



DYNAMICAL BEHAVIOR OF THE LINEARIZED VERSION OF THE FITZHUGH–NAGUMO NEURAL MODEL

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Received June 23, 2000; Revised November 27, 2000

For a linearized version of the FitzHugh–Nagumo model, firing and resetting conditions are defined by analogy with the Integrate and Fire model. The dynamical behavior of the model, subject to periodic synaptic inputs, is investigated both theoretically and numerically, with particular emphasis on the synchronization properties. The study is then extended to a network of two synaptically coupled units.

1. Introduction

There is now evidence that, in many sensory and motor areas of the cortex, the phase difference between action potentials fired from different neurons can encode information beyond that carried by the spike train of a single cell [Singer, 1999]. The visual information coded by our eyes comes to the primary visual cortex and complex information-coding processes occur in the neurons of this cortical area. A striking characteristic of the visual cortex is its columnar organization: the firing activity of each cell, within a given functional column, increases when the corresponding receptive field in the retina is activated with the preferred stimulus orientation [Gray & Singer, 1989; Gray *et al.*, 1989]. Current theories suggest that the brain processes the visual information by splitting it into its component features (color, motion, depth, etc.). A relevant question is how the brain rebinds these individual characteristics. Recently it was proposed that this aim could be achieved by synchronizing the firing times of the neurons that encode the features of the visual scene [Malsburg & Schneider, 1986]. Moreover, stimulus dependent synchronization between spatially separate neurons in the visual cortex of cats was also observed [Gray *et al.*, 1989]. These

experimental results suggest that the synchronization of the firing activity of different neurons could be the key to link together different features of a scene [Gray & Singer, 1989; Vershure & Köning, 1999]. How this task is obtained is not yet clear. However, the tangential excitatory connections between neurons in the cortex seem to play a fundamental role for the synchronization phenomena, the degree of synchronization being modulated by the characteristics of synaptic coupling, especially its strength; moreover, the phase locking between neurons could serve as a mechanism to achieve synchrony of neural activity [Singer, 1990]. All these neurophysiological findings propose new challenges, to be faced both experimentally and theoretically.

In a general setting, if ω_1 and ω_2 are the frequencies of two coupled oscillators (or those of an oscillator and its forcing signal), the synchronization condition is that $m/\omega_1 = n/\omega_2$, with m , n prime integers. A state for which the phase difference $\Delta\phi$ (measured in units of 2π) between the two interacting units is zero will be called, from now onwards, a completely synchronous state; while a state where $\Delta\phi = 0.5$ will be termed antisynchronous. All others are defined as states of intermediate synchrony.

Now, the realistic biophysical models of a neuron, like the Hodgkin–Huxley (HH) one, are quite complicated systems of nonlinear differential equations. So there is a considerable advantage (analytical and numerical) in using systems of equations that are simpler than the HH model, but retain many of its qualitative features: an example is represented by the FitzHugh–Nagumo equations (FHN). Even simpler is the well known Integrate and Fire (IF) neural model. In this paper we will use a neural model intermediate between FHN and IF. This model is obtained by linearizing the FHN model in the neighborhood of its resting state and introducing a firing mechanism similar to the IF one. Mainly, there are two reasons that justify using this linearized FHN model (LFHN). The first is the possibility of separating the dynamics of the FHN model into subthreshold and suprathreshold regimes. While the latter is associated to the generation of action potentials whose shape and duration are little affected by the input signal, the response of FHN to perturbations is mainly determined by its subthreshold dynamics. The second reason is related to the Hartman–Grobman theorem establishing that near a hyperbolic equilibrium a suitable change of coordinates linearizes the flow. Furthermore, it is worth noting that LFHN has been shown to reproduce many dynamical properties of the FHN model [Capurro *et al.*, 1998; Nozaki *et al.*, 1999; Di Garbo *et al.*, 2000].

Synchronization phenomena occurring in networks of synaptically coupled IF models have been studied by several authors [Van Vreeswijk, 1996; Coombes & Lord, 1997; Chow, 1998; Bressloff & Coombes, 1998; Coombes & Bressloff, 1999; Campbell *et al.*, 1999]. In particular, the first two papers show that a network of two coupled IF models exhibits a stable antisynchronous state for excitatory coupling and slow synaptic currents. For faster currents stable states of intermediate synchrony appear through a pitchfork bifurcation. For very fast synaptic currents the system gets the stable state of complete synchrony. More recently, Chow [1998] and Coombes and Bressloff [1999], established the conditions for stable phase locking of periodically forced IF models, and then extended their analysis to two or more synaptically coupled IF models.

In this paper we investigate the synchronization phenomena both for a single LFHN model driven by a periodic synaptic-like current and for a system of two LFHN models “synaptically” coupled. Given the importance that excitatory connections have in

the context of neurophysiology we limit our study to this kind of synaptic coupling. Noteworthy, a single LFHN unit can be considered to represent a neural population corresponding to a given functional column of the visual cortex. We will investigate how the features of the synaptic current, i.e. its duration and strength, influence the synchronization properties of the system. The extension of these researches to the general case (with excitatory and inhibitor synapses) will be presented elsewhere.

