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RANDOM GRAPH AND STOCHASTIC PROCESS CONTRIBUTIONS TO NETWORK DYNAMICS

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ABSTRACT. A fundamental question regarding neural systems and other applications involving networks is the extent to which the network architecture may contribute to the observed dynamics. We explore this question by investigating two different processes on three different graph structures, asking to what extent the graph structure (as represented by the degree distribution) is reflected in the dynamics of the process. Our findings suggest that memoryless processes are more likely to reflect the degree distribution, whereas processes with memory can robustly give power law or other heavy-tailed distributions regardless of degree distribution.

1. Introduction. In recent years, a number of studies have found interesting structure in data arising from biological systems, and data with power law structure have particularly garnered much interest [20, 7, 4, 27]. Explanations for how such structure arises have sometimes focused on the processes generating the data [7, 1, 16] and other times on the structure of the network on which the process occurs [22, 24]. The question naturally arises: if one is trying to understand data produced by a process on a network, should one study the process or the network? How can one understand the contributions of the network architecture and of the process itself in shaping the data? Surely the relative contributions vary; are there clues when one or the other dominates the effect?

The brain contains a great many neurons with synaptic connections forming an intricate neuronal network. The propagation of action potentials along an axon and its synaptic transmission from one cell to the next has been extensively studied and

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mathematically modeled. The architecture of connections between neurons within a nucleus and between different brain nuclei remains an active area of investigation. The collective activity of a group of neurons often has interesting structure that invites theoretical exploration. Recent innovations such as electrocorticography and *in vitro* cortical networks provide rich data of neuronal network activity with good spatial and temporal resolution. These technologies have led to reports of power law distributions of activity, in terms of the number of spikes per activity bout and the duration of activity bouts. Models for the generation of such power laws include branching processes [28] and processes occurring on scale-free graphs [23] (for which the network itself has a power law degree distribution).

While Beggs and colleagues [7, 14] argue that criticality may be desirable for dynamical reasons, critical processes require fine tuning of a parameter to a critical value, a feature that has led to criticism on the grounds that a biological system would likely require greater robustness. Abbot and Rohrkemper [1] partially deflect this criticism by providing a simple but plausible model demonstrating that self-tuning of a network to a critical value may not be difficult to achieve. Magnasco [18] presents a novel model in which a network uses an anti-Hebbian rule to self-tune, resulting in some range of scale-free dynamics. Teramae *et al.* [24] present a variation of a branching process model (a "critical wiring process") that is robust to perturbation. Their model results in a network that combines feed forward chains and recurrent circuits and may have implications for network topology in the cortex. Joshi and colleagues developed a simple model in which a small number of interacting neuronal populations produce power law distributed activity bouts via a doubly stochastic process [16, 17, 8].

Shkarayev and colleagues [22], on the other hand, focused more directly on the network architecture, showing that the topology of the network can control the dynamical properties of the network. They demonstrate, in a network of integrate-and-fire neurons, that a scale-free network can produce scale-free (power law) dynamics. These authors address possible relations between functional connectivity (as observed for example in fMRI imaging) and architectural connectivity.

In this paper we investigate the relative contributions to network dynamics made by the structure of the graph itself and by the nature of the process occurring on that graph. In particular, we are interested in what clues one may look for in evaluating the relative importance of these two factors. We consider randomly generated graphs with varied degree distributions, and we further vary the clustering within the graph by considering some small-world networks. We consider two different processes on the graphs, (i) a type of percolation and (ii) a neural spiking process.

In Section 2 we describe the graphs used in this investigation together with the processes that we put on the graphs. We describe in Section 3 the results produced, and we discuss the investigation and its results in the final section.

2. Methods. In order to investigate the relation between graph structure and dynamics, we selected three graph structures, Erdös-Rényi, small-world, and scale-free, and two stochastic processes to put on the graphs.

We chose representative graphs that differ in their degree distribution; *i.e.*, the probability distribution of the numbers of edges at each node in the graph. Vertex degree distribution is a distinguishing characteristic that captures important differences in graph structure (see for example [19]).

