Research paper

Synchronization domains in two coupled neural networks

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We investigate the dynamical properties of two coupled neural networks with 2,048 identical Hodgkin–Huxley type bursting neurons. The internal connection architecture of each network follows a small-world topology and the external connection scheme is based on the local mean field potential, where one network receives the signal from the other. To analyze the system, we use Kuramoto order parameter computed over each neuron data, and recurrence quantification analyses, particularly the ratio of recurrent points belonging to diagonal lines of the recurrence plot \textit{RP}, namely the determinism, computed over the local mean field potential of the networks, an easier experimentally accessible data. We analyze the complex synchronization scenario depicted by the network as a function of internal and external coupling parameters. Particularly, we identify regions of non-monotonic dependence of the synchronization level as a function of the coupling strength; coupling induced phase desynchronization (PD), where the synchronization levels are similar to those expected for randomly distributed phases; almost complete spike synchronization (SS) for which even spikes composing a burst are synchronized. This regime occurs as a product of the fast modulated signal imposed by the coupling between networks and weak internal coupling; finally, bursting synchronization (BS) regions are associated with slow modulated internal coupling.

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1. Introduction

The study of complex network behavior is used to understand distinct collective phenomena applied to physical, chemical, biological and even social problems \cite{1,2}. This approach is particularly useful to investigate dynamical properties of neural networks \cite{3}. In general, neural systems are composed of neural cells and its connections. A neural system can be composed of just few hundreds of neurons and thousands of synapses as is the case of the \textit{C. elegans} neural network \cite{4}, reaching much larger systems, composed of $10^{11}$ neurons and $10^{12}$ synapses, typical values found in human brains \cite{5}. An useful approach is to model real neural systems by complex mathematical networks where neurons are nodes and synapses are links \cite{5}. In fact, the literature shows different studies of single neural networks as well as neural systems composed of network of networks. Real connection architectures and pre-defined topologies such as small-world, random and scale-free networks are considered \cite{6–8}.

An important phenomenon of complex systems consists on the emergent behavior, where there is no central agent in the network and the global behavior depicts richer dynamics than the sum of individuals node dynamics \cite{9}. This characteristic

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is particularly important to neural network, since a set of collective phenomena such as phase synchronization, anomalous synchronization, complete synchronization and intermittent behavior are observed in real situations, contributing for a very rich dynamic behavior of the networks [10–13].

In general, the complexity of neural systems depends on neuron particular characteristics as well as the interactions among them. In real brains, neurons are classified according to their shape, location, and function, however, the connection structure influences much more than the neuron individual behavior [14]. It is observed in the literature many distinct connection topologies, mainly small-world, scale-free and random ones [7,15–17]. Furthermore, investigations of real neural systems relate the characteristics of these real connection schema to those well know connection topologies [4,18,19]. All these networks display transition from desynchronized to synchronized states as function of coupling strength parameter [7,10,15], even for the case of network of networks [20–23] where internal and external couplings have distinct roles. This is an important issue, since the transition to synchronization shows a great diversity of dynamical behaviors and these phenomena are not completely understood [24].

Neural networks depicting bursting behavior and under different connection topologies may present non-monotonous dependence of the phase synchronization level as a function of the coupling strength, which can be sometimes understood as an anomalous synchronization [10,11,20,25,26], leading to an excess of synchronization occurring for small coupling strengths. Such a phenomenon occurs associated to nonstationary behavior observed in regions of weak coupling and marks the beginning of the transition to phase synchronization. For some interval of the coupling parameter, the network can even display two stable states and the phenomenon of hysteresis is expected [27]. Long term numerical simulations also show that at the vicinity of the transition to a phase synchronized state, fluctuations in the asymptotic dynamics increase as expected for nonequilibrium systems [10,28]. The former situation turns the hysteresis scenario in a more general one, namely the coexistence of different locally stable but globally unstable states occurring in the network dynamics, a situation recognized as a two state on off intermittency [29]. Similar scenarios of anomalous synchronization are observed in identical and non-identical oscillators [10,11,25,30]. For large values of the coupling parameter, the sufficiently strong coupling, in general, leads the network to display a stable phase synchronized state, in general such a stability state observation is based on long term numerical simulations.

The understanding of these scenarios is of fundamental interest since the phase synchronization phenomenon has been linked to fundamental action of a healthy life, such as consciousness [31] and vision coordination [32]. On the other hand, there are also unhealthy phenomena related to (excess or lack of) synchronization, as Parkinson, autism and epilepsy [33–36].

In order to investigate more details of these scenarios, we propose a neural system composed of two coupled networks, where the internal connection architecture of each network consists on small-world topology with 2048 thermally sensitive identical Hodgkin–Huxley type neurons [37]. Each network has 8192 local and 1046 nonlocal connections, simulated through chemical synapses [38]. The coupling between networks is a mean field coupling. In this way, it is possible to study the neural system dynamics as function of internal and external coupling strengths, particularly, how the synchronization phenomena and its details varies as functions of coupling parameters.

