Neuronal avalanches: Where temporal complexity and criticality meet

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Abstract. The model of the current paper is an extension of a previous publication, wherein we have used the leaky integrate-and-fire model on a regular lattice with periodic boundary conditions, and introduced the temporal complexity as a genuine signature of criticality. In that work, the power-law distribution of neural avalanches was a manifestation of supercriticality rather than criticality. Here, however, we show that the continuous solution of the model and replacing the stochastic noise with a Gaussian zero-mean noise leads to the coincidence of power-law display of temporal complexity, and spatiotemporal patterns of neural avalanches at the critical point. We conclude that the source of inconsistency may be a numerical artifact originated by the discrete description of the model which may imply a slow numerical convergence of the avalanche distribution compared to temporal complexity.

1 Introduction

Diverse fields of research including neurophysiology, sociology, geophysics, and economics consider heavy tails and scale-free distributions as the signature of complexity [1]. The brain as a complex dynamic system and brain activities including neuronal membrane potentials, non-invasive electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI) signals observed at many spatiotemporal patterns exhibit a power-law behavior (PLB) [2].

Neuronal avalanches are a consequence of the bursting activity of neurons in intervals less than a specific time. At a critical state, avalanche size, and lifetime distributions display PL exponents limited to a specific range [3]. The widely varying profile of neural avalanche distribution in size is described by a single universal scaling exponent, $\beta$ in size, $p(S) \sim S^{\beta}$, and a single universal exponent in duration, $\tau$, $p(T) \sim T^{\tau}$, where $S$ and $T$ denote the size, and the duration of avalanches, respectively.

Criticality in neuronal avalanches is supported by the existence of a PL exponent, and shape collapse which are necessary criteria for criticality as proved in cultured slices of cortical tissue [4]. The existence of PLB in neuronal avalanches was detected in cortex slice cultures of rats in vitro [5,6], rat cortical layer 2/3 at the beginning and end of the second week postnatal [7], Local Field Potentials (LFPs) of anesthetized cats [8,9], and monkeys [9,10].

According to the popular view of Per Bak et al. [11], in most natural systems, criticality is realized spontaneously by Self-Organized Criticality (SOC) rather than requiring the fine tuning of a control parameter with a critical value. They proposed the term SOC as an operation of the system at criticality that generates the PLB in natural phenomena. However, the operation of the system at criticality does not imply that the system works with the SOC mechanism, and it has been convincingly shown that neural systems displaying critical avalanches are not an instance of SOC systems [12], and an adaptive or evolutionary mechanism may explain the emergence of criticality rather than SOC [12,13]. In [14,15], the level of excitability of the system changes the temporal organization of neural avalanches. This parameter explains the slow alternations of up and down states, which determines both the network and the single neuron behavior.

Moreover, there are widely empirical evidences showing that the resting brain works near criticality [4–6, 16, 17]. Furthermore, many studies have shown that criticality in the brain is often accompanied by other optimal operations including phase synchrony [6], information storage [17], communication, and information transition [3], optimal communication [3,16,18–22], transition
capability [22], computational power [18], and dynamic range [22, 23].

PL distributions may suggest that neural networks operate near a non-equilibrium critical point where the phase transition occurs [3]. A critical point sets a boundary between an ordered and a less ordered state with different scaling behaviors [4]. However, since many possible mechanisms generate PL, the appearance of them alone is insufficient to establish criticality, and also non-critical systems may produce PLs [16,24–26]. In [27,28], the authors argue that the methodology used in the analysis can amplify or create PLs that are not related to the critical structure in the underlying signal.

However, in [29–31], we have introduced another robust indicator of criticality, as temporal complexity, which is a complexity signature in time. Considering a complex system generating events in time, the probability that no event occurs up to time $t$ is properly termed survival probability, denoted by $\Psi(t)$. The temporal complexity signals the emergence of a form of survival probability called Mittag-Leffler (ML) function.

