

Fractal properties of percolation clusters in Euclidian neural networks

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Abstract

The process of spike packet propagation is observed in two-dimensional recurrent networks, consisting of locally coupled neuron pools. Local population dynamics is characterized by three key parameters – probability for pool connectedness, synaptic strength and neuron refractoriness. The formation of dynamic attractors in our model, synfire chains, exhibits critical behavior, corresponding to percolation phase transition, with probability for non-zero synaptic strength values representing the critical parameter. Applying the finite-size scaling method, we infer a family of critical lines for various synaptic strengths and refractoriness values, and determine the Hausdorff–Besicovitch fractal dimension of the percolation clusters.

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1. Introduction

The ground state of most biological neural networks is comprised of single neurons firing asynchronously at low rates, maintaining the global low level activity in the system [1,2]. Ground state destabilization by an external input leads to coherent states, which enable the information to be conveyed, and allow subsequent rapid relaxation of network structural units. Thus, the research conducted on neural populations receiving and transferring sensory input revealed high degree synchronization of single neuron firing times [3–7]. Recent results obtained in trained neural assemblies have proven that the excited state of a network, driven by the external input, may consist of sequential firing of smaller neuron groups with almost perfectly synchronized spike times [1,8–10]. In this dynamic mode, termed distributed synchrony mode, larger neural population dissolves into functional subassemblies of physically non-coupled neurons, enabling persistent transmission of precisely timed spike volleys through the whole network. Depending on the particular neural model and topology of neural couplings, different dynamic attractors may be obtained – from fixed points to large period limit cycles. Dynamics of such systems, for the appropriate set of parameter values, may exhibit the properties of critical phenomena. Thus, in some microscopic assemblies of *in vitro* neurons the self-organized criticality [11,12] has been identified as the principal mechanism for the origination of synchronized activity bursts, spanning the whole network. With the obtained burst size distribution displaying power-law behavior, the measured exponent value enabled the classification of bursting mode dynamics into the avalanche model universality class. Burst

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clustering according to single neuron firing time correlation revealed only a few statistically independent events, indicating that the activity spreading process is performed in several preferred paths [13]. Since the neural activity spatial patterns may be semantically significant in larger scale networks (temporal feature maps [14], mental representations), the scope of recent investigation shifted to assemblies comprised of medium-size populations, termed pools, representing the elementary units. The research of cooperative phenomena in mesoscopic scale neural networks has been hindered due to lack of comprehensive population dynamics model and failure to incorporate complex interactions between them, especially feedback. In our work, we were interested in modeling recurrent neural networks with continuous states of structural units, by applying the modified Gerstner model of population dynamics with two-step transfer function [15]. Local states are represented by the firing time distribution moments, with the zeroth moment (the integral activation) being the principal variable. Due to model complexity, we use the methods of statistical physics to assess the effects of varying network parameters on the propagation dynamics of integral activation.

The paper is organized in the following way. In Section 2, we introduce the details of the applied neuron model and define the variable expected to exhibit the long-range order. The results of computer simulation of pulse packet propagation, presented in Section 3, are applied to demonstrate the existence of percolation phase transition and to estimate its critical parameters. Finally, in Section 4 we consider the model validity comparing it to simulations of different scale networks and give our concluding remarks.

2. Model

Synchronization of neural spatio-temporal firing patterns is achieved either through local coupling or by neurons receiving the similar input. Since pools generally constitute functional assemblies of non-coupled neurons, common input may be provided by divergent/convergent all-to-all manner connecting of neurons in adjacent pools. Thus, a possible collection of connected pools can be created, with the synchronously firing neuron populations transferring their spike output through synaptic couplings to successive, structurally identical neural assemblies. Synchronicity in firing times, conveyed from pool to pool, comprises a synfire wave of activity. Synfire waves obviously resemble local excitations in other spatially extended media, especially solitons [19].

