# Modular Organization Enables Both Self-Organized Criticality and Oscillations in Neural Systems

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**Abstract** Neural networks in the brain display prominent hierarchical modular organization and complicated rhythmical oscillations. We systematically study the phenomenon of sustained activity in hierarchical modular networks, which are obtained by rewiring initially random networks. We find that a hierarchical modular architecture can generate sustained activity better than random networks. More importantly, the system can simultaneously support rhythmical oscillations and self-organized criticality, which are not present in the respective random networks. These results imply that the hierarchical modular architecture of cortical networks plays an important role in shaping the ongoing spontaneous activity, allowing the system to take the advantages of both the sensitivity of critical state and predictability and timing of oscillations for efficient information processing.

## 1 Introduction

Understanding the large-scale organization of the structure and dynamics in the brain from the viewpoint of complex networks has become a new frontier in neuroscience [1, 2], because the architecture of networks in brain always impacts neural system's dynamical behaviors and the dynamics underlie the mechanisms of the brain's functions.

One of the most prominent structural features in the neural system of the brain is the organization of modules, structured hierarchically from large-scale regions

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of the whole brain, via cortical areas and area subcompartments organized as structural and functional maps, to cortical columns, and finally circuits made up of individual neurons [3]. Meanwhile, the networks display self-organized sustained activity, which is persistent in the absence of external stimuli. At the systems level, such activity is characterized by complex rhythmical oscillations over a broadband background, such as α, θ, and δ oscillations [4]. While at the cellular level, neuronal discharges have been observed to display avalanches, indicating that cortical networks are at the state of self-organized criticality (SOC) [5]. Self-organized criticality is a concept proposed in physics that mimics the avalanche of sandpiles, and is an ubiquitous property of complex systems, such as piling of granular media, earthquakes, and forest fire, etc. [6–8]. The concept asserts that a system self-organized into a critical state is characterized by scale invariance. At such a critical state, signals and perturbations can efficiently propagate over broad spatio-temporal scales. Critical behavior in neural models has been shown to bring about optimal computational capabilities, optimal transmission, storage of information and sensitivity to sensory stimuli [9]. And SOC has been suggested playing an important role in human perceptual functions [10].

SOC is characterized by power-law distribution of the size of avalanches, indicating that there is no characteristic scale. On the contrary, rhythmic oscillations suggest that neural activity possesses typical scales and is predictable to certain extent. How these two apparently contradictory dynamical properties are unified in the neural dynamics is a question that has not been addressed in the studies of neurodynamics. In this work, we use numerical simulations to show that the modular network organization provides such a template to unify them.

Within the modules, the activity of the neural firing is characterized by SOC, while the weak interaction between the modules makes it possible that the avalanches of some modules can act as the weak input to other modules, leading to sustained activity without external stimulus.

## 2 Method/Models

We carried out intensive numerical simulations of a balanced neural network model [11]: there are 80% excitatory neurons and 20% inhibitory neurons. The dynamics of the membrane potential is described as

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

The value of the time constant is $\tau$=20 ms, the resting membrane potential is $V_{rest} = -60$ mV, reversal potentials of synapses for excitatory and inhibitory neurons are $E_{ex} = 0$ mV and $E_{inh} = -80$ mV. When an excitatory (or inhibitory) neuron fires, the synaptic variables $g_{ex}$ (or$g_{inh}$) of its postsynaptic targets are increased by $\Delta g_{ex}$ (or $\Delta g_{inh}$). Otherwise, synaptic variables decay exponentially with the time constants $\tau_{ex} = 5$ ms and $\tau_{inh} = 10$ ms.

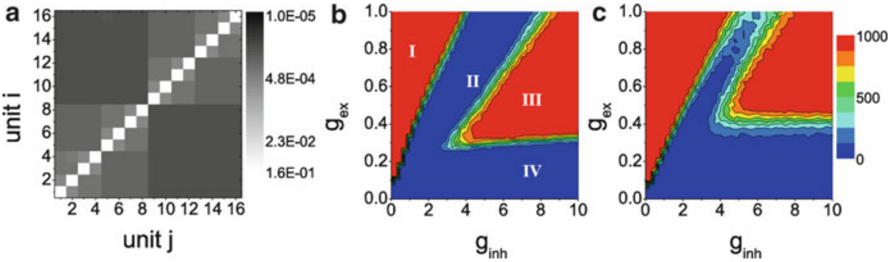


**Fig. 1** (**a**) Connection density matrix of a 4-level HMN. Network size is N = 10,000, $R_{ex} = 0.99$. (**b**, **c**) Average duration of network activity in the parameter space ($\Delta g_{inh}$, $\Delta g_{ex}$). The results are averaged over 100 realizations of (**b**) random networks and (**c**) 4-level HMNs with $R_{ex} = 0.99$, respectively

The strengths of excitatory and inhibitory neurons are such that in a broad range, the average input current of a neuron from the excitatory pool is roughly canceled by that of the inhibitory pool; however, the fluctuations can be so large to exceed the firing threshold in sparse random networks with large enough number of neurons (10,000 neurons in our simulations). This will lead to sustained irregular activity in such a balanced random network of neurons. In our study, we introduced modular structure into the network connectivity. Beginning with random networks, the neurons are divided into groups and the connections between groups are moved into groups with a probability $R$. Then connections are denser within the group but much sparser between the groups, while maintaining the total connections the same as the original random networks. We can further divide the modules into sub-modules to obtain a hierarchical modular network (HMN). See Fig. 1 for an example of a 4-level HMN with 16 modules, each having N/16 = 625 neurons. Considering the fact that inhibitory couplings form local connections and excitatory couplings provide long-distance interactions, we rewire inhibitory inter-module connections with the probability $R_{ex} = 1$, and rewire excitatory inter-module connections with $0 < R_{ex} < 1$.

