

Bursting synchronization in clustered networks of Hodgkin-Huxley-type neurons

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Abstract— We considered a clustered network of bursting neurons described by the Huber-Braun model [1]. In the upper level of the network we used the connectivity matrix of the cat cerebral cortex network, and in the lower level each cortex area (or cluster) is modelled as a small-world network [2]. There are two different coupling strengths related to inter and intra-cluster dynamics. Each bursting cycle is composed of a quiescent period followed by a rapid chaotic sequence of spikes, and we defined a geometric phase such that it is possible to investigate the onset of synchronized bursting, as the state in which the neuron start bursting at the same time, whereas their spikes may remain uncorrelated [3]. The bursting synchronization of a clustered network has been investigated using order parameter and the average field of the network, in order to identify regimes in which each cluster may display synchronized behavior, whereas the overall network does not. We introduce quantifiers to evaluate the relative contribution of each cluster in the partial synchronized behavior of the whole network.

1. Introduction

There are some neuroanatomic networks which have been intensively studied in the last years, which have served as paradigmatic models for computer simulations of neuronal networks. One of them is the cat cerebral cortex, consisting of $N = 53$ cortical areas, connected through $K = 826$ directed links [4]. These cortical areas are organized into four classes according to their common functionality: visual, auditory, somato-sensory-motor, and fronto-limbic[Fig. 1]. Each cortical area, on its hand, is a network itself formed by neurons connected through electrical and chemical synapses. Hence a proper description of the cat cortex would be a network of networks, or clustered network [5].

Each cortical area in such a clustered network is regarded as a network of neurons interacting with neurons from the same cortical area as well as from others. There have been considered many different connection architectures for clustered networks. One of them considers each cortical area as a small-world network in which, from the N

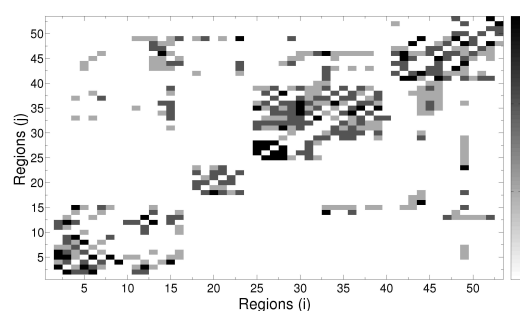


Figure 1: (color online) Matrix representation of the cortico-cortical connectivity of the cat, according to Ref. [5]. The connections among cortical areas are classified as null (white), weak (light gray), intermediate (dark gray) and strong (black), with respect to the axonal density of fiber projections.

neurons belonging to each area, 30 – 40% of them are connected with neurons belonging to different areas [6]. This can be modelled as a random network characterized by an inter-cluster probability (“random-plus-small-world”).

In this work we propose a different architecture for clustered networks based on the cat cortical connectivity matrix, where each cortical area is modelled by a small-world network of individual neurons. Instead of considering the synapses among neurons belonging to different cortical areas, we make the hypothesis that the cortical areas interact through their mean fields. In other words, we assume that the axonal fibers connecting two cortical areas are represented by a coupling between the corresponding microscopic mean fields. This is actually a coarse-grained description of neuron activity, and is expected to hold as long as we regard each cortical area as producing a coherent membrane potential. Hence, we expect the neurons from each cortical areas to act synchronously so as to generate a coherent signal which is represented by the mean field.