Pools participating in synfire wave propagation constitute synfire chains. The term was coined by Abeles [9], who proposed that neural activity transmission through directed subnetwork of pools may account for the complex cortical events, emerging as a response to external stimuli or subserving the establishing of cognitive motor processes. Since realistic neural networks have to allow a more complex topology than the one with feed-forward couplings, the issue of networks adequate to embed synfire chains was further investigated by Bienenstock [2]. Though multiple synfire chains may occur as subgraphs in random networks, it was determined that the response reproducibility would become susceptible to small stimuli perturbation, in contrast to the biological observations. In several cortical receptor areas with recorded synfire patterns robust to input variation, connection topology exhibits substantial recurrence. Bienenstock proposed that networks embedding synfire chains may include local feedback couplings, thus enabling chain subnetworks to subserve integrating complex information or neural encoding of mental representations.

The encoding mechanism particularities are specified through the local pool states, being usually characterized by spike packets, which represent the distribution of firing times in a given neural assembly. The two variables generally used to quantify the spike packet properties are the integral activation (percent of neurons activated on a single pool at small interval centered around mean firing time), and the dispersion of firing times around the mean firing time.

If the network topology were to allow robust response to stimuli variation, it would be plausible to assume that the spike packet propagation may exhibit attractor dynamics. Actually, synfire chains, with characteristic spreading times large compared to single axon conduction times, have already been observed in biological systems. Thus, it is our aim to infer the conditions necessary for stable and persistent transmission of synfire waves, with spike packets maintaining narrow width along the propagation path spanning the whole network. Since synfire chains constitute solely functional subnetworks, pools participating the synfire activity should not differ structurally or by the coordination number from the rest of the network pools.

Motivated by methods applied in recent studies on synchronization and clustering phenomena in several different areas (including coupled chaotic maps [16,17], oscillators or neural networks [18,21], with local, global or small-world connection topology [22]), we resort to simulating propagation of spike packets on a regular two-dimensional lattice, with sites being occupied by neural pools. Neurons constituting a pool are coupled with neurons from four neighboring pools in the manner presented in Fig. 1.

The couplings are weighted, but have only two possible values – zero, with probability $1 - p$ and non-zero $\omega_{ij} = \Omega$, with probability p . Given choice for synaptic weights is neurobiologically well justified, being based on spike-time dependent plasticity (STDP), which is the only plausible mechanism for synaptic coupling formation. It is believed that

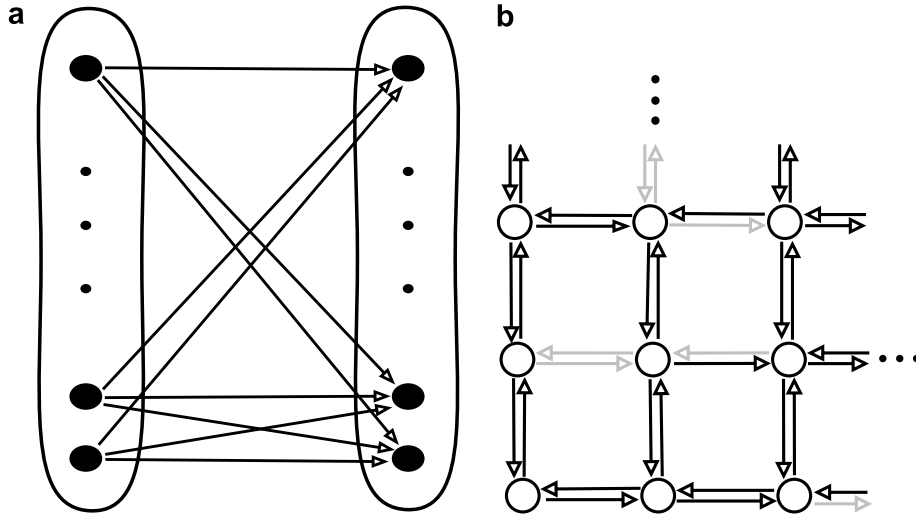


Fig. 1. (a) Neurons are organized in assemblies, i.e. neural pools, with common input provided by divergent/convergent all-to-all manner of interneuron connections projecting to adjacent pools. (b) Schematic representation of part of a network which is not fully connected. Open circles depict neural pools. Solid lines indicate connections between pools and their four nearest neighbors. Black lines are assigned to bonds with non-zero synaptic weights $\omega_{ij} = \Omega$, while the grey lines represent zero weight connections.

after elaborate training, with the STDP rules applied, synaptic weights cluster around the upper-bound non-zero value and zero [5]. We include feedback to allow reverberating activity in the network and control global activity levels. Synaptic weights connecting pools in opposite directions are identically and independently distributed. Since the weight change characteristic time is supposed to be large compared to duration of single volley, synaptic weights may be considered as quenched variables during the synfire wave propagation.

