

Energy aspects of the synchronization of model neurons

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We have deduced an energy function for a Hindmarsh-Rose model neuron and we have used it to evaluate the energy consumption of the neuron during its signaling activity. We investigate the balance of energy in the synchronization of two bidirectional linearly coupled neurons at different values of the coupling strength. We show that when two neurons are coupled there is a specific cost associated to the cooperative behavior. We find that the energy consumption of the neurons is incoherent until very near the threshold of identical synchronization, which suggests that cooperative behaviors without complete synchrony could be energetically more advantageous than those with complete synchrony.

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I. INTRODUCTION

Energy is an important aspect to be contemplated in the normal behavior of the brain. At just 2% of body mass, the human brain consumes 20% of human metabolic energy [1]. In the gray matter of rodent brain action potentials and postsynaptic effects are predicted to consume much of the energy, 81%, with the resting potential and glutamate recycling consuming a smaller amount, 16% [2]. Energy usage depends strongly on the action potential rate and the energy expended on signaling is a large fraction of the total energy used by the brain. In fact, energy is a constrain on the coding and processing of sensory information [3]. Some research approaches evaluate the required metabolic energy to maintain neural activity [1–4] and also to understand energy efficient neural codes compromising representational capacity and metabolic energy expenditure [5], but these approaches lack a comprehensive model of the electrical energy balance in the neuron. Although great effort is being devoted to the study of models showing the irregular spike bursting characteristic of some neurobiological systems [6–9], no extensive work has been done on the energy considerations of their dynamical behavior. Yet, in arrays of biological structures coherent oscillations are thought to play a substantial role in information processing [10,11] and the required collective behaviors could be influenced by their electrical energy cost [12]. One possible reason for this lack of energy models is that the available kinetic models of a single neuron [13–15] are usually qualitative models of motion with no clear connection with the source of energy that is required to maintain its activity. In that situation, the study of their dynamical properties from an energy perspective requires one to find an energy function for the specific model of the neuron under study. In Ref. [16] we developed a method to assign an energylike function to a chaotic system described by equations of motion. This energy function was used as a measure to study its dynamics and, in particular, to evaluate the cost of maintaining a certain degree of synchrony with other chaotic oscillators.

In this paper we find for the Hindmarsh-Rose model of a neuron [17] a function of the state space variables that can be

considered as the electrical energy of the neuron in each of the different states of its dynamical behavior. The Hindmarsh-Rose model, which exhibits a dynamical behavior similar in several aspects to the properties of real neurons, is described by the following equations of movement:

$$\begin{aligned}\dot{x} &= y - ax^3 + bx^2 + \xi I - \rho z, \\ \dot{y} &= c - dx^2 - y, \\ \dot{z} &= r[s(x - x_0) - z],\end{aligned}\quad (1)$$

where to ensure dimensional consistency we have added two additional parameters ξ and ρ . This is a qualitative model whose dimensional consistency does not usually deserve much attention. Nevertheless, the dimensional consistency of the model is relevant to our study in order to be able to ascertain whether the energy function that emerges from its dynamics is dimensionally consistent with the true physical energy for a neuron. In the model, variable x is a voltage associated to the membrane potential, variable y , although in principle associated to a recovery current of fast ions, has been transformed into a voltage, and variable z is a slow adaptation current associated to slow ions. Parameter I is a external current input. The time variable of the model is dimensionless. For the numerical results of this work we fix the usual parameters to the values $a=1$ (mV)⁻², $b=3.0$ (mV)⁻¹, $c=1.0$ mV, $d=5.0$ (mV)⁻¹, $s=4.0$ μ S, $x_0=-1.6$ mV, and $r=0.006$. These numerical values have been frequently used since Ref. [18]. The two new parameters are fixed to $\xi=1$ M Ω and $\rho=1$ M Ω . For values of the external current input 2.92 nA $< I < 3.40$ nA the system exhibits a multitime scale spike-burst chaotic behavior [10]. We have fixed the external current value to $I=3.2$ nA.

