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A critical study of network models for neural networks and their dynamics

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ABSTRACT

We use three network models, Erdős–Rényi, Watts–Strogatz and structured nodes, to generate networks sharing several topological features with the neural network of *C. elegans* (our target network). A new topological measurement, *incoming and outgoing edges heat maps*, is introduced and used to compare the considered networks. We run these networks as random recurrent neural networks and study their dynamics.

We find out that none of the considered network models generates networks similar to the target one both in their topological features and dynamics. Moreover, we find that the dynamics of the target network are very robust to the rewiring of its edges.

1. Introduction

In the previous years several fields of Biology saw important advances in the study of processes and phenomena when they are regarded as networks (Junker and Schreiber, 2008; Kleinberg and Easley, 2011). This study has been fuelled by the understanding of links between topology and dynamics (Milo et al., 2002, 2004; Alon, 2006) and by the definition of network models that are able to generate networks with topological features present in biological networks (Barabàsi and Albert, 1999; Chung et al., 2003; Frisco, 2011).

A similar development took place also in neural networks. Recent studies linked neural network topology and dynamics in a novel way (Bock et al., 2011; Ko et al., 2011; Perin et al., 2011; Sporns et al., 2000; Bassett and Bullmore, 2006; Lu et al., 2009; Lago-Fernández et al., 2000). These important discoveries have not been matched by new network models that are able to closely replicate neural networks. Researches using network models in order to generate networks similar to neural networks employed either classical network models (i.e., Erdös–Rényi) or more recent ones (e.g., Watts–Strogatz) that are able to replicate only some (often just one) topological features present in the neural networks.

The ability to generate networks similar to empirical neural networks is paramount: it allows us to test theories that cannot be tested in empirical networks, it allows us to understand how the network could behave under different stimuli, etc. Moreover, one should know that simulating the dynamics of a network is a costly undertaking and, even if very simplified network models, it is not possible to simulate in real-time the dynamics of a network with more than a few tens of thousands nodes (Izhikevich, 2003; Vogels et al., 2005), and an exhaustive exploration of the state space of a network with more than a few hundreds nodes is not feasible (Drossel, 2008). It would be helpful if the dynamics of a network could be inferred from the topological features of the network without any simulation on the dynamics. This would allow faster analysis of network dynamics and the ability to infer the dynamics of very large networks.

In this paper we take a critical look at the network models used to replicate neural networks. Some of the questions we address are as follows: How similar are the topologies of the networks generated by the network models to the ones of the empirical neural networks that they aim to replicate? Are there, for neural networks, topological properties describing these networks better than the others? Are the dynamics of empirical and generated networks comparable?

As a case study we consider the neural network of *C. elegans*. In the following we refer to this network as the *target network*. We chose this network because it is relatively small, its topology is completely known and it has been extensively used as a benchmark for several studies (Watts and Strogatz, 1998; Milo et al., 2002). We use the connected component of 297 neurons with the synaptic links between them. We included both chemical and electrical synapses (gap junctions) in the network and treat them equally (Majewska and Yuste, 2001). We aggregated multiple

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connections from one node to another as a single edge in the network, for this reason we cannot differentiate between different connection types. We computed several topological features of this neural network and we tested its dynamics under different stimuli when it is regarded as a random recurrent neural network. Then, using known network models, we generated networks having topological features as similar as possible to our case study, we treated these networks as random recurrent neural networks, and we tested their dynamics under different stimuli.

We found out that there is very little relation between similarities in dynamics and similarities in topology between our case study and the generated networks. This means that similar dynamics between a particular generated network and the target network do not imply similar topology. Also the opposite does not hold true: artificial networks having topological features similar to the target network do not share similar dynamics.

The present paper poses more questions than it actually answers (see Section 6). Overall, our findings can be summarised saying that none of the current network models seems to be appropriate to replicate the target network. If one wants to have networks similar (both in topology and dynamics) to the target network, then it is better to obtain other networks simply by perturbing (i.e., applying a filter/noise) the edges of the target network. Put in different terms, this research lets us realise even more the pitfalls in which it is possible to incur when trying to replicate complex networks. This proves that the classical network models considered by us are not appropriate to model neural networks. As a consequence, we conclude that other network models (possibly including other elements as development, topography, etc.) should be pursued to replicate neural networks.

