Spike-LFP Phase Coupling and Synchronization Transition in a Leaky Integrate-and-Fire Model

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Scale-invariant spatiotemporal dynamics in cortex indicates a critical state entailing interesting properties including efficient information processing, information transition, and maximal variability in phase synchrony. Hence, mechanisms that underlie, or are generated by criticality in neuronal networks are of particular interest. Therefore, we presume that the existence of a coupling between spikes and LFPs which measures the inter-neuronal interactions may enhance our understanding of the mechanisms governing the critical behavior in the cortex. To this end, we consider a network of N excitatory neurons that reside on a regular lattice with periodic boundary conditions. The connection between neurons, K, plays the role of the control parameter that is expected to generate criticality when the critical cooperation strength, Kc, is adopted. Here, we show that spike-LFP coupling (SPC), quantified by the phase locking value (PLV), is positively correlated with the inter-neuronal connectivity strength. We find a continuous transition from irregular spiking (i.e., zero PLV) to a phase locked state at a critical point, soaring to its maximum level (i.e., one). We also studied the effect of input noise and current to individual neurons, and found that SPC is attenuated as the noise or input current are increased. Moreover, we deploy the finite-size scaling analysis to obtain the universality of this transition. We also show that the neuronal avalanches created at this critical point, display a remarkable scaling behavior in a fair agreement with the predicted theoretical and experimental values reported before. We conclude that SPC can play the role of an order parameter in our neural model.

I. INTRODUCTION

Ongoing activity in cortex results from activities of many single neurons that transiently add up to larger events, traceable in various recording techniques including extracellular microelectrode arrays (MEAs) with local field potential (LFP), the electroencephalogram (EEG), the magnetoencephalogram (MEG), and the BOLD signal from functional magnetic resonance imaging (fMRI) [1]. An attractive yet controversial dynamical landscape explores emergent properties that speak for the brain collective behavior, proposing the concept of “neuronal avalanches”. Different from avalanches in critical sandpile models which generate stochastic patterns, neural avalanches of LFPs occur in spatiotemporal patterns, display stable scale-free patterns in the spatial extent of neuronal activity, i.e. patterns with temporal precision of 4 ms are reproducible over periods of as long as 10 hours [2, 3]. These properties suggest that avalanches could be used by networks as a substrate for storing information [4, 5]. Moreover, neuronal avalanche patterns are considered to be a signature of criticality, and many empirical evidence supports the hypothesis that the cortex operates near criticality, thereby enabling efficient information processing [2, 5–9], dynamic range [9–11], communication and information transition [2], optimal communication [2, 6, 10, 12–15], transition capability [10], computational power [12], and phase synchrony [8].

However, a natural question arises here is that “under what conditions do local cortical networks converge on criticality or deviate from criticality?” Royer and Pare [16] proposed that conservation of synaptic strengths is a possible mechanism responsible for maintaining a network in the vicinity of a critical point. Similarly, in [17], authors show that due to some combination of homeostatic regulation of excitability and Hebbian learning, the total sum of synaptic strengths remains near a constant value, hence the network operates near criticality. Competitive activity-dependent attachment and pruning [18, 19], dynamic synaptic plasticity [20], synaptic scaling [21], and neural coupling adjustment to generate criticality [22–25] are possible mechanisms for leading up the network into critical regime.

Thus, understanding the mechanisms that underlie, or are generated via criticality state in neuronal networks are of particular interest. This motivated us to take a novel approach, studying the coupling between sequences of spikes resembling avalanches [26, 27], and local population-level average activities, LFPs, two core components of extracellular neural activities at criticality. Extracellular neural activities are either studied within the scope of unit (single/multi) activities, or local field potentials (LFP); the former, reflective of the neurons’ axonal output and the latter, representative of the neighboring average synaptic activity [28]. Recent studies have been measuring the coupling between spikes and LFPs to shed light on what role the inter-neuronal interactions
play in cognitive functions [29]. Higher frequency components of LFPs mostly represent local activity [30], while lower frequency bands reflect the integration of neural activities across larger networks of neurons [31]. It has further been shown that neuronal spike times are locked to the phase of low frequency (< 10 Hz) LFPs in different cortical areas, including the visual [30] and the prefrontal cortex [32]. This evidence sheds light on how single neuron activities are coordinated within large neural populations. Several studies have shown that spike times are linked to the phase of low-frequency components of LFPs [30, 33], providing a potential mechanism for how low-frequency activity affects sensory processing, and is mediated by cognitive functions. For instance, low-frequency neural synchrony, as well as the trial-by-trial correlation of spike times across single neurons, is suppressed with attention [34, 35]. It has further been shown in different visual areas that attention decouples spikes from the phase of low-frequency LFPs [36, 37], and hypothesized that the mechanism by which attention desynchronizes neurons [38] could be mediated by decoupling the spiking activity from low-frequency LFPs [37]. The neural mechanisms underlying the changes of this spike-phase coupling (SPC) are not yet well understood. Computational modeling of this effect may, therefore, shed light on how this coupling regulates neural processing, in particular in the context of critical dynamics.