Different of the original model of Hodgkin–Huxley [39], the thermally sensitive neuron model of Braun et. al. [37,40] used here is capable to reproduce burst neural dynamic regime, which can be described as a sequence of chaotic spikes, or action potentials, followed by a quiescent period [41]. The bursting behavior is reported to be more robust regarding to noise than individual spikes [42]. This kind of behavior is characterized by the presence of two time scales, a fast one, related to chaotic spikes and a slow one, associated to the bursts. The scenario offers the possibility to analyze the burst synchronization, which is associated to (slow) temporal synchronization of bursting and the spike synchronization, where there is bursting synchronization associated to fast temporal coherence of spike of the action potential [43,44]. This neural dynamics was vastly experimentally observed [45–47].

Here, we show that a complex network of networks based on the thermally sensitive neuron model of Braun et. al. [37,40] shows different types of synchronization as a function of internal and external couplings. We also explore how a well known recurrence quantifier, namely the determinism, associated to other traditional synchronization quantifiers, the Kuramoto and standard deviation, may be combined to distinguish burst (phase) and spike synchronizations of networks.

The paper is divided as follows. In Section 2, we describe details of the used model and the major factors that influence neuron dynamics. In Section 3, we discuss the methodology used, mainly, Kuramoto order parameter, the determinism quantifier and statistical tools. In Section 4, we present the results and discussions which support our conclusions that are in Section 5.

2. Neuron model and connection architecture

The neuron dynamical properties are described by the model developed by Braun et. al. [37], based on the Hodgkin–Huxley model [39]. The main equation of the model is based on parallel-plate capacitor, mathematically described as

$$C_m \frac{dV_i}{dt} = -I_{i,Na} - I_{i,K} - I_{i,Na} - I_{i,K} - I_{i,L} + I_i^e,$$

(1)

where \( j = 1, 2 \) represents each network and \( i \) denotes the neurons belonging to the \( j \)th network. The action potential \( V \) and time are measured in millivolts (mV) and milliseconds (ms); \( C_m \) is the specific capacitance of the neuron membrane.
measured in $\mu F/cm^2$. $I_{Na}$, $I_K$ and $I_L$ are ionic and leak fluxes (current densities) measured in $\mu A/cm^2$, which are related to the ionic channels of neuron membrane. The terms $I_{sd}$ and $I_{sa}$ are the first change in the original Hodgkin–Huxley model [39], which refer to intrinsic sub-threshold and hyperpolarization oscillations. These terms can be understood as slow currents and are responsible for the sub-threshold activation. This modification leads the system to displays bursting behavior [37]. The last term on Eq. (1) intends for the external interaction of neuron, which can be understood as a signal of other neurons and/or an external stimulus, as considered in [11,26]. In this work we consider the contribution of other neurons in the same network as an internal coupling while the contribution of neurons of the second network is denominated an external coupling, supposed to act through the mean field of the network. In this way, $I_i^f$ has an internal and an external contributions.

$$I_i^f = I_i^{f,\text{int}} + I_i^{f,\text{ext}}.$$  

The term of internal contribution can be understood as chemical synapses, mathematically represented by synaptic currents [38]

$$I_i^{f,\text{int}} = \frac{e_{\text{int}}}{\chi} \sum_{k=1}^{N} e_{i,k}^f r_i^f (V_{\text{syn}} - V_i^f),$$  

where, $e_{\text{int}}$ is the internal coupling strength, $\chi = 8$ is the normalization factor given by the number of connections of the most connected neuron of the network, $N = 2048$ is the number of neurons from each network, $e_{i,k}^f$ is the adjacent matrix element (small-world topology), obtained through Newman-Watts route [48], $V_{\text{syn}} = 20 mV$ is the synaptic reversal potential and $r_i^f$ is a kinetic term related to chemical synapse dynamics of the ith neuron ($k = i$), which represents the fraction of receptors that is available to receive signal from other neurons [38],

$$\frac{dr_i^f}{dt} = \left( \frac{1}{\tau_r} - \frac{1}{\tau_d} \right) \frac{1 - r_i^f}{1 + \exp[-s_0(V_i^f - V_0)]} - \frac{r_i^f}{\tau_d},$$  

where $\tau_r = 0.5ms$ and $\tau_d = 8ms$ are characteristic times, $V_0 = -20mV$ is the characteristic potential and $s_0 = 1mV^{-1}$ is just a dimensional constant.