The rest of the paper is organised as follows. The initial sections give a background on networks and network topological properties we considered (Section 2), the network models we used (Section 3) and the model of neural networks we adopted (Section 4). The followed methodology and obtained results are described in Section 5. In Section 6 we give our remarks on our study. The appendices give further details on one of the considered network models.

2. Networks and their topological properties

In this section we introduce the network terminology that we employ together with short definitions of the topological features we considered. Further details on network topological features can be found in Junker and Schreiber (2008).

Networks are composed of *nodes* connected by *edges*. We consider directed connected networks. This means that any edge can be traversed in one way but not in the other and if edges were considered bi-directional, then there would be a path from any node to any other node in the network. The *in-degree (out-degree)* of a node is given by the number of incoming (outgoing) edges it has, the *path length* between two nodes in a network is given by the minimum number of edges that have to be traversed in order to go from one node to the other, while the *clustering coefficient* of a node with k neighbours having e edges between themselves is $2e/k(k-1)$ (when computing the clustering coefficient edges are regarded as bi-directional).

The network topological properties we considered as measures of similarity are as follows:

incoming (*outgoing*) *average degree*: the sum of the in-degree (out-degree) of each node divided by the number of nodes;
average path length: the sum of all shortest path lengths between any pair of different nodes divided by the number of pairs of different nodes;
average clustering coefficient: the sum of the clustering coefficients for each node divided by the number of nodes;
in(*out*)-*degree distribution*: the probability distribution indicating the probability to find in a network a node with a given in-degree (out-degree);
incoming (*outgoing*) *edges heat map*: let X be the set of nodes with a specific in-degree (out-degree). Let Y be the set of nodes having an edge to (from) any node in X. This 2D heat map shows the in-degree (out-degree) of the nodes in Y.

The incoming (outgoing) edges heat map is defined for the first time in the present paper. In other words this heat map shows the answer to this kind of question: What is the out-degree of all nodes receiving an edge from nodes with an out-degree α?

The reason why we introduced this measure is because, when dealing with dynamical networks, it is important to have an idea of how signals (or however the dynamics are defined) can propagate through the networks.

If, in a network, a node with many outgoing edges is connected to other nodes with many outgoing edges, then the signal from that first node would likely propagate quickly through the network. Contrary to this, a node with many outgoing edges that connect to the nodes with a few outgoing edges is likely to take longer for its signal to propagate through the network. As we will see, edges heat maps gave us a deeper understanding of the networks that could not be deducted from any other topological property.

We want to emphasise further that, when comparing networks, it is unusual to compare several topological features as we do. The vast majority of comparisons present in the scientific literature consider very few (often just one) topological features. Of course, when dealing with complex networks, the more features that are considered the more difficult it is to find networks matching all these features. We appreciate the difficulties in generating networks with several given topological features, but we believe that network comparison can be meaningful only if a broad range of topological features are considered. This view is also shared by others (Ratmann et al., 2007).

3. Network models

We generated networks using three network models briefly outlined in the following. Each of these three models constructs networks in a different fashion and the networks obtained by these models have very different topological properties.

The Erdős–Rényi (ER) model (Erdös and Rényi, 1959) (the networks generated by it are also known as *random networks*) starts from a fixed number of nodes and it adds edges with a fixed probability p_{ER}. Networks created by the ER model are likely to have a low average path length but they fail to account for the local clustering characterising many empirical networks. This model has been extensively used to model neural networks (Dauce et al., 1998; Siri et al., 2006; Sompolinsky et al., 1988).

The Watts–Strogatz (WS) model (Watts and Strogatz, 1998) starts from a lattice in which each node has degree n_{WS}, then it rewires each edge with probability p_{WS}. In our implementation nodes are arranged in a ring and each node has outgoing edges to its $n_{WS}/2$ clockwise and $n_{WS}/2$ counter-clockwise neighbours. When edges are rewired their direction is not changed. Networks created by the WS model are likely to have the small-world property (the minimum path length between any pair of nodes is approximately equivalent to a comparable random network but the nodes of the network have greater local inter-connectivity than a random network) found in many neural networks (Bassett and Bullmore, 2006; He et al., 2007; Sporns and Zwi, 2004).