

Effects of different connectivity patterns in a model of cortical circuits

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Abstract. Cortical circuits are usually modeled as a network of excitatory and inhibitory neurons with a completely regular or a random connectivity pattern. However, neuroanatomy of the macaque and the cat cortex shows that cortical neurons are organized into densely linked groups that are sparsely and reciprocally interconnected. Interesting properties arise in the average activity of an ensemble of cortical neurons when the topology of the network itself is an intrinsic parameter of the model that can vary with a given set of rules. In this work we show that both the temporal activity and the encoded rhythms in an ensemble of cortical neurons depend on the topology of the network.

1 Introduction

Graph theory [1] provides the most adequate theoretical framework in order to characterize the anatomical connectivity of a biological neural network. The representation of neural networks as graphs allows a complete structural description of the network and the comparison with different known connection patterns. The application of graph theory to modeling neural networks appears in theoretical neuroanatomy for the analysis of the functional connectivity in the cerebral cortex. In [2] it is shown that the connection matrices based on neuroanatomical data that describes the macaque visual cortex and the cat cortex, present structural characteristics that coincide best with graphs whose units are organized in densely linked groups that were sparsely but reciprocally interconnected. These kind of networks also provide the best support for the dynamics and high complexity measures that characterize functional connectivity.

There are some well known biological neural networks [3,4] that present a clear clustering in their neurons but have small distances between each pair of neurons. These kind of highly clustered, highly interconnected sparse networks are known as Small-World (SW) networks. SW topologies appear in many real life networks [6,7], as a result of natural evolution [4] or a learning process [8]. In [5] it is shown that on SW networks coherent oscillations and temporal coding can coexist in synergy in a fast time scale on a set of coupled neurons.

Cortical circuits are usually modeled as a network of excitatory and inhibitory neurons [9] with a completely regular or a random connectivity pattern [10,11].

However, as shown in [13], the connection substrate can have a major effect on the dynamical behavior of the elements in a network, even when these elements are highly synchronized. This means that it is necessary to consider the topology of the network as an additional parameter that can be modified. In this paper we study the different behavior of the average activity in a model of cortical circuits as a function of the network topology.

2 Network Models

We explore three topological models: a regular grid, a random network and a SW network.

In [15] a method to study the dynamic behavior of networks when a network is shifted from a regular, ordered network to a random one is proposed. The method is based on the random rewiring with a fixed probability p for every edge in the graph. We obtain the original regular graph for $p = 0$, and a random graph for $p = 1$. This method shows that the characteristic path length L (the average distance, measured as the minimal path length between them, between nodes) decreases with the increasing value of p much more rapidly than the clustering coefficient C (the average number of neighbors of each node that are neighbors between them) does. There is a range of values of p where paths are short but the graph is highly clustered, this range of values of p is known as the small-world area.

In this paper we take the architecture of the regular model as a directed and weighted grid where nodes connect to the two closest neighbors that are in each of the four possible directions in the grid. We take $p = 0.06$ for the generation of the SW network as this probability ensures the maximum distance between the value of C and L when the original substrate is a regular grid [14]. For the random model we have followed the same rewiring procedure with $p = 1$. In Fig. 1 we show the connectivity pattern of the cells in the regular, SW and random networks.

The values of L and C for the three models of graphs can be seen in Table 1. Random graphs present a low L and C while the regular grid present a high L and a high C . The SW model have L values similar to the values of random networks, but C values closer to those of regular networks.

	L	C
REGULAR GRID	13.005	0.214
SW	5.498	0.180
RANDOM	4.021	0.002

Table 1. Values of L and C for different graphs models. In the three models the number of nodes is 2500 and the average number of neighbors per node is 8.