The external contribution factor is modeled by mean field connection, where each element of jth network receives a signal of the mean local field potential of the other network,

$$I_i^{f,\text{ext}} = e_{\text{ext}} \sum_{k=1}^{2} g^{j,k} \nabla^k.$$  

Here, $e_{\text{ext}}$ is the external coupling strength, $g^{j,k} = 1$ ($g^{j,k} = 0$) represent the existence (absence) of a connection between network j and network k. At last, $\nabla^j$ is the mean field of the jth network,

$$\nabla^j = \frac{1}{N} \sum_{i=1}^{N} V_i^j.$$  

The global mean field of the network is given by

$$\overline{V}_{\text{global}} = \frac{1}{2N} \sum_{j=1}^{2} \sum_{i=1}^{N} V_i^j.$$  

The other flux terms of Eq. (1) that contribute to the neural dynamics are related to ions dynamics and leak process and they are defined by conductance-based expressions [49].

$$I_{i,U}^f = \rho_g^{i,u} \alpha_{i,U}^f (V_i^f - E_U), \text{ for } U = \text{Na, K, sd, sa}$$  

$$I_{i,L}^f = \rho_g^{i,L} (V_i^f - E_L).$$  

In Eqs. (8), (9) $\rho_{Na}$, $\rho_{K}$, $\rho_{sd}$, $\rho_{sa}$ and $\rho_{L}$ are the maximum specific conductances and $E_{Na}$, $E_{K}$, $E_{sd}$, $E_{sa}$ and $E_{L}$ are the reversal Nernst potentials. Theses values are used as described in [10,26,37]. The first temperature dependence of the model is described by

$$\rho = \rho_0 \frac{T}{T_0},$$  

where $\rho_0$, $T_0$, and $T_0$ are considered as in [37].

Following the original model [37] a possible temperature dependence in Eq. (9) is not considered, since the temperature dependence of leak channels is smaller in comparison to ion channels [50].

The dynamical variables $\alpha_{Na}^f$, $\alpha_{K}^f$, $\alpha_{sd}^f$ and $\alpha_{sa}^f$ are activation current densities and governed respectively by

$$\frac{d\alpha_{i,U}^f}{dt} = \frac{\phi}{\tau_{i,U}} (\alpha_{i,U,\infty}^f - \alpha_{i,U}^f), \text{ for } U = \text{Na, K, sd}$$  

...
Fig. 1. (a) Representative $V_i(t)$, Eq. (1), for a coupled Hodgkin-Huxley like neuron simulated through model of Braun et al. [37]. (b) $U_i^j = 1/\alpha_{i,sd}^j$, Eq. 12 giving the slow variable of the model, whose local maximums coincide with the start of each burst.

\[
\frac{d\alpha_{i,sd}^j}{dt} = -\phi \left( \eta \alpha_{i,sd}^j + \gamma \alpha_{i,sd}^j \right),
\]

where $\tau_{i,sd}$, $\tau_{K}$, $\tau_{sd}$, and $\tau_{sa}$ are characteristic times and their values are considered as in [40]. The parameter $\eta$ is related to the increasing calcium ion concentration and $\gamma$ consists on elimination of intracellular $Ca^{2+}$ [51]. The second temperature dependence is describe by the term

\[
\phi = \phi_0 T^{1/5},
\]

where $T = 38.0$ and $\phi_0$ is chosen following [37].

\[
\alpha_{i,u,\infty}^j = \frac{1}{1 + \exp[-s_u(V_i^j - V_{0u})]}, \quad \text{for } u = \text{Na, K, sd}
\]

where $s_{Na}$, $s_{K}$, and $s_{sd}$ are model constants, $V_{0Na}$, $V_{0K}$, and $V_{0sd}$ are activation potentials, all of them are considered following [10,26,37].

The integration was performed with 4th order Runge-Kutta method with time step of 0.01. Random initial conditions are used in order to avoid any trend and/or numerical divergence caused by the initialization of their values. The intervals are given by $\eta_i \in [-65:0]$ mV, $\alpha_{i,u} \in [0.1: 1]$, where $u$ represent Na, K, sd, sa, L and $r_i = 0.1$ in order to avoid any synchronization trend and numerical divergence.

