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Effective non-universality of the quorum percolation model on directed graphs with Gaussian in-degree

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HIGHLIGHTS

- Collective behavior of dissociated neuronal cultures.
- Continuous prolongation of the quorum percolation model.
- Thorough numerical calculations in the infinite limit behavior.
- Accurate thresholds and critical exponent associated with the percolation transition: non universal behavior.
- Relation between critical parameters and topological properties of the network.

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ABSTRACT

We investigate a model derived from bootstrap percolation on a directed random graph with Gaussian in-degree useful in describing the collective behavior of dissociated neuronal networks. By developing a continuous version of the model, we were able to provide accurate values of the critical thresholds and exponents associated with the occurrence of a giant cluster. As a main result, it turns out that the values of the exponents calculated over a numerical accessible range covering more than two orders of magnitude below the critical point exhibit a slight dependence upon the connectivity of the graph.

Percolation models have been successfully applied in describing the transmission of information through lattices of sites and links [1,2]. In this respect, they are expected to provide a useful framework for signal propagation in neural networks. The first theoretical attempt in describing the emergence of a giant cluster experimentally observed in dissociated neuronal cultures in vitro was based upon a link percolation model on a graph [3]. Later, a more sophisticated model, the so-called quorum percolation model derived from the bootstrap percolation one was proposed [4,5]. In its original version, bootstrap percolation [6] is a percolation model on a lattice, where each basic element is a two-level system (active or inactive) located at a node; more recently, bootstrap percolation has been studied on random graphs [7]. The main additional feature that a model of neuronal network has to take into account is the fact that electric action potentials cannot propagate along axons in both directions. Hence the underlying graph of such a quorum percolation model must be directed. The connectivity of the graph is encoded in the adjacency matrix whose elements a_{ij} are equal to 1 if the nodes indexed by i and j are connected, 0 otherwise. Starting from a state of the network where a given fraction f of nodes is initially set active, information spreads through the network according to a threshold rule: a node becomes active if a fixed number m of its first neighbors are active. Although critical phenomena associated with directed percolation on one hand and bootstrap percolation on the other hand

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have been widely investigated, a thorough analysis of the critical phenomena associated with the quorum percolation model described above is not available, and has to be carried out specifically. Although bootstrap and quorum percolation models are close, the fact that links are directed rather than symmetrical is expected to impact on the critical behavior; moreover, the dissymmetry of links makes analytical approaches much more difficult, and very scarce results are available. An issue of fundamental importance in studying percolation model on graphs is the possibility to extract information related to the connectivity of the network from a critical behavior [3]. In this way, E. Moses and his coworkers were able to deduce from an experimental phase diagram that the degree distribution of the neuronal cultures they studied was a Gaussian one and to estimate the mean connectivity of the neuronal networks. It should be pointed out that the connectivity should not be understood here in the usual geometrical sense in a physical space, but from the point of view of the information provided by the adjacency matrix: such-and-such node are connected by a directed link, no matter where they are in the embedding physical space.

This paper is devoted to a thorough numerical study of the critical behavior occurring in the framework of the directed quorum percolation model in the thermodynamical limit.

1. Theoretical framework and numerical method

The network is made up of N nodes, where each of them is a two-level system: it can be either active or at rest. For each node in the network, k incoming links are randomly chosen among the $N-1$ other nodes according to a probability p_k; the implemented algorithm rules out backlinks (if $a_{ij}=1$ then $a_{ji}=0$). Hence, the connectivity of the directed graph $\mathcal{G}$ is entirely determined by the degree distribution of incoming links per node. At $t=0$, a fraction f of the nodes drawn randomly among the network is activated. The activation process of the network is described by a discrete time dynamics [5] with a step Δt during which each node integrates the signals sent by its incoming first neighbors [8]. A variable $V_i(t)$, assigned to each node i, keeps track of the sum of the signals received from the beginning of the process. The transition from a time step to the next obeys the following rules.

Every node j activated between $t-\Delta t$ and t sends at time t one signal to each of its neighbors through its outcoming links; no further signals will be sent by such an activated node at later times. The variable $V_i(t)$ of each target node at rest is incremented by the sum of the number of signals it has received. If $V_i(t)$ is greater than or equal to an activation threshold m_i, the node i switches from the state at rest (at time t) to the state active (at time $t+\Delta t$).

Once a node has been activated it remains in such a state until the end of the process, but fired only once at the time step of its activation. Hence, calling $s_i(t)=\Theta(V_i(t)-m_i)$ the state of a node i at time t ($s_i(t)=1$ if the node is active, $s_i(t)=0$ otherwise), the transition from a time step to the next is given by the following relation:

$$s_i(t+\Delta t)=s_i(t)+(1-s_i(t))\,.\Theta\left(\sum_j a_{ij}s_j(t)-m_i\right) \qquad (1)$$

where Θ designates the Heaviside function and the sum runs over the incoming links of the node i.

In the original version of this integrate and fire model, each node has the same activation threshold (quorum) m, each signal the same profile and each link has the same weight. Moreover this model describes complex systems where the time step Δt is assumed to be much smaller than every characteristic time associated with other features. It is worth noticing that the quorum percolation model is very flexible: more sophisticated versions of this model taking in account additional relevant biological features can be implemented. For instance, the fact that the membrane of a neuron cannot be modeled as a perfect capacitor since it is continuously leaking ions leads to a decay of its potential with some time constant τ; it has been recently shown that the incorporation of such a decay in the model destroys criticality [8] (in the thermodynamical limit). From a statistical physics point of view, the process described by Eq. (1) converges towards a stationary state described by the fraction Φ of active nodes at equilibrium. On the other hand, in the framework of a mean field approach, such a stationary state can be viewed as one of the solutions which satisfy a self consistency equation [5,9]: the probability for a node to be active at equilibrium is the sum of the probability for a node to be initially activated and the probability to be connected to at least m active "in-neighbors" if not initially activated. Hence, the self consistency equation reads:

$$\Phi=f+(1-f)\sum_{k=m}^{\infty}p_k\sum_{l=m}^{k}\binom{k}{l}\Phi^l\,(1-\Phi)^{k-l}\,. \qquad (2)$$

A truncated binomial appears because nodes that have less than m incoming links remain forever inactive (unless they were initially activated). Moreover, we will restrict ourselves to topological properties of the network described by a Gaussian in-degree distribution p_k with a mean value $\bar{k}$ and standard deviation σ as observed in dissociated neuronal cultures [3]. When solving Eq. (2) in the physically meaningful range [0, 1] of the variable f, two regimes can be distinguished according to the value of the parameter m: For m smaller than a critical value m_c there is a range $f\in]f_0(m),f^*(m)[$ where three different real values of Φ satisfy Eq. (2), while for $m>m_c$, Φ is an increasing monotone function of f. Since the rules stated above require Φ to be an increasing function of f also when $m<m_c$, the behavior of Φ resolves the existence of an unstable branch in the range $[f_0(m),f^*(m)]$ in the following way: Φ follows the stable solution associated with the lowest branch for