II. HINDMARSH-ROSE ENERGY

The procedure followed to find an energylike function for a chaotic system has been reported in detail in Ref. [16] and can be summarized as follows. Consider an autonomous dy-

namical system $\dot{x}=f(x)$ where $x \in \mathfrak{R}^n$ and $f: \mathfrak{R}^n \rightarrow \mathfrak{R}^n$ is a smooth function. The velocity vector field $f(x)$ can be expressed as sum of two vector fields $f(x)=f_c(x)+f_d(x)$, one of them, $f_c(x)$, conservative containing the full rotation and the other, $f_d(x)$, dissipative containing the divergence [19]. Taking the conservative vector field, the equation $\nabla H^T f_c(x)=0$ defines for each dynamical system a partial differential equation from which a function $H(x)$ can be evaluated. This function $H(x)$ is a generalized Hamiltonian for the conservative system $\dot{x}=f_c(x)$ as long as it can be rewritten in the form $\dot{x}=J(x) \nabla H$ where J is a skew symmetric matrix that satisfy Jacobi's closure condition [20]. If that is the case, we consider $H(x)$ as an energy associated to the original system $\dot{x}=f(x)$. This energy is dissipated, passively or actively, due to the dissipative component of the velocity vector field according to the equation, $\dot{H}=\nabla H^T f_d(x)$.

In the Hindmarsh-Rose model given by Eq. (1) the vector field $f(x)$ can be expressed as sum of the following vector fields:

$$f_c = \begin{pmatrix} y - \rho z \\ -dx^2 \\ rsx \end{pmatrix} \quad \text{and} \quad f_d = \begin{pmatrix} -ax^3 + bx^2 + \xi I \\ c - y \\ -rsx_0 - rz \end{pmatrix}. \quad (2)$$

As it can be observed f_c is a divergence free vector that accounts for the whole rotor of the vector field and f_d is a gradient vector that carries its whole divergence. Consequently, the energy function $H(x, y, z)$ will obey the following partial differential equation, $(y - \rho z) \frac{\partial H}{\partial x} - dx^2 \frac{\partial H}{\partial y} + rsx \frac{\partial H}{\partial z} = 0$, which has the cubic polynomial solution

$$H = p \left[\frac{2}{3} dx^3 + rs \rho x^2 + (y - \rho z)^2 \right], \quad (3)$$

where p is a parameter. It can be proved the existence of a local skew-symmetric structure matrix $J(x, y, z)$ that guarantees that this H function is formally a generalized Hamiltonian (details will be published elsewhere) and so an energy for the Hindmarsh-Rose neuron. Note that as in the model time is dimensionless and every adding term in Eq. (3) has dimensions of square voltage, function H is dimensionally consistent with a physical energy as long as parameter p has dimensions of conductance. In this paper we fix parameter p to the arbitrary value $p=1$ S. Figure 1 shows the isosurface $H=45$ pJ. The Hindmarsh-Rose attractor is also shown.

The energy derivative $\dot{H}=\nabla H^T f_d(x)$ is given by

$$\begin{aligned} \dot{H}/2p = & (bd - r\sigma a)x^4 + \xi d I x^2 - y^2 - adx^5 + (c + prsx_0)y \\ & - \rho(c + prsx_0)z + \rho(1+r)yz + r\sigma p b x^3 + r\sigma p \xi I x \\ & - \rho^2 r z^2. \end{aligned} \quad (4)$$

It can be easily checked that the energy derivative is also dimensionally consistent with a dissipation of energy. The two first adding terms in Eq. (4) are definite positive, that is, they always contribute energy, and the third term is always definite negative helping to the quick release of energy in the membrane. As the time scale parameter r is very small, the last three adding terms can be neglected. The rest of the adding terms are not definite and their net contribution to the

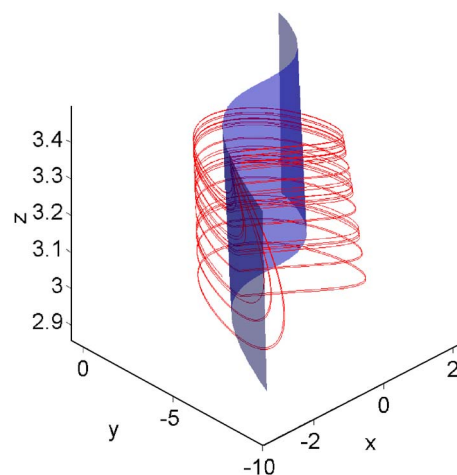


FIG. 1. (Color online) The energy isosurface of $H=45$ pJ for a Hindmarsh-Rose neuron. The neuron attractive manifold is also sketched.

balance of energy in the normal activity of the neuron depends on the particular parameterization of the model. To estimate the energy needed to generate action potentials the terms contributing energy will have to be identified. Figure 2(a) shows a series of action potentials (variable x in the model neuron) and Fig. 2(b) shows the energy derivative \dot{H} corresponding to that series. In Fig. 2(c) a detail of the energy derivative corresponding to a train of two action potentials is also shown. For each action potential it can be appreciated that the energy derivative is first positive, contributing energy to the spike, and then negative, quickly releasing part of that energy to relieve the membrane potential. During the resting state between the two spikes the energy derivative remains slightly negative, still releasing energy, until the onset of the following action potential.