Phases of a chaotic flow can be defined based on an appropriate Poincaré section with which the chaotic orbit crosses once each pseudo-period [52]. The dynamic of a coupled neuron is described as a sequence of chaotic spikes followed by a quiescent period [37]. Fig. 1 depicts an example of the bursts sequence (panel (a)) and the dynamical behavior of variable $U_i^j = 1/\alpha_{i,sd}^j$ (panel (b)). Every time a burst starts the variable $U_i^j$ assumes a local maximum defining a Poicaré section, so, in order to analyze the bursting synchronization of the system, we associate a geometric phase to burst periods, since we can evaluate each time they happen using the slow variable $U_i^j$ [52]. In this way, the phase is increased by $2\pi$ every time $U_i^j$ assumes a local maximum value. A continuous varying phase for each neuron in the system is obtained using linear interpolation, i.e. [52,53]

\[
\theta_i^j(t) = 2\pi k_i^j + 2\pi \frac{t - t_{k,i}^j}{t_{k+1,i}^j - t_{k,i}^j}, \quad t_{k,i}^j \leq t < t_{k+1,i}^j.
\]

where $t_{k,i}^j$ is the time of the $k$th burst of $i$th neuron belonging to the $j$th network. Considering just the bursting regime for the neuron dynamics, the Eq. (15) defines a suitable phase for each neuron, independently of the trajectory, and can be used for isolated or coupled neurons, it means that phase can be obtained equivalently by analyzing the maxima of the scalar chaotic time series ($U_i^j$) without reconstruction of the dynamics in a higher dimensional phase space [52]. Here we have used by Eq. (15), but other forms to rigorously define a phase based on trajectories and not restrict to bursting neurons are also possible to be used [54,55].

Each Newman-Watts small-world networks [48] contains $2,048$ neurons. The total number of connections ($K$) is

\[
K = 4N_{\text{local}} + N(N - 5)p,
\]

where the first term refers to a second neighborhood scheme, resulting in $8,192$ local connections and the second term refers to nonlocal connections, where we considered the probability $p = 0.00025$ resulting in $1,046$ nonlocal connections. Finally, $p = 1$ leads to a globally connected network.

We can evaluate the average path length ($L$) and the clustering coefficient ($C$) [7] to these networks using [56]. In this case, we obtain $C_{SW} = 0.3385 \sim 10^{-1}$ and $L_{SW} = 6.325 \sim 1$. On the other hand, these quantifiers for an equivalent random
network are: $L_{\text{random}} \sim \ln(N)/\ln(K/N)$ and $C_{\text{random}} \sim K/N^2$, where $N$ is the number of neurons and $K$ is the number of connections in the network considered [9].

Defining $\lambda_L = L_{sw}/L_{\text{random}}$ and $\lambda_C = C_{sw}/C_{\text{random}}$ we evaluate the merit variable $\sigma = \lambda_C/\lambda_L$ [57,58]. If $\sigma > 1$, than the network considered has a small-world topology. For the problem considered in this work $C_{\text{random}} \sim 10^{-3}$ and $L_{\text{random}} \sim 1$. Using the values before mentioned $C_{sw}$ and $L_{sw}$, it is possible to demonstrate that $\sigma \sim 10^2$, confirming that the networks used have small-world topology. The parameters $C$ and $L$ of the small-world networks considered are similar to those observed in real neural systems [7].

3. Synchronization quantifiers

To investigate phase synchronization we use the phase associated to the $i$th neuron on the $j$th network, Eq. (15) and the Kuramoto order parameter [59]

$$R^j(t) = \left| \frac{1}{N} \sum_{i=1}^{N} e^{i\theta^j_i(t)} \right|,$$

where $R(t)$ is naturally a spatial average, since it is measured over all neurons of the network. If the system displays burst synchronization, $R(t)$ gets close to one, while if the system is out of phase, $R(t)$ oscillates close to zero, indicating the unsynchronized states. In a similar approach, it is possible to evaluate the order parameter for the entire network, the global order parameter

$$R_{\text{global}}(t) = \left| \frac{1}{2N} \sum_{j=1}^{2} \sum_{i=1}^{N} e^{i\theta^j_i(t)} \right|.$$  

To evaluate synchronization as function of coupling parameters we use the mean value of the Kuramoto order parameter for each network

$$\langle R^j \rangle = \frac{1}{T_f} \sum_{t=0}^{T_f} R^j(t),$$

where $T_f = 100,000 \text{ ms}$ is the total simulation time, $t_0 = 70,000 \text{ ms}$ is the transient time, $A = (t_f - t_0)/h$, where $h = 0.01$ is the computation step.

To analyze synchronization phenomena of the global system as function of coupling parameters, a similar approach adopted to mean value of the order parameter is used, however, it is considered the global Kuramoto order parameter ($\langle R^\text{global} \rangle$), described by Eq. (18),

$$\langle R \rangle_{\text{global}} = \frac{1}{T_f} \sum_{t=0}^{T_f} R_{\text{global}}(t).$$

Another quantifier used to analyze dynamical properties of the network is based on the recurrence plot (RP) [10,60,61]. The RP is a graphical tool to identify recurrence of a trajectory $x_a \in \mathbb{R}^d$ phase space, $a \in 1, 2, \ldots, S$, where, $S$ is the size of the time series, and it is based on the recurrence matrix [61]

$$R_{a,b}(\delta) = \Theta(\delta - ||x_a - x_b||), x_a, x_b \in \mathbb{R}, a, b = 1, 2, \ldots, S.$$  

$\| \cdot \|$ is an appropriate norm, $\Theta$ is the Heaviside function and $\delta$ indicates the recurrence threshold.

