



Neural avalanches at the edge-of-chaos?

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Abstract—Does the brain operate at criticality, to optimize neural computation? Literature uses different fingerprints of criticality in neural networks, leaving the relationship between them mostly unclear. Here, we compare two specific signatures of criticality, and ask whether they refer to observables at the same critical point, or to two differing phase transitions. Using a recurrent spiking neural network, we demonstrate that avalanche criticality does not necessarily lie at edge-of-chaos.

1. Introduction

In the endeavour of understanding the functioning of the brain, the hypothesis has emerged that biological neural networks might be operating at criticality [1]. The promise of this hypothesis is that at the critical point the particular details of the system's individual elements and their interaction laws cease to be of importance. In this case, the phase transition itself dominates the behavior of the system and therefore the astounding anatomical and biophysical details of neural circuits would surrender to some very generic network properties, allowing to grasp the fundamentals of the information processing and computation in the brain. A “fingerprint” of criticality is power law distributions of the properties exhibited by local descriptors evaluated across the ensemble. Such a fingerprint was also discovered in the statistics of spontaneous activity avalanches of cortical neural tissue recorded with multi-electrode arrays [1]. While alternative explanations for power law observations have been proposed, the proponents of the *avalanche criticality* hypothesis attribute several advantages of this state: optimized information transmission and capacity, as well as increased flexibility of responses granted by diverse activity patterns [2, 3]. The notion of computation used in this context remained, however, rather vague, similar to the dynamical (in contrast to the topological) situation counterpart, where it has been contended that computation, in the sense of the ability of a system to transmit, store and modify information, would be optimized at *edge-of-chaos* [4] criticality. Links have been occasionally drawn in the literature between the edge-of-chaos and the avalanche criticality [5], however, the relationship between these two phase transitions in neural networks is far from established. Here, we examine whether avalanche criticality lies at the edge-of-chaos, characterized by a zero largest Lyapunov exponent.

2. Neural network model

The neural network model used in this study reflects the general features ascribed to cortical networks: sparsely connected and consisting of 80% excitatory and 20% inhibitory neurons, where inhibitory synapses are several times stronger than the excitatory ones. The network topology was a directed Erdős-Rényi random graph; this type of connectivity is more in line with the networks in dissociated cortical cultures [6]. The number of nodes in the network was set to $N = 128$, and the mean in-degree was set to $k = 5$, which is equal to 4% connectivity. The size of the network was chosen to satisfy a trade-off between obtaining enough statistics for the avalanche size distributions and minimizing the calculation time of the network's Lyapunov exponents.

To assess the dynamical stability properties of the network, we need nodes that exhibit dynamics similar as possible to the membrane potential dynamics of real neurons, which can be achieved by using the Rulkov map model (cf. Eq. 3, 4 in Ref. [7] where $u = y_n + \beta I_n^{\text{syn}}$ and $\sigma_n = I_n^{\text{syn}}$). The parameter values for excitatory and inhibitory neurons were identical: $\alpha = 3.6$, $\mu = 0.001$, $\sigma = 0.09$, $\beta = 0.133$. Synaptic input I_n^{syn} was modelled by exponential decay and step-like increase upon a presynaptic spike event, $I_{n+1}^{\text{syn}} = \gamma I_n^{\text{syn}} - \sum_j^N W_{scale} w_{ij} (x_n - x_{rp})$, where γ controls the decay rate of the synaptic current, w_{ij} is the synaptic strength between the presynaptic neuron j and the postsynaptic neuron i , x_{rp} is the reversal potential which determines whether the synapse is inhibitory or excitatory, and W_{scale} is a global scaling parameter of the synaptic weight. We used the following parameter values for excitatory (‘Ex’) and inhibitory (‘Inh’) synapses: $x_{rp}^{\text{Ex}} = 0$, $\gamma^{\text{Ex}} = 0.75$, $w_{ij}^{\text{Ex}} = 0.6$, $x_{rp}^{\text{Inh}} = -1.1$, $\gamma^{\text{Inh}} = 0.75$, $w_{ij}^{\text{Inh}} = 1.8$. Because this would pertain to self-organized criticality, which is not the goal of the present investigation, synaptic plasticity was not included in the network model.