2. Dynamics of the LFHN Model

Let us start with the FHN model, whose equations can be derived, under certain hypotheses, from the HH ones. In the presence of an external perturbation $P(t)$ they are

$$\varepsilon \frac{dv}{dt} = v(v - a)(1 - v) - w + \sigma P(t) \quad (1a)$$

$$\frac{dw}{dt} = v - w - b \quad (1b)$$

where $v(t)$ is the fast variable describing the membrane voltage and $w(t)$ is the slow recovery variable; σ is the amplitude of the perturbation $P(t)$. For the parameters we shall set the values $\varepsilon = 0.005$, $a = 0.5$. As parameter b increases, at the value $b_1 \simeq 0.2623$ the unperturbed system (i.e. with $\sigma = 0$) undergoes a Hopf bifurcation from the resting state (v_0, w_0) to subthreshold periodic orbits. Lastly, for $b \geq b_2$, the system generates full action potentials. Linearizing the equations (1) in the neighborhood of fixed point yields:

$$\varepsilon \frac{dx}{dt} = Rx - y + \sigma P(t) \quad (2a)$$

$$\frac{dy}{dt} = x - y \quad (2b)$$

with $R = -3v_0^2 + 2v_0(1 + a) - a$, $v(t) = v_0 + x(t)$ and $w(t) = w_0 + y(t)$. But Eqs. (2) do not have any mechanism to generate action potentials; thus, in analogy with the IF model we assume that, whenever the fast variable $x(t)$ crosses a threshold $H > 0$ with positive derivative, an action potential is generated and $x(t)$, $y(t)$ are reset to x_r , y_r , respectively. In this way the linearized FHN model is completely defined. Now, depending on the value of parameter b , LFHN can be in two dynamical regimes: in the first one the fixed point is stable whereas in the other it is unstable. In this paper we suppose LFHN

to be in the last regime (the other case may be handled similarly as long as the forcing is sufficient to produce repetitive firing).

If we denote by $\{t_n : n = 1, 2, \dots, N\}$ the set of firing times, the solution of Eqs. (2a) and (2b) for $t_n \leq t < t_{n+1}$ is given by

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = A(t - t_n) \begin{pmatrix} x_r \\ y_r \end{pmatrix} + \frac{\sigma}{\varepsilon} \int_{t_n}^t A(t - s) \begin{pmatrix} P(s) \\ 0 \end{pmatrix} ds, \quad (3)$$

where $A(t)$ is the fundamental matrix. It easily follows that

$$\begin{aligned} x(t) = e^{\gamma(t-t_n)} & \left\{ x_r \cos \beta(t - t_n) + \sin \beta(t - t_n) \right. \\ & \times \left. \frac{[(1 + \gamma)x_r - \beta^2 y_r - (1 + \gamma)^2 y_r]}{\beta} \right\} \\ & + \frac{\sigma}{\varepsilon} e^{\gamma t} \int_{t_n}^t P(s) e^{-\gamma s} \left[\cos \beta(t - s) \right. \\ & \left. + \frac{2 + \gamma}{\beta} \sin \beta(t - s) \right] ds, \quad (4) \end{aligned}$$

where $\gamma = (R - \varepsilon)/2\varepsilon$ and $\beta = \sqrt{2\varepsilon - (R + \varepsilon)^2}/2\varepsilon$. If we define $x(t) \equiv g(t, t_n, \sigma)$, the firing condition is $g(t_{n+1}, t_n, \sigma) = H$. Whenever locally $\partial g/\partial t_{n+1} \neq 0$ the implicit function theorem guarantees the existence of the explicit map $t_{n+1} = \psi(t_n)$. When this theorem does not hold the map $t_n \rightarrow t_{n+1}$ is implicitly defined by the firing condition. In the following we assume the perturbation in (2a) to be periodic with period T . An important property of the equation $H = g(t_{n+1}, t_n, \sigma)$ is that for any solution (t_{n+1}, t_n) , also $(t_{n+1} + T, t_n + T)$ is a solution. This leads to the following conclusion: if the explicit map exists and is invertible in some domain of the parameter space, then it is the lift of a circle map. In this case chaotic dynamics is not possible for LFHN, the rotation number is rational for periodic orbits (phase locking) and irrational for quasiperiodic ones. The loss of invertibility of the map $t_{n+1} = \psi(t_n)$ means that the rotation number is not defined and chaotic dynamics is possible [Guckenheimer & Holmes, 1983].

Let us assume now that the system itself fires periodically with a period Δ and condition $\Delta/T =$

p/q holds, where p, q are prime integers. To test the stability of this phase locked solution we perturb the firing time t_n to $t_n + \delta_n$ and study the evolution of the perturbation δ_n . By expanding $g(t_{n+1} + \delta_{n+1}, t_n + \delta_n, \sigma)$ and retaining only the linear terms we get the map $\delta_{n+1} = Q(t_n, t_{n+1})\delta_n$ with $Q(t_n, t_{n+1}) = -(\partial g/\partial t_n)/(\partial g/\partial t_{n+1})$. If $|Q(t_n, t_{n+1})| < 1$ for $n \in \mathbb{N}$ then $\lim_{n \rightarrow \infty} \delta_n = 0$ and the corresponding phase locked solution is stable. The borders of the regions where stable phase locking occurs (Arnold tongues) are typically defined by saddle-node and period doubling bifurcations. For such parameter values the Arnold tongues overlap and complex dynamical regime should occur.

In the following we present a simulative investigation of the forced LFHN model, with the perturbation $P(t)$ mimicking the current due to a presynaptic neuron firing regularly with period T : $P(t) = (\alpha^2 e^{-\alpha t}/(1 - e^{-\alpha T}))[t + (T e^{-\alpha T}/(1 - e^{-\alpha T}))]$ for $0 \leq t < T$ [Van Vreeswijk, 1996]. Parameter α is the reciprocal of the synaptic current duration. To characterize the phase locking states we use the rotation number $R = \langle I_n \rangle/T$, $I_n = t_{n+1} - t_n$ being the interspike interval (ISI). It is worth noting that for a $(p : q)$ phase locking state (q spikes in p forcing periods) it is $R = p/q$.