Based on the idea of recurrence matrix, it is possible to define recurrence quantifiers that synthesize dynamical properties of the systems [62,63]. From several structures that can be explored in a RP, one of the most important is the diagonal line statistics since diagonal line distributions are related to the regularity of the trajectories, in fact a diagonal line of length $\ell$ means that a segment of the trajectory is rather close during $\ell$ time steps to another segment of the trajectory in a different time [62]. The determinism gives us the ratio of recurrent points belonging to diagonal lines over all recurrent points evaluate from recurrence matrix defined by Eq. (21). This approach was already used to successfully evaluate transition to phase synchronization since the mean field of a phase synchronized network has a “periodic” oscillations (see Fig. 6) [10]. The determinism is expressed by

$$\Delta(\ell, \delta, \mathcal{V}) = \frac{\sum_{\ell = \ell_{\text{min}}}^{\ell_{\text{max}}} \ell P(\ell, \delta)}{\sum_{\ell = 1}^{\ell_{\text{max}}} \ell P(\ell, \delta)},$$

where $\ell$ is the length of diagonal lines and $\ell_{\text{min}}$ is the minimum diagonal line length considered. $P(\ell, \delta)$ is the probability distribution function of diagonals lines and $\mathcal{V}$ is the mean field, described by Eq. (6) for each network and by Eq. (7) for the global system.
Using Eq. (22), similar analysis done to the mean value of the Kuramoto order parameter can be done using only data of the local field potential of each network, Eq. (6) or the global mean field potential, Eq. (7). Again, we analyze the system as a function of the coupling parameter strengths, evaluating the mean value of the determinism of each network

$$\langle \Delta_j \rangle = \frac{1}{A} \sum_{t=t_0}^{t_f} \Delta_j(t),$$

(23)

or the global mean value of the determinism, where it is considered the mean local field of the entire system.

The use of the mean field potential is desirable due to its easier experimental acquisition. As a complementary analysis, we compute the standard deviation of the mean field potential of each network and the global mean field.

$$\sigma = \sqrt{\frac{\sum_{t=t_0}^{t_f} (\overline{V}(t) - \langle \overline{V} \rangle)^2}{A}},$$

(24)

where $\overline{V}$ is the temporal average of the local mean field potential. Here, higher (lower) values of $\sigma$ reveal a more (less) synchronized system, since the amplitude of mean field is related to synchronization level [11].

4. Results and discussions

Making use of the quantifiers described in Section 3, we investigate the dynamical behavior of a network of networks related to its synchronization and desynchronization processes as function of internal and external coupling strength, identifying synchronization domains.

Recurrence parameters were chosen in order to optimize the dynamical analysis. The parameter $\delta = 0.11$ is obtained from the condition of Max[$d(\Delta(\delta))/d\delta$] [64], resulting in a maximum sensitiveness of the determinism ($\Delta$). The minimum diagonal length considered is $l_{\text{min}} = 35$ avoiding small diagonal lines, such that synchronized and unsynchronized states can be better distinguished [17]. The determinism is evaluated using a moving window of 10,000 points, where 9,900 points are overlapped between two subsequent windows.

The set of parameters used leads the system to display ionic currents oscillating in the following intervals: $l_{i_{\text{Na}}}^i \in [-60, 0]$, $l_{i_{\text{K}}}^i \in [0, 60]$, $l_{i_{\text{Ca}}}^i \in [0, 10]$, $l_{i_{\text{Na}}}^j \in [-10, 0]$, $l_{i_{\text{L}}}^j \in [0, 7]$, $l_{i_{\text{ext}}}^j \in [0, 2]$ and $l_{i_{\text{ext}}}^j \in [-0.25, -0.15]$ $\mu$A/cm². All compatible values for a large class of biologic situations. In special $l_{i_{\text{int}}}^j$ and $l_{i_{\text{ext}}}^j$ have current densities lower than the maximum suggested by ICNIRP guidelines [65].

The main scenario of the synchronization and desynchronization processes as a function of coupling parameters of the network is found in Fig. 2. Panels (a), (b) and (c) depict mean values of the Kuramoto order parameter for each network obtained by using Eq. (19) (a, b), and for the entire system calculated from Eq. (20) (c). Panels (d), (e) and (f) depict the same scenario, but they are based on analyses using the determinism, Eq. (22), computed over the mean field of each network (d, e), Eq. (6), and the global mean field (e), Eq. (7). Finally panels (g), (h) and (i) display results from the standard deviation of the mean field of each network (g, h) and the global mean field (i).

