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Firing sequence storage using inhibitory synapses in networks of pulsatil nonhomogeneous integrate-and-fire neural oscillators

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We discuss a nonhomogeneous population of pulsatil integrate-and-fire neural oscillators, coupled through purely inhibitory synapses. For instantaneous communication, we provide a strategy to generate synaptic couplings to obtain simple periodic and stable firing patterns. We provide restrictions under which each stored firing pattern is a unique attractor for the population dynamics. In the case of Peskin's leaky integrator we show results obtained from numerical simulations.

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I. INTRODUCTION

There has been much interest on the study of systems of integrate-and-fire (IF) neurons [1–6]. This is mainly because the individual description of each unit can be simply accomplished through the use of one differential equation without losing the key aspects of neuron behavior, with the emphasis placed in the connectivity and interactions of large number of units. It is expected that the behavior of systems made of many of these simplified model neurons can shed light into phenomena that persist in systems of more realistic and complex neurons. The type of behavior studied in this paper has been touched before in discussions of synchronization in neural assemblies. Experimental evidence suggests that some neurobiological processes have as a crucial ingredient the synchronized firing of groups of neurons [7–14]. These intriguing phenomena have stimulated theoretical work by many authors. Mirollo and Strogatz [15] were able to demonstrate that fully connected homogeneous systems of rather general IF oscillators have the tendency to spontaneously synchronize when the communication among oscillators is pulsatil, instantaneous, and excitatory. Kuramoto [16] introduced a phase model for each oscillator and was able to study synchronization as a result of Hopf bifurcations in an evolution equation. His formulation also considered refractory periods and noise. The case of synchronization with inhomogeneous IF neurons with instantaneous excitatory pulsatil communication was studied by Tsodyks *et al.* [17]. These authors showed that even in the case of weak interactions in inhomogeneous systems, full synchronization was incomplete and a finite population of unlocked neurons persisted. Another recent study of synchronization with inhomogeneous populations of IF neurons is the work of Senn and Urbanczik [18], where synchronization of similar nonleaky IF neurons with excitatory interactions is discussed. In parallel, there has been interest in noncoherent firing states of systems of IF neurons. Abbott and van Vreeswijk [19] with a mean field approach have studied the stability of the noncoherent states and the influence of noise. A work along the same lines has been carried out by van Vreeswijk [20], with an homogeneous population of IF neurons. They studied in detail coherent and noncoherent states, their dependence on the quality of the excitation — whether excitatory or inhibitory —, as well as the delays of communication. In [21] they study the conditions for self-sustained firing in populations of IF neurons. Hopfield and Herz [22] study the potentialities of systems of homogeneous IF neurons to perform fast computations. These authors work in detail the case of the weak leaky integrator with excitatory interactions. Recent findings on the increased computational capabilities of pulsed neural networks of the IF type have promoted new efforts in the understanding of their capabilities [23]. A recent competing model for the IF neuron is the spike response model of Gerstner *et al.* [24], which also simplifies the description of each neuron to one integral equation with the advantage that the refractory period can be naturally included. Using this model, recent advances in the detailed study of coherence and incoherence in neural assemblies have been possible [25–27]. Another source of interest in the study of the generation of stable firing structures is the mounting experimental evidence showing that neural coding in some systems appears to be linked to precise timing information on spike events rather than on coarse rate values [28–34].

The aim of the present paper is the study of conditions that must be met by the synaptic couplings in populations of IF neurons in order to generate repetitive and structured firing patterns of simple period, in which one neuron fires once per cycle. This feature differentiates our approach from most of the work mentioned above on pulsatil IF neurons, generally dealing with generic synaptic couplings. We consider only the case of instantaneous and inhibitory interactions, but including nonhomogeneous populations of IF neurons of a fairly general type. We find the necessary restrictions on the dynamics that allow the synaptic couplings to store the information on the firing patterns. These patterns turn out to be attractors for that dynamics. In this respect we are able to extend the convergence conditions of Mirollo and Strogatz [15] to the case of nonhomogeneous populations and inhibitory synapses. The paper is organized as follows. In Sec. II we formulate the model and provide the conditions under which the synaptic prescription can lead to stable firing patterns. In Sec. III we explicitly demonstrate the theorem of convergence to the attractor. In Sec. IV we illustrate the analytical results with the use of Peskin's model [35] and pro-

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*Electronic address: imatus@dfi.uchile.cl vide results from numerical simulations. Finally, in Sec. V we discuss the results.