Our aim is to investigate bursting synchronization in a clustered network in which the outer level consists of the cat cerebral cortex network, as known in the literature, and the cortical areas (inner level) is a small world of burst-

Membrane capacitance	$C_M = 1.0 \mu F/cm^2$				
Maximum conductances (mS/cm^2)	$\bar{g}_{Na} = 1.5$	$\bar{g}_K = 2.0$	$\bar{g}_{sd} = 0.25$	$\bar{g}_{sa} = 0.4$	$\bar{g}_L = 0.1$
Characteristic times (ms)	$\tau_{Na} = 0.05$	$\tau_K = 2.0$	$\tau_{sd} = 10$	$\tau_{sa} = 20$	
Reversal potentials (mV)	$E_{Na} = 50$	$E_{sd} = 50$	$E_K = -90$	$E_{sa} = -90$	$E_L = -60$
	$V_{0Na} = -25$	$V_{0K} = -25$	$V_{0sd} = -40$		
Other parameters	$\phi_0 = 1.3$	$\phi_{Na} = 0.25$	$T_0 = 50^\circ C$	$\tau_0 = 10$	$\eta = 0.012 \mu A$
	$\gamma = 0.17$		$s_K = 0.25$	$s_{sd} = 0.09$	

Table 1: Parameter values of the neuronal dynamics model according to Ref. [1].

ing neurons. The coupling in the outer level is performed among the mean field of the networks representing each cortical areas. The dynamics of the latter is described by the Huber-Braun (HB) model of Hodgkin-Huxley-type thermally sensitive neurons [1].

2. Bursting neuron dynamics

In this Section we describe briefly the equations and parameters of the Huber-Braun (HB) model for thermally sensitive neurons [1]. The dynamics of the membrane potential V of the neuron is governed by the membrane equation (V is measured in mV and time in ms):

$$C_M \frac{dV}{dt} = -I_{Na} - I_K - I_{sd} - I_{sa} - I_L + I_{ext}, \quad (1)$$

where C_M is the membrane capacitance (measured in $\mu F/cm^2$). The current densities due to the Sodium, Potassium and leak channels are denoted respectively by I_{Na} , I_K , and I_L (measured in $\mu A/cm^2$). The external current density I_{ext} is either injected or due to the synaptic coupling with other neurons.

We associate a given ohmic conductance to each ion current, as

$$I_{Na} = \rho \bar{g}_{Na} a_{Na} (V - E_{Na}), \quad (2)$$

$$I_K = \rho \bar{g}_K a_K (V - E_K), \quad (3)$$

$$I_{sd} = \rho \bar{g}_{sd} a_{sd} (V - E_{sd}), \quad (4)$$

$$I_{sa} = \rho \bar{g}_{sa} a_{sa} (V - E_{sa}), \quad (5)$$

$$I_L = \rho \bar{g}_L (V - E_L), \quad (6)$$

where \bar{g}_{Na} , \bar{g}_K , \bar{g}_{sd} , \bar{g}_{sa} , \bar{g}_L are the maximum specific conductances (measured in mS/cm^2), and the reversal (Nernst) potentials for each ionic current are denoted by E_{Na} , E_K , E_{sd} , E_{sa} and E_L . The parameter ρ is a scale factor depending on the temperature T , given by

$$\rho = \rho_0 \frac{(T-T_0)}{\tau_0}, \quad (7)$$

where ρ_0 , T_0 and τ_0 are constants.

The time evolution of the activation currents a_{Na} , a_K , a_{sd} , and a_{sa} are governed by the following equations

$$\frac{da_{Na}}{dt} = \frac{\phi}{\tau_{Na}} (a_{Na,\infty} - a_{Na}), \quad (8)$$

$$\frac{da_K}{dt} = \frac{\phi}{\tau_K} (a_{K,\infty} - a_K), \quad (9)$$

$$\frac{da_{sd}}{dt} = \frac{\phi}{\tau_{sd}} (a_{sd,\infty} - a_{sd}), \quad (10)$$

$$\frac{da_{sa}}{dt} = \frac{\phi}{\tau_{sa}} (-\eta I_{isd} - \gamma a_{sa}), \quad (11)$$

where τ_{Na} , τ_K , τ_{sd} and τ_{sa} are characteristic times. The parameter η serves for increasing Calcium ion concentration following I_{sa} , while γ accounts for active elimination of intracellular Ca^{2+} . A second temperature-dependent scale factor is defined as