Using the leaky integrate-and-fire model (LIFM), we found that temporal complexity occurs in a narrow range of coupling parameters. To confirm the critical point, the cross-correlation and mutual information were computed, and we showed that information transfer from one network to another becomes maximal in the corresponding range. Moreover, two regular-lattice networks were identically selected, and we argued that if the enhancement of information transfer is interpreted as a signature of criticality, then PL avalanches are a manifestation of supercriticality rather than criticality. This finding, however, coincides with the finding of [32] that no clear evidence of PL scaling or self-organized critical states was found in the awake and sleeping brain of mammals including monkey, cat, and human. Nevertheless, if the temporal complexity is a valid indicator of criticality, these results would not conflict with the hypothesis that the brain works near criticality.

Yet, considering many inconsistent results reported from recordings in awake animals, and humans in appearance of PL scaling of avalanche data profile, we assumed that it may be a conflict that avalanche distributions in size and duration do not display PLB at the critical point indicated by temporal complexity. Hence, we were motivated to find the source of the conflict.

Hence, in this study, we show that by replacing the discrete stochastic noise with a continuous Gaussian noise, avalanche probability distributions display PLB at criticality indicated by temporal complexity, and show that the choice of noise may be the source of the conflict between our previous study [29] and the current one. However, in both studies, temporal complexity remains robust while spatial scale invariance of neural avalanches show slow numerical convergence.

Therefore, here, we first show that temporal complexity detects a critical point. We then examine whether avalanche distribution in size and time follow a PL exponent as found in [3]. Using the scaling theory [33] that predicts exponent relations, we confirm that neural avalanche data collapses onto the critical exponent suggested by temporal complexity.

2 Model description

The model used in the previous studies [29–31], and here is the LIFM [34].

$$\dot{x}_i = -\gamma x_i(t) + S + \sigma \xi_i(t), \quad (1)$$

where $x$ is the membrane potential, $1/\gamma$ is the membrane time constant of the neuron, $S$ is proportional to a constant input current. Note that $i = 1, \ldots, N$ where $N$ is the total number of neurons. Each neuron starts from a random value or zero, and fires when it reaches the threshold, $x = 1$. When one neuron fires, it forces all the neurons linked to it to make a step ahead by the quantity $K > 0$ which means that all neurons are excitatory. The parameter $K$ is the cooperation strength and plays the role of the control parameter that is expected to generate criticality when the special value $K_\ast$ is adopted. After firing, each neuron jumps back to the rest state $x = 0$.

In the absence of cooperation, $K = 0$, the vanishing noise condition yields the following expression for the time distance between two consecutive firings of the same neuron:

$$T_P = \frac{1}{\gamma} \ln \left( \frac{1}{1 - \frac{S}{\gamma}} \right). \quad (2)$$

If $K > 0$, after a few time steps all the neurons fire at the same time [35], thereby generating a sequence of quakes of intensity $N$ with the time period $T_P$ given by eq. (2).

The parameter $\sigma$ is the standard deviation of the noise which can also be considered as the noise intensity. In the previous solution of eq. (1), we adopted the integration time step $\Delta t = 1$ and $\xi(t)$ as a discontinuous random fluctuation taking with equal probability either the value of $\xi(t) = 1$ or $\xi(t) = -1$ [29,30].

However, the central limit theorem requires that a discrete noise with finite variance converges to a Gaussian distribution after a long time integration. Hence, in order to have results comparable with real neuronal behavior, it is natural to have a continuous time description of the LIFM. Therefore, we treat the time continuously and then consider $\xi$ to be a continuous Gaussian white noise with zero mean and unit variance, defined by

$$\langle \xi(t) \rangle = 0,$$
$$\langle \xi(t) \xi(t') \rangle = \delta(t - t'). \quad (3)$$

To reduce the number of the parameters, we define the dimensionless time variable $T = \gamma t$, hence, eq. (1) can be rewritten in the following form:

$$\dot{x}_i(T) = -x_i(T) + \frac{S}{\gamma} + \frac{\sigma}{\sqrt{\gamma}} \eta_i(T), \quad (4)$$

in which $\eta(T) = \frac{1}{\sqrt{\gamma}} \xi(T)$ is the dimensionless Gaussian noise with zero mean, and unit variance. To numerically
integrate the stochastic differential equation eq. (4), we use Ito’s interpretation, which is

\[ x_i(T+dT) = x_i(T) + \left[-x_i(T) + \frac{S}{\gamma}\right]dT + \frac{\sigma}{\sqrt{\gamma}} \eta_i(T) \sqrt{dT}. \]  

(5)

Here, we choose \( dT = 0.01, S = 0.001005, \gamma = 0.001, \) and \( \sigma = 0.0001. \) We assume that neurons are residing on the nodes of a two-dimensional square lattice with periodic boundary condition with size \( N = L \times L, \) where \( L \) is the linear size of the lattice (here, \( L = 10, 15, \) and \( 20). \) The duration of all realizations was \( 10^5 \) time steps.