All the results reported were obtained by numerical integration of Eqs. (2a) and (2b) using a fourth order Runge–Kutta method with integration step $\Delta t = 0.001$ and parameter value $x(0) = x_r = 1, y(0) = y_r = 0.15, H = 0.3$ and $b = 0.265$. For each trial a transient interval of 10 t.u. was discarded and the total integration time was 60 t.u. For such parameter values the free running period of LFHN is $T_0 = 0.2645$.

In Fig. 1, R and the corresponding ISIs are plotted against the forcing period for three couples of values of α and σ . In panels (a), (b) two well defined phase locking states, the (1:1) and (1:2) ones, clearly appear. We also found that out of the corresponding stability regions of phase locking the firing map is invertible and the orbits are quasiperiodic (data not shown). As α is increased the stability regions of these phase locking states widen [panels (c) and (d)]. Moreover, according to the Farey tree law, other states with narrower phase locking regions appear: those corresponding to (2:1), (3:2), (2:3), (2:5) and (1:3)

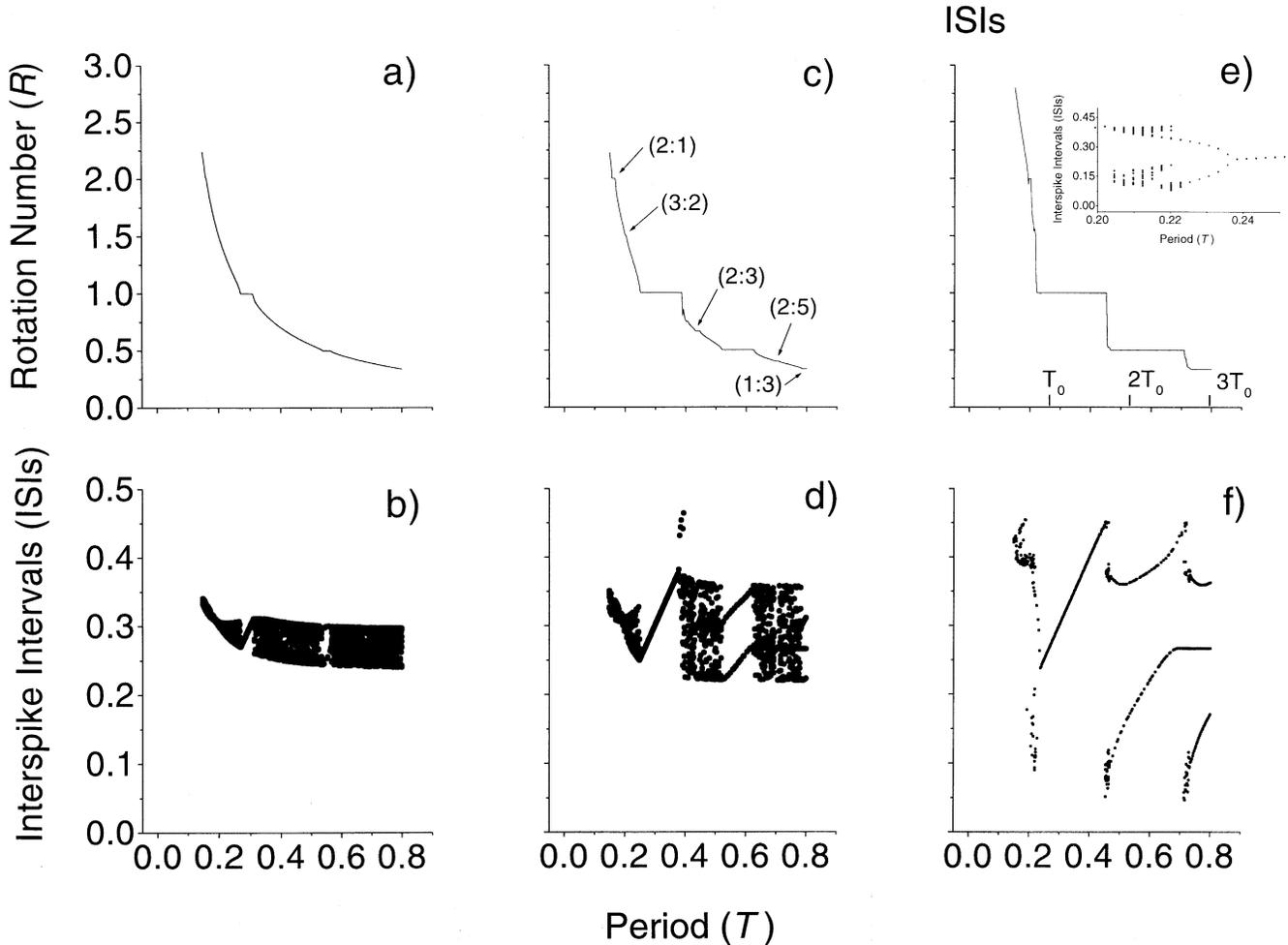


Fig. 1. In the top (bottom) panels the values of the R parameter (the corresponding ISIs) are plotted versus the forcing period T . (a and b) $\alpha = 8, \sigma = 0.02$; (c and d) $\alpha = 14, \sigma = 0.02$; (e and f) $\alpha = 14, \sigma = 0.04$. The vertical bars on the T axis of panel (e) correspond to T values representing integer multiples of the free running period of LFHN. The inset of panel (e) shows an enlarged view of the region $T \in [0.20, 0.25]$ of panel (f).

modes. Increasing the coupling σ and keeping α constant destroys some of these secondary phase locking states (panels (e) and (f) of Fig. 1). An example of period doubling bifurcation, starting at $T \approx 0.24$, is reported in the inset of panel (e) of Fig. 1. In the region around the period doubling bifurcation ($0.22 \lesssim T \lesssim 0.24$) the rotation number remains constant. Moreover, regions where the firing map is not invertible were found ($T \lesssim 0.21$): in these regions chaotic dynamics should be possible.