The graph structure introduced by Paul Erdös and Alfred Rényi in 1959 [10, 11] and now referred to as an Erdös-Rényi random graph assumes that, for a given set of nodes, any possible edge occurs independently of all other possible edges.

Watts and Strogatz [26] introduced small-world networks after recognizing that many naturally occurring networks, such as social networks, exhibit greater clustering than does an Erdös-Rényi graph: an edge is more likely to occur if it would complete a triangle. In social networks, this lack of edge independence expresses the observation that two individuals are more likely to be acquainted if they share another acquaintance. Small-world networks such as the Watts and Strogatz model are characterized by a high degree of clustering as well as a short average path length between any two nodes. They are not, however, characterized by degree distribution. Nonetheless, this class of networks has proved widely useful in applications, and we include here some judiciously chosen examples.

The third class of networks that we study here, scale-free graphs, is actually a distinguished subset of small-world networks [3]. These networks have a power law degree distribution; in particular, they include nodes with high degree known as hubs. In algorithms for creating scale-free graphs, an edge is more likely to occur if it would connect to a hub - a node that is already highly connected.

We consider here two processes occurring on each type of random graph. First, we look at a process based upon percolation of activity through a graph in which nodes can be in either an active or an inactive state. Beginning with some proportion of active nodes, one asks whether all nodes eventually become active. For cases in which activity percolates, one computes the distribution of percolation times. The second process is a simple neural-like process involving spiking activity. Nodes fire spikes at some Poisson rate, and each spike increases the firing rate of neighbor nodes, tending to prolong activity. We ask how long each bout of such activity lasts and calculate the distribution of active bout durations.

In the subsections below we describe in more detail the selection and construction of the graphs as well as the algorithm for each process on the graphs. In each case, the work was performed using the R programming language (version 2.9.0) [21] along with the igraph package [9].

2.1. Graph Families. Each random graph is generated by starting with a set of N nodes and adding edges between them according to a random process. For simplicity, we consider only undirected, connected graphs.

In the Erdös-Rényi model [10], we start with N nodes and connect each pair with probability p, independently of all other pairs of nodes. Since a node is equally likely to be connected to each of the N - 1 other nodes, the probability that a node has degree k is given by the binomial distribution

$$P(k) = \binom{N-1}{k} p^k (1-p)^{N-1-k}.$$

Here the expected degree of a node is $\lambda = (N-1)p$ which allows us to rewrite this expression as

$$P(k) = \binom{N-1}{k} \left[\frac{\lambda}{N-1-\lambda}\right]^k \left[1 - \frac{\lambda}{N-1}\right]^{N-1} \simeq \frac{\lambda^k}{k!} e^{-\lambda}.$$

Thus the degree distribution of an Erdös-Rényi graph becomes Poisson in the limit of large N.

The small-world graphs we consider are generated by the model of Watts and Strogatz [26]. We start with N nodes in a regular ring lattice where each node is connected to k of its nearest neighbors. Then with probability q, each edge is rewired. In other words, an edge is disconnected from one of its two nodes and then reconnected to another node chosen at random. This rewiring process introduces long-range connections, leading to small average path length characteristic of smallworld graphs. In addition, this graph is more highly clustered than an Erdös-Rényi random graph.

To generate scale-free graphs, we follow the model by Barabási and Albert [6] in which nodes are connected by a process with preferential attachment. We begin with a small network of $m_0 \ge 2$ nodes and add new nodes to the network one at a time until we have a total of N nodes. The probability that the new node will be connected to an existing node i, $p_i = \frac{k_i}{\sum_j k_j}$, is proportional to the degree k_i of node i. Highly connected hubs tend to quickly accumulate more links, while nodes of small degree are unlikely to gain new connections. Thus, new nodes have a "preference" to attach themselves to hubs. The degree distribution of a Barabási-Albert random graph is scale-free, and in particular, it follows a power law distribution

$$P(k) = Ak^{-\gamma}$$

where A is a constant that ensures that P(k) sums to 1, and the degree exponent γ typically lies in the range $2 < \gamma < 3$ [2]. Since scale-free graphs belong to the larger class of small-world graphs, they share the property of small average path length, but the extent of clustering is closer to that of an Erdös-Rényi random graph [6].