As the states of an isolated Hindmarsh-Rose neuron are confined to an attractive manifold, Fig. 1, the range of pos-

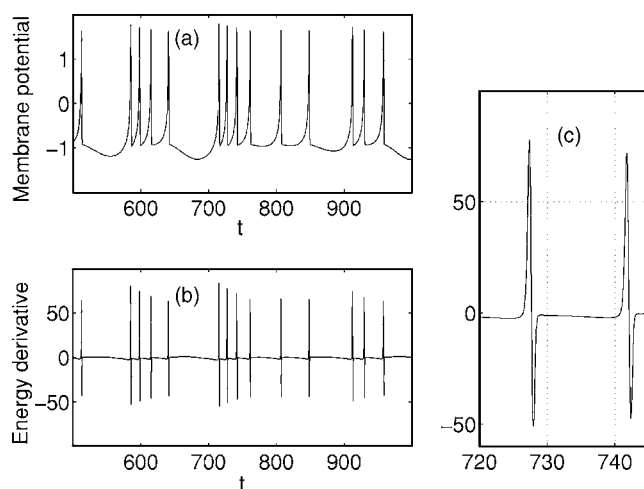


FIG. 2. (a) Action potentials and (b) energy derivative for the Hindmarsh-Rose model neuron. (c) Details of the energy derivative associated to two action potential spikes showing the energy contributed to the cell to generate the spike (positive area) and the ulterior release of that energy.

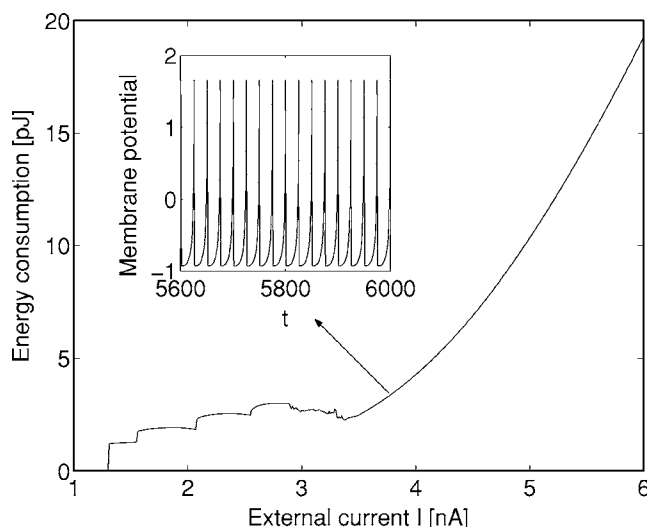


FIG. 3. Average consumption of energy vs external current I . The plateau at 0 corresponds to the nonenergy consuming quiescent state of the neuron. The energy consumption is sensitive to the different firing regimes of the neuron which are reflected in the successive plateaus. The nonsmooth region between $2.92 \text{ nA} < I < 3.40 \text{ nA}$ corresponds to the chaotic regime. Inset: High-frequency repetitive firing regime of the neuron at $I \approx 3.75 \text{ nA}$, the approximate frequency of the firing is 0.04 Hz .

sible values of its energy is recurrent and the long term average of its energy derivative is zero. This leads to the apparent paradox that the electrical activity of the isolated neuron occurs with no average energy consumption. However, it has to be considered that the average involves a global balance of energy. The model itself incorporates, in a nonexplicit way, components which are responsible of the energy consumption together with others which are the energy suppliers. Altogether, the whole balance is zero in the long run. However, the average energy consumption per unit time of the neuron, that is, the metabolic energy that has to be supplied to the neuron to maintain its activity, corresponds to the long term average of only the positive component of the energy derivative.

