Combined effect of chemical and electrical synapses in Hindmarsh-Rose neural networks on synchronization and the rate of information

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In this work we studied the combined action of chemical and electrical synapses in small networks of Hindmarsh-Rose (HR) neurons on the synchronous behavior and on the rate of information produced (per time unit) by the networks. We show that if the chemical synapse is excitatory, the larger the chemical synapse strength used the smaller the electrical synapse strength needed to achieve complete synchronization, and for moderate synaptic strengths one should expect to find desynchronous behavior. Otherwise, if the chemical synapse is inhibitory, the larger the chemical synapse strength used the larger the electrical synapse strength needed to achieve complete synchronization, and for moderate synaptic strengths one should expect to find synchronous behaviors. Finally, we show how to calculate semianalytically an upper bound for the rate of information produced per time unit (Kolmogorov-Sinai entropy) in larger networks. As an application, we show that this upper bound is linearly proportional to the number of neurons in a network whose neurons are highly connected.

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I. INTRODUCTION

Intercellular communication is one of the most important characteristics of all animal species because it makes the many components of such complex systems operate together. Among the many types of intercellular communication, we are interested in the communication among brain cells, the neurons, that exchange information mediated by chemical and electrical synapses [1].

The uncovering of the essence of behavior and perception in animals and human beings is one of the main challenges in brain research. While the behavior is believed to be linked to the way neurons are connected (the topology of the neural network and the physical connections among the neurons), the perception is believed to be linked to synchronization. This comes from the binding hypothesis [2], which states that synchronization functionally binds neural networks coding the same feature or objects. This hypothesis raised one of the most important contemporary debates in neurobiology [3] because desynchronization seems to play an important role in perception as well. The binding hypothesis is mainly supported by the belief that a convenient environment for neurons to exchange information appears when they become more synchronous.

Despite the explosive growth in the field of complex networks, it is still unclear for which conditions synchronization implies information transmission and it is still unclear which topology favors the flowing of information. Additionally, most of the models being currently studied in complex networks consider networks whose nodes (such as neurons) are either linearly or nonlinearly connected. But, recent works have shown that neurons that were believed to make only nonlinear (chemical) synapses make also simultaneously linear (electrical) synapses [4–8]. To make the scenario even more complicated, neurons connect chemically in an excitatory and/or an inhibitory way. In this work, we aim to study the relationship between synchronization and information transmission in such neural networks, whose neurons are simultaneously connected by chemical and electrical synapses.

The electrical synapse is the result of the potential difference between the neurons and causes an immediate physiological response of the latter one, linearly proportional to the potential difference. The chemical synapse is mediated by the exchange of neurotransmitters from the pre to the postsynaptic neuron and can only be released once the presynaptic neuron membrane achieves a certain action potential. The chemical interaction is described by a nonlinear function [9].

While the electrical synapses between neurons is localized in the neuron cell and therefore it is a local connection, the chemical synapse is in the neuron axon and is therefore mainly responsible for the nonlocal nature of the synapses.

Chemical synapses can be inhibitory and excitatory. When an inhibitory neuron spikes (the presynaptic neuron), a neuron connected to it (the postsynaptic neuron) is prevented from spiking. As shown in Ref. [10], inhibition promotes synchronization. When an excitatory neuron spikes, it induces the postsynaptic neuron to spike. Several types of synchronization were found in networks of chaotic neurons coupled with only electrical synapses. One can have complete synchronization, generalized synchronization and phase synchronization, the latter appearing for small synapse strength [11]. Complete synchrony strongly depends on the network structure and the number of cells. In networks of chemically coupled neurons [12], the net input a neuron receives from synaptic neurons emitting synchronized spikes is proportional to the number of connected units. Hence, for chemical synapses, if all the nodes in the network have the same degree, synchronization will be enhanced; if different nodes have different degrees, synchronization will be hampered [13]. In fact, Ref. [14] has shown analytically that the stability of the completely synchronous state in such net-

works only depends on the number of signals each neuron receives, independent of all other details of the network topology.

The most obvious possible role of electrical synapses within networks of inhibitory neurons is to couple the membrane potential of connected cells, leading to an increase in the probability of synchronized action potentials. This synchronous firing could coordinate the activity of other cortical cell populations. For example, it has been reported that the introduction of electrical synapses among GABAergic neurons that are also chemically connected can promote oscillatory rhythmic activity [6]. These possibilities have been addressed experimentally by several investigators and have been reviewed recently [7,8,15].

Motivated by these observations and also by the fact that the behavior of microcircuitry in the cerebral cortex is not well understood, we analyze the combined effect of these two types of synapses on the stability of the synchronous behavior and on the information transmission in small neural networks. In order to deal with this problem analytically we consider idealistic networks, composed of equal neurons with mutual connections of equal strengths (see Sec. II). A basic assumption characterizing most of the early works on synchronization in neural networks is that, by adding a relatively small amount of electrical synapse to the inhibitory synapse, one can increase the degree of synchronization far more than a much larger increase in inhibitory conductance [16,17].

Our results agree with this finding in the sense that for larger inhibitory synaptic strengths complete synchronization can only be achieved if the electrical synapse strength is larger than a certain amount. But in contrast, we found that for moderate inhibitory synaptic strengths, the larger the chemical synapse strength is the larger the electrical synapse strength needs to be to achieve complete synchronization. Additionally, we introduce in this work analytical approaches to understand when complete synchronization should be expected to be found and what is the relation of that with the amount of information produced by the network.

Information is an important concept [18]. It measures how much uncertainty one has about an event before it happens. It is a measure of how complex a system is. Very complicated and higher dimensional systems might be actually very predictable, and as a consequence the content of information of such a system might be very limited. But measuring the amount of information is something difficult to accomplish. Normally, there is always some bias or error on the calculation of it [19], and one has to rely on alternative approaches. Measuring the Shannon entropy of a chaotic trajectory is extremely difficult because one has to calculate an integral of the probability density of a fractal chaotic set. But for chaotic systems that have absolutely continuous conditional measures, one can calculate Shannon's entropy per unit of time, a quantity known as Kolmogorov-Sinai (KS) entropy [20], by summing all the positive Lyapunov exponents [21]. A system that has absolutely continuous conditional measures is a system whose trajectory continuously distribute along unstable directions. More precisely, systems whose trajectories continuously distribute along unstable manifolds at points that have positive probability measure. These systems form a large class of nonuniformly hyperbolic systems [22]: the Hénon family; Hénon-like attractor arising from homoclinic bifurcations; strange attractors arising from Hopf Bifurcations (e.g., Rössler oscillator); some classes of mechanical models with periodic forcing. The result in Ref. [21] extends a previous result by Pesin [23] that demonstrated that for hyperbolic maps, the KS entropy is equal to the sum of the positive Lyapunov exponents. We are not aware of any rigorous result proving the equivalence of the KS entropy and the sum of Lyapunov exponent for the Hindmarsh-Rose neural model neither to a network constructed with them. But the chaotic attractors arising in this neuron model are similar to the ones appearing from Homoclinic bifurcations. Additionally, for two coupled neurons, we show in Sec. VII (using the nonrigorous methods described in Appendix) that a lower bound estimation of the KS entropy is indeed close to the sum of all the positive Lyapunov exponents. Despite the lack of a rigorous proof, we will assume that the results in Refs. [21,22] apply in here in the sense that the sum of the positive Lyapunov exponents provide a good estimation for the KS entropy.

The KS entropy for chaotic networks has another important meaning. It provides one the so called network capacity [11], the maximal amount of information that all the neurons in the network can simultaneously process (per unit of time). A network that produces information at a higher rate is more unpredictable and more complex. Arguably, the network capacity is an upper bound for the amount of information that the network is capable of processing from external stimuli. In Ref. [11] we discuss a situation were that is indeed the case.