## 3 Results

In random networks, balance between excitation and inhibition exists in a region of the parameter space of the strength of the excitatory and inhibitory synapses ($\Delta g_{inh}$, $\Delta g_{ex}$), which allows the neural network to sustain irregular activity without external signals. In simulations, the networks were stimulated by noise in an initial period of time. Figure 1b and c show how long the activity sustained after noise is removed. The region III of the Fig. 1b represents the irregular sustained activity in random networks [12]. When the rewiring probability $R_{ex} = 0.99$, although modules are dense and small, the irregular sustained region is maintained in HMNs, as shown in Fig. 1c.

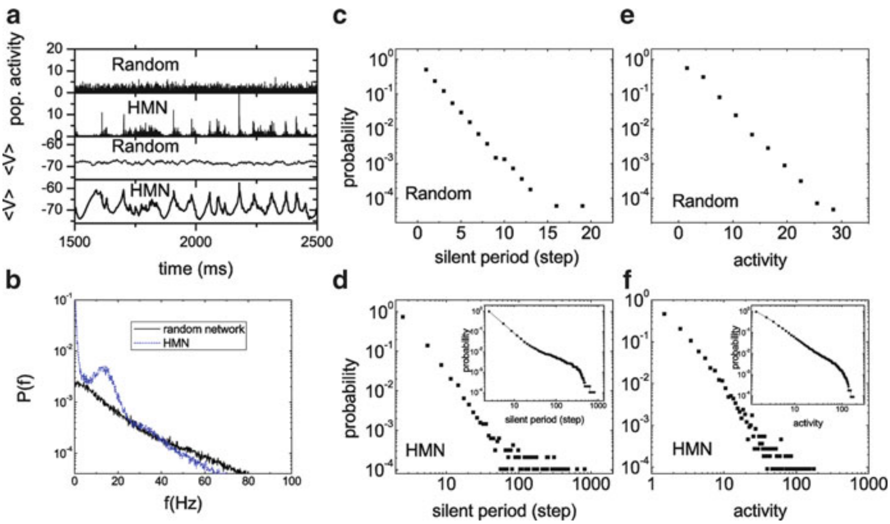


**Fig. 2** (**a**) Population activity of an ensemble of neurons in a random network and of a module in the HMN rewired from the random network (*upper panels*), and corresponding average membrane potentials (*lower panels*). (**b**) Power spectrum density of average potentials in random networks (*black*) and HMNs (*blue*). (**c**) and (**d**) Distributions of the silent period in an ensemble of neurons in random networks and in a module of HMNs. (**e**) and (**f**) Distribution of the activity size in networks corresponding to (**c**) and (**d**). The insets in (**d**) and (**f**) show the cumulative distributions of silent period and activity size in modules of HMNs

However, different from quite homogeneous random activity in random networks, the activity patterns in modular networks is very heterogeneous. In Fig. 2a, we compare the activity of one module in a 4-level HMN obtained at $R_{ex} = 0.99$ and the activity of the corresponding ensemble of neurons in the random network before rewiring. The HMN displays intermittence with bursts of relatively strong activity separated by distinct silent periods, while the activity in the random network continues at a lower level, but without discernible silent intervals.

The intermittent activity of modules in the HMN exhibits the characteristics of avalanche dynamics. We analyzed the distribution of the size of each activity of a module and the lengths of the silent interval between two activities. In Fig. 2c and e, distributions of both the silent interval and the activity size in random networks are straight lines when plotted in log-linear form, showing that the distributions follow exponential functions. On the contrary, the distributions of modules in HMNs display straight lines in the log-log plot (Fig. 2d, f). Therefore in the HMN both the silent interval and the activity size are distributed according to the power-law functions.

Power-law distribution of avalanche size is the fingerprint of the self-organized criticality [9]. These results show that HMNs are close to critical states, while the random networks are not. The observation of critical states is consistent with experimental data which showed a power-law distribution of the neuronal avalanche size [5] or the intervals between large energy fluctuations [13].

Another significant effect of the intermittent dynamics in HMNs is the emergence of low frequency activity. In Fig. 2a one can see the fluctuation of the average potential of modules in HMNs is more significant than that of random networks and exhibits the characteristics of rhythmic oscillations. We perform an analysis by calculating the power spectrum density of the average potential of networks. Figure 2b shows that in random networks the power decays monotonically as the frequency increases. In the HMNs with $R_{ex} = 0.99$, a pronounced peak appears at low frequency around 15 Hz.

## 4 Conclusion/Discussions

We studied the effect of hierarchical modular structure on the dynamics of the sustained activity of neural networks with both excitatory and inhibitory neurons. The modular property can support the irregular sustained activity. More importantly, we found that the coexistence of SOC and oscillations could be realized in modular neural networks. Our results provide a new mechanism of sustaining activity and generating oscillations in cortex-like neural network that captures the most prominent structural features: the hierarchical modular organization and the coexistence of excitatory and inhibitory neurons.

Our further analysis shows that cutting SOC off at finite size due the limited number of neurons within the module could be one of the reasons that leads to the oscillations of the network collective activity. Currently we are exploring the implications of the combination of SOC and oscillations in information processing, which should shed light on the structure-function relationship in the brain. Further studies on the role and advantages of HMNs in information processing are interesting, and are potentially useful for understanding neural activities underlying perceptual functions.

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