As an illustrative application, relevant to the investigation of energy efficient neuronal coding, we have calculated the average consumption of energy of the Hindmarsh-Rose neuron at different values of the external current I ranging from 1 to 6 nA. As it has been reported in Ref. [10] the external current I modifies the permanent regime of the isolated neuron. For sufficient low values of I the neuron is in a stable quiescent state. As I increases, a low frequency train of regularly spaced spikes appears. A further increase in I leads to periodic bursts of two or more spikes per burst. For intermediate values of I there is a chaotic regime. For large values of I the neuron is in a high-frequency repetitive firing state. Our results show, Fig. 3, that the energy consumption of the neuron during its signaling activity is discontinuous with I and very sensitive to the different firing states. The initial plateau at zero corresponds to the neuron in its quiescent state where no electrical energy is required and the next plateaus correspond to the subsequent firing states. The nonsmooth regime between $2.92 \text{ nA} < I < 3.40 \text{ nA}$ corresponds to the chaotic

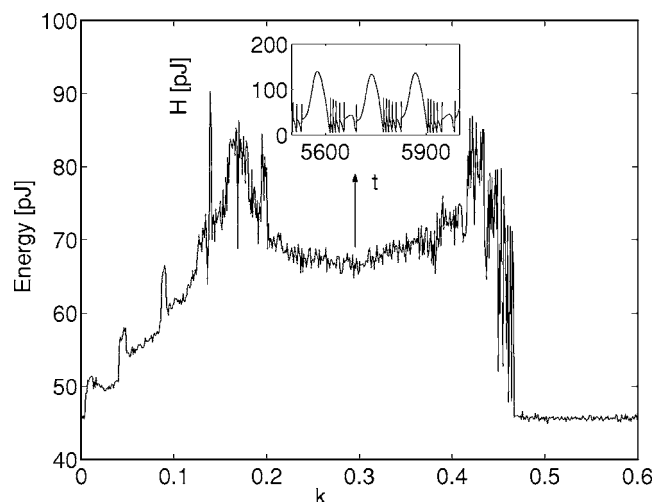


FIG. 4. Energy of one of the two bidirectionally coupled neurons averaged on the attractor at different values of the coupling strength k . In the inset a time series of its energy at $k=0.30$ is shown as an example of energy pattern.

regime, and the continuous, nearly linear, increase with I corresponds to the high-frequency periodic regime. The inset in Fig. 3 shows the firing regime of the neuron at $I \approx 3.75 \text{ nA}$, the approximate frequency of the firing is 0.04 Hz . The parallelism of this result of energy consumption with the one obtained in Ref. [10] for the time-averaged firing rates versus the external current I is remarkable. This parallelism supports the assumption that energy consumption increases linearly with the mean firing rate [5] and, consequently, with the representational capacity of a possible neuronal code.

III. SYNCHRONIZATION ENERGY

The possibility of assigning an energy value to a particular state of a given neuron permits evaluating its energy balance in the process of synchronization with other neurons. To do so, let us force two identical neurons to mutually synchronize via linear bidirectional feedback coupling to the x component, $\dot{x}_i = y_i - ax_i^3 + bx_i^2 + \xi I - \rho z_i + k(x_j - x_i)$, $\dot{y}_i = c - dx_i^2 - y_i$, and $\dot{z}_i = r[s(x_i - x_0) - z_i]$, where $k \geq 0$ is the coupling strength and $i, j = 1, 2$ and $i \neq j$ are the indices for the neurons.

We have computed the average energy and the average dissipation of energy of each of these neurons at different values of the coupling strength k ranging from $k=0$ to $k=0.6$. Figure 4 shows the energy of a neuron averaged on its respective manifold at different values of the coupling strength k . As soon as the coupling is engaged the average energy of the neuron starts to increase with the coupling strength. The average energy reaches a maximum at $k=0.17$ and begins a slow decline followed by a second rise to a maximum at about $k=0.42$. After that the average energy quickly falls, at $k=0.467$, to its initial uncoupled level. Although both neurons follow different temporal trajectories the aggregate data for their average energy and average dissipation are identical. The inset illustrates a time series of one of the neurons at $k=0.30$.