To introduce spontaneous activity, we modelled one of the neurons to spike intrinsically by setting its parameter $\sigma = 0.103$, which is just above the spiking threshold. By embedding this neuron in the network, the network's influence on spontaneous firing is much more realistic compared to if the network were solely external input-driven. Additionally, we also added a sparse, excitatory external input to all neurons in the form of independent Poisson

spike trains. The probability for a single neuron to receive an external input spike at any given iteration was $6 \cdot 10^{-4}$. This type of input models randomness similar to the spontaneous neurotransmitter vesicle release.

The parameters of the network model were kept fixed except for the synaptic weight scaling parameter W_{scale} that was varied for accessing subcritical, critical and supercritical activity states. For each of the three states we ran 50 simulations and pooled the results. For each simulation, the synaptic connections were randomized. A single simulation covered $5 \cdot 10^5$ iterations, and the first 5000 iterations were discarded.

3. Analysis of neuronal avalanches

Neuronal avalanches are generally defined as periods of uninterrupted neural activity, either local-field potential events or spikes, with respect to a given time binning. In our case we will analyse spike avalanches. Time is divided into bins of length Δt and an avalanche is a sequence of bins that each features at least one spike, preceded and followed by at least one bin without any spikes. The lifetime of the avalanche T is the number of bins in the sequence. The size of the avalanche S is the sum of the spikes in the sequence. A popular decision in the experimental studies is to use a temporal bin size equal to the average time between two subsequent events across all of the electrodes: the inter-event interval IEI_{avg} [1, 8, 9, 10]. In order to put our study in the same context as the experimental investigations of the avalanche criticality, we will follow the established approach of defining neural avalanches by using a binning size of $\Delta t = IEI_{avg}$ [1].

Power law distributions can be caused by several different mechanisms and not necessarily by a phase transition, which necessitates additional tests to confirm that the network is really at criticality. An important test for the scale-free property of the avalanches is the universal scaling of avalanche shapes [10]. The avalanche shape of length T is defined as the temporal profile of an avalanche, i.e., the number of spikes over time $V(T, t)$. The critical point is characterized by power laws in many variables and these relationships give rise to the fractal structure of avalanches: the average shapes are similar over different time scales and they collapse to one universal shape after rescaling. In contrast, subcritical or supercritical avalanche shapes should not collapse. We let $\langle V \rangle(T, t/T)$ be the average temporal evolution of the size of an avalanche with a normalized duration t/T and rescale the avalanches to $\mathbf{V}(t/T) = T^{1-\gamma} \langle V \rangle(T, t/T)$, where $\mathbf{V}(t/T)$ is the universal scaling function, i.e., the characteristic shape of all avalanches. The critical exponent γ can be obtained from $\langle S \rangle(T) \propto T^\gamma$, where $\langle S \rangle(T)$ is the mean size of avalanches as a function of the duration T , which can be easily estimated from the simulation results.

