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Statistical analysis of spatially embedded networks: From grid to random node positions

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Abstract

Many conceptual studies of local cortical networks assume completely random wiring. For spatially extended networks, however, such random graph models are inadequate. The geometry of neuronal dendrites and axons induces distance-dependent connectivity. Here, we investigated several types of spatial embedding that are widely used in modeling. Both regarding the spatial positions of nodes and in terms of node connectivity, we considered the full range between regularity and randomness, and characterized the various networks in the framework of stochastic graph theory. We found that many characteristic network properties are highly sensitive to the degree of randomness in the spatial arrangement of nodes, especially in the case of networks dominated by local connections. Our findings have potentially important implications for the design of large-scale network models.

Keywords: Spatially extended networks; Distance-dependent connectivity; Stochastic graph theory; Global network properties

1. Introduction

Current studies of the activity dynamics in local cortical networks assume sparse, but completely random wiring [4]. For spatially extended networks, however, this random graph approach is inadequate. The architecture of non-local cortical networks has a much richer structure, and in particular, it has a spatial dimension: Cortical wiring is, to some extent, distance-dependent [5–8], and it comprises both local and long-range connections [3]. In the simplest case, a non-local network is represented by a two-dimensional 'sheet' of neurons. This immediately raises the question how to adequately describe the spatial arrangement of nodes. Here, we investigated several different methods to position the nodes, before connecting them according to distance-dependent probabilities. Comparison with neuroanatomical data may then be used to derive more realistic models of non-local cortical networks.

We assumed an embedding of all neurons into a two-dimensional quadratic domain. This allows for distance-dependent connectivity reflecting the geometry of dendrites and axons. To assess the influence of the spatial embedding scheme on the emerging network topology, we considered the full range between regular lattices and randomly positioned nodes. The wiring schemes of all models were arranged to span the full continuum from local/regular wiring to completely random connectivity. We then employed the framework of stochastic graph theory [10,1] to define a set of characteristic network properties. This allowed us to compare networks based on widely different construction principles, and to compare the network models inspired by neuroanatomy with well-known types of abstract graphs, e.g. small-world networks [10,9].

2. Methods

A directed graph G is completely specified by its non-symmetric adjacency matrix $A(G) = (a_{ij})$, where $a_{ij} = 1$ if a link $j \to i$ exists, otherwise $a_{ij} = 0$. We specifically considered here sparsely connected networks of $N = 1024$ nodes. On

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average, only a fraction $c = 0.012$ of all $N(N-1)$ possible links was established in each particular network. Both the mean in-degree and out-degree was selected to be $\bar{k} = 12$, for reasons that will be explained in the following.

2.1. Spatially embedded graphs

We considered different spatial embeddings of networks into a two-dimensional quadratic domain of extent R, wrapped around to a torus to avoid boundary effects (Fig. 1a). First, the nodes were placed on the grid points of a rectangular lattice, with a distance $a = R/32$ between immediate neighbors. We then studied the effect of perturbing the grid. In the jittered lattice (JL) scenario, all grid points were randomly, uniformly and independently displaced by a step from $[-\Delta, \Delta]$ in each direction. For $\Delta = 16a = R/2$ we ended up with completely random node positions.

For each of these initial node embeddings, we then let each node of the network establish an axonal projection to all nodes within a local circular neighborhood of radius r. For the nodes placed on grid points, this neighborhood consists of the eight nearest neighbors and four additional next-to-nearest neighbors, leading to the determination of $\bar{k} = 12$ for all considered networks. Hence, the radius of the local neighborhood is $r = R\sqrt{c/\pi} \approx 0.062R$. For regular grids this resulted in a singular distribution of out-degrees, in the case of a strongly JL the out-degree distribution was binomial. We also considered a variant of this model, where we used regular lattice positions, but forced the in-degree distribution to be binomial (FB) by admitting randomly varying values for the radius r. Moreover, we applied the following rewiring procedure to introduce extra long-range connections (Fig. 1b): each individual link of the graph was, with probability ϕ, replaced by a randomly selected one. For $\phi = 1$ we again end up with a completely random graph.