To understand the scope of this paper and the methods used, we first justify the chosen network topologies in Sec. II. Then, in Sec. III, we describe the dynamical system of our network and derive the variational equations of it in the eigenmode form, a necessary analytical tool in order to be able to study the onset of complete synchronization (CS) and to calculate the rate of information produced by the network. Complete synchronization happens when the trajectories of all neurons are equal.

Our main results can be summarized as in the following:

(i) We show (Secs. IV and V) how one can calculate the synaptic strengths (chemical and electrical) necessary for a network of N neurons to achieve complete synchronization when one knows the strengths for which two mutually coupled neurons become completely synchronous.

(ii) We show numerically (Sec. VI) parameter space diagrams indicating the electrical and chemical synapse strengths responsible to make complete synchronization to appear in different networks. The analytical derivation from Sec. V are found to be sufficiently accurate. There are two scenarios for the appearance of complete synchronization for inhibitory networks. If the chemical synapse strength is small, the larger the chemical synapse strength used the larger the electrical synapse strength needed to be to achieve complete synchronization. Otherwise, if the chemical synapse strength is large, complete synchronization appears if the electrical synapse strength is lager than a certain value. In excitatory networks both synapses work in a constructive way to promote complete synchronization: the larger the

chemical synapse strength is the smaller the electrical synapse strength needs to be to achieve complete synchronization.

(iii) We show (Secs. VII) that the sum of the positive Lyapunov exponents provides a good estimation for the KS entropy. Additionally, we show that there are optimal ranges of values for the chemical and electrical strengths for which the amount of information is large.

(iv) If complete synchronization is absent, we show (Sec. VIII) that while in inhibitory networks one can typically expect to find high levels of synchronous behavior, in excitatory networks one is likely to expect desynchronous behavior.

(v) We calculate (Sec. IX) an upper bound for the rate of information produced per time unit (Kolmogorov-Sinai entropy) by larger networks using the rate at which information is produced by two mutually coupled neurons.

II. TOPOLOGY OF THE STUDIED NETWORKS

In order to consider the combined action of these two different types of synapses, we need to consider in our theoretical approach idealistic networks, constructed by nodes possessing equal dynamics and particular coupling topologies such that a synchronization manifold exists and CS is possible. If we had studied networks whose neurons were exclusively connected by electrical means, we could have considered networks with arbitrary topologies. On the other hand, if we had studied networks whose neurons are exclusively connected by chemical means, we would have considered networks whose neurons receive the same number of chemical connections. These conditions are the same ones being usually made to study complete synchronization in complex networks [14,24].

In order to analytically study networks formed by neurons that make simultaneously chemical and electrical connections, we have not only to assume that the neurons have equal dynamics and that every neuron receives the same number of chemical connections coming from other neurons, but also that the Laplacian matrix for the electrical synapses (that provides topology of the electrical connections) and the Laplacian matrix for the chemical synapses commute, as we clarify later in this paper. Naturally, there is a large number of Laplacian matrices that commute. In this work we construct networks that are biologically plausible. Since the electrical connection is local, we consider that neurons connect electrically only to their nearest neighbors. Since neurons connected chemically make a large number of connections (of the order of 1000), it is reasonable to consider that for small networks the neurons that are chemically connected are fully connected, i.e., every neuron connects to all the other neurons. Notice however that while reciprocal connections are commonly found in electrically coupled neurons, which is not typical for chemically connected neurons.

Since our small networks are composed of no more than eight neurons, we make an abstract assumption and admit another possible type of network in which neurons that are connected electrically can also make nonlocal connections, allowing them to become fully connected to the other neurons. Notice, however, that our theoretical approach remains valid for larger networks that admit a synchronization manifold.

III. NETWORKS OF COUPLED NEURONS AND MASTER STABILITY ANALYSIS

The dynamics of the Hindmarsh-Rose (HR) model for neurons is described by

$$\dot{p} = q - ap^3 + bp^2 - n + I_{ext},$$

$$\dot{q} = c - dp^2 - q,$$

$$\dot{n} = r[s(p - p_0) - n], \tag{1}$$

where p is the membrane potential, q is associated with the fast current, Na^+ or K^+, and n with the slow current, for example, Ca^{2+}. The parameters are defined as $a=1$, $b=3$, $c=1$, $d=5$, $s=4$, $r=0.005$, $p_0=-1.60$ and $I_{ext}=3.2$ where the system exhibits a multi-time-scale chaotic behavior characterized as spike bursting.

The dynamics of a neural networks of N neurons connected simultaneously by electrical (a linear coupling) and chemical (a nonlinear coupling) synapses is described by

$$\dot{p}_i = q_i - ap_i^3 + bp_i^2 - n_i + I_{ext} - g_n(p_i - V_{syn})\sum_{j=1}^{N} \mathbf{C}_{ij}S(p_j) + g_l\sum_{j=1}^{N} \mathbf{G}_{ij}\mathbf{H}(p_j),$$

$$\dot{q}_i = c - dp_i^2 - q_i,$$

$$\dot{n}_i = r[s(p_i - p_0) - n_i], \tag{2}$$

$(i,j)=1,\ldots,N$, where N is the number of neurons.

In this work we consider that $\mathbf{H}(p_i)=p_i$. But we preserve the function $\mathbf{H}(p_i)$ in our remaining analytical derivation to maintain generality. The chemical synapse function is modeled by the sigmoidal function

$$S(p_j) = \frac{1}{1 + e^{-\lambda(p_j - \Theta_{syn})}}, \tag{3}$$

with $\Theta_{syn}=-0.25$, $\lambda=10$, and $V_{syn}=2.0$ for excitatory and $V_{syn}=-2.0$ for inhibitory. For the chosen parameters and all the networks that we have worked $|p_i|<2$ and the term $(p_i - V_{syn})$ is always negative for excitatory networks and positive for inhibitory networks. If two neurons are connected under an inhibitory (excitatory) synapse then, when the presynaptic neuron spikes, it induces the postsynaptic neuron not to spike (to spike).

The matrix $\mathbf{G}_{ij}$ describes the way neurons are electrically connected. It is a Laplacian matrix and therefore $\Sigma_j \mathbf{G}_{ij}=0$. The matrix $\mathbf{C}_{ij}$ describes the way neurons are chemically connected and it is an adjacent matrix, therefore $\Sigma_j \mathbf{C}_{ij}=k$, for all i. For both matrices, a positive off-diagonal term placed in the line i and column j means that neuron i perturbs neu-

ron j with an intensity given by $g_l\mathbf{G}_{ij}$ (or by $g_n\mathbf{C}_{ij}$). Since the diagonal elements of the adjacent matrix are zero, k represents the number of connections that neuron i receives from all the other neurons j in the network. This is a necessary condition for the existence of the synchronous solution [14] by the subspace $P=P_1=P_2=\ldots=P_N$, $P_i=(p_i,q_i,n_i)$.

Under these assumptions and, as previously explained, we consider networks with three topologies: **topology I**, when all the neurons are mutually fully (all-to-all) connected with chemical synapses and mutually diffusively (nearest neighbors) connected with electrical synapses; **topology II**, when all the neurons are mutually fully connected with chemical synapses and mutually fully connected with electrical synapses; **topology III**, when all the neurons are mutually diffusively (nearest neighbors) connected with chemical and electrical synapses. We consider networks with two, four, and eight neurons. By nearest neighbors, we consider that the neurons are forming a closed ring.