$$\phi = \phi_0 \frac{(T-T_0)}{\tau_0}. \quad (12)$$

The activation functions $a_{Na,\infty}$, $a_{K,\infty}$, $a_{sd,\infty}$, depend on the membrane potential by the relations

$$a_{Na,\infty} = \frac{1}{1 + \exp[-s_{Na}(V_i - V_{0Na})]}, \quad (13)$$

$$a_{K,\infty} = \frac{1}{1 + \exp[-s_K(V_i - V_{0K})]}, \quad (14)$$

$$a_{sd,\infty} = \frac{1}{1 + \exp[-s_{sd}(V_i - V_{0sd})]}, \quad (15)$$

where s_{Na} , s_K , and s_{sd} are constants and V_{0Na} , V_{0K} , and V_{0sd} are activation voltages.

A typical bursting event in such a neuron starts when a neuron fires a large number of fast spikes, and ends with the ensuing quiescent period. The beginning of each burst has been found to be a local maximum of the recovery variable $1/I_{isa}$. It is possible to define a geometric bursting phase, which increases by 2π after each burst, even though the dynamics in each timescale is actually chaotic. Let t_k the time at which the k th bursting cycle begins. The phase is obtained by a simple linear interpolation as

$$\varphi(t) = 2\pi k + 2\pi \frac{t - t_k}{t_{k+1} - t_k}, \quad (t_k < t < t_{k+1}), \quad (16)$$

and increases monotonically with time.

3. Dynamics of the neuronal network

The neuronal network to be studied in this work consists of two levels: in the outer level the nodes are cortical areas and the links are the respective connections (axonal fibers). The architecture of these links is given by the corticocortical connectivity of the cat, represented by its weighted adjacency matrix A_{ij} , whose elements are depicted in Fig. 1. Each cortical area, on its hand, is a small-world network of neurons, obtained from the NW scheme with a given probability p .

Hence we consider S cortical areas, each of them with N neurons, i.e. the whole network has SN nodes (note that in Section II we denoted by N the number of neurons of the whole network). Each neuron will be identified by two

Characteristic times(ms)	
$\tau_r = 0.5$	$\tau_d = 8$
Reversal potentials(mV)	
$V_{syn} = 20$	$V_0 = -20$

Table 2: Parameter values for the synaptic dynamics according to Ref. [7].

labels $V_i^{(j)}$: the area j to which it belongs ($j = 1, 2, \dots, S$) and its index i within the j th area ($i = 1, 2, \dots, N$). The dynamics of the coupled neurons is described by the HB model, whose membrane equation is

$$C_M \frac{dV_i^{(j)}}{dt} = -I_{i,Na}^{(j)} - I_{i,K}^{(j)} - I_{i,sd}^{(j)} - I_{i,sa}^{(j)} - I_{i,L}^{(j)} + I_{i,ext}^{(j)}, \quad (17)$$

where the ionic currents for the j th neuron are given by Eqs. (2)-(6) and (8)-(15).

The coupling term for the j th neuron, denoted by $I_{i,ext}^{(j)}$, is represented by two synaptic currents of different nature: (i) an inner coupling, which stands for chemical synapses with a small-world connectivity within each area, and (ii) an outer coupling, by which the areas connect to each other through their corresponding mean potentials. The contribution of the inner coupling can be modelled as

$$I_{i,IN}^{(j)} = g_{IN} \sum_{k=1}^N A_{ik}^{(j)} r_k^{(j)} (V_{syn} - V_k^{(j)}), \quad (18)$$

with g_{IN} is the inner coupling strength with conductance dimensions, $A_{ik}^{(j)}$ are the elements of the adjacency matrix for the j th area, V_{syn} is the synaptic reverse potential, and $r_k^{(j)}$ is the fraction of bond receptors of the k th neuron belonging to the j th area, whose evolution is described by

$$\frac{dr_k^{(j)}}{dt} = \left(\frac{1}{\tau_r} - \frac{1}{\tau_d} \right) \frac{1 - r_k^{(j)}}{1 + \exp(-V_k^{(j)} + V_0)} - \frac{r_k^{(j)}}{\tau_d}, \quad (19)$$

where $V_k^{(j)}$ is the membrane potential of the post-synaptic neuron, τ_r and τ_d are characteristic rise and decay times, respectively, of the chemical synapse. The numerical values of the parameters used here are given in Table 2. We suppose that their values are the same for each area. However, each cluster has a different adjacency matrix $A_{ik}^{(j)}$, since it describes a different realization of a small-world network obtained (from the Newman-Watts prescription).