2.2. Characteristic network properties

The following descriptors were used to characterize and compare the different network models: (A) histograms of the numbers of incoming or outgoing links for all nodes of a graph give an estimate of the characteristic distribution of in-degrees $P_{\text{in}}(k)$ or out-degrees $P_{\text{out}}(k)$, respectively. The two-node degree correlation $K_c = \langle \sum_{(i,j)} k_i * k_j \rangle$ describes in-degree or out-degree relations between any two connected nodes i and j, respectively. (B) The length of the shortest path L_{ij} is the minimal number of hops necessary to get from node j to node i respecting link directions. We considered the average length of shortest paths $L = 1/N(N-1)\sum_{i \neq j} L_{ij}$ for all pairs of distinct nodes. (C) The cluster coefficient C_i is the fraction of all potential links actually established between any two nodes receiving a link from node i. We considered the mean cluster coefficient $C = 1/N \sum_i C_i$. Additionally, we calculated the degree-dependent cluster coefficient $C(k)$ [2]. (D) For any graph G, we numerically determined the N complex eigenvalues λ of its adjacency matrix $A(G)$, and we estimated the eigenvalue density $p(\lambda)$ from ensembles of graphs of the same type. (E) The corresponding eigenvectors v of $A(G)$ were also numerically determined [1]. To quantify the spatial concentration of a normalized vector v, we used the weighted two-dimensional circular variance

$$V = 4 - 2\left|\sum_k |v_k|^2 \mathrm{e}^{2\pi \mathrm{i} x_k / R}\right| - 2\left|\sum_k |v_k|^2 \mathrm{e}^{2\pi \mathrm{i} y_k / R}\right|,$$

where v_k are the components of v satisfying $\sum_k v_k^2 = 1$, and (x_k, y_k) denotes the spatial coordinates of node k. For this definition, it holds that $0 \leqslant V \leqslant 4$. Small values of V indicate that the 'mass' encoded by the squared components of v is concentrated in a compact spatial region, larger values of V imply that it is more uniformly spread over the whole domain.

3. Results

Networks with random node positions ($\Delta = 16a$) exhibit binomial degree distributions, irrespective of the value of ϕ, the relative abundance of non-local connections. For JL networks with $\Delta < 16a$, these distributions are binomial only for $\phi = 1$, corresponding to a random graph. Only few non-local connections in combination with only mildly

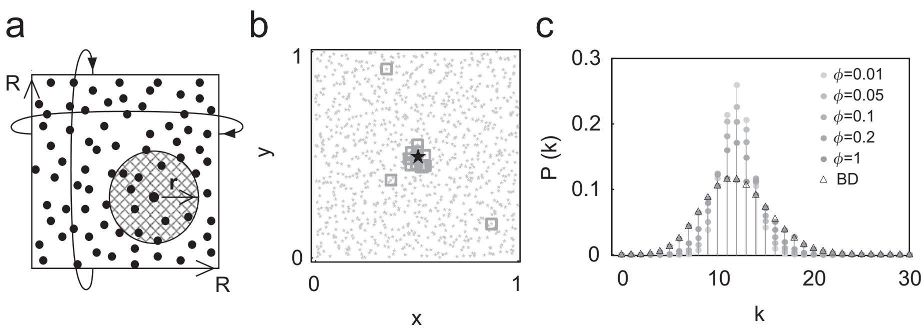

Fig. 1. (a) Scheme describing the construction of spatially embedded networks with distance-dependent connectivity. (b) Random node positions (dots) for a sample network of $N = 1024$ nodes. Local and distant targets (squares) of one particular node (black star). (c) Distribution of out-degrees in the FB model (see text), for various rewiring probabilities ϕ, and the corresponding theoretical binomial distribution (BD).

jittered node positions generally lead to more narrow degree distributions. The unconstrained out-degree distribution of the FB model is not as narrow as for lattice position networks, but it is far from being binomial (Fig. 1c). The degree correlation turned out to be a sensible indicator for the type of spatial embedding (Fig. 2a). In case of random positions, K_c decreases with increasing ϕ, while for lattice positions it decreases towards the common value of $K_c = 156$ for $\phi = 1$. The JL networks with $0 < \Delta < 16a$ fill up the range in-between these two extremes. For the FB model, K_c of the unconstrained out-degree results in a curve very similar to the grid model, while the in-degree correlation is constant with respect to ϕ. The average spatial concentration of eigenvectors also depends on the jitter parameter Δ. The stronger the nodes are displaced from their original grid points, the more locality we observe (Fig. 2b). Again this effect varies with ϕ: for mainly locally connected networks, larger differences are obtained. Spatially embedded rewired networks exhibit a strong 'small-world' effect (Fig. 2c), according to which only very few long-range connections suffice to dramatically decrease the average shortest path length L, while the cluster coefficient C is still relatively high [10]. Concerning the spatial regularity, we found that C is highest for random positions, and decreases for smaller values of Δ. Here again, the FB model shows a curve similar to lattice position networks. Additionally, $C(k)$ of the FB model resembles the $C(k)$ curves for the JL networks with small Δ, i.e. little jittering (Fig. 2d). In the case of completely random connectivity, the cluster coefficient is independent of the degree k [2], indicated in Fig. 2d by a horizontal line. However, for spatially embedded networks with $\Delta < 16a$ and low rewiring probabilities ϕ, the $C(k)$ curve shows a decrease with increasing k.