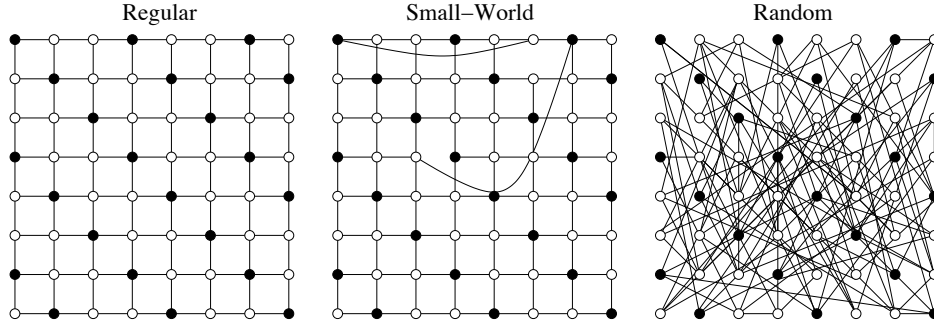


Fig. 1. Regular, SW, and random networks. Empty circles represent excitatory neurons. Filled circles represent inhibitory neurons. The three networks are composed of 64 nodes and each node is connected in average to 4 neighbors.

As shown in [15] synchronization in a network of automaton is favored by low values of L due to the efficiency in the transmission of information when short paths are present in the network. On the other hand, high values of C tend to favor local effects. This makes us expect that in the SW model, encoded rhythms that come both from global synchronization and local effects [18] can coexist .

3 Neuron Model

In this work we will consider a network of simple integrate and fire (IF) neurons. This model of neuron is often utilized in simulation studies. Simple IF neurons have been shown to provide good approximations to the dynamics of more complex model neurons [12]. We consider a network of N neurons, $N^1 = 0.75N$ of them excitatory and $N^2 = 0.25N$ of them inhibitory. We name the population of excitatory neurons as population 1 and the population of inhibitory neurons as population 2. Each neuron is connected in average to 8 neurons; this value ensures the sparsity of the network. Each neuron also receives an input from excitatory neurons outside of the network.

The connection between the i -th presynaptic neuron of population k and the j -th postsynaptic neuron of the l population will be denoted W_{ij}^{kl} where $k, l = 1, 2$. The connections provient from neurons of the first population (excitatory) W_{ij}^{1l} , are positive meanwhile the connections provient from neurons of the second population W_{ij}^{2l} are negative (see fig 2).

The state of each neuron is a binary variable σ . Each neuron can present two different states, 0 meaning a quiescent state or refractory state and 1 representing a fire state. The state of neuron j of population l at time $t + 1$ comes determined by the following update rule.

$$\sigma_j^l(t + 1) = \Theta(u_j^l(t)) \quad (1)$$

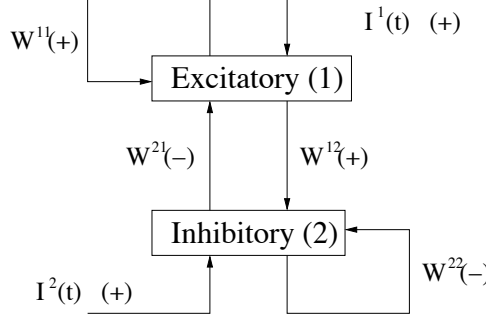


Fig. 2. Scheme of the network, the sign of each connection is noted between parentheses.

Where Θ is the usual Heaviside function

$$\Theta(x) = \begin{cases} 0 & \text{if } x \leq 0 \\ 1 & \text{otherwise} \end{cases} \quad (2)$$

The total synaptic input to neuron j of population l at time t , $u_j^l(t)$ comes determined by the following expression:

$$u_j^l(t) = \left(\sum_{k=1}^2 \sum_{i=1}^{N^k} W_{ij}^{kl} \sigma_i^k(t) \right) + I_j^l(t) + \theta^l \quad (3)$$

Where $I(t)$ represents the external input and θ represents a bias. The state of each neuron is calculated synchronously at fixed time intervals τ^l for each population l . In this work we assume $\tau^1 = \tau^2 = 1$. Each time the neuron fires (i.e., $\sigma_j^l(t) = 1$) the neuron enters in a refractory state r^l . During the refractory state the neuron can't fire and its status σ is assumed as 0. In this work we will use $r^1 = 3$ and $r^2 = 11$ for excitatory and inhibitory neurons respectively, these values correspond with anatomical estimates for neocortex.

This model presents a large parameter space, we choose $W_{ij}^{11} = 1$, $W_{ij}^{12} = 1$, $W_{ij}^{21} = -2$ and $W_{ij}^{22} = -1.8$. The bias will be taken as $\theta^1 = -1$ $\theta^2 = -0.7$.