The contribution of the outer coupling can also be described by a current density in the form

$$I_{OUT}^{(j)} = g_{OUT} \sum_{\ell=1}^S A_{j,\ell}^{(j)} M(j), \quad (20)$$

with g_{IN} is the outer coupling strength (conductance), $A_{j,\ell}$ are the elements of the adjacency matrix of the cat cortex

connectivity, and

$$M(j) = \sum_{i=1}^N V_i^{(j)}, \quad (21)$$

is the mean field of the j th cluster, i.e. the cat matrix connects two cortical areas characterized collectively by their mean potentials. The total coupling current acting on the i th neuron belonging to the j th area is thus

$$I_{i,ext}^{(j)} = I_{i,IN}^{(j)} + I_{OUT}^{(j)}. \quad (22)$$

Moreover, the values of the inner and outer coupling strengths, denoted by g_{IN} and g_{OUT} respectively, are varied over an interval chosen as to always preserve a bursting behavior of the coupled neurons (a too large coupling may drive the neuron off the bursting regime into an irregular spiking one).

4. Bursting synchronization

An assembly of neurons is said to exhibit bursting synchronization if their phases coincide for all times. This assembly can be, for example, a whole cluster, or the entire network. Since bursting synchronization is an instance of phase synchronization, a useful quantitative diagnostic is provided by Kuramoto's order parameter z . Let N be the number of neurons in a given cluster j . The complex order parameter magnitude for the j th cluster is then defined as

$$R_j(t) = \left| \frac{1}{N} \sum_{i=1}^N e^{i\varphi_{ij}} \right|, \quad (j = 1, 2, \dots, S) \quad (23)$$

If all neurons in a cluster are completely synchronized, all the corresponding bursting phases coincide and thus the terms in (23) add coherently such that $R_j \rightarrow 1$. If, on the other hand, the neurons are completely non-synchronized their bursting phases are totally uncorrelated and $R_j \rightarrow 0$. We may estimate that, in this case, $R \sim 1/\sqrt{N}$ for a finite network, since there will be a number of chance coincidences that eventually yield a nonzero sum. We choose the value of R_j at time $t = 3 \times 10^4 ms$, for which the transients have died out.

We can take the whole network into account in two ways: either we compute the (ensemble) average over all clusters

$$R_{mean} = \frac{1}{S} \sum_{j=1}^S R_j, \quad (24)$$

or we calculate the order parameter magnitude for the whole network

$$R_{global} = \left| \frac{1}{NS} \sum_{i=1}^N \sum_{j=1}^S e^{i\varphi_{ij}} \right|, \quad (25)$$

In Fig. 2 we plot the values of the clustered-averaged order parameter R_{mean} as a function of the two coupling parameters g_{IN} (inside each cluster) and g_{OUT} (connections

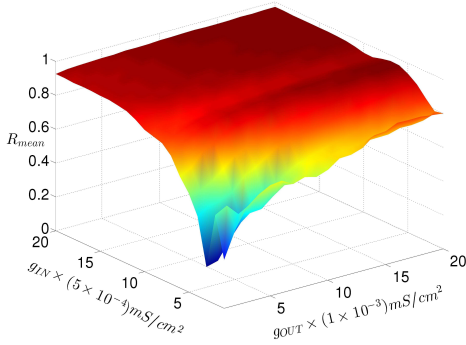


Figure 2: (color online) Cluster-averaged order parameter as a function of the two coupling parameters g_{IN} and g_{OUT} , for a network of $S = 53$ clusters and $N = 256$ neurons *per* cluster. Each cluster is a small-world network obtained from the Newman-Watts scheme with probability $p = 0.01$. The clusters are connected through their mean fields using the cat cortical connectivity matrix.