Neural population dynamics is based on the spike response model with stochastic firing. The effects of all-but-one last firing on the neuron following spike time are neglected, so that the applied model belongs to the class of input dependent renewal processes. All the possible noise effects (membrane potential fluctuations, synaptic and ion-channel noise) contribute to the temporal jitter in firing times on a pool. With the neuron model exhibiting no non-linear transfer function or firing threshold, a single hazard-function is sufficient to account for stochasticity in neural ensemble activation process. The chosen hazard function assumes that the single neuron firing probability equals the positive part of membrane potential:

$$f(u) = \begin{cases} u, & u \geq 0 \\ 0, & u < 0 \end{cases} \tag{1}$$

According to statistical calculations conducted in [15], the membrane potential on a neuron k of the given pool i (the index applies to the coordinate set) relates through a recurrent formula to the input activation from the n neighboring pools:

$$u_i^k = \sum_{j \in n,n} \frac{\omega_{ij}}{n+1} \int_0^\infty \varepsilon(t') A_j(t-t') dt' \tag{2}$$

with $\varepsilon(t)$ representing the neuron response function, defined as $\varepsilon(t) = t e^{-t} \Theta(t)$.

The effects of membrane potential reset after spiking and refractoriness (time period after spiking during which further spike is impossible to elicit) are taken into account through a single refractoriness variable. The actual activation at time t on the considered pool is related to the membrane potential on each neuron constituting pool according to:

$$A(t) = (1 - \int_{t-\delta}^t A(t') dt') u(t) \exp\left(-\int_0^t u(t'') dt''\right) \tag{3}$$

The $(1 - \int_{t-\delta}^t A(t') dt')$ part on the right side of Eq. (3) accounts for the refractoriness effects, decreasing the activation of the given neural population. Increasing refractoriness value may partly dampen the effects of feedback couplings, making the activity loops less likely.

Applying Eqs. (2) and (3) we numerically study the propagation of synfire waves through neural networks. Its dynamics should satisfy three key conditions: stability (with non-increasing time dispersion of spike packets), reproducibility (with synfire waves appearing as a response to similar input provided to the network), and long-time duration (with synfire waves spanning the whole network) [2]. Since the integral activation (time integral of Eq. (3)) is believed to carry all the semantic content in our model, we observe the values of integral activation in consecutive layers of the network. With the large enough external input provided, long-range order of pool integral activation is to be expected.

3. Numerical simulation of pulse propagation

Two-dimensional network is introduced with a single high activation spike packet to enable the neural activity spreading through the whole system. Clustering of pool integral activation values is observed in three-dimensional parameter space. With varying values of synaptic strength Ω , refractoriness δ and probability p for pool connectedness, we find pool ensemble dissolving into classes (subgroups), with, up to the computational bin, identical value of integral activation. Connected pools belonging to the same class comprise clusters. For fixed refractoriness and weight values, clusters spanning the whole network appear only after a certain pool connectedness probability is surpassed. Thus, our model is transformed into an example of bond percolation, with percolation clusters, equivalent to synfire chains, appearing only above a threshold value of non-zero weight probability. Correspondingly, there are three-dynamical modes observed in our simulation, each occupying a distinct subspace of the parameter space. Firstly, the system is in subcritical state, if the pools belong to many different classes and thus form only small clusters. The system of neural pools is in critical state for the parameter set values that enable the appearance of percolation clusters. Finally, in supercritical state, most of the pools pertain to same class, or even the same cluster (see Fig. 2).