To elucidate the behavior of R in the transition region from (1:1) to (1:2) phase locking modes, we performed other simulations. In Fig. 2, R is plotted against T for $T \in [0.42, 0.482]$. The transition from mode (1:1) to (1:2) shown in panel (e) of Fig. 1 appears so sharp due to the large range of values

used for T . As shown in panel (b) of Fig. 2, in the transition region the dynamics of LFHN looks irregular with an apparent superposition of states with $R = 1$ and $R = 1/2$. The small fluctuations of the ISI values in the transition region suggest that the dynamical behavior of LFHN can be chaotic on some segments of this range. In fact, the firing map evaluated numerically for $T = 0.452$ is not invertible, while the Poincaré map of the interspike intervals exhibits four distinct and well separated attractors (data not shown).

In Fig. 3, R is plotted against T and σ for the case $\alpha = 14$. Two main Arnold tongues dominate the dynamical behavior of the periodically forced LFHN, corresponding to phase locking modes (1:1) and (1:2). Other very narrow tongues are those

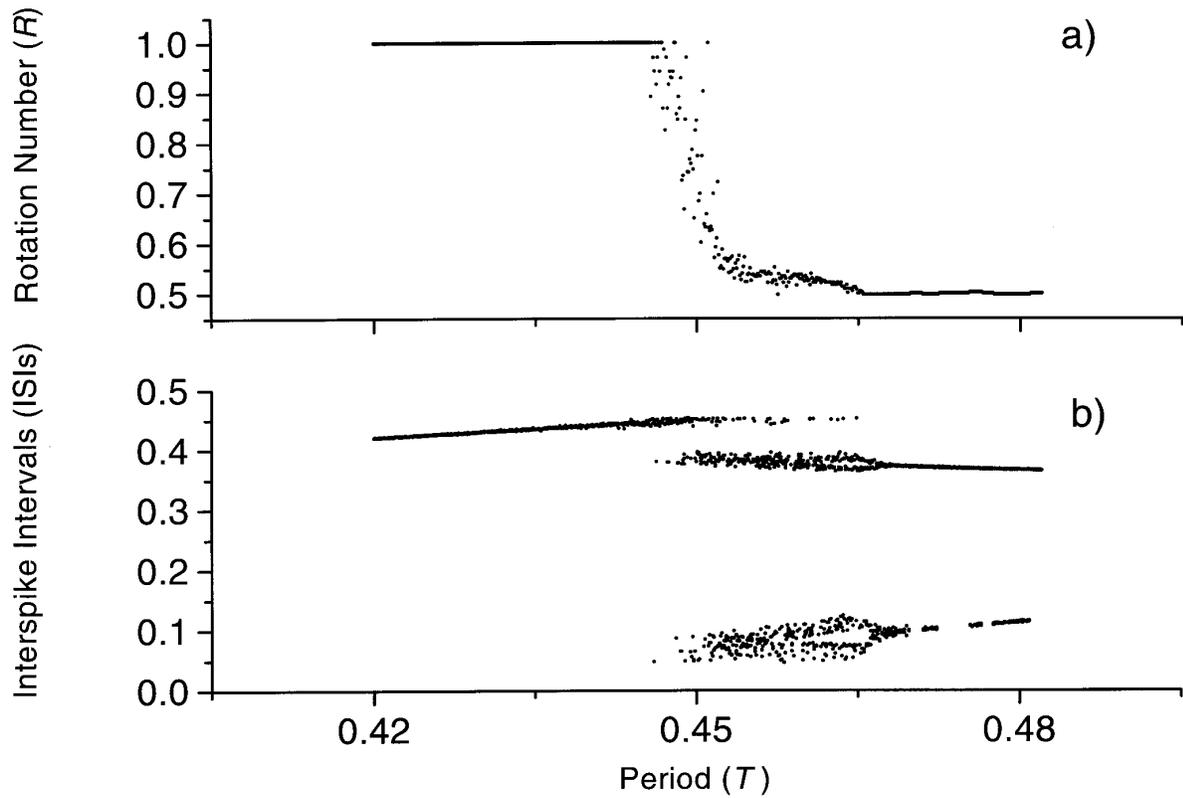


Fig. 2. Enlarged view of a narrow band of panels (e) and (f) in Fig. 1 containing the transition region between the phase locking states (1:1) and (1:2).