among clusters). Considering first $g_{OUT} = 0$, i.e. the clusters are not connected among themselves, we find that the variation of R_{mean} with g_{IN} has the typical shape of a continuous phase transition: for small g_{IN} the clusters do not display phase synchronization, and so R_{mean} is correspondingly small. After a critical value of $g_{IN,cr}$, however, the order parameter for each cluster (and their average) begins to increase according to a scaling law $R_{mean} \sim (g_{IN} - g_{IN,cr})^\varpi$, where $\varpi = 1/2$ for the Kuramoto model of phase oscillators. Since we have for each cluster a small-world network, the exponent ϖ is expected to be different, though.

As we increase the coupling among clusters ($g_{OUT} \neq 0$), the transition to synchronized behavior in the clusters continue to exist, but with smaller values of the critical parameter $g_{IN,cr}$, which is an effect of the increasing coupling strength caused by the outer network. Roughly speaking, the same scenario happens if we switch off the inner coupling and increase the outer coupling. In this case, however, the coupling between neurons is mediated by the mean fields of the clusters they belong to, and thus the effect is not so pronounced as before. Nevertheless we have a transition scenario but with bumps and fluctuations that come from the indirect nature of the coupling.

5. Conclusions

We choose the parameters to be varied the synaptic conductances within each area (g_{IN}) and among different clusters (g_{OUT}). As a general trend, the larger the values of both, the more synchronized is the entire network. In fact the effect of g_{IN} is more pronounced than g_{OUT} to achieve the same effect. Hence the internal cluster dynamics influences more the overall result than the inter-cluster coupling.

It may well happen that a number of clusters are synchronized at different levels, what results in a non-synchronized behavior, when considered from a global point of view. This is clearly different, however, from a situation when all clusters are themselves non-synchronized. We have defined, to distinguish between these situations, suitable quantities based on the order parameters computed for both the entire network and for the average taken over various cortical areas. We have found that large values of this quantity are observed for intermediate values of g_{IN} and large values of g_{OUT} . The reason for this is still unclear but probably results from the dynamics of the coupled system.

References

- [1] U. Feudel, A. Neiman, X. Pei, W. Wojtenek, H. Braun, M. Huber and F. Moss, “Homoclinic bifurcation in a Hodgkin-Huxley model of thermally sensitive neurons”, *Chaos*, vol. 10, pp. 231-239, 2000.
- [2] C. A. Batista, E. L. Lameu, A. M. Batista, S. R. Lopes, G. Zamora-López, J. Kurths and R. L. Viana, “Phase synchronization of bursting neurons in clustered small-world networks”, *Physical Review E*, vol. 86, pp. 016211(12), 2012.
- [3] C. A. Batista, R. L. Viana, F. A. S. Ferrari, S. R. Lopes, A. M. Batista and J. C. P. Coninck, “Control of bursting synchronization in networks of Hodgkin-Huxley-type neurons with chemical synapses”, *Physical Review E*, vol. 87, pp. 042713(13), 2013.
- [4] J. W. Scannell, G. A. P. C. Burns, C. C. Hilgetag, M. A. O’Neil, and M. P. Young, *Cerebral Cortex* **9**, 277 (1999).
- [5] G. Zamora-López, C. Zhou, and J. Kurths, *Frontiers in Neuroscience* **5**, 83 (2011).
- [6] G. Zamora-López, C. Zhou, and J. Kurths, *Frontiers in Neuroinformatics* **4**, 1 (2010).
- [7] Y. Hao, Y. Gong, L. Wang, X. Ma, and C. Yang, *Chaos, Solit. & Fract.* **44**, 260 (2011).