

Fast Response and Coherent Oscillations in Small-World Hodgkin-Huxley Neural Networks

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1 Introduction

In a recent letter by Watts and Strogatz [1] it was shown that small-world (SW) networks, half way between regular and completely random ones, enhance signal-propagation speed, computational power, and synchronizability. The main properties of SW networks are a high clustering like in regular networks and, at the same time, a small path length like in random ones. Therefore, SW networks may have properties given neither in regular nor in random networks [2].

In this work we have extended Watts and Strogatz's general framework by introducing dynamical elements in the network nodes. The cooperative behavior of large assemblies of dynamical elements has been the subject of many investigations [3]. However, in all of them the connectivity between the elements of the network was either regular or completely random. None of the previous studies incorporates a comparative analysis of network dynamics for all the different connectivity topologies. We pretend to show that in order to provide the typical behavior observed in biological systems, namely fast response, coherent oscillations in the local field potential (LFP) and temporal coding, a neural network with SW connectivity topology is required. We will show that regular topologies are able to produce temporal coding and coherent oscillations, but in a time scale that would imply much slower responses than those observed in biology. On the other hand, completely random connectivities provide a fast response, but the coherent oscillations typically observed in the LFP are lost. The SW topology seems to be the only one capable to produce all these features in synergy within a biologically plausible time scale.

2 Model and Methods

The model we propose for this study is made of an array of non-identical Hodgkin-Huxley elements coupled by excitatory synapses. We have used the original functions and parameters employed by Hodgkin and Huxley [4]. The synaptic transmission is modelled using the method and parameters described by Destexhe et al. [5]. The system was integrated using the Runge-Kutta 6(5) scheme with variable time step based on [6].

Three different kinds of connectivity patterns have been tested: regular, random and small world. To interpolate between regular and random networks we follow the procedure described by Watts and Strogatz [1]: starting from a ring lattice with N vertices and k edges per vertex, each edge is rewired at random with probability p . The limits of regularity and randomness are for $p = 0$ and $p = 1$ respectively, and the SW topology lies somewhere in the region $0 < p < 1$.

The quantification of the structural properties of these graphs is performed using their characteristic path length $L(p)$ and their clustering coefficient $C(p)$ [1] (see Fig. 1a).

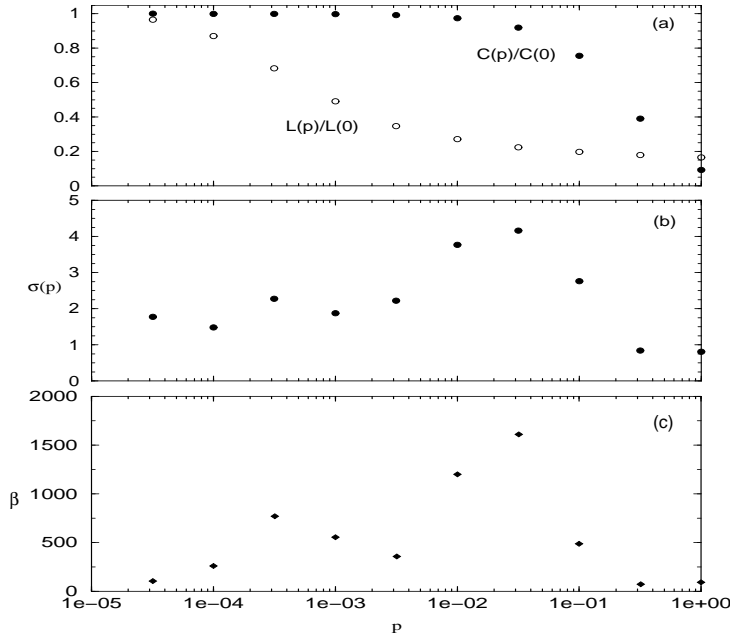


Figure 1: (a) Characteristic path length $L(p)$ and clustering coefficient $C(p)$ for the family of randomly rewired graphs, normalized to the values $L(0)$ and $C(0)$ of the regular case. (b) Average activity oscillation amplitude $\sigma(p)$, and (c) degree of coherence $\beta(p)$ for the whole range of networks, calculated between $T_1 = 100$ and $T_2 = 200$. All curves are averages over ten realizations of the simulation with parameters $N = 797$, $k = 30$ and $g = 0.015$. An input signal $I_0 = 1.5$ was injected, at $t = 50$, to 80 contiguous neurons.