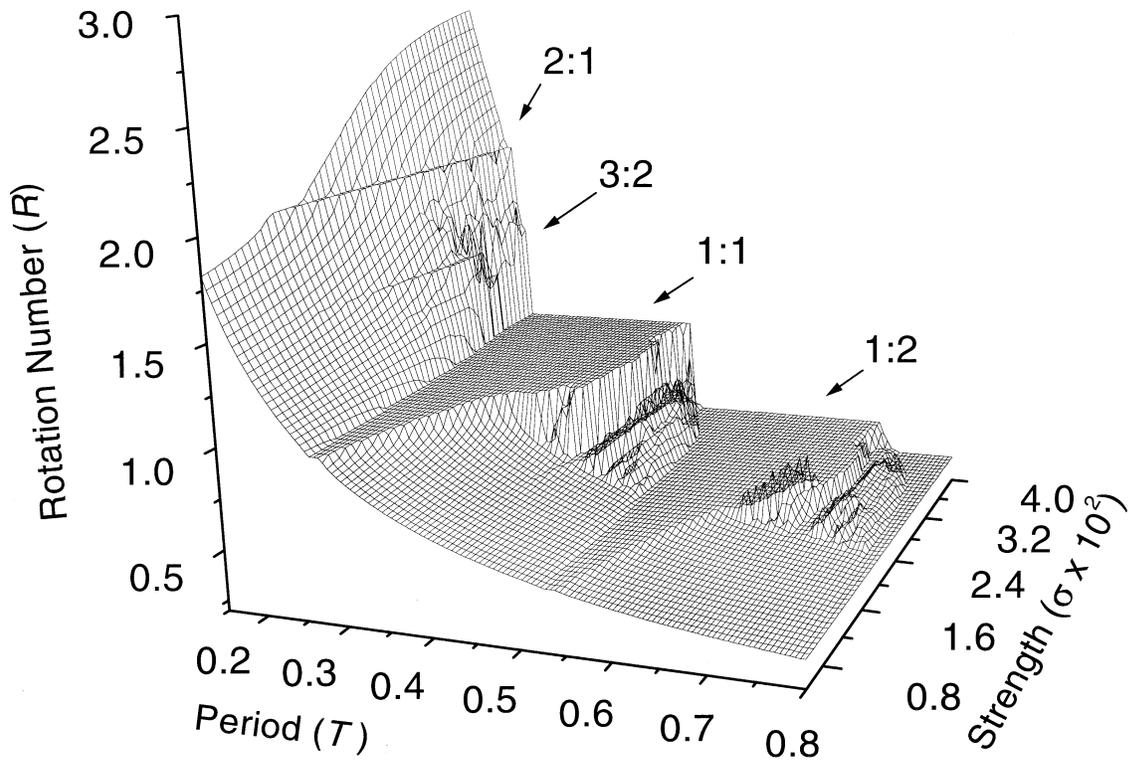


Fig. 3. Phase locking domains of the forced LFHN: the values of R are plotted against the period T and strength σ of the synaptic input.

corresponding to (3:2) and (2:1) modes. The borders of the tongues are clearly defined only for low values of σ . At high values of σ these borders overlap and consequently the dynamics become more complex. The characterization of the system dynamics in the critical regions where a complex behavior occurs, will be addressed in a future work.

3. Two Coupled LFHN Models

Let us begin with the equations describing two LFHNs synaptically coupled

$$\varepsilon \frac{dx_i}{dt} = Rx_i - y_i + \sigma_i P_i(t), \tag{5a}$$

$$\frac{dy_i}{dt} = x_i - y_i, \tag{5b}$$

where $P_i(t) = \sum_{n \geq 1} \Gamma(t - t_n^j)$, $i, j = 1, 2$ and $i \neq j$. The α -function $\Gamma(t)$, vanishing for $t \leq 0$ while holding $\alpha^2 t e^{-\alpha t}$ for $t > 0$, describes the synaptic current following the generation of an action potential in a presynaptic neuron. Let $\{t_n^j : n \geq 1\}$ ($j = 1, 2$) be the firing times of each LFHN model. In what follows, we assume the parameter values to be such to generate, for both LFHNs, periodic firing activity with the same period T . To evaluate the synaptic input to the second LFHN model we suppose that the last spike of the first model occurred at $t_L^1 < t$, whence $P_2(t) = P(t - t_L^1)$, with $P(t)$ as written in the previous section. Similarly, to get the synaptic input to the first LFHN we assume that $t_L^2 = t_L^1 - \theta T$ with $0 \leq \theta < 1$, where θ is the phase difference between the two oscillators, then $P_1(t) = P(t - t_L^2)$.

Now, to determine the unknowns θ and T we could perform a numerical integration of Eqs. (5) and search for stationary states where both firing activities are periodic with period T . However, we follow a different approach based on the knowledge of the explicit solution of Eqs. (5): $x_1(t) = g(t, t_L^1, \sigma_1)$ (for $t_L^1 \leq t \leq t_L^1 + T$) and $x_2(t) = g(t, t_L^2, \sigma_2)$ (for $t_L^2 \leq t \leq t_L^2 + T$), the function g being defined as in the previous section. For simplicity, the same reset values, x_r, y_r , have been assumed for both LFHNs. The firing conditions for both LFHNs are expressed by $x_1(t_L^1 + T) = H$ and $x_2(t_L^2 + T) = H$. So, to determine θ and T we search for the roots of the equation $E(T, \theta) = x_1(t_L^1 + T) - x_2(t_L^2 + T) = 0$ ($t_L^2 = t_L^1 - \theta T$),

being

$$E(T, \theta) = \exp^{\gamma t} \int_0^T \exp^{-\gamma s} \left[\cos \beta(T - s) + \frac{2 + \gamma}{\beta} \sin \beta(T - s) \right] \left[\frac{\sigma_1}{\varepsilon} P_1(s + t_L^1) - \frac{\sigma_2}{\varepsilon} P_2(s + t_L^1 - \theta T) \right] ds. \tag{6}$$