II. MODEL

Let us start with the description of a network of integrate-and-fire oscillators with instantaneous interactions,

$$\frac{dx_i}{dt}=F_i(x_i(t))+G_i(x_i(t))\sum_{j=1}^{N}\sum_{f} J_{ij}\delta(t-t_j^f). \tag{1}$$

In Eq. (1) $x_i(t)$ is a dynamic variable associated with oscillator *i*. In the usual interpretations it corresponds to the membrane potential of the given neural oscillator. The function $F_i(x_i(t))$ drives oscillator *i* to fire in the absence of mutual interactions. Firing occurs when $x_i(t)=\theta_i$, where θ_i is the firing threshold of oscillator *i*. Once a given unit fires, its dynamic variable *x* is immediately reset to zero. Simultaneously, the effect of the firing is sensed by the rest of the population as impulses to their respective *x*. The second term on the right-hand side of Eq. (1) represents the net effect of the firings of all the oscillators connected to unit *i*. The summation over *j* considers the indices of the rest of the population and the summation over *f* picks up their respective firing times t_j^f. The effect of each impulse received by unit *i* and emitted by unit *j* is weighed by! the product of the constant synaptic couplings J_{ij} and the function $G_i(x_i(t))$. When the mutual interactions are inhibitory the product is negative. J_{ij} is null if unit *i* does not receives pulses from unit *j*. In the absence of mutual interactions, all the synaptic couplings are null. In this case the oscillators fire periodically with a period that depends on the function $F_i(x_i(t))$. As we require that the units raise their dynamic variables *x* from rest, taken as zero, to the threshold $\theta>0$ it is necessary that $F_i(x_i(t))>0$ when $0\leqslant x_i(t)\leqslant\theta_i$. Anticipating events of hyperpolarization that occur when the effect of the inhibitory interactions may drive $x_i(t)$ under zero we require that $F_i(x_i(t))>0$ for all range of values of $x_i(t)$ under the thresholds.

To proceed further we make a usual change of variables and define $y_i(t)$ as the phase of unit *i* as follows:

$$y_i(t)=g_i\int_0^{x_i(t)}\frac{dx'}{F_i(x')}. \tag{2}$$

In Eq. (2) the constant g_i allows to normalize $y_i(t)$ such as $y_i(t)=1$ when $x_i(t)=\theta_i$. This means that $g_i^{-1}=\int_0^{\theta_i}dx'/F_i(x')$. The constants g_i correspond to the natural or intrinsic frequencies of each unit. As $F_i(x')>0$ the phase $y_i(t)$ is univocally defined from $x_i(t)$. On the other hand, $dy_i(t)/dt=[g_i/F_i(x_i(t))][dx_i(t)/dt]$. These results allow to recast Eq. (1) as

$$\frac{dy_i(t)}{dt}=g_i+\sum_{j=1}^{N}\sum_{f} H_{ij}(y_i(t_j^f))\delta(t-t_j^f), \tag{3}$$

where

$$H_{ij}(y_i(t))=y_i(x_i(t)+G_i(x_i(t))J_{ij})-y_i(x_i(t)). \tag{4}$$

Equation (3) shows that each unit evolves freely between firing events with constant phase velocities g_i. In addition, the effect of each pulse sent by an oscillator depends on the value of the phase at the instant it is received. Now, we are in a situation to write down the prescription to store phase information in the synaptic couplings J_{ij}.

Assume that we want the whole population to fire periodically with a common period T_l but preserve the phase differences between firings of different units. We start the population at $t=0$ with phases $y_i(0)=y_i^0$. There is one unit that will fire first at time t^1. Rename this unit $j=1$. All the other units have phases less than 1. After firing, unit $j=1$ resets its phase to zero. The synaptic couplings J_{k1} are obtained from unit $j=1$ to the rest imposing that $H_{k1}(y_k(t^1))=(1-g_kT_l)/(n-1)$. Here the subscript *k* labels each unit other than $j=1$. Now apply the effect of the pulse from unit $j=1$ to the rest, using the calculated synaptic coefficient. It is clear that the net effect on every unit is an impulse of magnitude $(1-g_kT_l)/(n-1)$. If T_l is chosen such that $T_l>1/g_k$ for every unit *k*, the synapses are inhibitory. After resetting of the unit $j=1$ and the instantaneous phase decrements of the other units have taken place, the whole population continues their free evolution to threshold until a second unit fires at t^2. Rename this unit $j=2$ and calculate a synaptic coupling J_{k2} to every other unit *k* from $H_{k2}(y_k(t^2))=(1-g_kT_l)/(n-1)$. As before, unit $j=2$ is reset to zero and we apply the pulse from $j=2$ weighed by J_{k2}. The net effect on every unit that is not firing is an inhibitory pulse of magnitude $(1-g_kT_l)/(n-1)$. The series of firing events and calculations of J_{kj} continue until every unit has fired once, i.e., the last pulse is emitted at t^n by unit $j=n$. In the construction of J_{kj}, it is crucial that all units fire once and only once in the period T_l. This imposes some restrictions on the values for the initial phases y_i^0.