The synchronous solutions $P=(p,q,n)$ take the form

$$\dot{p} = q - ap^3 + bp^2 - n + I_{ext} - g_n k(p - V_{syn})S(p),$$

$$\dot{q} = c - dp^2 - q,$$

$$\dot{n} = r[s(p - p_0) - n]. \tag{4}$$

The variational equation of the network in Eq. (2) [calculated around the synchronization manifold Eq. (4)] is given by

$$\begin{aligned}\dot{\delta p}_i &= \delta q_i - 3ap_i^2\delta p_i + 2bp_i\delta p_i - \delta n_i - g_n(p_i - V_{syn})S'(p)\\ &\times\left(k\delta p_i + \sum_{j=1}^{N}\tilde{\mathbf{G}}_{ij}\delta p_j\right) - kg_nS(p)\delta p_i\\ &+ g_l\sum_{j=1}^{N}\mathbf{G}_{ij}D\mathbf{H}(p)\delta p_i,\end{aligned}$$

$$\dot{\delta q}_i = 2d\delta p_i - \delta q_i,$$

$$\dot{\delta n}_i = r(s\delta p_i - \delta n_i). \tag{5}$$

The matrix $\mathbf{C}_{ij}$ has been transformed to a Laplacian matrix by $\tilde{\mathbf{G}}=\mathbf{C}_{ij}-k\mathbb{I}$. $D\mathbf{H}(p)$ represents the derivative of $\mathbf{H}$ with respect to p, which in this work equals 1.

The term $S'(p)$ refers to the spatial derivative $\frac{dS(p)}{dp}$ and equals

$$S'(p) = \frac{\lambda\exp^{-\lambda(p-\Theta_{syn})}}{[1+\exp^{-\lambda(p-\Theta_{syn})}]^2}. \tag{6}$$

Notice that if $S(p)=1$ (what happens for $p\gg\Theta_{syn}$), then $S'(p)=0$ and if $S(p)=0$ ($p\ll\Theta_{syn}$), then $S'(p)=0$. $S'(p)$ is not zero when the value of $S(p)$ changes from 1 to 0 (and vice-versa) and $p\approx\Theta_{syn}$.

Equation (5) is referred to as the variational equation and is often the starting point for determining whether the synchronization manifold is stable. This equation is rather complicated since, given arbitrary synapses g_n and g_l, it can become quite higher dimensional. Also the coupling matrices $\mathbf{G}$ and $\tilde{\mathbf{G}}$ can be arbitrary making the situation to become even more complicated. However, assuming that whenever there is a chemical synapse (and $g_n>0$), the matrices $\mathbf{G}$ and $\tilde{\mathbf{G}}$ commute, then the problem can be simplified by noticing that the arbitrary state δX (where $\delta X=(\delta p_i,\delta q_i,\delta n_i)$ is the deviation of the ith vector state from the synchronization manifold) can be written as $\delta X=\Sigma_{i=1}^{N}\mathbf{v}_i\otimes\kappa_i(t)$, with $\kappa_i(t)=(\eta_i,\psi_i,\varphi_i)$. The $\mathbf{v}_i$ be the eigenvector and γ_i and $\tilde{\gamma}_i$ the corresponding eigenvalues for the matrices $\mathbf{G}$ and $\tilde{\mathbf{G}}$, respectively. So, if that is the case, by applying $\mathbf{v}_j^T(t)$ (with $\mathbf{v}_j^T(t)\cdot\mathbf{v}_i=\delta_{ij}$ where δ_{ij} is the Kronecker delta), to the left (right) side of each term in Eq. (5) one finally obtains the following set of N variational equations in the eigenmode,

$$\dot{\eta}_j = (2bp - 3ap^2)\eta_j - \varphi_j + \psi_j - \Gamma(p)\eta_j,$$

$$\dot{\psi}_j = 2d\eta_j - \psi_j,$$

$$\dot{\varphi}_j = r(s\eta_j - \varphi_j),$$

$$j = 1,2,3,\ldots,N, \tag{7}$$

where the term $\Gamma(p)$ is given by

$$\Gamma(p) = kg_nS(p) - g_n(V_{syn} - p)S'(p)(k + \tilde{\gamma}_j) - g_l\gamma_j \tag{8}$$

in which γ_j (with $\gamma_1=0$, and $\gamma_j<0$, $j\geq 2$) are the eigenvalues of $\mathbf{G}$ and $\tilde{\gamma}_j$ are the eigenvalues of $\tilde{\mathbf{G}}$. The eigenvalues γ_j are negative because the off-diagonal elements of $\mathbf{G}$ are positive.

TABLE I. Values of γ_2 in absolute value and k for the considered networks.

	All-to-all	Nearest-neighbor
$N=2$	$\gamma_2=2$, $k=1$	$\gamma_2=2$, $k=1$
$N=4$	$\gamma_2=4$, $k=3$	$\gamma_2=2$, $k=2$
$N=8$	$\gamma_2=8$, $k=7$	$\gamma_2=0.585786402$, $k=2$

For networks with $N=2$ we have that $|\gamma_2|=2$ and $k=1$, meaning that the neurons are connected in an all-to-all fashion. For networks with $N=4$, if the neurons are connected in an all-to-all fashion, we have that $|\gamma_2|=4$ and $k=3$ or if the neurons are connected with their nearest neighbors we have that $|\gamma_2|=2$ and $k=2$. For $N=8$, $|\gamma_2|=8$ and $k=7$ (all-to-all) and $|\gamma_2|=0.585\,786\,402$ and $k=2$ (nearest neighbor). These values are placed in Table I for further reference.

The previous equations are integrated using the fourth-order Range-Kutta method with a step size of 0.001. The calculations of the Lyapunov exponents are performed considering a time interval of 600 [sufficient for a neuron to produce approximately 600 spikes ($p>0$)]. We discard a transient time of 300, corresponding to 300 000 integrations.

IV. STABILITY ANALYSIS

The stability of the synchronization manifold can be seen from the perspective of control [14,25–27] by imagining that

the term $\Gamma(p)$ stabilizes Eq. (7) at the origin. This term can be interpreted as the main gain of a feedback control law $u(t)=\Gamma(p)\eta_j$ such that η_j (respectively, ψ_j and φ_j) tends to 0 as t tends to infinity. In fact, the controlling force $u(t)=\Gamma(p)\eta_j$ could be designed with no previous knowledge of the system under consideration assuming that it has a parametric dependence. A drawback of such a general control approach is that it leads to nonfeedback control strategy, which have not guaranteed stability margins. More robust approaches for determining the structural stability of the synchronization manifold of systems whose equations of motion are partially unknown have been recently developed [25–27].

In this work, however, we determine the stability of the synchronization manifold from the master stability analysis of Refs. [14,24]. A necessary condition for the linear stability of the synchronized state is that all Lyapunov exponents associated with γ_j and/or $\tilde{\gamma}_j$ for each $j=2,3,\ldots,N$ (the directions transverse to the synchronization manifold) are negative. This criterion is a necessary condition for complete synchronization only locally, i.e., close to the synchronization manifold.

V. RESCALING OF EQS. (4) and (7)

When working with networks formed by nodes possessing equal dynamical rules, we wish to predict the behavior of a large network from the behavior of two coupled nodes. That can always be done whenever the equations of motion of the network can be rescaled into the form of the equations describing the two coupled nodes. That means that, given that two mutually coupled neurons completely synchronize for the electrical and chemical synapse strengths $g_l^*(N=2)$ and $g_n^*(N=2)$, respectively, then it is possible to calculate the synapse strengths $g_l^*(N)$ and $g_n^*(N)$ for which a network composed by N nodes completely synchronizes.