For the rest of the paper we assume that the coupling between the two LFHNs is symmetric, that is: $\sigma_1 = \sigma_2 = \sigma$. By evaluating $P_1(t + t_L^1)$ and $P_2(t + t_L^2)$ and using their periodicity it follows that, for each $T, \theta = 0$ and $\theta = 0.5$ are always solutions of the equation $E(\theta, T) = 0$. The existence of the solution $\theta = 0.5$ follows from the identities $P_1(t + T_L^1) = P(t + \theta T)$, $P_2(t + T_L^2) = P(t - \theta T)$ and the periodicity of $P(t)$. Moreover, for any solution (T^*, θ^*) , $(T^*, 1 - \theta^*)$ is another solution. It can be seen that by suitably choosing the values of H and σ , any solution (T, θ) of equation $E(\theta, T) = 0$ can be mapped to a solution of both equations $x_1(t_L^1 + T) = H$ and $x_2(t_L^2 + T) = H$. So we can simplify our investigation by limiting ourselves to this equation. As shown for the case of two coupled IFs [Coombes & Lord, 1997], the stability of any solution (T, θ) of the same equation is guaranteed by the condition $(\partial E(T, \theta) / \partial \theta) > 0$.

Let us come to the results obtained by solving the equation $E(\theta, T) = 0$ numerically — to this aim we used the programs *dqag.f* and *root.f* of the NETLIB library (see <http://www.netlib.no/netlib/>) allowing for the integration and the computation of the roots of a nonlinear equation, respectively and firstly look to the dependence of the phase difference θ between the two oscillators on the duration of the synaptic current for a fixed value of the period T .

Figure 4 shows the bifurcation diagrams of θ versus α for three values of the firing period of the two oscillators. A pitchfork bifurcation is exhibited in all the cases. Below the bifurcation point the antisynchronous states are stable, while those of complete synchrony are unstable. Above the bifurcation point stable states of intermediate synchrony appear, while the antisynchronous states become unstable. The states of complete synchrony become stable when the branches of intermediate synchrony cross the horizontal axis $\theta = 0$ (or $\theta = 1$). These results are in keeping with those reported for the case of two α -coupled IF models [Van Vreeswijk,

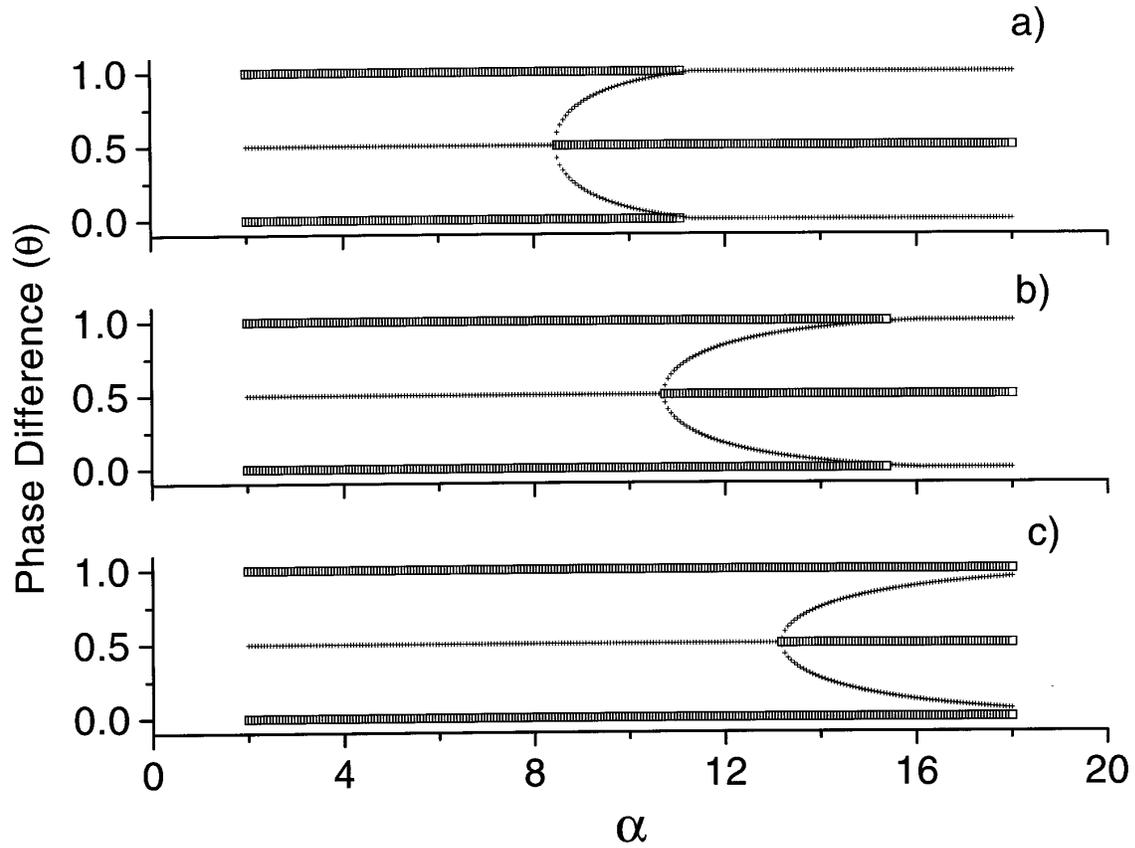


Fig. 4. Bifurcation plots of the phase difference θ between the two LFHN units versus α . Panels: (a) $T = 0.35$; (b) $T = 0.33$; (c) $T = 0.31$. Open squares: unstable states; crosses: stable states.