We note that the integral activation values on pools constituting percolation clusters are loosely coupled to the stimuli activation, which elicited them. This fact is in accordance with the experimental observations conducted in biological neural networks [3].

We measure the critical probabilities p_c and critical exponents $\frac{\beta}{\nu}$ to characterize the critical behavior of the percolation phase transition in the observed neural system. The order parameter is defined as:

$$m = \left| \rho - \frac{1}{2} \right| \quad (4)$$

with parameter m being the normalized number of pools belonging to the percolation cluster. The subtraction of $\frac{1}{2}$ is necessary to account for the transition from the site occupancy to Ising-like variables, enabling the proper definition of the magnetization-like order parameter. The actual order parameter values are obtained through averaging over many copies (replicas) of the system (maintaining identical input and coupling parameters), due to the quenched character of pool connectedness variables. Since, owing to the large computational demand, only small networks can be simulated, we apply the finite-size scaling method to determine the critical probability value and to evaluate the critical exponent ratio required to calculate the percolation cluster fractal dimension.

Critical probability value may be obtained utilizing the appropriate features of finite size scaling of Binder cumulants [20,27,28]. In vicinity of the percolation threshold, for fixed synaptic weight and refractoriness values, Binder cumulants (i.e. reduced fourth-order cumulant) are calculated according to:

$$U_L(p) = 3 - \frac{\langle m^4(p) \rangle}{\langle m^2(p) \rangle^2} \quad (5)$$

where $\langle m^4(p) \rangle$ and $\langle m^2(p) \rangle$ denote the fourth and second moments of the normalized parameters m of cluster sizes. Binder cumulants are indexed with L , indicating general dependence on lattice size. On the other hand, finite size scaling relation reveals that Binder cumulant value

$$U_L(p) = \hat{U}((p - p_c)L^{1/\nu}) \quad (6)$$

is size independent at the critical probability p_c . So, we find Binder cumulant curves for different lattice sizes, by sampling them in the percolation threshold vicinity. The intersection points of these curves are observed at the values p_c . Then, we plot the Binder cumulant curves as function of probability for several lattice sizes to determine their intersection point probability coordinate, declaring it's value to be the best estimate for the critical probability. The obtained p_c values may provide information on the connectivity degree necessary for the network to sustain synfire chains.

Critical probabilities are evaluated for various refractoriness δ and synaptic weight values Ω . We present the results in the weight-probability parameter space, with critical probabilities for fixed refractoriness values comprising critical

