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Simulating global properties of electroencephalograms with minimal random neural networks

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Abstract

The human electroencephalogram (EEG) is globally characterized by a $1/f$ power spectrum superimposed with certain peaks, whereby the "alpha peak" in a frequency range of 8–14 Hz is the most prominent one for relaxed states of wakefulness. We present simulations of a minimal dynamical network model of leaky integrator neurons attached to the nodes of an evolving directed and weighted random graph (an Erdős–Rényi graph). We derive a model of the dendritic field potential (DFP) for the neurons leading to a simulated EEG that describes the global activity of the network. Depending on the network size, we find an oscillatory transition of the simulated EEG when the network reaches a critical connectivity. This transition, indicated by a suitably defined order parameter, is reflected by a sudden change of the network's topology when super-cycles are formed from merging isolated loops. After the oscillatory transition, the power spectra of simulated EEG time series exhibit a $1/f$ continuum superimposed with certain peaks.

Keywords: EEG; Field potentials; Leaky integrator units; Random graphs; Phase transitions; Order parameter

1. Introduction

The electrical activity of the brain can be measured with the electroencephalogram (EEG). Its origin is due to the synchronized activity of large formations of cortical neurons, the pyramidal cells. These nerve cells possess an axial symmetry and they are aligned in parallel perpendicular to the surface of the cortex thus forming a palisade of cell bodies and dendritic trees [11,45]. They receive excitatory input at the superficial apical dendrites from thalamic relay neurons and inhibitory input at the basal dendrites and at their somata from local interneurons [11,45,18]. Excitatory and inhibitory synapses cause different ion currents through their cell membranes thus leading to either depolarization or hyperpolarization, respectively. When these synapses are activated, a single pyramidal cell behaves as a microscopic electric dipole surrounded by its characteristic dendritic field in the extracellular space. The *dendritic field potentials* (DFP) of a large assembly of cortical pyramidal cells superimpose to the *local field potential* (LFP) of a dipole layer which eventually contributes to the EEG measurable at the human's scalp [11,56,5,40].

One of the most obvious features of the EEG are oscillations in certain frequency bands. The *alpha waves* are sinusoidal-like oscillations between 8 and 14 Hz, strongly pronounced over parietal and occipital recording sites which reflect a state of relaxation during wakefulness, with no or only low visual attention. Alpha waves are related to awareness and cognitive processes [41,4,30,47]. In the power spectrum of the EEG, these oscillations are represented by particular peaks superimposed to a broad-band $1/f$ continuum [11,7].

The $1/f$ behavior and the existence of distinguished oscillations in the EEG such as the alpha waves are cornerstones to evaluate computational models of the

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EEG. Yet, modeling these brain rhythms has a long tradition. Wilson and Cowan [53] were the first who used a population model of excitatory and inhibitory neurons that innervate each other. They introduced a two-dimensional state vector whose components describe the proportion of firing McCulloch–Pitts neurons [38] within a unit volume of neural tissue at an instance of time. Lopez da Silva et al. [35] pursued two different approaches: a distributed model of the thalamus where relay cells and interneurons are considered individually, and a "lumped" model analogous to the neural mass model of Wilson and Cowan [53]. Lopez da Silva et al. [35,36] were able to show that their model reproduces a peak around 10 Hz, i.e."alpha waves", in the spectrum.

The neural mass model [35] has been further developed by Freeman [17], Jansen et al. [24,25], Wendling et al. [51,52], and researchers from the Friston group [12–14] in order to model the EEG of the olfactory system, epileptic EEGs, and event-related potentials (ERP), respectively.

On the other hand, Rotterdam et al. [50] generalized the model [35] to spatiotemporal dynamics by considering a chain of coupled cortical oscillators. A similar approach has been pursued by Wright and Liley [55,54] who discussed a spatial lattice of coupled unit volumes of excitatory and inhibitory elements obeying cortical connectivity statistics. The most important result that we shall appreciate here is that the power spectrum exhibits the alpha peak, and that there is a shift of that peak towards the beta band with increasing input describing arousal.