In order to rescale the equations for the synchronization manifold and for its stability, Eqs. (4) and (7), respectively, we need to preserve the form of these equations as we consider different networks. Concerning Eq. (7), we need to show under which conditions it is possible to have $\Gamma(p,N=2)=\Gamma(p,N)$, where Γ is the term responsible to make the stability of the synchronization manifold to depend among other things on the topology of the network and on the coupling function $S(p)$.

Notice that $S(p)$ assumes for most of the time either the value 0 or 1. For some short time interval $S(p)$ changes its value from 0 to 1 (and vice-versa) and at this time $S'(p)$ is different from zero [see Eqs. (3) and (6)]. For that reason we will treat $S'(p)$ as a small perturbation in our further calculations and will ignore it, most of the times. That leave us with two relevant terms in both Eqs. (4) and (7) that need to be taken into consideration in our rescaling analyses. These terms are $g_l\gamma_j$ and $kg_nS(p)$. While the first term comes from the electrical synapse, the second term comes from the chemical synapse.

The first term depends on the eigenvalues of $\mathbf{G}_{ij}$ (which varies according to the number of nodes and the topology of the network) and on the synapse strength g_l. If this term assumes a particular value for a given network, for another network one can suitably vary g_l in order for the whole term to assume this same value in the other network. So, the term $g_l\gamma_j$ can always be rescaled by finding an appropriate value of g_l.

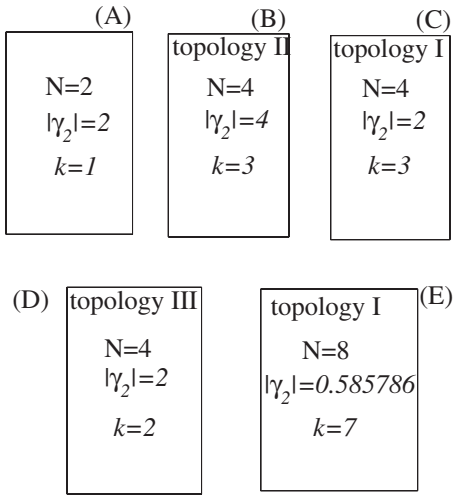

FIG. 1. The topology of the networks considered in Figs. 2–5 and the values of N, $|\gamma_1|$, and k.

The rescaling of the second term, $kg_nS(p)$ is more complicated because it depends on the trajectory (p) of the attractor. Naturally, we wish to find a proper rescaling for the function $S(p)$, which implies that the attractors appearing as solutions on the synchronization manifold should present some kind of invariant property.

In order to find such an invariant property, we study the time average $\langle S(p)\rangle$ of the function $S(p)$ for attractors appearing as solutions of Eq. (4) for five network topologies. In Fig. 1 we show in the boxes (A–E) the values of N, $|\gamma_2|$, k, and the type of topology considered in the networks of Figs. 2–5.

The result for excitatory networks can be seen in Figs. 2(A)–2(E), which shows this value as a function of kg_n.

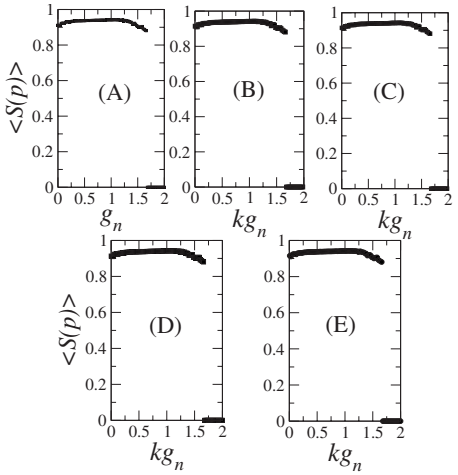

FIG. 2. (A–E) The value of $\langle S(p)\rangle$ with respect to a rescaled chemical synapse strength kg_n for excitatory networks with a configuration shown in Figs. 1(A)–1(E). Initial conditions of the neurons are set to be equal (and $g_l=0$).

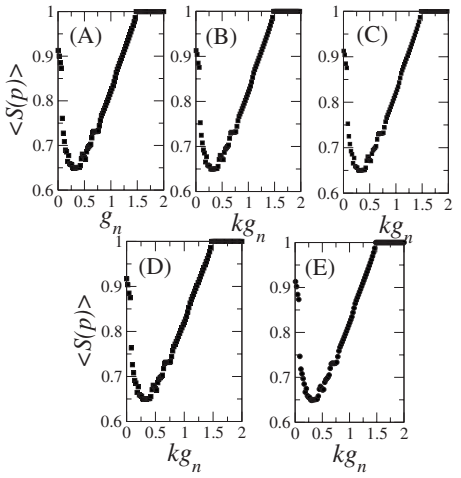

FIG. 3. (A)–(E) The value of $\langle S(p)\rangle$ with respect to a rescaled chemical synapse strength kg_n for inhibitory networks with a configuration shown in Figs. 1(A)–1(E). Initial conditions of the neurons are set to be equal (and $g_l=0$).

Apart from some small differences, the function $\langle S(p)\rangle$ remains invariant for the different networks considered. We identify two relevant values for $\langle S(p)\rangle$. Either $\langle S(p)\rangle \cong 0.9$, for $g_n < g_n^{(c)}$ or $\langle S(p)\rangle = 0$, for $g_n \geq g_n^{(c)} \cdot g_n^{(c)} \approx 1.67$.

We also find an invariant curve of $\langle S(p)\rangle$ for inhibitory networks. In Figs. 3(A)–3(E) we show this curve for the same networks of Fig. 2. For these networks, we define $g_n^{(c)} \approx 1.5$ as the value of g_n for which the curve of $\langle S(p)\rangle$ reaches its maximum. In the considered inhibitory networks, $\langle S(p)\rangle = 1$ is a consequence of the fact that the neurons loose their chaotic behavior and become a stable limit cycle. Notice that the value of $\langle S(p)\rangle$ does not depend on the value of the electrical synapse strength g_l. This is due to the fact that g_l is not present in the equations for the synchronization manifold [Eq. (4)].

Let us rescale Eq. (4). First notice that the average $\langle (p - V_{syn})\rangle$ has the same invariant properties of the average

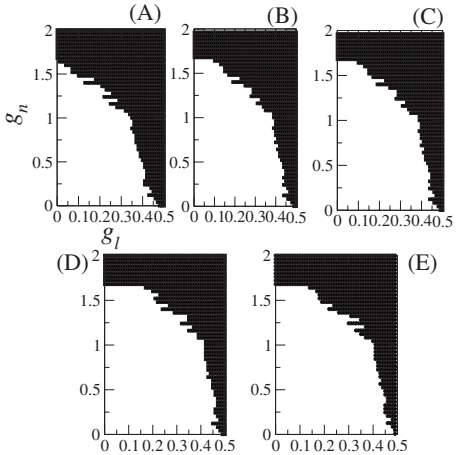

FIG. 4. Excitatory networks. Black points represent values of the synapse strengths for which all transversal conditional exponents are negative. In (B–E) the horizontal axis represent $g_l(N)|\gamma_2(N)|/2$ and the vertical axis kg_n. Initial conditions of the neurons are set to be equal.

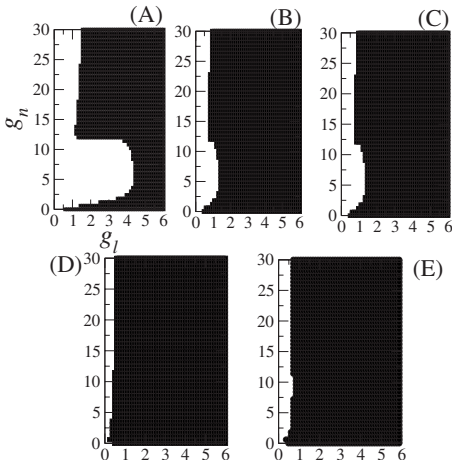

FIG. 5. Inhibitory networks. Black points represent values of the synapse strengths for which all transversal conditional exponents are negative. In (B–E) the horizontal axis represent $g_l(N)|\gamma_2(N)|/2$ and the vertical axis kg_n. Initial conditions of the neurons are set to be equal.