For vanishing values of $\varepsilon_{\text{ext}}$, all panels of Fig. 2 show the traditional non-monotonic transition to burst synchronization (BS), a phase synchronized domain of the network of Hodgkin–Huxley like neuron-model [10,11,25]. In this region of the parameter space the network displays an almost phase synchronized domain occurring for low values of $\varepsilon_{\text{int}}$, as observed in the region near $\varepsilon_{\text{int}} = 8 \times 10^{-3}$ and better visualized in panels (d), (e) and (f) using the determinism. This burst synchronization domain occurs for values of $\varepsilon_{\text{int}}$ at least four times smaller than the asymptotic value observed for the threshold of stable bursting synchronization. For vanishing values of $\varepsilon_{\text{ext}}$, the influence of one network on the other is negligible and as recently discussed [10], small values of $\varepsilon_{\text{int}}$ make the network to show locally stable but globally unstable asymptotic states, where intermittent phase synchronization is observed [10]. Further increases of $\varepsilon_{\text{int}}$ results in a transition to a stable phase synchronized state, what we call burst synchronization in Fig. 2. Large values of the $\varepsilon_{\text{ext}}$ imply in an external current $l_{\text{ext}}$ strong enough to modulate the behavior of each neuron and the intrinsic differences among neuron behaviors are suppressed.

Increasing $\varepsilon_{\text{ext}}$, and for intermediate values of $\varepsilon_{\text{int}}$ it is observed a phase desynchronization domain (PD) resulting from a combined destructive effect of $\varepsilon_{\text{ext}}$ and $\varepsilon_{\text{int}}$. This area the level of synchronization measured by the order parameter fluctuates around to that one expected for a random distribution of phases and given by $R_{\text{Residual}} \sim 1/\sqrt{N} \approx 0.016$ [66] for a network of 4,096 oscillators (see inset of Fig. 4(b)). As $\varepsilon_{\text{int}}$ grows a transition area is observed and finally a stable bursting synchronization domain is again reached. The global bursting synchronization is inferred since panels (a,b), (d,e) and (g,h) are similar to panels (c), (f) and (i) respectively. For vanishing values of $\varepsilon_{\text{int}}$ and growing values of $\varepsilon_{\text{ext}}$, the network also displays an non-monotonic transition to stable BS, as observed in the region $8 \times 10^{-4} \leq \varepsilon_{\text{ext}} \leq 24 \times 10^{-4}$. Such results seem to be consistent with the fact that, in this case, $\varepsilon_{\text{ext}}$ makes the same hole of $\varepsilon_{\text{int}}$ for vanishing values $\varepsilon_{\text{ext}}$, modulating the bursting nature of the neurons, generating a BS. For larger values of the $\varepsilon_{\text{ext}}$ and small or intermediate values of $\varepsilon_{\text{int}}$ the network suffers another transition from bursting (BS) to spike (SS) synchronization. In this region the external coupling between network, $l_{\text{ext}}$ in Eq. (2), is composed of two frequencies, a low one related to the burst frequencies and a high one associated to the spike frequencies. As $\varepsilon_{\text{ext}}$ grows the external current works as a forcing for both networks, imposing a new high frequency modulation that results in a spike synchronization. For larger values of $\varepsilon_{\text{int}}$ just BS is observed for all
Fig. 2. General scenario of synchronization as function of internal ($\varepsilon_{\text{int}}$) and external ($\varepsilon_{\text{ext}}$) couplings. Panels (a), (b) and (c) depict the mean value of the Kuramoto order parameter for network 1, network 2 obtained from Eq. (19) and global network, Eq. (20). Panels (d), (e) and (f) show mean value of the determinism, Eq. (23) from network 1, network 2 and global neural system. Panels (g), (h) and (i) display the standard deviation of the local field potential, Eq. (24) for the same situation explored in panels (a-f). BS and SS intend for burst and spike synchronization domains, PD localizes the phase desynchronized domains while TR are transition domains.

Simulated intervals of $\varepsilon_{\text{ext}}$ since for this regime the high frequency modulation of $I_{\text{ext}}$ is again lost. An immediate conclusion is that SS domains occur for large $\varepsilon_{\text{ext}}$ but only conjugated to small or moderate $\varepsilon_{\text{int}}$ since high values of $\varepsilon_{\text{int}}$ destroy the high frequency modulation of $I_{\text{ext}}$, inhibiting SS and giving rise just to BS on the network.