3 Results

We are interested in the functional significance of SW topologies for the dynamics of the network. To study the global behavior of the network we compute its average activity (equivalent to the LFP). The quantities used to detect the onset and degree of coherent oscillations are the average activity oscillation amplitude [7] and the degree of coherence [8]. The amplitude of the oscillations is measured by

$$\sigma^2(p) = \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} [\langle \overline{V_p(t)} \rangle_t - \overline{V_p(t)}]^2 dt \quad (1)$$

where $\overline{V_p(t)}$ is the average activity of the network for a given value of the probability p , and the angle brackets denote temporal average over the integration interval. A high value of $\sigma(p)$ would imply a high amplitude of the oscillations of the average activity, while a low value would indicate an almost non-oscillatory behavior.

The degree of coherence is determined by fitting a gaussian to the highest peak of the power spectra and calculating:

$$\beta = H\omega/\Delta\omega \quad (2)$$

where H is the height of the peak, ω is the frequency at which it appears and $\Delta\omega$ is the width of the peak at the half maximum height [8].

In Fig. 1b we plot $\sigma(p)$ for each of the different networks characterized by its probability p , and in Fig. 1c we do the same for $\beta(p)$. Notice that coherent oscillations increase in the region in which a high $C(p)$ and a low $L(p)$ occur simultaneously; this is precisely the SW region.

In many biological systems, temporal coding is represented by the timing of action potentials with respect to an ongoing coherent collective oscillatory pattern of activity. When a stimulus is presented, some neurons respond to it with some particular timing with respect to the LFP. As a measure of this temporal coding, we have divided time in periods of the global average activity, and calculated for each period the quantity:

$$A_i(n) = \frac{1}{C} \int_T [a_i(t) - \overline{V(t)}]^2 dt \quad (3)$$

where i represents a particular cluster, n a particular period of the average activity, $a_i(t)$ is the average activity of cluster i , and C is a normalization constant to get the value of $A_i(n)$ in the range 0–1. In Fig. 2 we show the results for three different clusters chosen at random in a network within the SW connectivity regime. It can be observed that the activities of the different clusters are out of phase and reach their maximum values at different periods of the average activity. The ability to represent this kind of temporal coding can be observed in regular networks as well. However, we remind the reader that regular networks have very slow activation times.

4 Conclusions

In conclusion, regular networks produce coherent oscillations in a slow time scale; whereas random networks give rise to fast response but without coherent oscillations. We have observed that SW networks show both coherent oscillations with the ability of temporal coding and fast reaction times. The dynamical system introduced in the nodes of the network is the Hodgkin-Huxley model that presents a saddle-node bifurcation to the limit cycle.

Although we have not performed a detailed analysis of the mechanism that generates coherence, the simulations show that: i) it takes longer to synchronize in regular networks because the localized input needs to propagate through the ring; ii) the SW topology overcomes this problem because of the existence of a few long range connections; and iii) in the random case the clustering coefficient is too low, which implies that a specific neuron receives signals from many neurons that do not communicate among themselves, so difficulting synchronization.

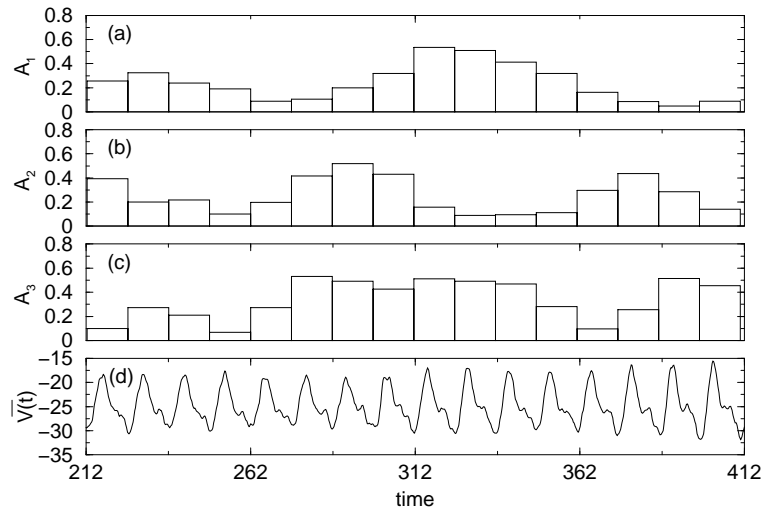


Figure 2: (a)-(c) Average activity of three different clusters of neurons promediated over periods of the global mean activity. The simulation corresponds to a probability within the SW region. (d) Average activity of the whole network showing the coherent oscillations over which the activities of clusters are promediated.

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