2.2. **Percolation.** The first of the two stochastic processes we consider on random graphs is based upon percolation of activity through the network. Assume that each node can be in one of two possible states: active or inactive. We start the percolation-type process at time t = 0 with a proportion ρ of initially active nodes in the graph. We then define an updating rule for the spread of activity: in the next time step, a node with k active neighbors becomes active with probability p_a , which depends on k. If a node was active in the previous time step, it stays active. In contrast to classical bootstrap percolation, we are not considering a fixed threshold above which nodes become activated with probability 1. We use a saturating function to define the activation threshold. In particular, for each node $i \in \{1, \ldots, N\}$ we compute the proportion of active neighbors y_i and then take

$$p_a = \frac{cy_i}{y_i + d}$$

where c and d are constants such that $p_a \in [0, 1]$. For cases in which activity percolates throughout the network, we look at the distribution of percolation times, *i.e.* the time it takes for all nodes in the graph to become active. This is a variation on a classical question in random graph theory that we describe below.

For a given graph with N nodes where each node is initially active with probability p, let E be the event that all nodes are eventually active. Identify p_{-} and p_{+} such that for $p < p_{-}$ (respectively, $p > p_{+}$), the probability of event E is essentially 0 (respectively, 1). In particular, show the existence of a phase transition window $[p_{-}(N), p_{+}(N)]$ and quantify how quickly it shrinks to 0 as $N \to \infty$.

Balogh and Pittel [5] give results for this question in the case of d-regular random graphs, but for other types of random graphs and more complicated percolation processes, little is known.

2.3. **Spiking Model.** The second process we consider is a simple neural-like process involving spiking activity. Nodes fire action potential spikes at a Poisson rate, and each spike increases the firing rate of neighboring nodes, tending to prolong activity on the graph. Here we are interested in the length of each bout of activity in order to compute the distribution of active bout durations.

The spiking model we consider is similar to a model by Abbott and Rohrkemper [1], but with different network structure and without critically tuning any parameters. These authors consider a neural network that grows and shrinks in response to intracellular calcium concentration C, a measure of activity in the network. Their model involves tuning parameter C to a critical value in order to produce power law distributions of activity.

We generate and fix a random graph with N nodes from one of the three families described above. We then put a Poisson spiking process on the graph according to the firing rate equations from [1]: their equation (1) and a modified version of (2). These are equations (1) and (2) below.

$$\tau_r \frac{dr_i}{dt} = r_0 - r_i \tag{1}$$

Here r_i is the firing rate for node $i \in \{1, ..., N\}$, r_0 is the background firing rate which is constant for all nodes in the graph, and τ_r is a time constant. When node i fires an action potential, the firing rate of each of its neighboring nodes j gets incremented by a constant g:

$$r_j \to r_j + gA_{ij}.\tag{2}$$

A is the adjacency matrix of the graph, *i.e.*, entry $A_{ij} = 1$ if nodes *i* and *j* are connected, otherwise $A_{ij} = 0$. Hence, node *i*'s neighbors are the non-zero entries in row *i* of *A*.

We simulate the above processes on random graphs via Gillespie's Stochastic Simulation Algorithm [12] implemented in R. All simulations are done with a fixed graph for 100,000 replications of the process on that graph. We record the length of each bout of activity separated by a period of inactivity of at least length Δ , and then compute the distribution of active bout durations for a range of parameter values for each of the three graph families.

3. **Results.** We present the results of our investigation of the relation between graph structure and dynamics, focusing on three graph structures and two stochastic processes occurring on the graphs. The percolation process is considered in the first subsection and the spiking model in the second.