We can consider the procedure described above as a learning stage. Notice that after this stage, unit *i* has received a net effect resulting from the $(n-1)$ pulses from the rest of the population, whose magnitude is equal to $(n-1)(1-g_iT_l)/(n-1)=(1-g_iT_l)$. The net phase change of unit *i* after the period T_l is $y_i(T_l)=g_i(T_l-t^i)+(n-i)/(n-1)(1-g_iT_l)$, where we have used the fact that after the firing of unit *i* at t^i its phase is reset to zero; consequently, after that instant there are $n-i$ other firing events, each generating impulses of size $(1-g_iT_l)/(n-1)$ to unit *i*. We can determine t^i from the condition $y_i(t^i)=y_i(0)+g_it^i+(i-1)/(n-1)(1-g_iT_l)=1$, which gives $t^i=[1-y_i(0)-(i-1)/(n-1)(1-g_iT_l)]/g_i$. Replacing this value in the equation for $y_i(T_l)$ we finally obtain $y_i(T_l)=y_i(0)=y_i^0$. This result is valid for every unit *i* and it states that the behavior of the whole population is periodic with period T_l, and also that the information of the phase differences at the moment of the individual firings have been stored in the synaptic couplings J_{ij}.

In what follows we provide conditions that ensure that every unit fires once and only once in the period T_l. As before we identify the index of each unit with the temporal order in which each of them originally fired; i.e., unit *s* fires at t^s and unit *p* fires at t^p. For unit *s* to fire and unit *p* not to fire at t^s it must simultaneously happen that $y_s(t^{s-1}) + g_s(t^s - t^{s-1}) = 1$ and $y_p(t^{s-1}) + g_p(t^s - t^{s-1}) < 1$. Obtaining $(t^s - t^{s-1})$ from the first equation and inserting the value into the second one, we get

$$\frac{y_p(t^{s-1})}{g_p} < \left(\frac{1}{g_p} - \frac{1}{g_s}\right) + \frac{y_s(t^{s-1})}{g_s}. \tag{5}$$

But from the construction procedure at the learning stage, we know that for $p \geqslant s$, $y_p(t^{s-1}) = y_p(0) + g_p t^{s-1} + (s-1)/(n-1)(1 - g_p T_l)$ and that for $p < s$, $y_p(t^{s-1}) = y_p(0) + g_p t^{s-1} + (s-2)/(n-1)(1 - g_p T_l) - 1$. The subtraction of 1 in the latter equation arises from the fact that units with $p < s$ have already fired and have been reset. Notice that for these units we cannot consider, in the total stimulation, a unit of the pulse emitted by itself.

Introducing the condition for the case $p \geqslant s$ in Eq. (5) we obtain

$$\frac{y_p(0)}{g_p} < \left(\frac{1}{g_p} - \frac{1}{g_s}\right)\left(\frac{n-s}{n-1}\right) + \frac{y_s(0)}{g_s}, \tag{6}$$

and repeating the procedure for the case $p < s$ we get

$$\frac{y_s(0)}{g_s} > \left(\frac{1}{g_p} - \frac{1}{g_s}\right)\left(\frac{s-n}{n-1}\right) + \frac{y_p(0)}{g_p} + \left(\frac{1}{n-1}\right)\left(\frac{g_p T_l - n}{g_p}\right). \tag{7}$$

As these relations must hold for every s and p we can interchange s and p in Eq. (6) obtaining for $p \leqslant s$,

$$\frac{y_s(0)}{g_s} < \frac{y_p(0)}{g_p} + \left(\frac{1}{g_s} - \frac{1}{g_p}\right)\left(\frac{n-p}{n-1}\right). \tag{8}$$

