

Sensitive Stochastic Oscillation in Self-Organized Critical States of Small Neural Systems

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Abstract—Self-organized critical states and stochastic oscillations are simultaneously observed in neural systems. Here we show that stochastic oscillations can emerge in self-organized criticality of small size neuronal networks. As a result, the oscillation is very sensitive to weak external input and displays phase sensitivity. Our results suggest that finite-size, columnar neural circuits may play an important role in generating neural oscillations around the critical states, potentially enabling functional advantages of both self-organized criticality and oscillations for sensitive response to transient stimuli.

1. Introduction

Oscillation in brain activity has been observed for more than 80 years [1]. Several different oscillation bands exist and appear in different states of the brain [1]. In the spectrum of these oscillations, broad noise background always accompanies with the peaked frequency of the oscillation. Therefore these oscillations are stochastic oscillations. Oscillations characterized by repetition of activities with typical scales are believed to be essential to brain functions, especially to provide timing, predictability, coherence and integration in neural information processing [2]. However, the neurobiological and dynamical mechanisms of oscillations may be different and most of them are not well understood [1], and are topics of active research. The synchronization between inhibitory neurons has been found crucial for fast rhythms, such as gamma oscillations (30-70Hz)[3, 4]. Neural field models [5] based on population firing rate indicated that resonance between thalamus-cortex can generate alpha oscillations (8-13Hz). Despite many modelling studies, a commonly accepted mechanism of alpha rhythm is still lacking [?]. This slow oscillation is particularly obvious during the resting states without systematic external stimuli (i.e., eye closed).

Recently, self-organized criticality is observed in the resting states of cat and monkey's cortex networks in experiments [6, 7, 8, 9, 10]. It was shown that the critical-

ity plays an important role in the development of neural systems [11, 12, 13]. The self-organized criticality in neural networks are also studied intensively in computational models [10, 14, 15, 16, 17]. It has been shown that critical states have functional advantages for both the sensory system [18] and memory [19].

Experiments on self-organized criticality of neural activity actually also showed pronounced oscillations of local field potentials (LFPs) [6, ?, 20]. The coexistence of self-organized criticality and oscillation has been explicitly analyzed in the maturation of cortex [21]. Modelling studies found that they can indeed coexist in biologically plausible neuronal networks [22, 23]. In hierarchical modular networks, when neurons in modules are densely connected and modules are coupled sparsely, modules can exhibit both self-organized criticality and stochastic oscillation [22].

A natural property of criticality is the sensitivity to weak perturbation. This property of criticality raises a question that if the oscillation in resting state has sensitivity to perturbation. In the present work, we use numerical simulation to demonstrate the sensitivity of stochastic oscillation in self-organized criticality.

2. Model

The neural network model consists of both excitatory and inhibitory neurons. E-I balance has been demonstrated experimentally [24, 25]. Large and sparsely connected balanced model was proposed to explain irregular [26] and self-sustained neural activity [27], but local circuits are more densely coupled. To mimic the modules of local cortical networks, we analyze an isolated, small and dense random network (connectivity $p = 0.16$, 80% of excitatory neurons). In the model only weak background input is added to the network in order to simulate the resting states. The dynamics of neurons reads [27]

$$\tau \frac{dV}{dt} = (V_{rest} - V) + g_{ex}(E_{ex} - V) + g_{inh}(E_{inh} - V). \quad (1)$$

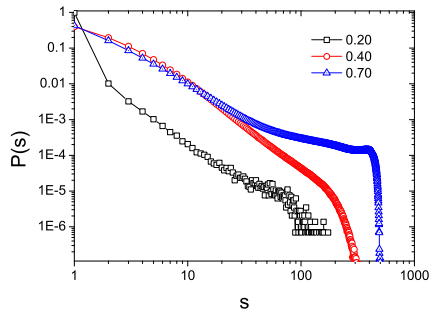


Figure 1: Distribution of avalanche size $P(s)$ for critical (circles), subcritical (squares) and supercritical (triangles) regimes. The network size is $N=500$. The inhibitory coupling strength is $\Delta g_{inh}=4.0$. The excitatory coupling strengths for subcritical, critical and supercritical states are $\Delta g_{ex}=0.2, 0.4$ and 0.7 , respectively.

