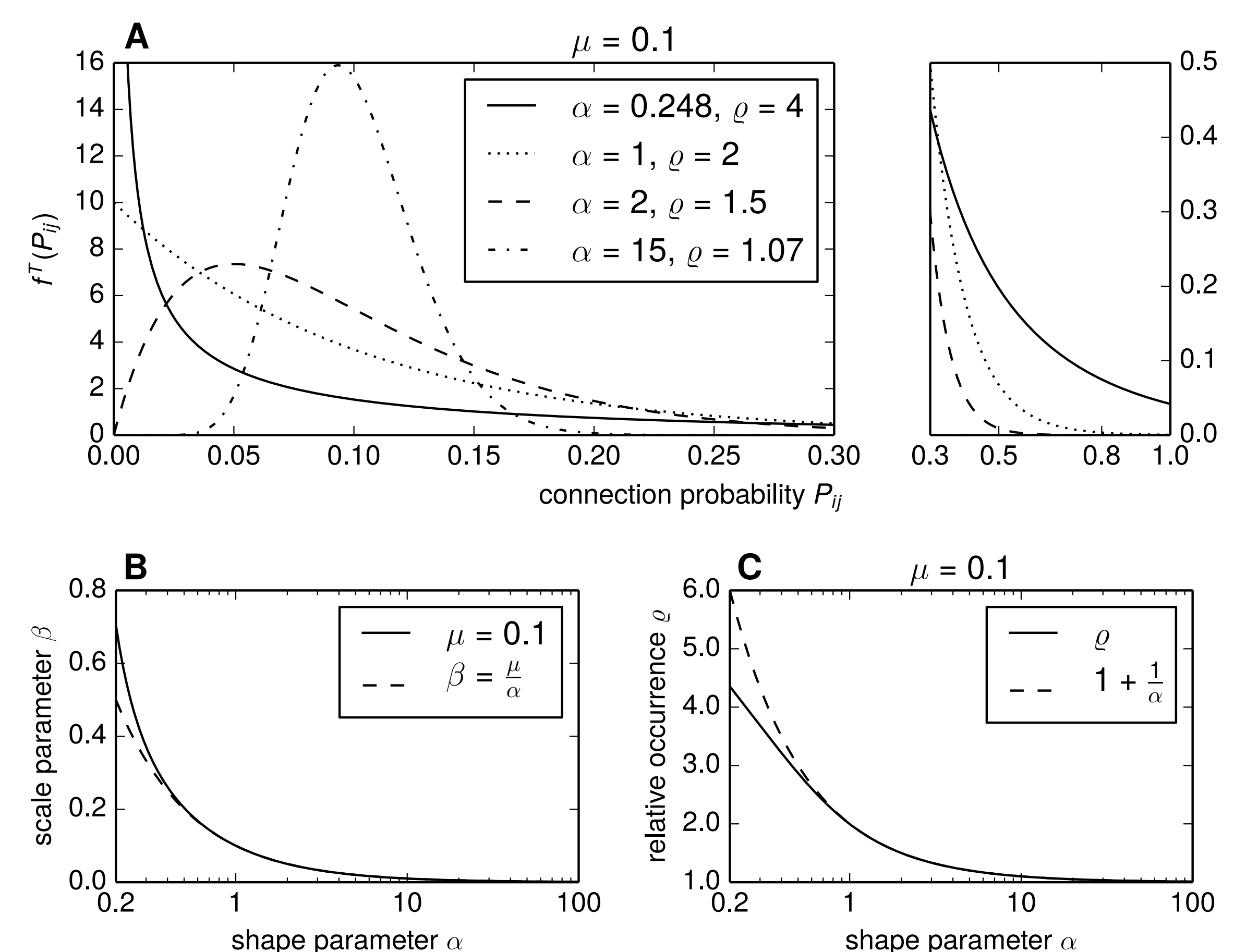


Figure 2: **A** Probability density functions of the truncated gamma distribution for different shape parameters α and the induced relative overrepresentation ϱ in the network with such distributed connection probabilities P_{ij} . For a given α , the scale parameter β was chosen such that $\mu = 0.1$. **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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