$\langle S(p)\rangle$. Then, we assume that both $S(p)$ and $(p - V_{syn})$ make small oscillations around their average value. That implies that $S(p)(p - V_{syn}) \cong \langle S(p)(p - V_{syn})\rangle$. From Figs. 2 and 3 we have that the average $\langle S(p,N)\rangle$ can be written as a function of $g_n(N)$, as well as $\langle (p - V_{syn})\rangle$. Therefore, we can write $\langle S(p)(p - V_{syn})\rangle$ as a function of $g_n(N)$. It is clear that the value of this average obtained for $g_n(N=2)$ should be approximately equal to the value obtained for $kg_n(N)$, and so this average function can be rescaled by $kg_n(N) \cong g_n(N=2)$. Therefore, Eq. (4) describing a large network can be rescaled into this same equation describing two mutually coupled neurons by

$$g_n(N) = \frac{g_n(N=2)}{k}. \tag{9}$$

Now, we need to show that it is also possible to do the same to Eq. (7), the equation responsible for the stability of the synchronous solution.

Assuming again that $S(p)$ make small oscillations around its average value allows us to write $\Gamma(p,N)$ as a function of $\langle S(p)\rangle$ as in $\Gamma(p,N) \cong kg_n(N)\langle S(p,N)\rangle - g_l(N)\gamma_j$. Notice from Figs. 2 and 3 that the average $\langle S(p,N)\rangle$ can be written as a function of $g_n(N)$. In order to rescale Eq. (7), describing a network of N nodes in terms of a network of 2 nodes, we need to have that $\Gamma(p,N) = \Gamma(p,N=2)$ leading to

$$kg_n(N)\langle S[g_n(N)]\rangle - \gamma_2 g_l(N) = g_n(N=2)\langle S[g_n(N=2)]\rangle + 2g_l(N), \tag{10}$$

where we have considered only the second largest eigenvalue γ_2, the one responsible for the stability of the synchronization manifold; we have ignored terms that appear together with S' in Γ.

We make now a reasonable hypothesis that if a stable synchronous solutions for Eq. (4) exists for $g_n(N=2) = g_n^*(N=2)$ (for a two mutually coupled neurons), then this same stable synchronous solution exists for $kg_n^*(N)$ (for a network

composed by N neurons mutually connected). This hypothesis is constructed from the observation that equivalent attractors can be found in different networks if the rescaling in Eq. (9) is employed. We are assuming that if $g_n^*(N=2)$ represents the chemical synapse strength for which complete synchronization appears in two mutually coupled neurons, then complete synchronization would appear in a network of N nodes if

$$g_n^*(N) = \frac{g_n^*(N=2)}{k}. \tag{11}$$

If the previous hypothesis is satisfied, i.e., Equation (11) is satisfied, we see from Figs. 2 and 3 that $\langle S[g_n(N)]\rangle \approx \langle S[g_n(N=2)]\rangle$ and assuming that these two averages are equal, then Eq. (10) takes us to

$$g_l^*(N) = \frac{2g_l^*(N=2)}{|\gamma_2(N)|}, \tag{12}$$

where $g_l^*(N)$ represents the electrical synapse strength for which complete synchronization occurs in a network composed by N neurons.

In the following, we analyze two special cases of Eq. (10) when the function $S(p)$ is constant and the previous approximations (expanding Γ around its average and that $\langle S[g_n(N)]\rangle = \langle S[g_n(N=2)]\rangle$) to arrive to Eqs. (11) and (12) are exact.

A. Rescaling in excitatory networks ($V_{syn}=2.0$)

Case 1. A large chemical synapse strength, $kg_n(N) > g_n^{(c)}$, with $g_n^{(c)} \approx 1.67$, makes for all the time $p < \Theta$, leading to $S(p)=0$ and $S'(p)=0$ (see Fig. 2). The neurons become completely synchronous to a stable equilibrium point.

B. Rescaling in inhibitory networks ($V_{syn}=-2.0$)

Case 2. a large chemical synapse strength, $kg_n(N) > g_n^{(c)}$, with $g_n^{(c)} \approx 1.50$, makes for all the time $p > \Theta$ and as a consequence $S(p)=1$ and $S(p)'=0$ (see Fig. 3). The neurons become completely synchronous to a limit cycle.

VI. COMBINED EFFECT OF THE CHEMICAL AND ELECTRICAL SYNAPSES ON THE SYNCHRONOUS BEHAVIOR

The analytical derivations done in the previous section are approximations, except for some special values of the synaptic strengths (case 1 and 2). However, as we show in this section, our calculations provide a good estimation of what to expect from parameter spaces of larger networks when the parameter space of two mutually coupled neurons is known. The parameter space is constructed by considering the synapses (g_l, g_n) and they identify the regions where the state of complete synchronization is stable.

The stability is determined from Eqs. (7), by verifying whether there are no Lyapunov exponents associated with transversal directions to the synchronization manifold. These exponents are numerically obtained, without any approximation.

In Fig. 4, we show in black the synchronous regions (all transversal conditional exponents are negative) for the excitatory networks and in Fig. 5 the same network topologies but for inhibitory networks. To simplify the understanding of these two figures, in Fig. 1 we show in boxes (A–E) the values of N, $|\gamma_2|$, k and the type of topology considered in the networks of Figs. 4(A)–4(E) and 5(A)–5(E). The values of g_l and g_n were rescaled by using Eqs. (11) and (12). As expected, in excitatory networks our rescaling works very well and roughly in inhibitory networks. So, the vertical axis of Figs. 4(B)–4(E) and 5(B)–5(E) show the quantity $kg_n(N)$ and the horizontal axis of these same figures show the quantity $\frac{|\gamma_2| g_l(N)}{2}$.

To assist the analysis of the parameter spaces, imagine a curve Σ that is the border between the regions defining parameters for which the synchronization manifold is unstable (white regions) and regions defining parameters for which the synchronization manifold is stable (black regions). There are four main characteristics in these two types (excitatory and inhibitory) of networks concerning the occurrence of complete synchronization.

In excitatory networks, the electrical and the chemical synapses act in a combined way to foster synchronization. The neurons become completely synchronous to a stable equilibrium point. The asynchronous neurons (white regions) are chaotic. The curve Σ would look like a diagonal line with a negative slope. Such a curve could be defined by an equation similar to $kg(N) + \gamma_2 g_l \approx C$, C being a function that is approximately constant (see Fig. 4).

In excitatory networks, with $kg_n(N) > 1.67$, Neurons are completely synchronous to a stable equilibrium point (see Fig. 4).

In inhibitory networks, with $kg_n(N) < 5$, the larger the chemical synapse strength is the larger the electrical synapse strength needs to be to achieve complete synchronization. Neurons become completely synchronous to either a limit cycle (large chemical synapse strength) or to a chaotic attractor (small chemical synapse strength). The curve Σ would look like a diagonal line with a positive slope. Such a curve could be defined by an equation similar to $kg(N) - \gamma_2 g_l \approx C$, C being a function that is approximately constant (see Fig. 5).