For any value of Δ in the JL scenario, the distribution of eigenvalues changes its shape from flat (all eigenvalues real) with a heavy tail of large positive eigenvalues for mainly locally coupled networks ($\phi \approx 0$) to circular with radius $\sqrt{Nc(1-c)}$ in the case of $\phi \approx 1$ (not shown). However, for intermediate values of ϕ, the FB model (Fig. 3f, h) exhibits significantly more complex eigenvalues than the corresponding JL networks (Fig. 3e, g), irrespective of Δ. The difference between lattice and random position networks is most apparent in the probability density of $\mathrm{Re}(\lambda)$ (Fig. 3a–d). A less regular spatial embedding ($\Delta > 0.15a$) results in a smooth, curve with triangular shape, with a peak at $\mathrm{Re}(\lambda) = -1$. In comparison, the FB model shows no peak, but a smooth triangular shape, and for $\mathrm{Re}(\lambda) > 2$ the density 'fluctuates' as much as for the JL model with $\Delta = 0.075a$.

4. Conclusions

We examined the graph theoretic properties of several different network architectures with spatially embedded

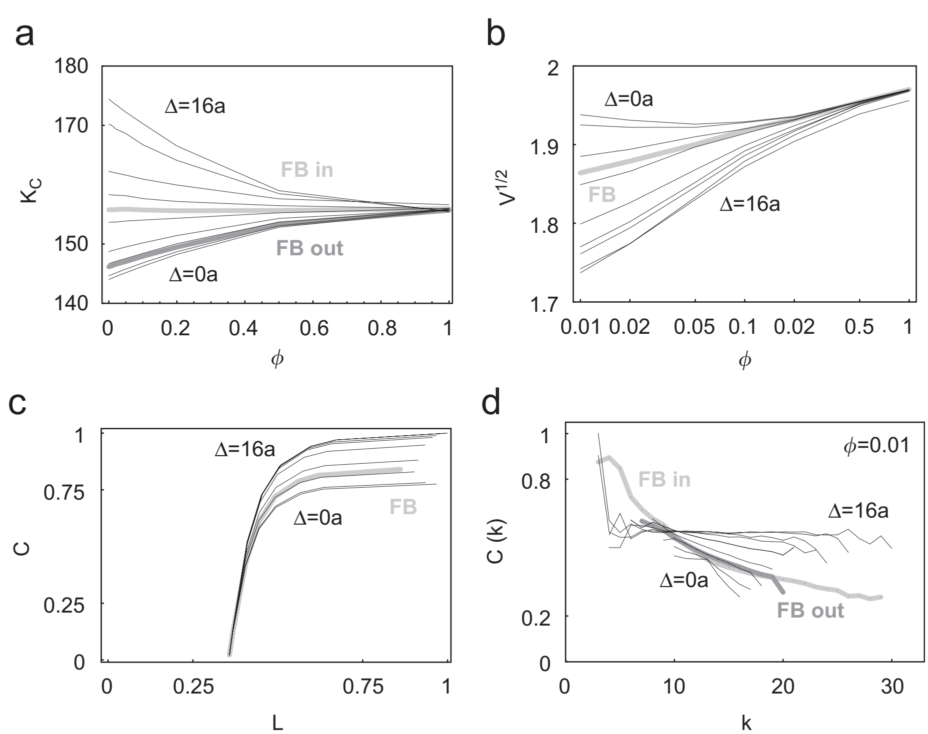

Fig. 2. Some characteristic properties of jittered lattice position networks (JL, black lines) and networks on regular grids with forced binomial degree distribution (FB, gray lines). Each curve represents the average over 20 independent network realizations. (a) Two-node degree correlation in dependence of the rewiring probability ϕ, for jitter amplitudes $\Delta/a = 0, 0.075, 0.15, 0.5, 1, 1.5, 2, 4, 16$. (b) Square root of spatial concentration V, averaged over all eigenvectors, in dependence of ϕ. (c) Cluster coefficient C and average shortest path length L. Both quantities are normalized to their respective maximum for all networks considered here. (d) Degree-dependent cluster coefficient $C(k)$ for all networks with rewiring probability $\phi = 0.01$.