Combining Eqs. (7) and (8) we obtain for $p < s$,

$$L_S(p,s) < \frac{y_p(0)}{g_p} - \frac{y_s(0)}{g_s} < R_S(p,s), \tag{9}$$

with

$$L_S(p,s) \equiv \left(\frac{1}{g_p} - \frac{1}{g_s}\right)\left(\frac{n-p}{n-1}\right)$$

and

$$R_S(p,s) \equiv \frac{n-s}{n-1}\left(\frac{1}{g_p} - \frac{1}{g_s}\right) + \frac{1}{n-1}\left(\frac{n - g_p T_l}{g_p}\right).$$

Equation (9) provides the restrictions that must be satisfied by the initial conditions for the phases in order to ensure that each unit fires only once during the period T_l. In addition to requiring $T_l > 1/g_p$ for every p, Eq. (9) also requires that $L_S(p,s) < R_S(p,s)$, leading to

$$T_l < \frac{n}{g_p} - \left(\frac{1}{g_p} - \frac{1}{g_s}\right)(s-p)$$

for every p,s with $p < s$.

In the case of identical neurons, Eq. (9) reduces to

$$y_s(0) < y_p(0) < y_s(0) + \frac{1}{n-1}\left(\frac{n - g_p T_l}{g_p}\right) \tag{10}$$

for $p < s$. Equations (9) and (10) illustrate the fact that the initial phases at $t = 0$ will determine the order of firing, and whenever these equations are satisfied there will not occur any crossings in which some units might fire a second pulse before the first firing of any other unit.

Before leaving this section we will rewrite Eq. (4)—dropping for the moment all indices associated with neurons—using the index o to refer to the learned sequence and the superscript $-$ to refer to the value just prior to the arrival of the pulse as $H(y_o) = y(x_o^- + G(x_o^-)J) - y(x_o^-)$. If we set $H(y_o) = \kappa$ we obtain J as $J = [x(\kappa + y(x_o^-)) - x_o^-]/G(x_o^-)$, where we have used $x(y) = y^{-1}(x)$. Since usually $|\kappa| \ll 1$, we can write to first order in κ that

$$J = \kappa \frac{dx(y_o)}{dy} \frac{1}{G(x_o^-)} = \frac{\kappa}{g} \frac{F(x_o^-)}{G(x_o^-)} = \frac{\kappa}{g} \frac{dx(t_o^-)}{dt} \frac{1}{G(x(t_o^-))}.$$

This expression has to be evaluated at the moment prior to the effect of the pulse that we denote by t_o^- . This form is very attractive from the point of view of a possible hardware implementation. The mechanism to create the synaptic coupling requires the measurement of the temporal derivative of the potential (as well as the potential itself, if $G \neq 1$) just prior to the arrival of the pulse. Once we have selected J between a pair of neurons on the learning stage, it is fixed afterwards. If we were to start a new sequence from initial conditions slightly different from those used to build J we would have an equation like $P = y(x^- + G(x^-)J) - y(x^-)$ with P equal to the impulse to the phase y, in the new trajectory. For inhibitory synapses, where $G(x^-)J < 0$, we observe that $y' > 0$ implies that $P < 0$ everywhere. In addition, $P = P(\Delta y^-)$, where we have $y(x^-) = y(x_o^-) + \Delta y^-$ and $x^- = x_o^- + \Delta x^-(\Delta y^-)$, with Δy^- and Δx^- being the perturbations in the values of y and x prior to the arrival of the pulse, respectively. They are univocally related by Eq. (2) as $\Delta y^- = g\int_{x_o^-}^{x_o^- + \Delta x^-} 1/F(x')dx'$. Besides, notice that $d\Delta x^-/d\Delta y^- = (d\Delta y^-/d\Delta x^-)^{-1} = 1/gF(x^-)$ and $y'(x) = g/F(x)$; therefore, we can calculate the important quantity $P' = dP/d\Delta y^-$ as follows:

$$P' = \left(\left[1 + J\frac{dG(x^-)}{dx^-}\right] y'(x^- + G(x^-)J) - y'(x^-)\right)\frac{d\Delta x^-}{d\Delta y^-}. \tag{11}$$

Considering that $d\Delta x^-/d\Delta y^- > 0$ the sign of P' depends on the concavity of the function $y(x)$. At this point we anticipate that we are interested in situations where $P' < 0$. These cases arise when

$$[1 + JG'(x^-)]y'(x^- + JG(x^-)) < y'(x^-).$$

For inhibitory synapses we have two important cases to consider: (i) $G = 1$ and $J < 0$ and (ii) $JG(x^-) < 0$ and $JG'(x^-) < 0$ as in models such as $JG(x) = J(A - x)$ with $A < 0$ and

$J>0$. In both cases the condition $P'<0$ is guaranteed if the function $y(x)$ has $d^2y/dx^2=-g/F^2F'>0$, which leads to $F'<0$.