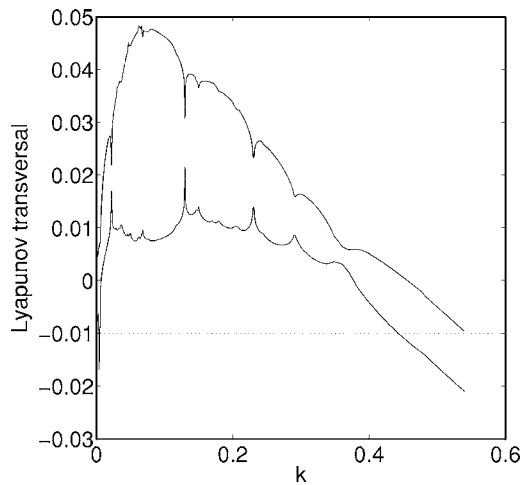


FIG. 5. The two largest Lyapunov exponents of the transversal system of two bidirectionally linearly coupled Hindmarsh-Rose neurons at different values of the coupling strength k .

Several considerations are pertinent. As at every value of k the average energy corresponds to the average on a trajectory virtually covering the whole manifold we can contemplate this average energy as characterizing the manifold itself. From this perspective the process of increasing the gain k leads the neuron through a set of manifolds of different energies. For a linear feedback coupling identical synchronization implies that the interaction term equals zero, consequently, identical synchronization can only occur at the same value of the energy that corresponds to the original non-coupled situation at $k=0$. This occurs at $k=0.467$, as it can be seen in Fig. 4.

For the two coupled neurons that we have analyzed it has been reported [21] that synchrony is a multiscale phenomenon that involves synchrony of bursts, that occurs at $k \approx 0.45$, and synchrony of spikes, that occurs at $k \approx 0.5$. According to our energy results identical synchronization, that is, synchronization of both bursts and spikes occurs at $k=0.467$ a little before than what has been reported. This result is confirmed by the evolution of the two largest Lyapunov exponents of the transversal system that are shown in Fig. 5. From $k=0.462$ both Lyapunov exponents are negative indicating that the neurons can be completely synchronized. Our results for the Lyapunov exponents show some degree of discrepancy with the ones presented in Ref. [21] for the same neurons. The discrepancy could be attributed to the possibly inaccurate linear approximation performed there.

Note that evolving on manifolds of the same energy is a necessary precondition for identical synchronization of two neurons and that bidirectional coupling guarantees always that precondition. Thus, a change in the mechanism of coupling in such a way that the interaction term did not go to zero at identical synchronization could permit both neurons to synchronize at values of the gain parameter others than $k=0.467$. For instance, enhancement of neural synchrony by time delay has been recently published [22].

The fact that the whole curve of average energy versus k is very nonsmooth is a reflection of the complex structure of

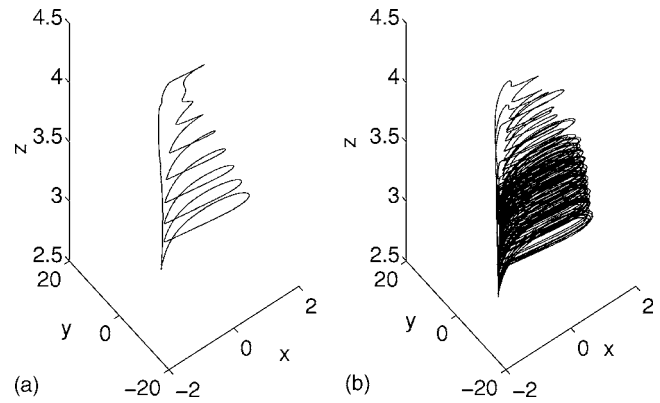


FIG. 6. State space portrait of a neuron for values of the coupling strength (a) $k=0.170$ showing periodic behavior and (b) $k=0.171$ showing an apparent chaotic regime.

manifolds for each neuron at different values of the coupling strength k . Figure 6(a) shows the periodic appearance of the neuron dynamics at $k=0.170$ while Fig. 6(b) shows the chaotic appearance for $k=0.171$. This changeable dynamics very much conditions the quality of the synchrony between both neurons.

As we have said before, although the average energy on the manifold at every value of k is the same for both neurons it does not mean that they follow an identical pattern of energy. Figure 7(a) shows the cross correlation of the energies of both neurons at different values of the coupling strength ranging from $k=0$ to $k=0.5$. The evolution of the cross correlation is very illuminating of the behavior of both neurons. At the very beginning both energies are uncorrelated but very soon reach a high degree of coherence that, with the remarkable exception of the region $0.15 < k < 0.25$, further increases monotonically until complete coherence at $k=0.467$. In the region of gains approximately between $0.15 < k < 0.25$, the cross correlation of both energies constantly jumps from positive values very near to one to very significant negative values. That is so because, in that region,