To this end, we use our previously introduced leaky integrate-and-fire model (LIFM) [22–25] to explore whether SPC connects to criticality, indicated by neural avalanches. SPC is a proxy to capture synchrony of single neurons’ activity with accumulated electric current from all active neurons within the network. Previously, we used the temporal complexity approach as a robust indicator of criticality [22, 23]; an approach that relies on events generated in time and captures the emergence of criticality in a form of a function, called Mittag-Leffler (ML) function. Despite its robustness in detection of criticality compared to neural avalanches [25], a lack of a dynamical theory for the origin of the ML function led to the lack of a theory and a robust order parameter for the form of criticality generated by the neural model. Here, however, using SPC quantified by Phase-Locking Value (PLV), we illustrate that by increasing the coupling (connection strength, K) between neurons, a second-order transition from desynchronized firing with low SPC to a synchronized firing state with high SPC is realized; suggesting SPC to play the role of an order parameter in the model. Moreover, using the finite size scaling analysis, we evaluate the critical exponents incorporating in this transition and show that the model’s critical behavior is preserved when the system’s size increases; in good agreement with the predicted theoretical [39] as well as experimental exponents [7].

The paper is organized as follows. The neuronal model and simulation details are introduced in section II. Section III discusses the spike-LFP phase coupling and its role as the order parameter of a critical transition in the model. The scaling of neuronal avalanches are studied in section IV, and section V is devoted to the discussion and conclusion.

II. MODEL DESCRIPTION

N excitatory neurons reside on a two-dimensional square lattice with the periodic boundary condition of size \(L\), where \(N = L \times L\). We use the leaky integrate-and fire model (LIFM) [40] as used in our previous studies [22–25]

\[
x_i = -\gamma x_i(t) + S + \sigma \xi_i(t),
\]

where \(x\) is the membrane potential, \(1/\gamma\) is the membrane time constant of the neuron and \(S\) denotes the constant input current. \(\xi(t)\) is a continuous Gaussian white noise with zero mean and unit variance, defined by

\[
\langle \xi(t) \rangle = 0, \\
\langle \xi(t) \xi(t') \rangle = \delta(t-t'),
\]

The parameter \(\sigma\) is considered as the noise intensity. Starting from a random value or zero, we consider \(x = 1\) as the firing threshold for each neuron. After reaching the threshold, the neuron adds a value \(K\) to the input currents of its neighboring neurons and jumps back to a rest state with \(0 < x < 0.5\). The quantity \(K > 0\) implies that all the neurons linked to a firing neuron, makes a step forward by \(K\) which is called the cooperation strength. This parameter plays the role of the control parameter, and we later refer to it as the generator of criticality when \(K_c\), critical cooperation strength is adopted. Therefore, in our analysis, we investigate the system’s behavior while we vary coupling strength for each realization. Note that the model generates spikes simply extracted from numerical analysis.

For numerical analyses, we chose \(S = 0.001005\), \(\gamma = 0.001\), and \(\sigma = 0.0001\) and the lattices with the linear size \(L = 20, 25, 30, 35, 40\). We adopted the integration time step \(\Delta t = 0.01\), and the duration of analysis were \(10^7\) time steps. Computations were carried out using the Python programming language (Python Software Foundation. Python Language Reference, version 3.7.2. Available at https://www.python.org/).