Another useful result is derived when we substitute the values of y' and $d\Delta x^-/d\Delta y^-$ in terms of the function F. We obtain

$$P'=\left(\left[1+J\frac{dG(x^-)}{dx^-}\right]\frac{F(x^-)}{F(x^-+JG(x^-))}-1\right). \qquad (12)$$

In the cases where $[1+JdG(x)/dx]>0$, we have that $0>P'>-1$. This result will be used in the following section when we demonstrate the convergence of a perturbed firing sequence to the learned one.

When $P<0$, the condition $P'<0$ means that the magnitude of the pulse gets more negative for neurons receiving the pulse with a phase closer to threshold as compared with the learned trajectory ($\Delta y^->0$) and less negative for neurons receiving the pulse with a phase closer to the resetting point as compared with the learned trajectory ($\Delta y^-<0$). Both effects contribute to shift the reception phases of the pulses closer to the values of the learned trajectory. This is the essence of the argument that proves the stability of the learned trajectory and is in complete agreement with the conditions given by [15] for the case $G=1$. In Sec. III we will expand the argument and explicitly prove that the learned trajectory is the unique attractor when the evolution dynamics keep the firing order of the neurons equal to that in the learned trajectory.

III. THEOREM OF CONVERGENCE

In this section we demonstrate that the learned trajectory, according to the prescription given in Sec. II, is an attractor for the dynamics of the oscillators, provided the firing order is maintained equal to that used at the learning stage. We assume for the moment that this is the case and afterwards we find the conditions that have to be met to comply with the conservation of the firing order.

We concentrate on the study of the variable $\Delta y_i(t_j^f)\equiv y_i(t_j^f)-y_{io}(t_o^j)$, which measures the departure of the actual trajectory of a unit from the learned one, at each firing event. These individual trajectories, when plotted in the (t,y) plane, are sets of straight lines associated with the time intervals during which there is free evolution. These lines with slope g_i end at points with sharp decrements in the variable y, corresponding either to instantaneous inhibitions from incoming pulses or resettings after firing. Let us focus on two consecutive firing events taking place at times t^s and t^{s+1}. To keep track in the demonstration we choose subscripts to identify quantities associated with each oscillator and superscripts to identify the times at which firing occurs. Thus, for the actual and learned trajectories of oscillator $s+1$ between times t^s and t^{s+1}, we can write $g_{s+1}(t^{s+1}-t^s)+y_{s+1}^s=1$ and $g_{s+1}(t_o^{s+1}-t_o^s)+y_{s+1o}^s=1$, respectively. Here g_{s+1} and y_{s+1} are quantities associated with the unit that fires at t^{s+1}. Also, y_{s+1}^s is the phase value of unit $s+1$ as a result of the firing by unit s at time t^s. When we include in the equations the subscript o, we are referring to the same quantities at the learned trajectories. Subtracting both equations we obtain $(t^{s+1}-t_o^{s+1})-(t^s-t_o^s)=-(y_{s+1}^s-y_{s+1o}^s)/g_{s+1}=-\Delta y_{s+1}^s/g_{s+1}$.

Let us consider the actual and learned trajectories of a different unit k between t^s and t^{s+1}. We can write $y_k^{s+1}=y_k^s+g_k(t^{s+1}-t^s)+P_k^{s+1}$ and $y_{ko}^{s+1}=y_{ko}^s+g_k(t_o^{s+1}-t_o^s)+P_{ko}^{s+1}$, where P_k^{s+1} and P_{ko}^{s+1} are the pulses received by unit k as the result of the firing events at t^{s+1} and t_o^{s+1}, respectively. In these equations it is useful to single out the phases at t^{s+1} and t_o^{s+1} before the pulse has taken effect. They are $y_k^{s+1-}=y_k^s+g_k(t^{s+1}-t^s)$ and $y_{ko}^{s+1-}=y_{ko}^s+g_k(t_o^{s+1}-t_o^s)$. The difference of these phases modulates the effect of the pulses P_k^{s+1}. Subtracting the equations for y_k^{s+1} and y_{ko}^{s+1}, we obtain $\Delta y_k^{s+1}=\Delta y_k^s+g_k([t^{s+1}-t_o^{s+1}]-[t^s-t_o^s])+P_k^{s+1}-P_{ko}^{s+1}$. Introducing the value for $(t^{s+1}-t_o^{s+1})-(t^s-t_o^s)$ obtained, we have

$$\Delta y_k^{s+1}=\Delta y_k^s-\frac{g_k}{g_{s+1}}\Delta y_{s+1}^s+P_k^{s+1}-P_{ko}^{s+1}. \qquad (13)$$