The adoption of a periodic boundary condition is to ensure the total equivalence of the cooperating units, so as to avoid the doubt that the onset of firing bursts may be triggered by units with a favorable topology. However, numerical calculations not reported here show that the adoption of a periodic boundary condition is not crucial for the results of this paper. Also, due to computational expenses, the number of neurons in the current research is limited to \( N = 400. \) In [30], we have studied networks up to size \( N = 2500, \) and have extensively discussed the finite size effect.

Using the temporal complexity approach, we study the cumulative probability distribution of the time distances between two consecutive firings as a possible indicator of criticality. In the lack of cooperation, the dynamic is a Poissonian process and the probability distribution function is defined by an exponential

\[ \Psi_{ML}(t) = \exp(-Gt), \]  

(6)

which indicates the survival probability with \( G = \frac{N}{\langle \tau \rangle}. \) \( G \) indicates a constant firing rate, and \( \langle \tau \rangle \) is the mean time between firings of a given neuron. For \( \sigma \ll 1, \langle \tau \rangle = T_P \) of eq. (2). According to [36], cooperation generates scale invariance, that is for the short times increasing \( K \) leads to a transition from the exponential form of eq. (6) to a form of stretched exponential that reads as follows:

\[ \Psi_{ML}(t) = \exp(-\lambda t^\alpha), \]  

(7)

with \( \alpha < 1. \) It is evident that the exponential function of eq. (6) corresponds to the ML function with \( \alpha = 1 \) and \( \lambda = G. \) This suggests that temporal complexity becomes evident when the parameter \( \alpha, \) as determined by means of the fitting procedure, becomes significantly smaller than 1.

Figure 1 shows how neural network deviates from an exponential to a regular behavior by changing the control parameters, \( K. \) Two distinctive time regimes characterize the survival probability: a short-time regime that can be fitted by a stretched exponential of eq. (7) with \( \alpha < 1, \) and a long-time regime fitted by an inverse PL, \( 1/t^\alpha. \) Fitting parameters, \( \alpha, \) and \( \lambda \) can be found under a fitting procedure. \( \alpha \) indicates the PL exponent of the survival probability meeting \( 0 < \alpha < 1, \) and \( \lambda \) indicates the scale of the stretched exponential of the survival probability distribution.

As an example, the fitting procedure for a value of \( K = 0.0018 \) is shown in fig. 2(a). The procedure is accomplished on each time regime in two steps: fitting of the stretched exponential, and fitting of the inverse PL. However, fitting on the Laplace transformation of the survival probability can be done in a single step on the total observation time. It is important to note that the fitting parameters found in both cases are equal. Hence, it is more convenient to use the Laplace transform of the survival probability and find the fitting parameters. We assign \( \Psi_{ML}(u) \) to the Laplace transform of the ML survival probability, by adopting the notation for the Laplace transform of \( (\Psi(u) = \int_0^\infty d\psi(t) e^{-ut}), \) on eq. (7)

\[ \Psi_{ML}(u) = \frac{1}{u + \lambda u^{1-\alpha}}. \]  

(8)

Similar to the earlier studies [29,31], we find the parameters \( \alpha, \) and \( \lambda \) by relying on fitting the Laplace transform with the variations of the cooperation strength, \( K. \) In [37], the authors illustrate the effect of establishing a cooperative interaction in the case of the random growth of surfaces. A growing surface is a set of growing columns whose height increases linearly in time with fluctuations that, in the absence of cooperation, would be of Poisson type. The effect of cooperative interaction is to turn the Poisson fluctuations into complex fluctuations: the interval between two consecutive crossings of the mean value being described by an inverse PL waiting time distribution \( \psi_{ML}(t), \) corresponding to a survival probability, whose Laplace transform is given by eq. (8).