The scenario depicted here by a network of networks and the role played by internal and external couplings should be better understood since internal and external connections are related to distinct neural mechanisms in real networks. All these features are observed using Kuramoto order parameter as well as the determinism. The standard deviation of the mean field also brings some similar results to the analyses, but in this case the evidences are less pronounced, showing the importance of the determinism in the analyses based on just mean field. Nevertheless, the use of the standard deviation must be used to infer (des)synchronization domains of the network evidenced by the determinism, namely low values of $\Delta$ and standard deviation lead to PD, large values of $\Delta$ and moderate values of the deviation characterize BS, small values of
Δ conjugated to large values of the deviation lead to SS. In particular the small values of Δ for the SS domain are justified since the synchronized spikes impose a smaller determinism to the time series of the mean field. So Δ and the standard deviation of the mean field give results similar to the order parameter, characterizing all synchronization domains of the network. Since the Kuramoto order parameter is computed over the phases defined by Eq. (15), it does not quantify spike synchronization. In this case, R ≈ 1 means phase or burst as well as spike synchronizations. The recurrence parameter Δ is computed over the mean field of each network defined by Eq. (6) or the global mean field defined by Eq. (7). So it can capture differences among phase and spike synchronizations (BS and SS). For the phase synchronization, R and Δ grow and decay in phase. But for the spike regime, R grows but Δ decays since from the recurrence point of view the spike regime is less deterministic (due to the spikes observed in the mean field) than the phase synchronized one (see Fig. 6). Different values of the standard deviation computed for the spike and phase synchronization regimes corroborate the fact that both regimes have distinct dynamical properties. The standard deviation is used to reinforce the results of Δ.

Fig. 3 depicts the mean value of Kuramoto order parameter (black line), determinism (red line) and the standard deviation of the mean field (blue line) as a function of the internal coupling for two values of external coupling (a) $\varepsilon_{\text{ext}} = 3 \times 10^{-4}$, a burst (phase) synchronization (BS) scenario and (b) $\varepsilon_{\text{ext}} = 22 \times 10^{-4}$ a spike synchronization (SS) situation. For the case of BS, all quantifiers follow the same trend, on the other hand, when the SS is reached, the determinism decays and the other quantifiers increase (see panel (b)).

Details of the contribution of the external coupling to the synchronization phenomena of the network of networks are shown in Fig. 4, where it is depicted the mean value of the Kuramoto order parameter as a function of $\varepsilon_{\text{ext}}$ for each network (black and red lines), Eq. (19), and for the global network (blue line), Eq. (20), for 4 representative values of $\varepsilon_{\text{int}}$. For a
vanishing $\epsilon_{\text{int}} = 8 \times 10^{-4}$. Fig. 4(a) shows that the increase of $\epsilon_{\text{ext}}$ makes the network to transit very quickly to a BS domain. An additional increase of $\epsilon_{\text{ext}}$ leads the network to a subtle partial desynchronization, denouncing a possible explosive (des)synchronization, as observed in [27]. A further increase of $\epsilon_{\text{ext}}$ leads the network to a SS domain. Fig 4(b) depicts the case of coupling induced PD. For domains of moderate $\epsilon_{\text{int}} = 14 \times 10^{-3}$, the PD domain extends until $\epsilon_{\text{ext}} = 10 \times 10^{-4}$. In this regime the synchronization level of the network is very low, as observed in the inset graph where the dashed line gives the expected value of the order parameter for random selected phases [66]. For larger external coupling, PD gives place to a progressive and monotonic (sigmoid shaped) transition to BS and finally SS domains ($R \approx 1$). For relatively larger value of $\epsilon_{\text{int}} = 26.4 \times 10^{-3}$ (c) the PD domain is absent and the network transits monotonically to BS and SS domains as a function of the external coupling. Once again the network depicts the traditional sigmoid shaped transition from partial synchronized to synchronized states, characteristic of non-inertial oscillators [59]. For larger internal coupling, Fig 4 (d), $\epsilon_{\text{int}} = 48 \times 10^{-3}$ the network exhibits BS domains ever for a vanishing $\epsilon_{\text{ext}}$. The level of synchronization is almost independent of the value of the external coupling. Nevertheless the asymptotic level of synchronization is lower than observed for smaller values of the $\epsilon_{\text{int}}$. For this domain SS seems to be suppressed and only BS can be acquired.

The scenario described so far shows that the interplay between different values of $\epsilon_{\text{int}}$ and $\epsilon_{\text{ext}}$ allows the network to display distinct synchronization characteristics, from a complete desynchronization till almost complete spike synchronization, both phenomena absent when just on network is studied.

Closer analyses of dynamical characteristics of the network bring more information of the synchronization domains and explain better the main scenario depicted in Figs. 2 and 4. Fig. 5 depicts the neuron membrane potential for PD (a), SS (b) and BS(c) domains. The PD domain dynamics is evident on panel (a) that depicts a completely incoherent network dynamics. The SS domains can be characterized by almost white horizontal lines in panel (b) since lighter gray and white tones denote higher values of the neuron membrane potential, evidencing the spatio-temporal coherence of the membrane potential of all neurons occurring even in high frequency spike regimes. Similar SS scenario was observed in [44]. Finally, panel (c) depicts the traditional raster plot observed for BS, where no fast scale spike synchronization is observed but only synchronization in the slow time scale [67].