The expression for the external input is:

$$I_i^k(t) = \begin{cases} 2.26E^k & \text{if } i \in S \text{ and } t < 100 \\ 0.56E^k & \text{otherwise} \end{cases} \quad (4)$$

where S is a set of 400 neurons (300 excitatory and 100 inhibitory) and $E^1 = 1$ and $E^2 = 0.8$; i.e., there is an initial overexcitation of a subset of the network. These values are selected as they correspond to the numerical values presented in [10] and [11].

4 Experimental results

In order to detect the oscillatory activity of the network, we study for each population of neurons, both the activity of the network at time t , $a^k(t) = \left(\sum_{i=1}^{N^k} \sigma_i^k(t) \right) / N$ where N is the total number of cells in the network and the modulus of the Fourier transform of the activity $|\hat{a}^k|^{1/2}(f)$ $k = 1, 2$, where f represents the frequency.

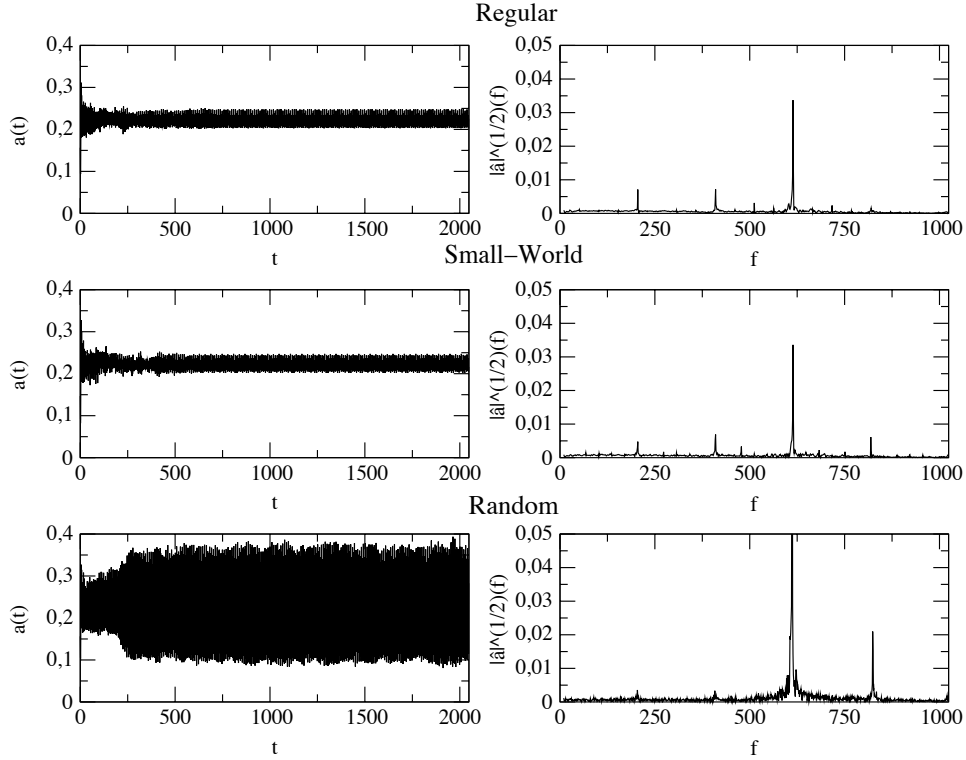


Fig. 3. Temporal activity (left) and power spectrum (right) of the set of excitatory neurons for the regular (top), SW (middle) and random (bottom) models

In figure 3 the network activity of the set of excitatory neurons and its Fourier transform are plotted. In the three models the temporal average activity of the network $\sum_{t=1}^T a^i(t)/T$ has the same value 0.22, where T is the simulation time limit; this average value coincides with the one obtained in [10]. However, the standard deviation of the average activity varies sensibly in the case of the random network. Regular and Small-World network present an standard deviation of 0.01 indicating a low level of overall synchronization meanwhile in the random model the standard deviation is 0.09.