3.1. **Percolation Results.** First we consider the percolation process described in Section 2.2 on the three different graph structures. All graphs in this section are generated with N = 1000 nodes. The time to percolation is measured in terms of the number of integer time steps it takes for all nodes in the network to become active. In general, we see that the percolation process reflects the degree distribution for a wide range of ρ values and certain activation threshold functions.

For an Erdös-Rényi random graph generated with edge probability p = 0.005, Figure 1 shows the degree distribution and distribution of time to percolation. Here the percolation process starts with 1% of the nodes initially active, *i.e.* $\rho = 0.01$, and the saturating function constants are c = d = 1. We see that the distribution of time to percolation has the same general shape as the degree distribution. As ρ increases, the mean time to percolation decreases while the shape of the distribution remains roughly the same.



FIGURE 1. Percolation process on an Erdös-Rényi random graph with N = 1000 nodes and edge probability p = 0.005. On the left is the degree distribution, and on the right is the distribution of time to percolation for the case with 1% of nodes initially active.

Next we use a Watts-Strogatz random graph generated with k = 5 and rewiring probability q = 0.4. Figure 2 shows the corresponding degree distribution and distribution of time to percolation when the process starts with 1% of the nodes initially active and c = d = 1. Again, the shape of the distribution of time to percolation resembles the degree distribution. As ρ increases, the mean time decreases as in the Erdös-Rényi case, and the variance also shrinks slightly.



FIGURE 2. Percolation process on a Watts-Strogatz random graph with N = 1000 nodes, number of neighbors k = 5 in initial ring lattice, and rewiring probability q = 0.4. On the left is the degree distribution, and on the right is the distribution of time to percolation for the case with 1% of nodes initially active.

Lastly, Figure 3 shows the distributions of node degree and time to percolation for a Barabási-Albert random graph generated as described in Section 2.1. The percolation process starts with 1% of nodes initially active ($\rho = 0.01$), but in this

case we averaged over a range of saturating functions by choosing c and d uniformly at random from [0.2, 1] and [0.5, 2], respectively. These distributions are plotted on a log-log scale; thus a straight line is consistent with a power law distribution.



FIGURE 3. Percolation process on a Barabási-Albert random graph with N = 1000 nodes and linear preferential attachment. On the left is the degree distribution, and on the right is the distribution of time to percolation for the case with 1% of nodes initially active.

3.2. Spiking Model Results. For the spiking process, we define bouts of activity as periods of time (measured in milliseconds) during which at least one node in the network fires an action potential spike and there has not been a gap in activity of more than Δ milliseconds. For the numerical results we present below, we use $\Delta = 1$ ms. Other parameters values used are $r_0 = 0.002$ Hz, g = 0.00001 Hz (except as noted), and $\tau_r \in [0.1, 1000]$ ms; the vector of firing rates $\mathbf{r} = \{r_1, \ldots, r_N\}$ was always initialized to the background firing rate r_0 for each node *i*.

As illustrated in Figure 4 (left and middle panels), the spiking model results in approximately power law distributed bout durations over a wide range of parameter values for the Erdös-Rényi and Bárbasi-Albert graphs; power laws were also observed when the underlying graph had Watts-Strogatz structure (not shown).

There are, of course, parameter choices that do not result in a power law. Note that if τ_r is too small, then firing rates raised by excitatory inputs are almost instantly reset to r_0 , so that the network remains approximately a union of independent Poisson processes and therefore approximately a Poisson process, by the Superposition Theorem [13]. In such cases, the bout distribution is approximately exponential.

When τ_r is large enough (in relation to g), the increment in firing rate due to an incoming spike does not have time to dissipate before the next spike arrives; the newly increased firing rate in turn impacts the neighbors' rates. As nodes engage in such positive feedback across an activity bout, firing rates of many nodes increase. The increased firing rates decrease the probability of a gap in firing sufficient to end the active episode, thereby leading to longer active bouts and a heavier tail in the distribution of bout durations. In this case, each node fires as an inhomogeneous Poisson process with rate $\lambda_i(t)$; the resulting bout distribution can approximate a power law for appropriate $\lambda_i(t)$. Note that if $\lambda_i(t)$ grows too quickly, the resulting active bout distribution will be more heavy-tailed than power law. The right panel of Figure 4 provides an illustration on an Erdös-Rényi graph.