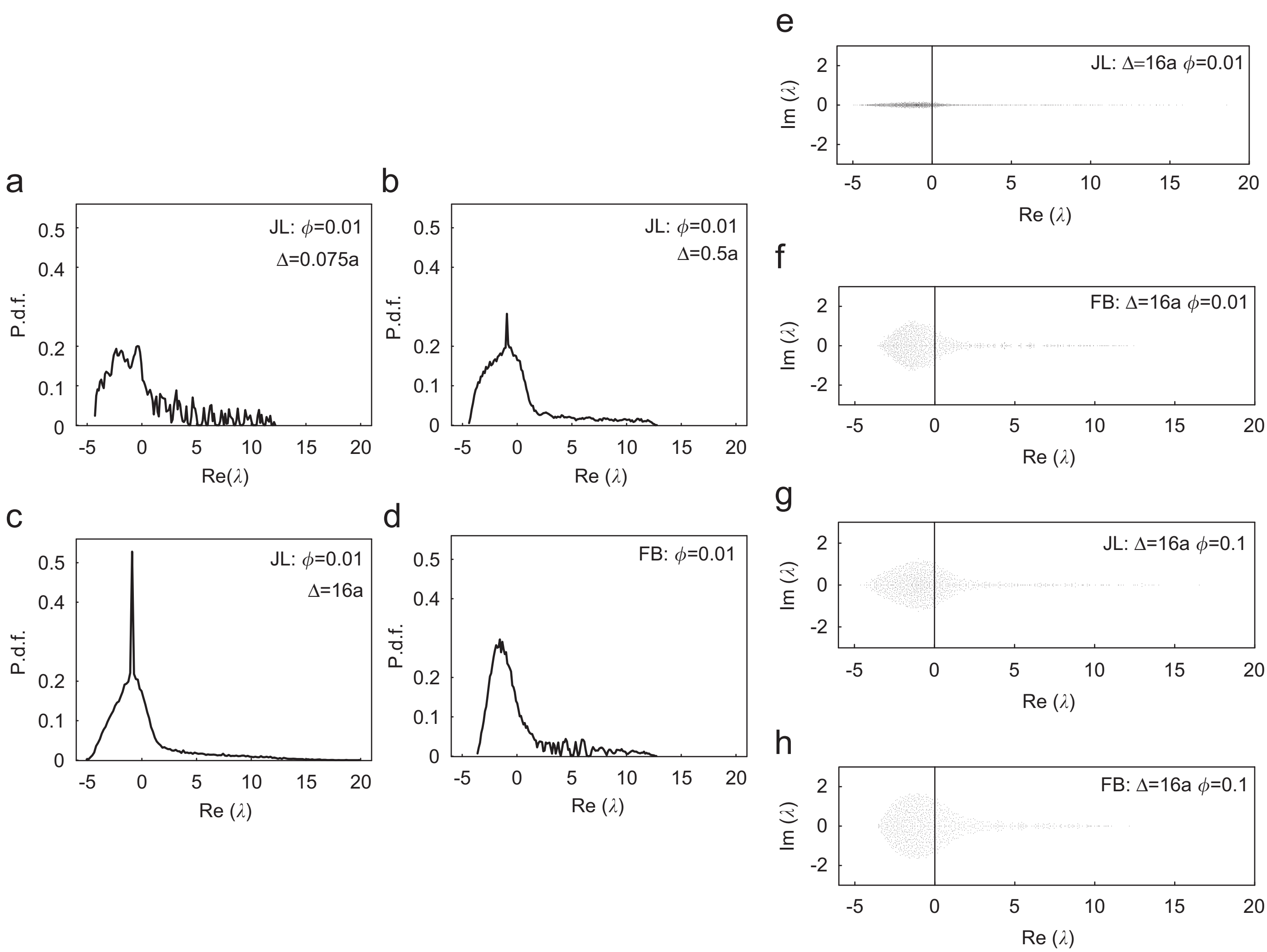

Fig. 3. (a–d) Probability density of the real part of eigenvalues of three types of JL networks and the FB model, for a fixed rewiring probability $\phi = 0.01$. (e–h) Distribution of complex eigenvalues for random position networks (JL; $\Delta = 16a$) and the FB model, each for $\phi = 0.01$ and 0.1. Each plot represents an average over 20 network realizations.

nodes and distance-dependent connectivity. Both the spatial arrangement and the connectivity was varied from regular to random. In a comparative numerical study of the resulting network models, we found that the degree of regularity imposed on the network of either level has a significant impact on its statistical structure. This was manifest in almost all of the characteristic network properties considered here. It may be expected that the signature of regularity, which is present on the architectural level, has also a strong impact on the activity dynamics exhibited by such networks. We conclude that the spatial embedding of nodes is critical in the design of large-scale network models. In particular, we found that lattice networks with a forced binomial degree distribution are much more similar to lattice position networks than expected. Therefore, they are not an adequate substitute for random position networks.

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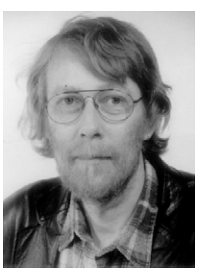

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