In inhibitory networks, for large values of $kg_n(N)$, complete synchronization appears for $\gamma_2 g_l > C$ and neurons become completely synchronous to a stable limit cycle, which is unstable if $\gamma_2 g_l < C$. The curve Σ would look like a straight vertical line. Such a curve could be defined by an equation similar to $\gamma_2 g_l \approx C$. C being a function that is approximately constant (see Fig. 5).

If the neurons are set with different initial conditions, but sufficiently close, complete synchronization is found for similar synaptic strengths for which the synchronization manifold is stable.

If the neurons are set with sufficiently different initial conditions, and we construct parameter spaces that represent synaptic strengths for which CS takes place, we would have obtained parameter spaces with similar structure as the one observed in Figs. 4 and 5. However, the network can become completely synchronous to other synchronous solutions of Eq. (4), different from the synchronous solutions observed

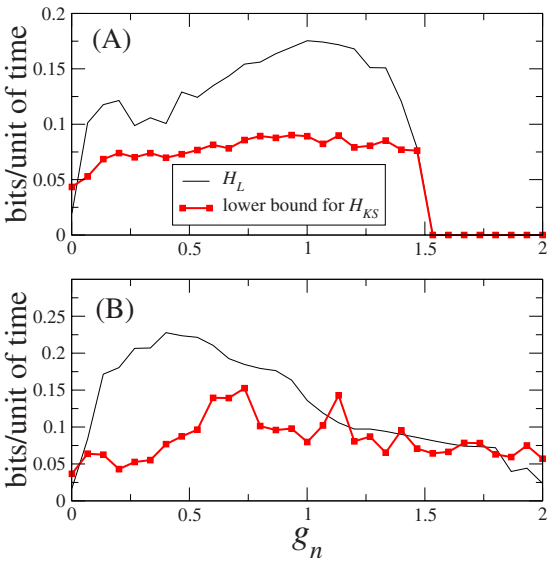

FIG. 6. (Color online) We show the value of the sum of all the positive Lyapunov exponents H_L in black line and an estimation of the lower bound for the KS entropy in filled squares (red line online) for two mutually chemically coupled neurons under an excitatory synapse (a) and an inhibitory synapse (b), as we vary the chemical synapse strength. We consider a constant electrical synapse of strength g_l=0.1. Initial conditions are not equal.

for the parameters used to make Figs. 4 and 5. In other words, parameter spaces that show CS in networks whose neurons are set with different initial conditions constructed for the same synaptic strengths and networks considered in Figs. 4 and 5 would present additional black points in the white areas of Figs. 4 and 5.

VII. COMBINED EFFECT OF THE CHEMICAL AND ELECTRICAL SYNAPSES ON THE AMOUNT OF INFORMATION

First, we calculate the sum of all the positive Lyapunov exponents of the attractor obtained from integrating the neural network [Eq. (2)] and represent it by H_L. The Lyapunov exponents are calculated from the variational equation of the network in Eq. (2). As previously discussed, it is reasonable to assume that $H_L \approx H_{KS}$, where H_{KS} represents the KS entropy [20], which measures the amount of information (Shannon's entropy) produced per time unit.

In Figs. 6(A) and 6(B) we show in the thin line H_L for two mutually chemically and electrically coupled neurons (g_l =0.1) for excitatory synapse (A) and for inhibitory synapse (B). To confirm that the sum of the positive Lyapunov exponents have an entropic meaning for the studied Hindmarsh-Rose neuron model, we have estimated a lower bound for the KS entropy, represented by the tick line with filled squares (red online) in Figs. 6(A) and 6(B).

We see that for both cases, as one increases the synaptic strength, H_L decreases. For the excitatory case, for $g_n > 1.52$, the neurons trajectories go to an equilibrium point and we obtain H_L=0. If H_L=0, that means that there are no positive Lyapunov exponents and therefore no chaos. The maximal value of H_L, calculated varying the synaptic strengths, is almost equal for both types of synapses. One sees that there is a range of strength values in both figures within which H_L is large. For example, in (A) H_L is large for $g_n \in [0.7, 1.2]$ and in (B) H_L is large for $g_n \in [0.3, 0.7]$. This was also observed in 3D parameter space diagrams (not shown in here) that show the value of H_L versus g_n and g_l. These diagrams indicate that there is an optimal range of values for g_n and g_l for which H_L remains large.

The reason we have shown results for two coupled neurons is because for such a configuration a lower bound estimation of the KS entropy can be calculated by encoding the trajectory into a binary symbolic sequence. Since the sequence is binary, this method is only capable of measuring an information rate that is less or equal than 1 bit/symbol or 1 bit/unit of time. Since that for two coupled neurons, $H_L < 1$ bit/unit of time, and assuming that H_L is a good estimation for H_{KS}, then the employed method to calculate a lower bound of the KS entropy is appropriate. The details of this estimation can be seen in Appendix.

Notice that in Fig. 6(A) and 6(B) for $g_n \approx 0$ [as well as in (B) for $g_n \approx 2$] the estimations of H_{KS} are larger than H_L. That is the result of a known problem in the estimation of entropic quantities which prevents the estimation to be small. The problem arises because the symbolic sequences considered are not infinitely long for one to realize that there exists a few or only one symbolic sequence encoding the trajectory. For example, a long periodic orbit would be encoded by a series of short symbolic sequences making the estimation of H_{KS} to be positive instead of zero as it should be.

VIII. SYNCHRONIZATION (AND DESYNCHRONIZATION) VERSUS INHIBITION (AND EXCITATION) VERSUS INFORMATION

To understand the relation between synchronization (desynchronization) and inhibition (excitability), when *complete synchronization is absent* we do the following. But notice that the following results are based on a conjecture that is currently not demonstrated.

We calculate the Lyapunov exponents along the synchronization manifold, which are just the Lyapunov exponents of the network by assuming that all neurons are completely synchronous. We call these exponents conditional Lyapunov exponents and the sum of all the positive ones is denoted by H_C. There are two ways for calculating them, either using Eqs. (5) or (7), Eq. (7) being simpler because of the dimensionality of the orthogonal vectors employed to calculate the Lyapunov exponents. While the use of Eq. (5) requires $3N$ vectors, each one with dimensionality $3N$, the use of Eq. (7) requires N vectors each one with dimensionality 3. Additionally, once the function that relates the conditional exponents of two mutually coupled neurons with g_n and g_l is known, then one can calculate this function for all the conditional exponents of larger networks as long as Eqs. (4) and (7) can be rescaled.

We can then classify these neural networks into two types. The types UPPER or LOWER. More specifically,

$$H_C(N, g_n, g_l) > H_L(N, g_n, g_l), \quad \text{UPPER}, \tag{13}$$

$$H_C(N,g_n,g_l) < H_L(N,g_n,g_l), \quad \text{LOWER}. \tag{14}$$

To understand what H_C and H_L exactly mean and the reason for such a classification, notice that the networks here considered admit a synchronous solution. This synchronous solution might be unstable (an unstable saddle) and typical initial conditions depart from the neighborhood of the synchronous solution and asymptotically tend toward a stable solution, the chaotic attractor. This attractor describes a network whose nodes are not synchronous. In such a situation, the network admits at least two relevant solutions: a stable desynchronous one (the chaotic attractor) and an unstable synchronous one (the synchronization manifold). While H_C can be associated with the amount of information produced by the unstable synchronous solution, H_L can be associated with the amount of information produced by the desynchronous chaotic attractor. If the complete synchronous state is stable, then, $H_C=H_L$, and the network in Eq. (2) possesses only one stable synchronous solution, for typical initial conditions. The nomenclature in Eqs. (13) and (14) comes from the fact that if $H_C(N,g_n,g_l)>H_L(N,g_n,g_l)$ then, H_C is an upper bound for H_L, otherwise it is a lower bound [29].