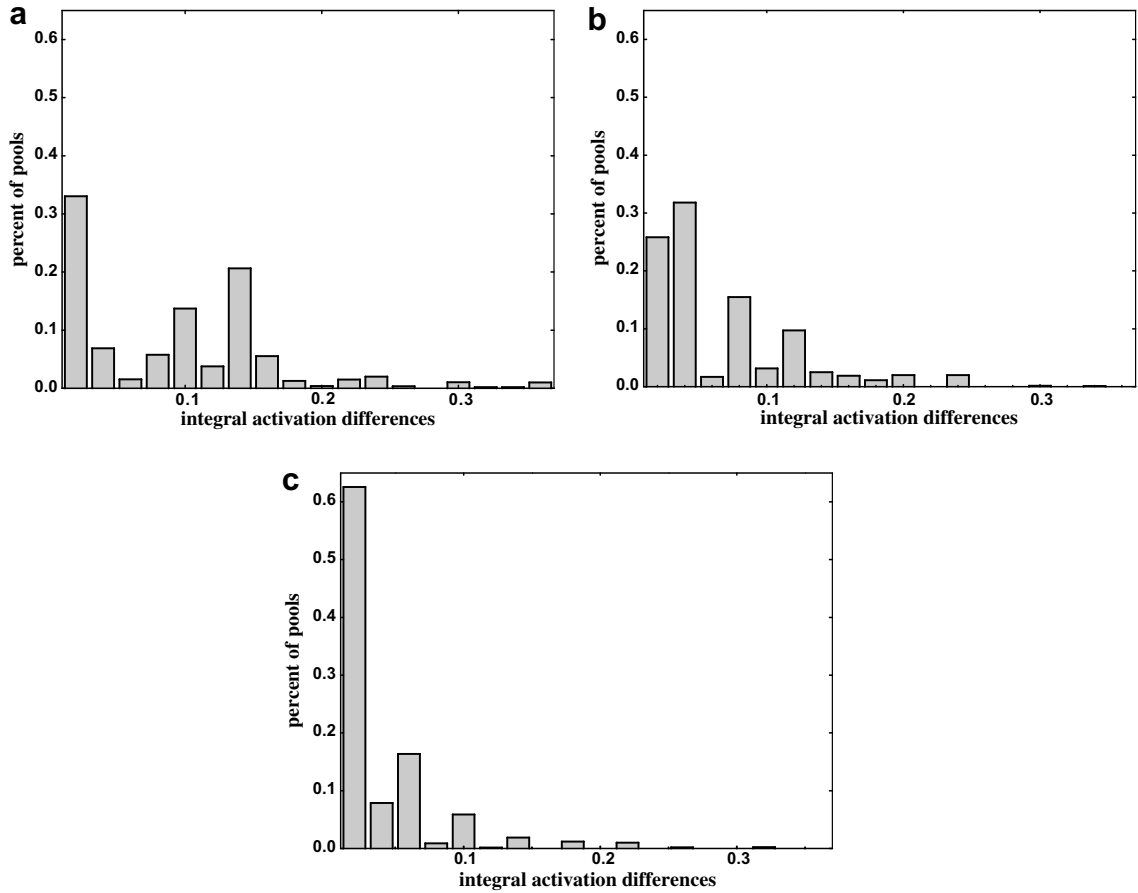


Fig. 2. Distribution of integral activation differences on pairs of pools, before (a), in the vicinity (b) and beyond (c) critical probability p_c . With increasing probability values, pools are persistently clustered in growing classes. The particular distribution example is obtained for the neural network with synaptic weight value 0.4 and zero refractoriness value.

lines (Fig. 3). The obtained family of critical lines clearly displays that higher δ decreases the corresponding critical probability p_c , enabling synfire chain formation in less connected networks.

The synfire chain fractal dimension D is calculated by applying the well-established hyperscaling relation:

$$d - D = \frac{\beta}{\nu} \quad (7)$$

with d representing the lattice dimensionality, and $\frac{\beta}{\nu}$ equaling the main critical exponent ratio. The required critical exponent ratio is evaluated by applying the finite size scaling relation of the order parameter:

$$\rho_L(p_c) \propto L^{-\beta/\nu} \quad (8)$$

Consequently, we make a log–log plot of the order parameter for several lattice sizes at previously determined critical probabilities, with the line slope representing a good estimate for the $\frac{\beta}{\nu}$ value. An example of the log–log plots for fixed synaptic weight $\Omega = 0.3$ and three refractoriness values is displayed in Fig. 4.

The synfire chain fractal dimensions, estimated for several weight and refractoriness values, are presented in Table 1. The obtained fractal dimensions obviously cluster in two classes, corresponding to zero and non-zero refractoriness values. Accordingly, the percolation phase transition at zero refractoriness belongs to the universality class other than the non-zero refractoriness phase transition. We further believe that phase transitions at non-zero refractoriness values pertain to the directed percolation (DP) universality class [23–25], suggesting that higher refractoriness contributes to more directed propagation of neural activity. We also examined the issue of crossover to the DP universality class at low refractoriness values. The apparent transition to DP seems to happen already at $\delta = 0$, since the fractal dimensions obtained for $\delta = 1$ closely resemble those at higher refractoriness values.