The procedure is as follows: i) apply a Laplace transform on the survival probability gained from neural dynamics, ii) fit the data given in step i) into eq. (8) to find \( \alpha \) and \( \lambda. \) We repeat this procedure for different values of coupling strengths, \( K. \) The Laplace transform of the survival probability of the same \( K \) is calculated as shown in fig. 2(b). As can be inferred from the figure, the result of numerical fitting fully matches with the analytical prediction of eq. (8).

The corresponding fractal exponents of each curve, \( \alpha, \) is plotted in fig. 3. The arrow in this figure indicates the
value of $\alpha < 1$ corresponding to the cooperation parameter $K \sim 0.0018$, for which the widest PLB is observed in the survival probability for a lattice of linear size $L = 10$ (see fig. 2(a)). We have repeated the calculation for two networks of larger sizes ($L = 15$, and $L = 20$), and found that for all these sizes the widest critical region corresponds to a value of $\alpha < 1$. Hence, criticality accompanies with a crossover from the Poissonian to the ML regime in temporal complexity.

In our former study [29], we have extensively analyzed the emergence of criticality using the aging experiment, and information transfer from one network to another that essentially rely on temporal firing patterns. The emergence of criticality is confirmed and the results not shown here indicate that the critical regime suggested by the current solution of the model also coincides with that of the previous solution. Therefore, we encourage readers to see sects. 5 to 7 of [29] for more details.

However, neural avalanches did not display PLB in the range suggested by fig. 3. We presumed that the source of the conflict is due to the discrete solution of the model, generating a numerical artifact. Therefore, here, we focus on neural avalanches, and set out to address whether the continuous solution of the model will result in the appearance of the PLB of avalanche distributions around the critical regime suggested by temporal complexity. Hence, we explore whether the avalanche data satisfies the scaling theory relation which is interpreted as an indicator of criticality [4,33].

Moreover, the model of the current paper is a generalization of the model proposed by Mirollo and Strogatz [35], and by adding a noise to the model, in order to generate temporal complexity, a competition is set between the adjustable coupling parameter, $K$, and the noise. Figure 4 shows how coupling has to be adjusted to the noise to maintain the criticality and phase transition. As can be inferred from the figure, the critical coupling, $K_c$, approx-
approximately has a linear dependence on the noise intensity, and as we increase the noise in the system, cooperation has to level up in order to maintain the system at criticality.

3 Neural avalanches

As predicted by the renormalization group theory [33], the neural avalanche data collapse onto universal scaling functions near a critical point and follow

\[ p(S) \sim S^{-\beta}, \]
\[ p(T) \sim T^{-\tau}, \]
\[ \langle S \rangle(T) \sim T^{1/z}, \]

where \( p(S) \) and \( p(T) \) are the probability density functions of the avalanche size and duration, respectively. \( \langle S \rangle(T) \) is the average of avalanche size conditioned on a given duration [33]. \( \beta, \tau, \) and \( 1/z \) are the critical exponents of the system, and are independent of the details of the model or system [4]. Therefore, \( P(S) \), and \( P(T) \) are the cumulative probability distributions, \( P(S) = \int_S^\infty p(s)ds \), and \( P(T) = \int_T^\infty p(t)dt \), respectively, and scale as

\[ P(S) \sim S^{1-\beta}, \]
\[ P(T) \sim T^{1-\tau}. \]

The scaling theory requires the following relation between the exponents:

\[ \frac{\tau - 1}{\beta - 1} = \frac{1}{z}. \]

The mean field theory predicts for \( \beta = 3/2, \tau = 2.0, \) and \( 1/z = 2.0 \) that eq. (11) is satisfied [33]. In our previous study [29], we did not observe the coincidence of the PL distribution of neural avalanches at criticality that was realized by temporal complexity.

Hence, we plot the size, duration, and the average avalanche size of the neuronal avalanches creating as the results of our LIFM in fig. 5. For this purpose, we count the number of firing neurons in time bins of 5 simulation steps (\( \Delta T = 0.01 \)). An avalanche is recorded whenever a burst of neurons is followed by quiescent duration of a minimum of 5 steps. The number of neurons fired during this active region is called the avalanche size, \( S \), and the duration of this activity is called the avalanche duration \( T \). The average avalanche size exponent is defined according to the last term of eq. (9).