The temporal average activity in the random model present a value of .1, indicating a higher synchronization in the network. This can be clearly seen when we consider the Fourier transform of the average activity. The random network has the strongest components of the Fourier transform values in the high frequency area, loosing the low frequency components. The regular network, on the other side, has the strongest components of the Fourier transform only in the low frequency area. The SW model has frequency components both in the high and low frequencies area. This behavior is due to the fact that the low frequency oscillations come from both local interactions between neurons [18] and the frequency associated to the refractory time of the inhibitory neurons, while high frequency components are favored by the overall synchronization of the excitatory neurons in the network. The SW network allows both local and global interaction. The highest component in frequency for the three models corresponds to a frequency over $612Hz$ that best corresponds to the firing period of the excitatory neurons, which is closely related to their refractory time.

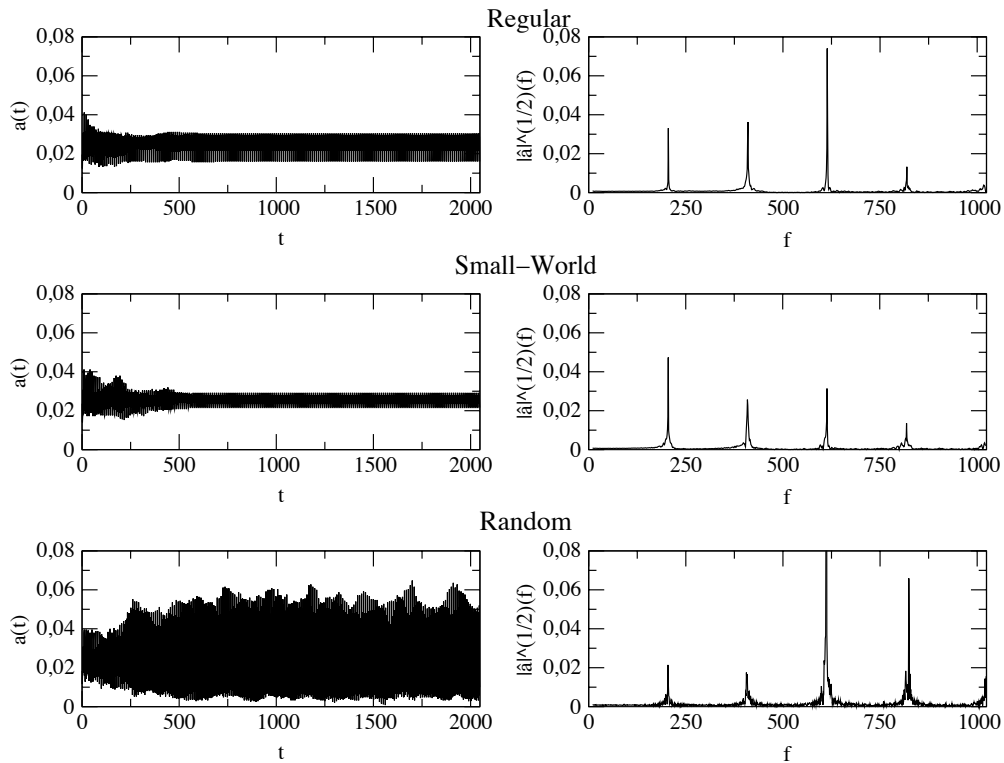


Fig. 4. Average activity (left) and power spectrum (right) of the set of inhibitory neurons for the regular (top) , SW (middle) and random (bottom) models

In figure 4 the activity of the set of inhibitory neurons and its Fourier transform is plotted. The three models present again the same overall average activity 0.02 for inhibitory neurons, and the highest standard deviation 0.02 corresponds to the random model being very close to 0 in the case of the regular and random networks.

In the case of inhibitory neurons, both high and low frequencies are present in the three topological models. In the random model the larger components of the Fourier transform correspond again to high frequencies, with the maximum corresponding to the period of the excitatory neurons. In the regular case, frequencies are concentrated in the low frequencies area, and the maximum value of the Fourier transform corresponds to the frequency associated to the excitatory neurons. In the SW there exist similar values for the high and low frequencies; however, the maximum frequency component corresponds to the firing period of the inhibitory neurons.

5 Conclusions

The previous results allow us to establish the following conclusions.

- The selected topology affects the dynamics of an ensemble of excitatory-inhibitory neurons.
- The overall activity of the network does not depend on the selected topology, while the temporal behavior does.
- The regular model tends to favor low frequency oscillations in the network.
- The random model tends to synchronize the network in a frequency corresponding to the period of the excitatory neurons.
- The SW model presents a good balance between low and high frequency oscillations.

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