FIGURE 4. Spiking model. All graphs are generated with N = 100 nodes. Left panel shows the length of active bout durations on an Erdös-Rényi graph, g = 0.00001 Hz and $\tau_r = 1000$ ms. In the middle is the active bout durations for a Barabási-Albert graph, g = 0.00001 Hz and $\tau_r = 10$ ms. Right panel shows the active bout durations on an Erdös-Rényi graph, g = 0.00002 Hz and $\tau_r = 1000$ ms.

4. **Discussion.** We have reported here our numerical investigation of the relative contributions of network structure and of node dynamics in determining the collective dynamics of a network. In ongoing work, we have been developing analytical calculations that shed light on the reasons for the results of these computer simulations. We have focused on the presence or absence of power law dynamics, a feature of interest in many recent studies [1, 7, 16, 22, 24].

We looked at a percolation-like process and a spiking neural process on randomlygenerated graphs with various degree distributions. We found that the percolation process reflected the degree distribution, while the spiking process did not. For the spiking process, the distribution of active bout durations was either exponential (when the parameter τ_r was too small, relative to g, to allow firing rate increments to accumulate) or heavy-tailed (typically power law or heavier tail).

Together with the results of Shkarayev *et al.* [22], this work suggests that memoryless processes such as percolation-like processes and spiking of integrate-and-fire neurons, in which the neurons integrate inputs and fire spikes without altering their intrinsic propensity to fire (modeled here as firing rate), may reflect the degree distribution of the graph. We refer to these processes as memoryless because the nodes show neither potentiation nor depression. That is, in response to being stimulated to fire frequently, they neither increase their response (as in long term potentiation, [25]) nor do they adapt to the stimulus and show a dampened response (long term depression, [15]). We find that processes with memory, for instance processes in which the nodes change their firing rate in response to inputs, can robustly produce heavy-tailed distributions of activity, including power laws. Thus the underlying graph structure may be obscured when the process has a memory mechanism such that the dynamics of the process can change in time. We observe that the behavior of firing rates of individual nodes in the network is one of the distinguishing features of different mechanisms for generating power law distributions via network dynamics. In the memoryless model of Shkarayev and colleagues [22], nodes fire in response to neighbors and in response to Poisson inputs. In their network, the nodes manifest a power law distribution of firing rates [23]. The spiking model with memory considered here behaves quite differently, with the firing rates increasing throughout a bout of activity.

Neuronal connectivity patterns vary substantially in different regions of the brain, likely reflecting different functions and needs in addition to evolutionary and developmental history. Though details of connectivity are often unknown, even partial information concerning circuit architecture can help distinguish between some of the possible mechanisms underlying the collective dynamics of the network. Knowing properties of nodes (adapting or potentiating synapses, for example) or of the network (*e.g.*, variance of firing rate among nodes) can be useful in ruling out some mechanisms.

One of the questions we address in this study is whether scale-free graph structure makes power law dynamics more robust. It was known that one could achieve power law dynamics in a non-scale free network with a critically tuned parameter [28, 1, 24], and we previously constructed an example of a simple network with power law dynamics without tuning [16, 17]. It was also known that a power law structure in the graph could give rise to power law dynamics [22]. A natural question is, can a scale-free network structure contribute to power law dynamics, thereby making power law behavior more robust or more likely to be observed than on a graph with some other structure? Perhaps surprisingly, we have not found evidence for such a conclusion. In the examples studied here, either the graph structure was entirely responsible for the power law, or the dynamics were robustly capable of producing power law dynamics on a wide range of graph structures. This conclusion may depend on other properties of the graph or process not studied here. We have not yet considered a directed graph, nor have we considered inhibitory connections. Nonetheless, this work contributes to the understanding of power law dynamics and begins to identify criteria according to which one may probe a network to determine what factors contribute to power law dynamics.

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