In order to show the results for networks of larger sizes, we run the model for three lattice sizes (\( L = 10, 15, \) and 20) at \( K_c = 0.0018 \) (see fig. 6). In this figure, panels (a), and (b) show the scaling of the probability density functions of the avalanche size and duration, respectively. Panel (c) is devoted to the conditional average avalanche size, \( \langle S \rangle(T) \) in terms of the duration \( T \). This is another proof that the critical point suggested by temporal complexity is, in fact, the system’s critical point.

Figure 6(a) illustrates \( p(S) \), the avalanche size distribution for \( K_c = 0.0018 \). We see that the crucial power

![Fig. 5. (Color online) Cumulative probabilities of (a) avalanche size \( P(S) \), (b) avalanche duration \( P(T) \). (c) Scaling of the conditional average of avalanches with duration \( T \) for \( K = 0.0010, 0.0014, 0.0016, 0.0018, 0.0020, 0.0024, 0.0030 \). The results are obtained using \( \gamma = 0.001, \sigma = 0.0001, S = 0.001005, and the lattice with the linear size \( L = 10 \. The arrow indicates the critical curve at \( K = 0.0018 \).](image-url)
Fig. 6. (Color online) Scaling of the probability density function of (a) avalanche size $p(S)$, (b) avalanche duration $p(T)$. (c) Scaling of the conditional average of avalanches with duration $T$. The results are obtained using $\gamma = 0.001$, $\sigma = 0.0001$, $S = 0.001005$ at $K = 0.0018$ and the lattices with the linear size $L = 10, 15$, and 20.

4 Concluding remarks

Here, by the continuous solution of LIFM, and using Gaussian zero-mean noise, we explored if at the critical point suggested by temporal complexity, avalanche data collapses onto a universal scaling function as predicted by the scaling relation [33], and whether it is consistent with the empirical findings of [3].

More specifically, we illustrate a neural model where the time interval between two consecutive firings, in the absence of cooperation, is described by an ordinary exponential function, corresponding to $\alpha = 1$. The effect of cooperation is to make $\alpha$ decrease in a monotonic way when increasing the cooperation strength, $K$.

Our results provide a compelling evidence that temporal complexity, and neural avalanches both display PLB at the critical point. Therefore, we may conclude that the choice of noise leads to the inconsistency of the result. Notably, the continuous time description is more natural and makes our model comparable to the empirical results.

Being dependent on a control parameter, we have shown that the model of the current research in not an instance of a SOC system, and some type of self-tuning mechanism needs to be invoked for the emergence of criticality as suggested in [12–15]. The critical region is extended to a narrow region, and tuning the coupling constant drives the system from a Poissonian (Random) regime, to a critical, and finally to a regular (fully synchronized) regime. Therefore, we refer to the mechanism of our model as a cooperation-induced criticality model.

We emphasize that the exponents of the avalanche data collapse on the scaling exponents that are model independent, and identical for all systems in the same universality class. On the other hand, the results of the paper indicate that a simple model using a regular lattice successfully sheds light into the cooperation-induced criticality in a neural system. However, for further analysis, and making our model closer to the real brain networks, we have incorporated inhibitory connections in the network. The results which will appear in our next publication indicate that introducing a small fraction of inhibitory neur-
rons does not change the global behavior of the system, and only slows down the tuning mechanism through different regimes.

In the light of these results, we conclude that temporal complexity is a robust indicator of criticality regardless of the solution method. Hence, what we have claimed based on temporal complexity before [29] is still valid in the current solution of the model. Also, we illustrated that neuronal avalanches are indicators of criticality if a continuous time description is applied to the LIFM model. This may also indicate that the spatial scale invariance given by the avalanche cumulative probability distribution in size displays a relatively slow numerical convergence compared to the temporal complexity measure, and the temporal complexity is more robust with respect to the choice of the noise.

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Author contribution statement

All the authors were involved in the preparation of the manuscript. All the authors have read and approved the final manuscript.

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