Assume now that the more information a network produces, the more desynchronization is observed among pair of neurons [29,30]. If $H_C(N,g_n,g_l)>H_L(N,g_n,g_l)$ (UPPER), then $H_L(N,g_n,g_l)$ is limited. As a consequence, the production of information in the network is limited and therefore the level of desynchronization is small. On the other hand, if $H_C(N,g_n,g_l)<H_L(N,g_n,g_l)$ (LOWER), then $H_L(N,g_n,g_l)$ can be large implying a large level of desynchronization. Another way of understanding the relationship between synchronization and information is by using a result from Ref. [29], which shows that for two coupled maps (but this result is trivially extended to networks), the largest transversal conditional exponent, when the maps have a LOWER character, is larger than this exponent for when they have an UPPER character. Since this exponent provides a necessary condition for the stability of the synchronization manifold, it can be interpreted as a measure of the level of desynchronization in the network. The larger this exponent is, the more desynchronous the network is. Therefore, UPPER networks should have neurons more synchronous than LOWER networks.

If $H_C(N,g_n,g_l)>H_L(N,g_n,g_l)$ (UPPER), the synapse forces the trajectory to approach the synchronization manifold and, as a consequence, there is a high level of synchronization in the network. On the other hand, if $H_C(N,g_n,g_l)<H_L(N,g_n,g_l)$ (LOWER), the synapse forces the trajectory to depart from the synchronization manifold and, as a consequence, there is a high level of desynchronization in the network.

One can check that in Fig. 7, which shows as gray, the parameter regions for which $H_C>H_L$ and as black the parameter regions for which the synchronization manifold is stable and there is complete synchronization (and therefore, $H_C=H_L$) for typical initial conditions. Gray points appearing on black regions represent synaptic strengths for which in fact one has $H_C=H_L$, but numerically we obtain that $H_C=H_L+\epsilon$, with ϵ being a very small positive constant. Typically, neurons coupled via an excitatory synapse [(A–D)] present a LOWER character while via an inhibitory synapse [(E–H)] present an UPPER character.

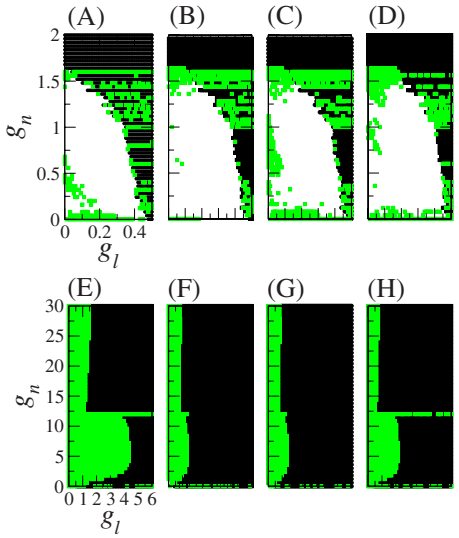

FIG. 7. (Color online) Gray regions (green online) indicate (g_n,g_l) values for which $H_C>H_L$ (UPPER) and black regions indicate (g_n,g_l) values for which the complete synchronization state is stable, in excitatory networks (A–D) and inhibitory networks (E–H). The networks considered in (A–D) as well as in (E–H) have the parameters shown in Fig. 1(A)–1(D). In (B–D) and (F–H) the horizontal axis represent $g_l(N)|\gamma_2(N)|/2$ and the vertical axis kg_n. Gray points (green online) appearing on black regions represent synaptic strengths for which in fact one has $H_C=H_L$, but numerically we obtain that $H_C=H_L+\epsilon$, with ϵ being a very small positive constant.

This classification is also important because as it was shown in Ref. [29], once two coupled neurons are UPPER (or LOWER) there is always a synaptic strength range for which a large network is UPPER (or LOWER). And these synaptic strength ranges can be calculated using the rescalings in Eqs. (11) and (12).

In Figs. 7(B), 7(C), and 7(F)–7(H), we show that the UPPER and LOWER character of two mutually coupled neurons is preserved in networks composed by a number of neurons larger than 2, if one considers the rescalings of Eqs. (11) and (12). This result is of fundamental importance, specially for synaptic strengths that promote the network to have an UPPER character because it allows us to calculate an upper bound for the KS entropy of larger networks by knowing the value of H_C for two mutually coupled neurons. Such a situation arises for inhibitory networks for a large range of both synaptic strengths. One finds an UPPER character in excitatory networks for a small value of the chemical synapse strength.

The electrical synapse favors the neurons to synchronize. As a consequence, it is expected that networks with neurons connected exclusively by electrical synapses are of the UPPER type. This can be checked in all figures for when $g_n \approx 0$.

We are currently trying to prove the conjecture in Ref. [29] by studying the relationship between the stability of unstable periodic orbits [34] embedded in the attractors appearing in complex networks and the stability of the equilibrium points. All the equilibrium points of a polynomial network can be calculated by the methods in Refs. [31–33].

IX. UPPER BOUND FOR THE RATE OF INFORMATION

According to Ruelle [28], the sum of all the positive Lyapunov exponents is an upper bound for the Kolmogorov-Sinai entropy [20]. Therefore, whenever $H_C(N) > H_L(N)$ (UPPER) it is valid to write that

$$H_C(N) > H_{KS}(N), \tag{15}$$

where $H_{KS}(N)$ denotes the Kolmogorov-Sinai entropy of a network composed of N neurons.

As we have previously seen, the UPPER character of two mutually coupled neurons is preserved in the special larger networks here studied. In addition to this, if the positive conditional exponents of two mutually coupled neurons are known for a given g_n and g_l, allowing us to calculate $H_C[N=2,\ g_n(N=2),\ g_l(N=2)]$, then one can calculate the positive conditional exponents of a network with N neurons, $H_C[N,g_n(N),g_l(N)]$. In other words, if the ratio of information production of two mutually coupled neurons that have equal trajectories, $H_C(N=2)$, is known and the neurons have an UPPER character, one can calculate the upper bound for the ratio of information production in larger networks, as long as Eqs. (4) and (7) can be rescaled. Therefore, in UPPER networks connected simultaneously with electrical and inhibitory chemical synapses we can always calculate an upper bound for the rate of information production in terms of this quantity in two mutually coupled inhibitory neurons.

Consider two mutually coupled neurons. Denote $\lambda_1(N=2,g_n)$ as the sum for the positive Lyapunov conditional exponents associated with the synchronization manifold for a chemical synapse strength g_n and $\lambda_2(N=2,g_n,g_l)$ as the sum of the positive Lyapunov exponents associated with the only one transversal direction for a chemical synapse strength g_n and an electrical synapse strength g_l. Remind that λ_1 and λ_2 are calculated using Eq. (7) for the index $j=1$ and $j=2$, respectively.

Now, consider a network formed by N neurons. Using similar arguments than the ones presented in Sec. V and based on the conjecture proposed in [29], the value of the synapse strengths $g_l(N),g_n(N)$ for which the exponent $\lambda_1(N)$ has the same value of $\lambda_1(N=2)$ can be calculated by

$$g_n(N) = \frac{g_n(N=2)}{k} \tag{16}$$

and the value of the synapse strengths $g_l(N),g_n(N)$ for which the sum of the positive conditional exponent $\lambda_w(N,g_n,g_l)$ (for $w \geq 2$) has the same value of $\lambda_2(N=2,g_n,g_l)$ can be calculated by

$$g_n(N) = \frac{g_n(N=2)}{k}, \tag{17}$$

$$g_l(N) = \frac{g_l(N=2)|\gamma_2(N=2)|}{|\gamma_w(N)|}. \tag{18}$$

Denote $\lambda_1^{\max}(N=2)$ and $\lambda_2^{\max}(N=2)$ as the maximal values of $\lambda_1(N=2,g_n)$ and $\lambda_2(N=2,g_n,g_l)$ with respect to g_n and g_l.