When the membrane potential V crosses a threshold (-50 mV), the neuron fires a spike. Then V is reset to the rest value of the membrane potential, $V_{rest}=-60$ mV. After the spike the membrane potential is fixed for a refractory period which is 5 ms in the model. The spike of excitatory (or inhibitory) neuron increases the synaptic conductance of postsynaptic targets by Δg_{ex} (or Δg_{inh}). The synaptic conductance decay exponentially and follows the equations

$$\tau_{ex} \frac{dg_{ex}}{dt} = -g_{ex}, \quad (2)$$

$$\tau_{inh} \frac{dg_{inh}}{dt} = -g_{inh}. \quad (3)$$

The time constant are τ_{ex} or τ_{inh} , respectively. The biological values of the parameters [27] are used in the model. The membrane potential time constant is $\tau=20$ ms. The reverse potentials for excitatory and inhibitory gates are $E_{ex}=0$ mV, $E_{inh}=-80$ mV, respectively. The decay time constants of excitatory and inhibitory conductance are $\tau_{ex}=5$ ms and $\tau_{inh}=10$ ms. Each neuron receives an independent external excitatory Poisson spike train with rate η . Here we study the network under weak stimuli.

3. results

In simulations we obtained the coexistence of self-organized criticality and stochastic oscillation (Figs. 1 and 2). The avalanche is defined as a period of activity that is initiated by an external input and terminates when no further neuron fires spikes. The size of avalanche is measured by the number of spiking neurons during an avalanche. In Fig. 1 the distribution of avalanche size is presented. At the balance region between excitatory and inhibitory couplings, the avalanche size is distributed by power-law (circles in Fig. 1). When the excitatory coupling is weak, subcritical states are obtained, the distribution of avalanche

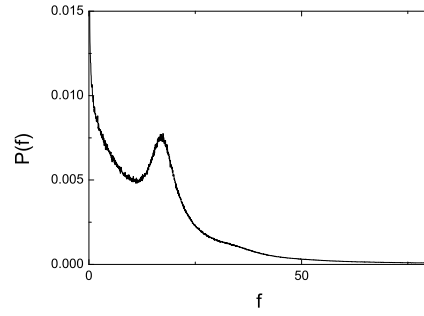


Figure 2: The power spectrum density of mean membrane potential $\langle V \rangle$ in the critical regime for network size $N=500$. The coupling strengths are $\Delta g_{inh}=4.0$ and $\Delta g_{ex}=0.4$.

size changes into exponential function. When the excitatory coupling is strong, supercritical states occur, and the probability of large avalanches is higher. The subcritical and supercritical distributions were also plotted (squares and triangles in Fig. 1).

We use the time series of the mean membrane potential of all neurons in the network to represent the temporal behavior. The power spectrum of the mean membrane potential is computed. When the network is at the critical state, a pronounced peak is shown at low frequency on the power spectrum of $\langle V \rangle$ (Fig. 2). It is consistent with the characteristics of alpha EEG of resting human brain [1], where a peak is overlapped on a noisy background.

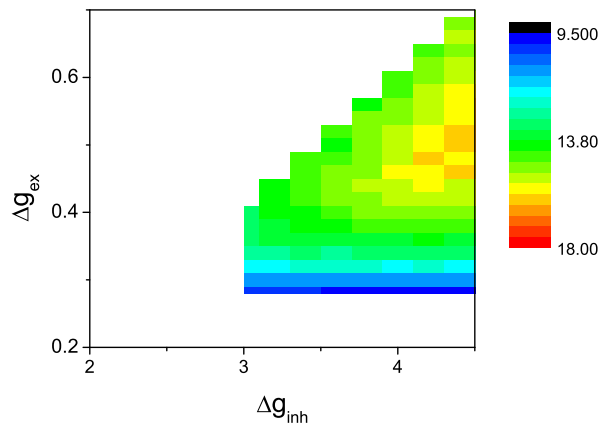


Figure 3: (Color online) The parameter region where oscillations can exhibit a single peak in the power spectrum. Color represents the peak frequency. The parameters are $\Delta g_{ex}=0.4$, $\Delta g_{inh} = 4.0$ and $N = 500$.