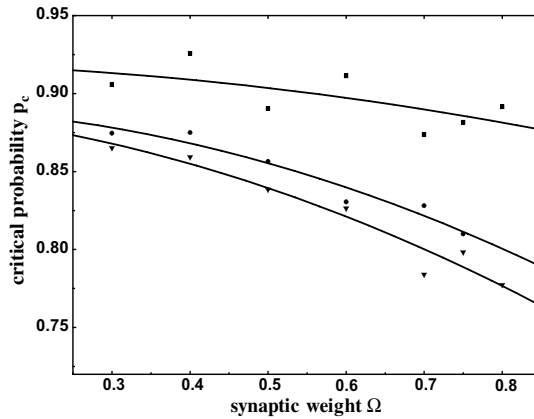


Fig. 3. Family of critical lines for refractoriness taking values 0 (squares), 4 (circles) and 8 (triangles). The results are presented in the weight-probability parameter space, with critical probabilities for fixed refractoriness values comprising critical lines. The network is in subcritical state for $p < p_c$ and each refractoriness value. The system is at criticality for $p = p_c$, while for $p > p_c$ neural network pertains to supercritical state.

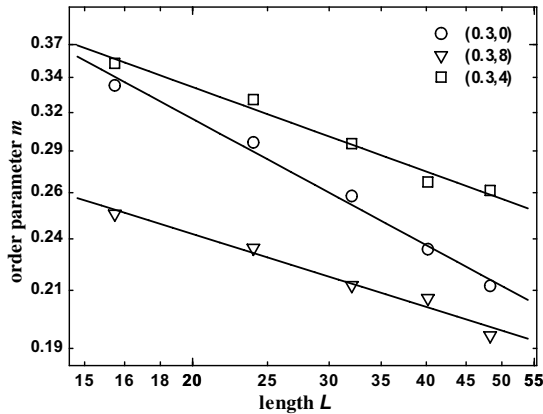


Fig. 4. Calculating the $\frac{\beta}{\nu}$ ratios. Log-log plots of the order parameter values m vs. system size are presented at the critical probabilities p_c . Curve slopes represent an estimate of the critical exponent ratios $\frac{\beta}{\nu}$. The particular curves are obtained for synaptic weight value $\Omega = 0.3$ and refractoriness $\delta = 0.4$ and 8.

Table 1
The Hausdorff–Besicovitch fractal dimension for a set of different refractoriness and synaptic weight values

	Refractoriness			
	0.3	0.5	0.7	0.8
0	1.557	1.553	1.554	1.574
1	1.782	1.736	1.762	1.797
4	1.725	1.768	1.735	1.663
8	1.746	1.729	1.768	1.740

Each table entry was obtained by performing 100 simulations of the neural system.

4. Summary and discussion

The presented model aims to reproduce the features of mesoscopic scale neural networks, since local coupling of elementary units is not characteristic for both the microscopic networks (being randomly diluted) and the networks

on macroscopic scale (with large neural populations having targeted long-range or mixed local-global connections). On the other hand, critical behavior in our model does resemble the results obtained for the two-dimensional network of random cellular automata, which may be considered as a model of microscopic scale neural network. Actually, the authors of [26] proposed the network topology allowing a certain percent of neurons to exhibit a single long-range connection. We note that the same type of crossover to the DP universality class, induced by the refractoriness parameter change in mesoscopic scale networks, is controlled in microscopic systems by the change in the percent of units having a long-range coupling. Specifically, the critical exponents we obtained for zero-refractoriness value correspond to the exponents calculated in [26] for all the neurons allowed a single long-range connection. This fact suggests that feedback effects, supported by $\delta = 0$, may have similar impact on signal propagation as the long-range couplings.

We introduced a percolation model to describe the propagation of synfire waves, representing the global excitation mode in the ensemble of neural pools with recurrent couplings. It is determined that the dynamics of synfire chain formation exhibits critical behavior, with probability for pool connectedness standing for the critical parameter. We find that refractoriness plays an important part in determining the properties of spike packet propagation. Increasing refractoriness lowers the critical probability for the given synaptic weight value, thus enhancing propensity for the synfire waves to occur. Refractoriness is also the key parameter to differentiate between the two universality classes of the observed phase transition, with classes corresponding to zero and non-zero refractoriness values. Judging by the decreasing critical probabilities for growing refractoriness values, it is possible that the topology with asymmetrical connections, favoring directed activity propagation, may also be sufficient to embed synfire chains. We believe further study is needed in the effects of pool asymmetric coupling and modifying network topologies on the synfire wave formation.

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