III. SPIKE-LFP COUPLING AND CRITICALITY IN NEURONAL SYSTEMS

In order to evaluate the inter-neuronal interaction, we study SPC which is the coupling between the phase of LFP and neuronal spike timing. LFP is accumulated electric current from all active neurons within a local volume of the brain, and is measured in frequency ranges below a few hundred Hertz. To calculate LFP, we sum all
FIG. 1. (Color online) Spike-LFP coupling (a) subcritical regime, \( K = 0.0004 \), (b) critical regime, \( K = 0.0025 \). (c) supercritical regime, \( K = 0.004 \). LFP peaks coincide with silent periods of spikes.

Potential values at each time step: \( \text{LFP}(t) = \sum_{i=1}^{N} x_i(t) \), where \( x_i(t) \) is the membrane voltage of the \( i \)th neuron at the time \( t \). Figure 1 illustrates the LFP and number of spikes spikes (summed across the population of neurons) for three values of parameter \( K = 0.0004 \) (subcritical), \( K = 0.0025 \) (critical), \( K = 0.004 \) (supercritical). To this end, for each spike-LFP pair, the parameter \( M_j \) is defined as

\[
M_j = \frac{1}{n} \sum_{k=1}^{n} \exp i\phi_k^j,
\]

(3)

Where \( n \) is the number of spikes in each spike train (for every single neuron), \( (\phi_k^j) \) is the instantaneous phase of LFP corresponding to the \( k \)th spike of the \( j \)th neuron and is extracted from the Hilbert transform of the low-frequency band of LFP signal. To obtain the phase locking value (PLV) of each trial, vector \( M \) was computed for each spike train and then the mean vector was calculated across them using the following [41]

\[
\text{PLV} = \frac{1}{N} \sum_{i=1}^{N} M_i.
\]

(4)

In the case of random phase spiking, PLV goes to 0 for large spike trains (\( n \to \infty \)), and for full synchrony at which all neurons spike at the same phase of LFP, the absolute value of PLV reaches its maximum 1.

Therefore, an estimation of the strength of SPC is given by the absolute value of PLV (\( m = |\text{PLV}| \)). Indeed, \( m \) can be considered as an order parameter indicating the transition from irregular to synchronous spiking state.

FIG. 2. (Color online) (a) Dependence of absolute value of PLV (\( m \)) on the parameter \( K \) for lattices with the linear size \( L = 20, 25, 30, 35, 40 \). (b) Collapse of \( m - K \) plots for different system size as the result of rescaling.
FIG. 3. (Color online) Density plot of spike-phase coupling strength, $m$ in (a) $K$-$\sigma$ and (b) $K$-$S$ planes, for $L = 20$. The variations of the order parameter $m$, versus cooperation parameter $K$ for $L = 20, 25, 30, 35, 40$, illustrated in the top panel of Fig. 2 suggests a continuous transition from irregular to synchronous condition as $K$ increases. To verify the continuous transition and critical behavior in this system, we use the finite size scaling theory. Hence, we assume the following scaling of the dependence of the order parameter on the coupling strength (cooperation), $K$

$$m = L^{-\beta/\nu} \mathcal{M}(|K - K_c|L^{1/\nu})$$

where $K_c$ is the value of critical cooperation and $\beta$ and $\nu$ are the critical exponents corresponding to order parameter and correlation length, respectively. $\mathcal{M}(x)$ is the scaling function, for which one expects the following behavior at large system size

$$\mathcal{M}(x) \sim x^\beta \text{ as } x \to \infty.$$  

FIG. 4. (Color online) Schematic plot of calculating the neuronal avalanches.

This property gives rise to the following behavior for the order parameter in infinite system size limit, for $K > K_c$

$$m \sim (K - K_c)^\beta,$$

which is an indicator of a continuous phase transition.

The bottom panel of Fig. 2 clearly shows the data collapse of the different lattice sizes by choosing $K_c = 0.0025 \pm 0.0001$, $\beta = 0.85 \pm 0.05$ and $\nu = 1.7 \pm 0.2$.

We also investigated the effect of noise and input current on the strength of SPC. The variations of the order parameter, $m$, as a function of noise intensity $\sigma$, as well as the input current $S$, are illustrated in density plots (See Fig. 3). The figure shows that SPC is attenuated as the noise or input current are increased. Moreover, while the critical cooperation strength, $K_c$, grows linearly as the function of $\sigma$, it displays a nonlinear growth in terms of the input current.