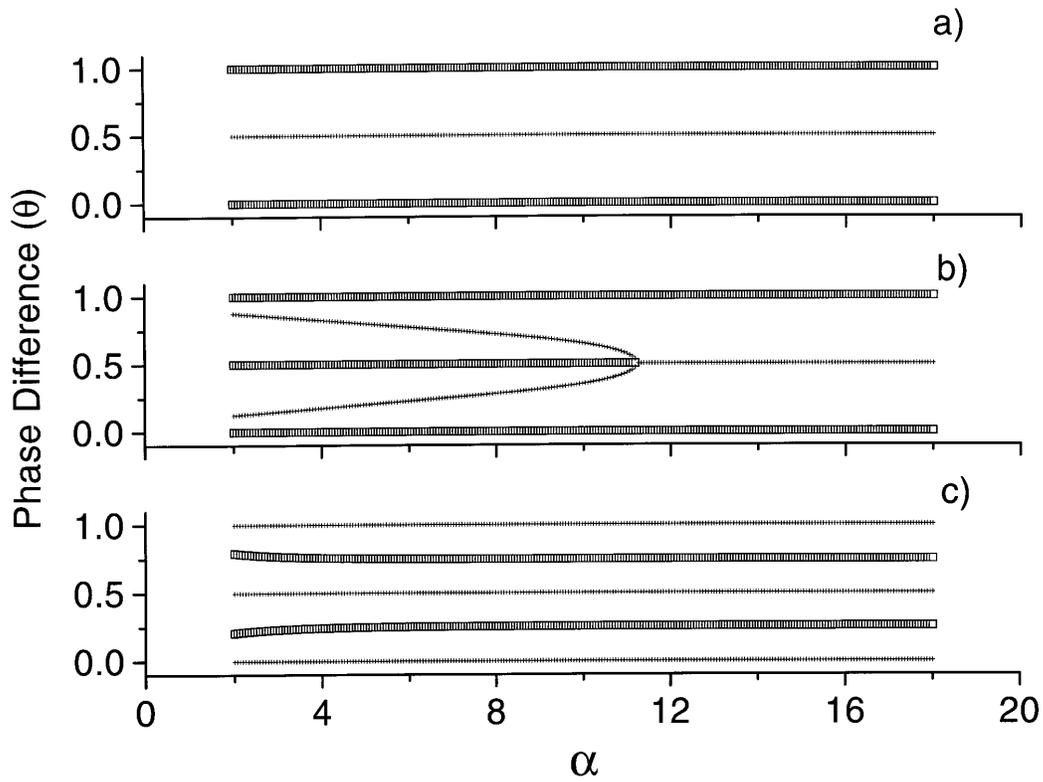


Fig. 5. As for Fig. 4. Panels: (a) $T = 0.2$; (b) $T = 0.7$; (c) $T = 0.9$.