The co-organization of self-organized criticality and stochastic oscillation occurs in a broad region of the parameters $(\Delta g_{ex}, \Delta g_{inh})$ (Fig. 3). The critical region broadly overlaps with the region of oscillation with only one pro-

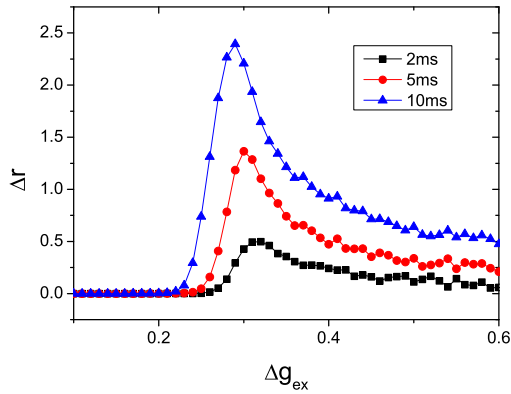


Figure 4: (Color online) (a) The stimulus-increased firing rate Δr versus Δg_{ex} . The stimuli last for 2 ms, 5 ms, and 10 ms. The firing rate is computed in 50 ms after the stimulation. Here $\Delta g_{inh} = 4.0$ and $N = 500$.

nounced peak at the main frequency (Fig. 3). In the subcritical states, there is no peak on the power spectrum, while in the supercritical states, multiple peaks appear. Previously, neural oscillations were explained by the synchronization between inhibitory neurons [4] or the alternating activation between excitatory and inhibitory populations (E-I loop) [28]. Here oscillations can emerge due to the accumulation-release process in small systems at self-organized critical states, where the quick release activates the E-I loop. The E-I loop becomes dominant in the supercritical states without a pronounced accumulation interval.

The co-organization of self-organized criticality and stochastic oscillation enables the system to display responsiveness of both self-organized criticality and oscillations in the presence of weak transient stimuli. Critical states can respond sensitively as shown in Fig. 4, where a transient stimuli of different duration with $\eta_1 = 50$ Hz are added on the background external driving ($\eta = 20$ Hz). With the background stimuli, the average firing rate of neurons is $r = 4.5$ Hz. The firing rate increases clearly at the critical region, similar to critical state in network of excitatory elements [18]. Meanwhile, due to oscillation, the response of critical states can display “phase sensitivity” (Fig. 5): the response depends on the mean membrane potential $\langle V \rangle$ at the onset of the stimuli. Dependence of the stimulus-driven activation on the phases of ongoing brain waves has been observed in cognitive experiments [29].

4. Conclusion

We simulated self-organized critical states of densely connected small networks. At the critical states, the network exhibits stochastic oscillation under a weak input. The stochastic oscillation has the responsiveness of both critical states and oscillation. We showed that the stochastic oscillation of critical states is sensitive to transient exter-

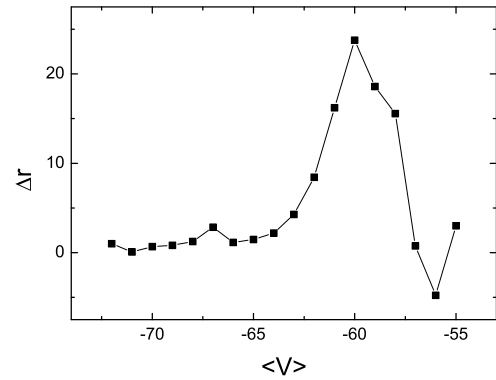


Figure 5: (Color online) Phase-sensitive response of critical oscillations to weak transient stimuli. The response of critical states versus the mean membrane potential at the timing of adding stimuli (lasting for 1 ms). Here $\Delta g_{inh} = 4.0$ and $N = 500$.

nal stimuli. Meanwhile the response depends on the phase of the oscillation at the onset of the stimuli. All these properties could be useful for efficient neural information processing.

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