IV. SCALING OF THE NEURONAL AVALANCHES

In our former studies [22, 23, 25], we have extensively analyzed the emergence of criticality in the LIFM model described above using temporal complexity and avalanche analysis. In this section, we complement our former analyses to prove the existence of criticality using finite-size scaling theory. We are interested to find the special $K_c$ or a narrow region at which the system displays the critical behavior. As documented previously, the emergence of criticality is indicated by the existence of PL exponent of avalanche size, lifetime distributions are limited to a specific range [2], and the shape collapse as suggested by Friedman and colleagues, in cultured slices of cortical tissue [7]. The widely varying profile of
neural avalanche distribution in size is described by a single universal scaling exponent, $\tau$ in size, $p(S) \sim S^{-\tau}$, and a single universal exponent in duration, $\alpha$, $p(T) \sim T^{-\alpha}$, where $S$ and $T$ denote the size, and the duration of avalanches, respectively.

According to the single scaling theory, the avalanche data collapse onto universal scaling functions near a critical point as follows [42]:

$$
p(S) = L^{-\mu \tau} S(L^{-\mu}) \langle S \rangle(T),
\quad p(T) = L^{-\mu \alpha} T(L^{-\mu}) \langle T \rangle(S),
\quad \langle S \rangle(T) = L^\mu F(TL^{-\mu}),$$

(8)

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 [42]. $\tau$ and $\alpha$, are the scaling exponents of the probability density functions of size and duration of the avalanches, respectively. $\mu$ denotes the scaling exponent of the size of avalanches versus the linear size of the lattice and $z$ is the dynamical exponent which determines the scaling relations of the duration and size of the avalanches.

$\langle S \rangle$, $\langle T \rangle$, and $F$ are the universal functions whose behavior at small $x$ limit (large $L$) are as the following

$$\lim_{x \to 0} \langle S \rangle \sim x^{-\tau},
\lim_{x \to 0} \langle T \rangle \sim x^{-\alpha},
\lim_{x \to 0} F \sim x^{1/z},$$

(9)

and at large $x$ limit (small $L$) each function tends to a constant value. In this way at the infinite lattice size, one finds

$$p(S) \sim S^{-\tau},
\quad p(T) \sim T^{-\alpha},
\quad \langle S \rangle(T) \sim T^{1/z},$$

(10)

The scaling theory requires the following relation between the exponents [7]

$$\frac{\alpha - 1}{\tau - 1} = \frac{1}{z}.$$ 

(11)

The mean field prediction for the scaling exponents are $\tau = 3/2$, $\alpha = 2.0$, and $1/z = 2.0$ [42].

To determine the neuronal avalanches, we count the number of spikes in successive time steps until a silent period of equal or more than 5 time steps ($\delta t = 5$). Avalanche duration is considered to be the interval of neuronal activity between any two silent periods and the number of firing during this activity indicates the avalanche size (see Fig. 4). In our simulation, we find that the neuronal avalanches show good scaling behavior at $K_c = 0.0025$. Fig. 5 illustrate s the logarithmic plots of the probability density functions of avalanche size and duration, and also the dependence of the average avalanche size versus the duration at $K = 0.0025$ for the lattices with the linear size of $L = 20, 25, 30, 35, 40$. The data shown in this figure are rescaled base on the relations (8) to properly collapse to a single plot. Fig. 6
represent such a data collapse which is achieved by $\mu = 2.0 \pm 0.1$, $\tau = 1.6 \pm 0.1$, $\alpha = 1.8 \pm 0.1$ and $1/z = 1.4 \pm 0.05$ and $K_c = 0.0025 \pm 0.0001$. It can be seen that the scaling relation (11) is satisfied within the simulation precision. The value of $\mu = 2.0$ indicates that the size of the avalanches grows proportionally with the lattice size.

Our estimation for the critical exponents $\tau$, $\alpha$ and $1/z$ are in fair agreement with the values reported in the pioneering theoretical study of avalanches in a IFM [39] and experimental values in the cortical slices of the brain in [7].

To close this section, we calculate the power spectra of avalanche size and avalanche duration time series generated according to the explanation above and shown in Fig. 4. The results in logarithmic scale are sketched in Fig. 7, indicating the $1/f$ scaling of these time series. From these results, one concludes that there might be a close connection between EEG and LFP data and the neuronal avalanche, as the same $1/f$ behavior is observed in LFP and EEG recordings.