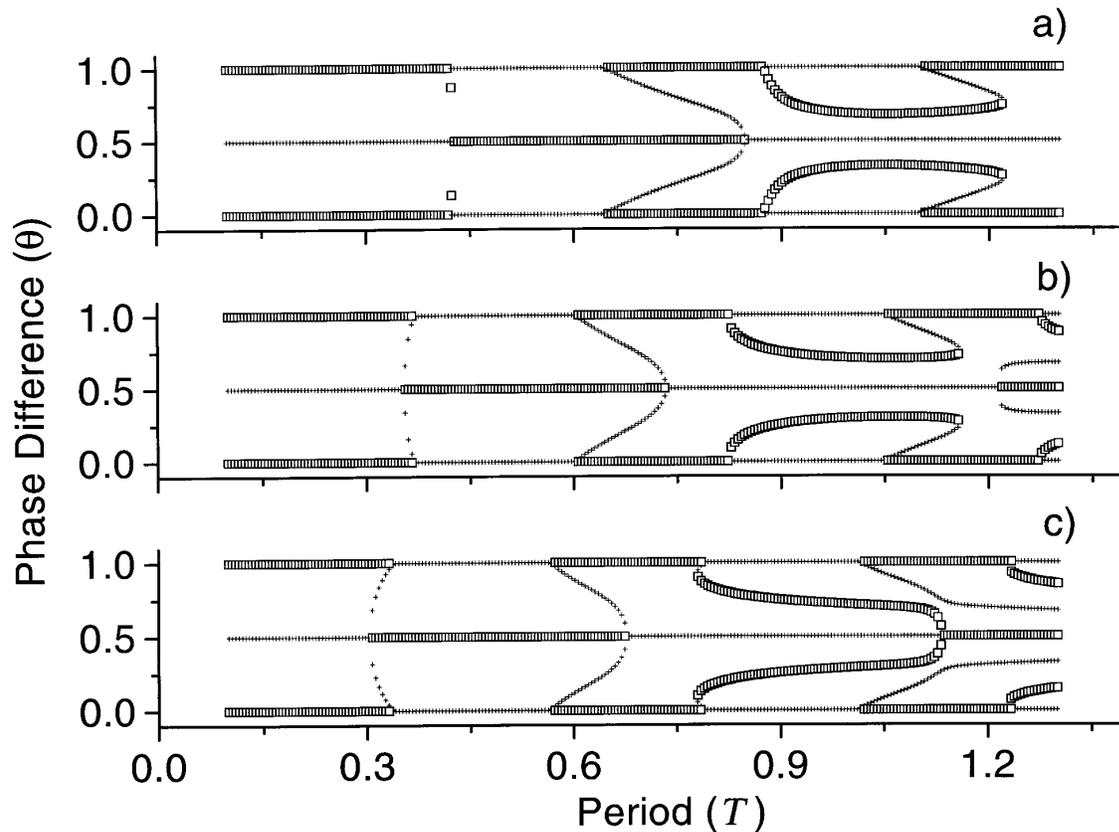


Fig. 6. Plots of the solutions of equation $E(\theta, T) = 0$ for some fixed values of α . Panels: (a) $\alpha = 2$; (b) $\alpha = 8$; (c) $\alpha = 14$. Open squares: unstable states; crosses: stable states.

1996; Coombes & Lord, 1997]. However, our system seems to be more sensitive to changes of α or T than the corresponding network of IF models.

Another interesting feature shown in Fig. 4 is the shift of the bifurcation point for small variations of T . Moreover, as T decreases the branches of the states of intermediate synchrony become smoother and of the bifurcation point moves to higher values of α . These effects, produced by changes of T , are similar to those occurring in the network of IF models by changing the delay time of the synaptic current [Coombes & Lord, 1997]. As shown in Fig. 5, larger variations of T lead to dramatic changes in the system dynamics: from the simplest case of panel (a) (stable antisynchronous and unstable synchronous states) to the more complex ones of panels (b) and (c). In this latter case, in the range of α values explored, stable states corresponding to synchrony and antisynchrony, together with unstable states of intermediate synchrony, appear.

Figure 6 shows the bifurcation diagrams of θ versus T for different α values. For each α a critical

value $T_{c,1}$ exists such that only states of complete synchrony (unstable) or antisynchrony (stable) occur for $T < T_{c,1}$. Moreover, as α increases, $T_{c,1}$ decreases. As T increases over the critical value $T_{c,1}$ new solutions, of intermediate synchrony, branch out (pitchfork bifurcation). For $\alpha = 2$ these states are unstable, while for $\alpha = 8$ and $\alpha = 14$ they become stable. Above $T_{c,1}$ there is, for each α , another critical point $T_{c,2}$. For $T_{c,1} < T < T_{c,2}$ stable and unstable states of any kind of synchrony are present. As for the case of $T_{c,1}$, the critical point $T_{c,2}$ moves to the left as α increases. For $T > T_{c,2}$ the solutions (θ, T) exhibit more complex geometry, with many branches originating from the different bifurcation points.

4. Summary and Discussion

A lot of experimental studies revealed that many biological oscillators (like neurons) may become entrained or phase locked to periodic perturbations [Glass & Mackey, 1988]. In addition, in some experimental conditions, irregular or aperiodic

dynamics was also observed. Likewise, many experimental results show that coherent or synchronized activity can be found between groups of neurons [Gray *et al.*, 1989]. In particular, it should be of great relevance to identify the conditions underlying the coherent activity of single neurons or groups of them; surely, the synaptic interaction between neurons and its features (strength and duration) play a key role in these phenomena.

In this paper we firstly investigated the synchronization properties of the LFHN model subject to a periodic synaptic current. We showed that both the strength and the duration of synaptic inputs are relevant parameters to change the synchronization properties of LFHN. Two main phase locking modes, (1:1) and (1:2), occur in a wide region of the forcing parameter space. Moreover, domains where the forced LFHN exhibits complex phase locking states or aperiodic dynamical behavior were found, the latter being located in the overlapping regions of the Arnold tongues. These results are similar to those obtained with the IF or FHN models subject to periodic perturbation [Coombes & Bressloff, 1999; Yoshino *et al.*, 1999]. In experiments where periodic current pulses were injected into the giant axon of the North Atlantic squid *Loligo pealei*, phase locking states of different order were found (depending on the period and amplitude of the injected current) and, for some parameter values, aperiodic-like rhythms were also observed [Clay & Shlesinger, 1983]. These experimental results seem to be in qualitative agreement with those found with the forced LFHN neural model.

We also studied a network of two synaptically coupled LFHNs to investigate its synchronization properties. By changing either the duration of the synaptic current or the firing period of the LFHN units, we found a wide range of synchronization regimes of all kinds of synchrony and with different stability properties. Part of our results reproduce those obtained for a network of two synaptically coupled IFs [Van Vreeswijk, 1996; Coombes & Lord, 1997]. Nevertheless, the network of two LFHNs seems to be more sensitive to variations in the duration of the synaptic current and firing period than that of two IF models. For a fixed value of α , the plots of the phase difference between the two LFHNs against the firing period, show complex patterns characterized by several bifurcations and by states of different stability.

Neurophysiological experiments demonstrate that cells in the visual cortex exhibit synchronous firing when their responses refer to a single object, for instance a moving light bar [Singer, 1999]. However, the same cells could desynchronize when they are responding to different objects (for instance two bars with different orientation). It was suggested in [Singer, 1990] that the switching between synchronous and asynchronous firing activity could be explained by a change in the synaptic coupling. Our theoretical results on two coupled LFHNs show that changing the duration of the synaptic current yields different synchronization states, so confirming that hypothesis. These theoretical findings suggest, as hypothesized elsewhere [Singer, 1990], that the features of synapses play a key role in the synchronization of a neural population.

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