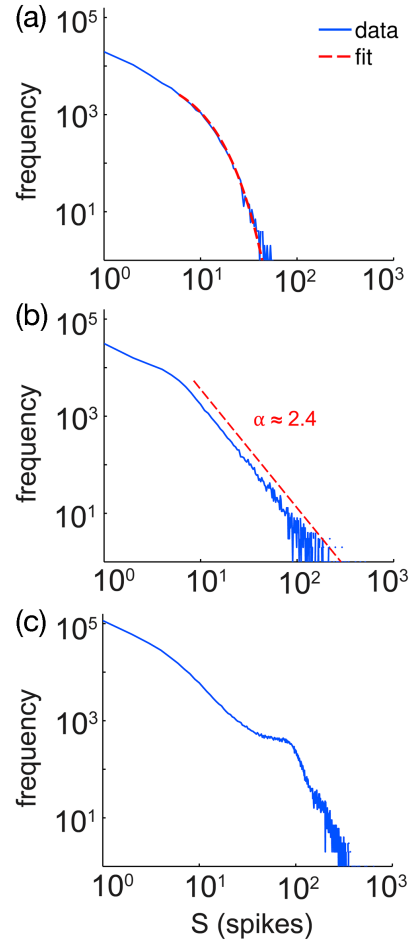


Figure 1: Avalanche size S distributions: (a) subcritical, (b) critical, (c) supercritical networks. The critical network shows a power law behavior for $S \geq 6$, with $\alpha \approx 2.4$ (fitted using the maximum-likelihood estimation; goodness of fit evaluated using the Kolmogorov-Smirnov distance with 1000 synthetic samples [11], p-value = 0.52). The decay of the subcritical distribution can be fitted by an exponential with exponent $\lambda \approx 0.21$ (p-value = 0.26).

4. Results and discussion

By globally increasing the synaptic strength of the connections with the parameter W_{scale} , we observed an overall increase in network activity and an evolution of the topological network state from subcritical, to critical, to supercritical (Fig. 1). The values of W_{scale} corresponding to subcritical, critical and supercritical networks were 0.13, 0.139 and 0.15, respectively. The mean $IEI_{avg} \pm SD$ was 110 ± 8 (subcritical network), 48 ± 6 (critical network) and 8 ± 2 (supercritical network) iterations. Changing W_{scale} appeared to have a similar effect to changing the levels of excitation in biological experiments by using pharmacological agents that alter the efficiency of neurotransmitter receptors [3]. The avalanche size distribution of the critical network follows a power law with the exponent $\alpha \approx 2.4$ (Fig. 1(b)),

with a power law noise cut-off at about $S \approx 100$. This is expected because the network is a finite system of the size $N = 128$ and in most of the avalanches a single Rulkov neuron fires only once. In the subcritical case, the avalanches were smaller and their size decayed exponentially, while in the supercritical case there was an increased number of large avalanches signified by the hump at the end of the distribution. If the synaptic strength were to be increased further, the hump would become even more prominent. Similar metamorphosis of the distribution shape was also observed for avalanche lifetimes. At criticality, the lifetime distribution could be fitted with a power law for $T \geq 10$, with an exponent $\tau = 2.9$.

The critical exponent $\alpha = 2.4$ of our avalanche size distribution is different from the slope $\alpha = 1.5$ measured in the original experiments [1]. However, in subsequent reports of critical spike avalanches the exponents have varied substantially, in the range from 1.5 to 2.1 [8, 9]. Some researchers explicitly reject the idea of a universal exponent (such as $\alpha = 1.5$) because of insufficient experimental and theoretical basis [12]. Our critical avalanche size distribution is rather similar to that of dissociated rat cortical neurons reported in Ref. [9], which had $\alpha = 2.1$ at the tail of the distribution and another scaling regime for very small avalanches.

The critical network showed a rather noisy collapse of the avalanche shapes of duration $T \geq 20$ (Fig. 2(a)), but overall the avalanche shapes were more self-similar than in the case of the supercritical network (Fig. 2(b)). The scaling could not be assessed for the subcritical network, as the maximum lifetime of the subcritical avalanches was only $T_{max} = 26$. A collapse similarly noisy to ours was reported for avalanches recorded in dissociated neuron cultures [10], which have a topology similar to our network model [6].

As the final test, we examined the relation among critical exponents $\frac{\tau-1}{\alpha-1} = \gamma$ [10]. The critical exponents of avalanche lifetime distribution ($\tau = 2.9$), avalanche size distribution ($\alpha = 2.4$), and the function of the mean avalanche size depending on the lifetime ($\gamma = 1.37$) fulfills this relation. Taken together: power law distributions, the similarity of avalanche shapes and an excellent fulfillment of the fundamental relation between critical exponents, strongly suggests that our ‘critically tuned’ network is indeed critical.