V. DISCUSSION

Neural avalanches are the hallmark of critical neural dynamics in cortex, extensively studied both in vivo and in vitro. However, it is not yet clear how local cortical networks converge on criticality giving rise to many
functional advantages such as efficient information processing or broadly speaking a healthy brain, and how they deviate from criticality leading to abnormalities in brain; whether its operation is signaled by random or high synchronicity. Hence, in this research, we set out to address this question with exploring the transitional behavior of LIF neurons residing on a regular lattice of different sizes. We based our analysis on exploring the inter-neuronal correlations, the coupling of spikes to the LFP phase. While the coupling of spikes to the LFP phase has been widely documented to play a critical role in encoding the spatial location in the mammalian hippocampus, it has only recently been proposed that this coupling may play a role in sensory areas to encode sensory information. While the preferred phase of LFP where spikes tend to occur is the encoding feature in the above studies, it has remained unknown how the strength of this coupling may contribute to the neural processing. However, our main focus was to study this mechanism at criticality and investigate if that mechanism enhances our understanding of the cortical dynamics. Therefore, we explored how spike-LFP phase coupling (SPC) depends on different parameters of our neural network. Our results suggest that the strength of SPC is: 1) positively correlated with the strength of inter-neuronal connectivity, 2) negatively correlated with the level of input noise to single cells, 3) negatively correlated with the magnitude of the input current.

SPC has been used as a proxy to capture the temporal synchrony between neighboring neurons, as well as different compartments of the neural circuitry. However, the exact link between this coupling and the inter-neuronal connectivity has not been revealed. Our evidence indicates a tight association between the strength of the inter-neuronal coupling and SPC strength: starting to climb to its maximum level at criticality. This suggests that SPC at criticality could be used to indirectly target the anatomical connectivity of neighboring neurons/neural subnetworks, helping to attribute variants of cognitive functions to more fine-grained dynamics in the topology of neural networks. As an instance, the architectural dynamics of neural networks under different conditions of selective attention is not yet fully known, although previous studies have documented an attentional suppression of SPC (in low-frequency bands). Our results here, support the hypothesis that attention may involve dynamic modifications of the neural networks’ structural topology. This not only opens a window towards understanding the link between high-level cognitive functions and structural properties of neural networks near criticality, but also supports the notion that structural properties may mediate different levels of information capacity.

The impact of input noise to individual neurons on neural information processing has been a recent controversial question. The role of correlated noise in information processing has been the focus of numerous recent studies, however how uncorrelated noise may influence neural network information processing capacity is not yet fully clear. Our modeling study indicates that the noise input to individual neurons suppresses SPC. The noise we fed to neurons here, was independently assigned for different neurons, leading to an uncorrelated noise across the membrane potential of cells. These suggest a suppressive effect of uncorrelated noise on SPC. Given the negative correlation of SPC strength with information content (especially in the context of selective attention), our results importantly suggest a role of uncorrelated noise in modulating information capacity within neural networks. Whether the noise influence on SPC, mediates a change in inter-neuronal connectivity structure or not, remains a question for future studies.

Our results further document that the overall input to a neural population could have a suppressive effect on SPC. This is consistent with the previous report that input from upstream cortical areas synchronizes the target neural population; which is further in line with previous studies indicative of a negative correlation between information capacity and the coupling of local neural activities (reflected by spike rate/gamma frequencies) to low-frequency LFPs. Our approach could contribute to understanding the resultant effects of the attentional stabilization of this shared input, in sensory neural networks.

In summary, we studied a linear leaky integrate and fire model on a square lattice. We found that the coupling of spike timing and the phase of local field potential, quantified by PLV, acts as an order parameter in our model. We showed that the increase in inter-neuronal cooperation parameter K, gives rise to a continuous phase transition from random phase irregular spiking (subcritical) to a synchronous spiking (supercritical), coupled tightly to the LFP. This finding is in line with the hypothesis that the strength of SPC might be a control parameter that is used to harness the information processing capacity of the neural system frequently manifested in the form of neural avalanches in many empirical studies. Using the finite size scaling analysis, we estimated the critical exponents corresponding to this transition. We also observed that at this critical point, the neuronal avalanches show power-law behavior with the scaling exponents close to the theoretical and experimental values. Moreover, the $1/f$ scaling in the power spectra of the avalanche time series indicate the connection between the neuronal avalanches and LFP and EEG data. This work suggests that the criticality observed in the neuronal systems is actually the critical point of a synchronization transition.

VI. ACKNOWLEDGMENT

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