As an example of how to use Eqs. (16)–(18) in order to calculate the upper bound for the rate of information produced in the network, we consider that the neurons in the network with N nodes are coupled via electrical and excitatory chemical synapses in an all-to-all configuration (topology II), then $k=N-1$, $|\gamma_w(N)|=N$ and $|\gamma_2(N=2)|=2$.

Now, we search for a synapse strength range for which two mutually coupled neurons have an UPPER character. For example, let us say the range $g_l(N=2) \in [0,1]$ and $g_n(N=2) \in [2,10]$, in Fig. 7(E), for two inhibitory mutually coupled neurons.

From Eqs. (17) and (18), as long as the network with N nodes has $g_n(N) \leq \frac{1}{2(N-1)}$ and $\frac{0.3}{k} \leq g_l(N) \leq \frac{1}{N}$, then $\lambda_1^{\max}(N) = \lambda_1^{\max}(N=2)$ and $\lambda_w^{\max}(N) = \lambda_2^{\max}(N=2)$, and therefore for this synapse range, the maximum of H_C is

$$\max_{g_n,g_l}[H_C(N,g_n,g_l)] = \lambda_1^{\max}(N=2) + (N-1)\lambda_2^{\max}(N=2) \tag{19}$$

Notice that Eq. (19) is valid to any network topology as long as Eqs. (4) and (7) can be rescaled.

For very large networks that are very well connected, $g_l(N)$ and $g_n(N)$ will be very small, since k and N are large. As a consequence, $\lambda_1^{\max} \approx \lambda_2^{\max}$, since neurons are equal, and we can write

$$\max_{g_n,g_l}[H_C(N,g_n,g_l)] = N\lambda_2^{\max}(N=2), \tag{20}$$

which means that the rate of information produced by large UPPER neural networks whose neurons are highly connected has an upper bound that increases linearly with the number of neurons. A similar result is obtained when the neurons are connected with only electrical synapses [29].

X. CONCLUSION

We have studied the combined action of chemical and electrical synapses in small networks of Hindmarsh-Rose (HR) neurons in the process of synchronization and on the rate of information production.

There are mainly two scenarios for the appearance of complete synchronization for the studied inhibitory networks. If the chemical synapse strength is small, the larger the chemical synapse strength used the larger the electrical synapse strength needs to be to achieve complete synchronization. Otherwise, if the chemical synapse strength is large, complete synchronization appears if the electrical synapse strength is larger than a certain value. In the studied excitatory networks both synapses work in a constructive way to promote complete synchronization: the larger the chemical synapse strength is the smaller the electrical synapse strength needs to be to achieve complete synchronization.

When neurons connect simultaneously by electrical and chemical ways, there is an optimal range of synaptic strengths for which the production of information is large. For strengths larger than values within this optimal range, the larger the electrical and chemical synaptic strengths are the smaller the production of information of coupled neurons.

In the absence of complete synchronization, it is intuitive to expect that excitatory networks have neurons that are more desynchronous while inhibitory networks have neurons that are more synchronous. This intuitive idea can be better

formalized by understanding the relationship between excitation (inhibition), synchronization (desynchronization) and the rate of information production. For that we classify the network as having an UPPER or a LOWER character. In a UPPER (LOWER) network, the sum of all the positive Lyapunov exponents, denoted by H_L, is bounded from above (below) by the sum of all the positive conditional Lyapunov exponents, denoted by H_C, the Lyapunov exponents of the synchronization manifold and the transversal directions. Networks that have neurons connected simultaneously by inhibitory chemical synapses and electrical synapses can be expected to have an UPPER character. In such networks, one should expect to find synchronous behavior, since the synapses force the trajectory to approach the synchronization manifold. On the other hand, networks whose chemical synapse are of the excitatory type might likely have a LOWER character. In such networks one should expect to find desynchronous behavior since the synapses force the trajectory to depart from the synchronization manifold.

Notice that $H_L(N)$ can only be numerically obtained whereas $H_C(N)$ can be calculated from the conditional exponents numerically obtained for two mutually coupled neurons that have equal trajectories. For UPPER networks, $H_C(N) > H_L(N)$, and by Ruelle [28] $H_L(N) \geq H_{KS}(N)$, where H_{KS} is the Kolmogorov-Sinai entropy, the amount of information (Shannon's entropy) produced by time unit; we have then that H_C is an upper bound for $H_{KS}(N)$. That can be advantageously used in order to calculate the rate of information produced by a large network, composed of N neurons by using only the rate at which information is produced in two mutually coupled neurons that are completely synchronous and have equal trajectories.

We have worked with idealistic networks. However, our results can be extended to more realistic networks [12]. For UPPER networks, our numerical results show that more realistic networks constructed with nonequal nodes (or networks of equal nodes but with random synapse strengths [30]) have H_L smaller than the networks with equal nodes. Therefore, even though networks with equal nodes might not be realistic, their entropy production per time unit is an upper bound for the entropy production of more realistic networks.

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APPENDIX: LOWER BOUND FOR THE KS ENTROPY

Imagine a 2D chaotic system as the one studied in Ref. [11] [Eqs. (5) and (6)]. Following the same ideas from there, the KS entropy of two coupled maps with variables x^α and x^β can be estimated from the Shannon's entropy of the probabilities that a trajectory point makes a given itinerary in the phase space (x^α, x^β), divided by the time interval for the trajectory to make that itinerary.

In practice, calculating the Shannon's entropy [18] for all possible itineraries on the phase space (x^α, x^β) of a chaotic trajectory is equivalent to calculating the joint entropy between the probabilities of finding a point following simultaneously an itinerary along the variable the variable x^α and another itinerary along the variable x^β.

Since we are unable to make a high resolution partition of the phase space (nor we do not know the Markov partition) in the neural networks studied in this work, we estimate a lower bound for the KS entropy by calculating the joint entropy between symbolic sequences encoding the trajectory. Such calculation of probabilities involves large matrix operations and for that reason we restrain ourselves to the calculation of the joint entropy between two neurons.

It is a lower bound due to two reasons. The first one is because the entropy will be measured considering the probabilities of occupation of a projected trajectory in a subspace of the network. The second one is because we calculate the entropy considering the probabilities of binary symbolic sequences and obviously a binary sequence may contain much less information than the content of a continuous signal [19].

In the following, we show in more details how this estimation is done. The way we encode the trajectory is partially based on the time encoding proposed in Ref. [30].

Given two symbolic sequences S_1 and S_2, generated by neuron 1 and 2, respectively, a lower bound for the KS entropy can be estimated by

$$H_{low} = \frac{1}{\langle \tau \rangle} H(S_1; S_2) \tag{A1}$$

with $H(S_1;S_2)$ representing the joint entropy between the symbolic sequences S_1 and S_2. To create the symbolic sequences, we represent the time at which the nth maxima happens in neuron 1 by T_1^n, and the time interval between the nth and the $(n+1)$-th maxima, by δT_1^n. A maxima represents the moment when the action potential reaches its maximal value. The quantity $\langle \tau \rangle$ represents the average time between two spikes. We then encode the spiking events using the following rule. The ith symbol of the encoding is a "1" if a spike is found in the time interval $[i\Delta, (i+1)\Delta[$, and "0" otherwise. We choose $\Delta \in [\min(\delta T_1^n), \max(\delta T_1^n)]$ in order to maximize H_{low}. Each neuron produces a symbolic sequence that is split into small nonoverlapping sequences of length $L=8$.

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