Moreover, Liley et al. [34] suggested a distributed model of cortical alpha activity using a compartmental description of membrane potentials [31]. In such an approach, nerve cells are thought to be built up by cylindrical compartments that are governed by generalized Hodgkin–Huxley equations [21]. Liley et al. [34] reported two oscillatory regimes of this dynamics: one having a broad-band spectrum with a peak in the beta range of about 20 Hz, and the other narrowly banded with a peak around the alpha frequency.

Surveying these attempts, one recognizes two main lines of research. In the first approach, relatively small networks of neurons, or even of neural masses, are hand-crafted in order to meet anatomical and physiological constraints [1,16,17,34–36,50–55,24,25,12–14]. In the second one, statistical properties of the nervous tissue are treated by field theoretical approaches [40,28,26,42,43,56,57]. Yet, the recent developments of random graph theory describing networks with complex topology [2,10,9,39,23,8,44,46,29] suggest a third, medial, way of brain modeling using complex networks whose nodes are attached to dynamical neuron models [46,27,48,22,58,32].

In this paper, we shall pursue this third approach by proposing a *minimal dynamical network model* where the onset of oscillatory behavior is correlated with the emergence of super-cycles in the network's topology. The network is provided by an evolving directed and weighted Erdős-Rényi graph of N nodes where all connections between two nodes are equally likely with increasing probability [2,10,9]. To each node of the graph a simple neuron model, the *leaky integrator neuron*, is attached [53,20,33,22].

2. Minimal random neural networks

In this section, we describe our minimal neural network model, namely an evolving directed and weighted Erdős–Rényi graph. The nodes of this most simple network type are occupied by a rather simple neuron model, the leaky integrator unit. We argue that the net input to such a unit can be regarded as a rough approximation of the DFP, and demonstrate how the superposition of the DFPs of a neural mass give rise to an estimator of the LPF. Finally, the superposition of the LFPs should be considered as our model EEG.

2.1. A minimal network model

A directed Erdős–Rényi graph consists of a set of vertices V that are randomly connected by arrows taken from an edge set $E \subset V \times V$ with equal probability q. The topology of the graph is completely described by its *adjacency matrix* $\mathbf{A} = (a_{ij})$ where $a_{ij} = 1$, if there is an arrow connecting the vertex j with the vertex i (i.e. $(j,i) \in E$ for $i,j \in V$) while $a_{ij} = 0$ otherwise. A directed and weighted Erdős–Rényi graph is then described by the *weight matrix* $\mathbf{W} = (w_{ij})$ which is obtained by element-wise multiplication of the adjacency matrix with constants g_{ij}, $w_{ij} = g_{ij}a_{ij}$.

The weights w_{ij} may be positive or negative. In the former case the connection $j \to i$ is called *excitatory*, in the latter *inhibitory*. Biologically plausible models must satisfy Dale's law saying that excitatory neurons have only excitatory synapses while inhibitory neurons only possess inhibitory synapses [15]. Therefore, the column vectors of the weight matrix are constrained to unique sign. We meet this requirement by randomly choosing a proportion p of the vertices to be excitatory and the remainder to be inhibitory.

In our model the weights become time-dependent due to the following evolution algorithm:

(i) Initialization: $\mathbf{W}(0) = 0$.
(ii) At evolution time t, select a random pair of nodes i,j.
(iii) If they are not connected, create a synapse with weight $w_{ij}(t+1) = \delta_{\mathrm{ex}}$ if j is excitatory, and $w_{ij}(t+1) = \delta_{\mathrm{in}}$ if j is inhibitory. If they are already connected, enhance the weight $w_{ij}(t+1) = w_{ij}(t) + \delta_{\mathrm{ex}}$ if $w_{ij}(t) > 0$ and $w_{ij}(t+1) = w_{ij}(t) + \delta_{\mathrm{in}}$ if $w_{ij}(t) < 0$. All other weights remain unchanged.
(iv) Repeat from (ii) for a fixed number of iterations L.

For the excitation-to-inhibition ratio for balanced activity [49] to be of the order of magnitude of 1:4 [42], we chose as the "learning rates" $\delta_{\mathrm{ex}} = +1$ for excitatory synapses and