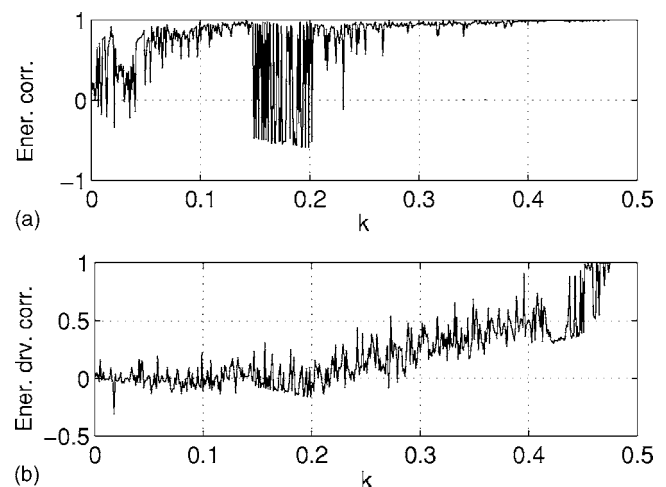


FIG. 7. (a) Cross correlation between the instantaneous values of the energies of both neurons at different values of the coupling strength k . (b) Cross correlation of the energy derivatives.

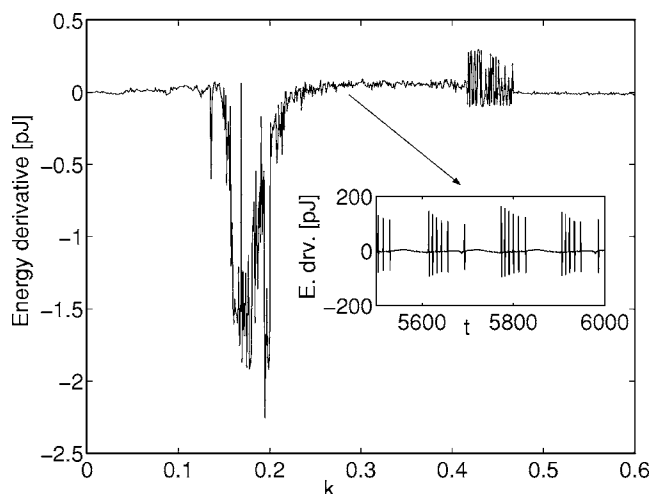


FIG. 8. Average energy derivative of any of the two bidirectionally coupled neurons at different values of the coupling strength k . In the inset, a time series of the actual energy derivative at $k=0.3$ is shown.

both neurons often change with parameter k from a regime in which both are close to complete synchrony with chaotic appearance, to a regime in which both are periodic and in complete synchrony although shifted by half a period. This shifted periodic synchrony has been called antiphase synchrony [23].

If the neurons are forced to synchronize via a coupling device their oscillatory region in the state space is different from the one that corresponds to their free oscillation and, consequently, their total average energy derivative is no longer zero. That means that energy must be provided by the coupling mechanism to balance the flow of energy [16]. This energy is dissipated by the neurons and it is a direct and specific consequence of their cooperative behavior. Figure 8 shows the pattern of the average dissipation of energy of one of the neurons as a function of the coupling strength k . The average dissipation of energy is zero at the starting point and remains in general very near to zero except for a clear burst between approximately $k=0.15$ and $k=0.25$. This result shows that, in general, all the different regimes of synchrony that the two neurons attain at different values of the coupling strength work with a low net dissipation of energy but that there is a region of values of the coupling strength, $0.15 < k < 0.25$, where the activity of the neurons is more energetically demanding. As we have seen before, Fig. 7(a), in that region the qualitative behavior of the neurons is particularly changeable and antiphase synchronization is frequent. A smaller second burst occurs for values of the coupling strength between $k=0.42$ and $k=0.46$. After this second burst the average dissipated energy returns to zero at $k=0.467$ which means that the movement is again on the synchronization manifold [16]. This fact confirms complete synchronization at $k=0.467$.