The largest Lyapunov exponents for the three network states, calculated using the network’s Jacobian matrix evaluated at points along the trajectory of the state vector [13], were, however, all positive and practically the same for subcritical and supercritical networks and slightly smaller for the supercritical network: $\lambda_1 \approx 18 s^{-1}$ for subcritical and critical networks and $\lambda_1 \approx 16.5 s^{-1}$ for the supercritical network (applying the time rescaling of [7] with one iteration accounting for about 0.5 ms).

The Lyapunov spectra in the three cases provided more insight by showing that the number of positive Lyapunov exponents increased with coupling strength. The upper

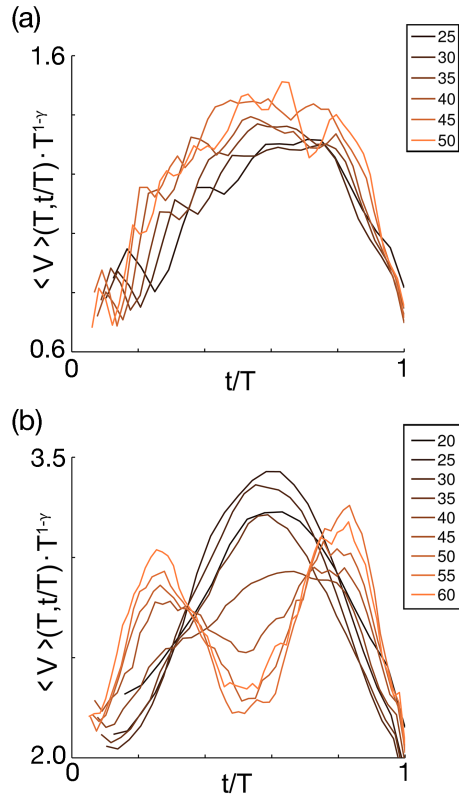


Figure 2: Time-rescaled avalanches: (a) critical, (b) supercritical case. Colors indicate avalanche lifetime T .

bound of the Kolmogorov-Sinai entropy $H = \sum_{\lambda_i > 0} \lambda_i$ in our networks increased with a higher coupling strength and was the highest for the supercritical network: $28 s^{-1}$ (subcritical), $46 s^{-1}$ (critical), $88 s^{-1}$ (supercritical). Although the supercritical network has a slightly smaller largest Lyapunov exponent, it loses the information about the past states at the fastest rate.

As chaotic dynamics could be a collective effect of the network interactions or arise simply because the nodes themselves have chaotic dynamics, we measured the largest Lyapunov exponent of the intrinsically spiking neuron and found it to be positive ($\lambda_1 = 20 s^{-1}$), in the absence of network input. In the presence of external input, the neuron was occasionally silenced, a behavior that can be also observed in Class II neurons. As a result, the neuron’s largest Lyapunov exponent decreased to $\lambda_1 \approx 18 s^{-1}$ which is in agreement with λ_1 of our networks. This suggests that the largest Lyapunov exponent of the network might be capturing the dynamics of the intrinsically spiking neuron. In the subcritical and critical cases there were 3-4 other positive Lyapunov exponents, which is close to the number of neurons that receive inputs from the intrinsically spiking neuron. Therefore, the source of chaos in our networks resides in the single neuron dynamics; the increase of coupling strength made the chaos more intensive because it allowed more neurons to spike.

5. Conclusion

Our network showed chaotic dynamics, for all choices of the synaptic weights. The main result of the present study is that we did not observe a coincidence of avalanche and edge-to-chaos criticality in our network type. This suggests that in neural networks with non-trivial node dynamics these are two separate phase transitions. Both phase transitions have been occasionally mentioned in the same context in the literature; our demonstration also elucidated that any computational benefits of one criticality cannot be directly translated to the other, and that in this regard the internal neuronal processes appear to play a decisive role.

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