Fig. 6 shows the characteristic of the mean field potential of each network (black and red lines) and global mean field (blue line) described by Eqs. (6) and (7) respectively for PD (panel (a)), SS (panel (b)) and BS (panel (c)) for a representative set of couplings sampled in Fig. 5. For the PD case, all mean local field potential depicts a vanishing amplitude oscilla-
tion around a negative value, indicating the absence of synchronization. On the other hand for the SS case, almost all high frequency individual spikes can be observed. The time series distinguish two time scales synchronized signals, a slow one indicating burst synchronization and a fast one indicating the spike synchronization. Similar behavior between global and individual signals denounces the global burst and spike synchronizations of the network. At last, for the BS case, it is observed only the slow frequency synchronization [11].

Another approach to analyze network synchronization can be done using the spatial standard deviation of the membrane potential signal of each neuron

$$\phi(t) = \sqrt{\frac{1}{N} \sum_{i=1}^{N} (V_i(t) - \overline{V}(t))^2}.$$  \hspace{1cm} (25)

For desynchronized networks small amplitude stochastic oscillations of the signal of $\phi(t)$ are expected due to the incoherent effect resulting from a large number of out of phase neurons. This behavior is clear in the black curve of Fig. 7 that depicts results for the network with $\varepsilon_{\text{ext}} = 5 \times 10^{-4}$ and $\varepsilon_{\text{int}} = 14 \times 10^{-3}$, representative of PD domains. The red line of Fig. 7 shows the spike domain of synchronization (SS), where the network is characterized by $\varepsilon_{\text{ext}} = 25 \times 10^{-4}$ and $\varepsilon_{\text{int}} = 26.4 \times 10^{-3}$. In this case the coherent effect of a large amount of spike synchronized neurons is evident, leading $\phi(t)$ to show clear sequence of high frequency spikes. The blue line shows the BS domain where $\varepsilon_{\text{ext}} = 30 \times 10^{-4}$ and $\varepsilon_{\text{int}} = 48 \times 10^{-3}$. In this case only the slow frequency oscillations due to the synchronized bursting nature of the neurons are observed.

Moreover, it is possible to evaluate the temporal average of $\phi(t)$, given by $\langle \phi \rangle = \frac{1}{T} \int_0^T \phi(t) dt$ [20]. For cases considered in Fig. 7, we expect to obtain smallest values for SS domains due to the large level of synchronization of this case. In fact, for PD domains, we obtain $\langle \phi \rangle = 10.48$, while for SS domains we obtain a lower value, $\langle \phi \rangle = 6.27$. For BS, $\langle \phi \rangle = 9.04$ points out to a intermediate level of synchronization.

5. Conclusions

We have studied the dynamical properties of the parameter space $\varepsilon_{\text{int}} \times \varepsilon_{\text{ext}}$ of a neural network composed of two coupled (sub)network of 2048 Hodgkin–Huxley type neurons, under small-world internal topology and externally coupled through individual network mean field. We have shown that identical coupled neurons show distinct complex collective behaviors as a function of internal and external coupling strengths. In special, varying the internal and external coupling strengths, the network displays domains of anomalous (non-monotonic) synchronization, coupling induced desynchronization, bursting and spike synchronization.

The quantification of synchronization properties is done based on data from each neuron through the computation of the Kuramoto order parameter and using the recurrence quantifier known as the determinism and obtained using just mean field of the network, a simpler experimental data. Statistical tools have also been used to corroborate and to complement the recurrence analyses.

The model itself and all synchronization features studied here have biologic interest since it extends the knowledge about synchronization of complex networks resulting in a better understanding of the role of internal and external couplings of a neural network of networks. The results can find applications in healthy and unhealthy scenarios, particularly, those associated to the lack or excess of many kind of synchronization [31,32]. It also can support theoretical background to the understanding of special details associated to collective phenomena of neurons related to neural dysfunctions [33–35].

The great diversity of dynamical behaviors found in the study and imposed by the interplay between internal and external couplings reveals the importance of neural networks composed of network of networks, in special, the observation that
the small-world topology allows the existence of coupling induced desynchronization domains, where the synchronization level of the network drops to values as low as those expected for randomly selected phase. Such desynchronization domains are surrounded in the parameter space $\epsilon_{\text{int}} \times \epsilon_{\text{ext}}$ by domains of almost complete spike synchronization, allowing the network to jump from one domain to the other as internal and/or external coupling strengths are slightly varied showing the great malleability of this kind networks.

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