Data from the cross correlation between the energy derivatives of both neurons at different values of the coupling strength are shown in Fig. 7(b). At low values of k correlation remains around zero until it starts a slow linear increase from $k=0.2$. The cross correlation of the energy derivatives

remains fundamentally low in an ample range of values of k which means that, in contrast with what happens with the energy level, the consumption of energy is fundamentally incoherent. Although the average dissipation of energy of the neuron is in general small it does not mean that its instantaneous demand of energy is necessarily small, as can be seen in the inset of Fig. 8. Moreover, in a neural network, a coherent instantaneous demand of energy by each individual neuron might be energetically very demanding. Our results show that a coherent demand of energy only happens at the threshold of identical synchronization whereas coherence is quickly lost if the need of complete synchrony is slightly relieved. This fact suggests that a cooperative behavior near synchrony could be energetically less demanding than in complete synchrony.

IV. DISCUSSION AND CONCLUSIONS

We have deduced for a Hindmarsh-Rose model neuron a function of the state space variables that can be used to evaluate the electrical energy of the neuron throughout the different states of its dynamics. This function permits calculation of the temporal derivative of the energy and thus, the energy consumption of the neuron in different circumstances can be estimated. Coding is the most specific activity of neurons and its understanding remains as an important open problem in neuroscience. It has been reported that energy consumption by neurons in their normal signaling activity is very high and seems to be a real constrain for neural coding [3]. Codes maximizing the representational capacity seem to be too energy demanding and it has been suggested that nature might have developed a compromise between the energy consumption and the representational capacity [5]. Energy efficient codes would then be codes that maximize the ratio of the representational capacity to the energy expended [5]. As a relevant application of our work on the investigation of energy efficient neuronal coding, we have calculated the average consumption of energy of the Hindmarsh-Rose neuron at different values of the external current I and found that the energy consumption of the neuron during its signaling activity is very sensitive to the different firing regimes. Our result for the energy consumption is in remarkable agreement with the one obtained in Ref. [10] for time-averaged firing rates, which supports the assumption that the energy consumption increases linearly with the mean firing rate [5] and, consequently, with the representational capacity of a possible neuronal code. Understanding energy efficient codes is a promising area of research where models of the electrical energy of the type described in this work can find a particular area of application.

We have also studied the energy and the global balance of energy of two bidirectionally coupled neurons at different values of the coupling strength k . When the two neurons are coupled they are forced to oscillate in regions of the state space where the long run average of their energy derivative is no longer zero. That means that an extra flow of energy is required to maintain the synchronized regime. This fact is a consequence of the different oscillatory regime of the neuron when coupled, and remains true for whatever type of cou-

pling is used for the synchronization. As it has been analyzed in Ref. [12] the extra flow of energy required for the collective behavior must be provided by the coupling mechanism itself. For the central nervous system it has been proposed the existence of a specialized structural site, for glycolytic generation of ATP, localized at the postsynaptic site [24]. According to Ref. [25] the temporal pattern of the presumed glycolytic response would directly follow the presynaptic input in order to meet the metabolic needs induced by the processing of nerve signal transduction. Our results are consistent with this proposal as they anticipate the need of a source of energy linked to the coupling mechanism in order to maintain synchronized kinetics between the two neurons. They also make it clear that that requirement is only for a cooperative behavior, not for an isolated activity of the neurons.

For the Hindmarsh-Rose studied case, we have seen that the average flow of energy required for the synchronized regime is low in an ample range of values of the gain parameter k but that there is a region, $0.15 < k < 0.25$, where the energy dissipation is higher. In this region the interrelation in the dynamics of both neurons is very changeable and antiphase synchronization is frequent. Cross correlation of instantaneous values shows that the consumption of energy of

both neurons is basically incoherent until very near the threshold of identical synchronization, which indicates that a behavior near synchrony is energetically less stringent than in complete synchrony. Incoherence in the energy consumption could facilitate a cooperative behavior especially in a large net of assembled neurons. Nevertheless, as we have shown, the specific cost of maintaining the cooperative regime also has to be considered and might strongly depend on the topological characteristics of the network couplings.

The Hindmarsh-Rose model of a neuron is useful for studying neural behaviors as it properly reproduces qualitatively some of the temporal dynamics of a real neuron. It will be of interest to experimentally ascertain whether the energy pattern exhibited by this Hindmarsh-Rose model is in fact reproducing energy characteristics of real neural synchronization. In Ref. [26] the synchronization between an electronic oscillatory circuit and a real neuron from the inferior olivary nucleus of the rat brain has been reported. To accommodate the oscillation between the circuit and the neuron, an electronic coupling consisting of adjustable gain amplifiers is used. Experiments of this type seem to support that a flow of energy must be provided by the coupling mechanism, and could be used to obtain information of the energy required for the synchronization of real neurons.

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