By hypothesis we know that oscillator $s+1$ fires in the actual and learned trajectories at firing event $s+1$. In both trajectories it has phase zero after resetting; therefore, it must hold that

$$\Delta y_{s+1}^{s+1}=0. \qquad (14)$$

We remark that $\Delta y_k^{s+1-}\equiv y_k^{s+1-}-y_{ko}^{s+1-}=\Delta y_k^s-g_k/g_{s+1}\Delta y_{s+1}^s$ is the difference in phases of unit k in the actual and learned trajectories, just previous to the effect of the pulse received at t^{s+1}.

We have $P_k^{s+1}=P_k(\Delta y_k^{s+1-})$ as was discussed at the end of Sec. II. Also, we want to stress that when there is full connectivity among the neurons, the functional form of P_k depends only on the identity of the receptor oscillator through F_k and G_k. On the other hand, $P_{ko}^{s+1}=1/(n-1)(1-g_kT_l)\equiv P_{ko}$ is fixed at the learning stage. Let us define $z_k^s=\Delta y_k^s-g_k/g_{s+1}\Delta y_{s+1}^s$ and the function $T_k(z)=z+P_k(z)-P_{ko}$. Notice that $P_k(0)=P_{ko}$ because when there is no perturbation in the trajectory, the received pulse is equal to the learned one. Therefore, we can write $z_k^{s+1}=\Delta y_k^{s+1}-g_k/g_{s+2}\Delta y_{s+2}^{s+1}$ and using the evolution equation (13) written in terms of the function $T(z)$, we have $z_k^{s+1}=T_k(z_k^s)-g_k/g_{s+2}T_{s+2}(z_{s+2}^s)$. To absorb constants we define the variables $v_k^r\equiv z_k^r/g_k$ and $R_k(x)\equiv 1/g_kT_k(g_kx)$; then we can write a new evolution equation

$$v_k^{s+1}=R_k(v_k^s)-R_{s+2}(v_{s+2}^s). \qquad (15)$$

We verify that $v_{s+2}^{s+1}=0$, as is required by Eq. (14). Equation (15) allows to write $v_{k1}^{s+1}-v_{k2}^{s+1}=R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)$.

Now, let us study in more detail the function $R_k(x)$. We have

$$\frac{dR_k}{dv_k^s}=\frac{dT_k}{dz_k^s}=1+\frac{dP_k}{d\Delta y_k^{s+1-}} .$$

In Sec. II we showed—with the restrictions on function G—that $-1<dP_k/d\Delta y_k^{s+1-}<0$. Therefore, we have the important result

$$0<\frac{dR_k}{dv_k^s}<1.$$

We are interested in $|v_{k1}^{s+1}-v_{k2}^{s+1}|=|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|$. As $0<dR_k/dv_k^s<1$ and $R_k(0)=0$ we have $|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|<\max_{k1,k2}|v_{k1}^s-v_{k2}^s|$ for any v_{k1}^s,v_{k2}^s. Here $\max_{k1,k2}$ means the maximum value over the variables $k1,k2$. In effect, for those pairs v_{k1}^s and v_{k2}^s that have opposite sign, we have $|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|<|v_{k1}^s-v_{k2}^s|$ and for those pairs that have the same sign, $|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|<\max_{k1,k2}(|v_{s+1}^s-v_{k2}^s|,|v_{s+1}^s-v_{k1}^s|)$, where we have used $v_{s+1}^s=0$. Then, we can write $|v_{k1}^{s+1}-v_{k2}^{s+1}|=|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|<\max_{k1,k2}|v_{k1}^s-v_{k2}^s|$. Following the recursion, we have $|v_{k1}^{n+p}-v_{k2}^{n+p}|<\max_{k1,k2}|v_{k1}^p-v_{k2}^p|$. These relations show that the difference in the variables v_k^s for a pair of oscillators, identified with the subindexes k, gets smaller as the number of firing events, identified with the superindex s, grows. After a large number of firing events, we finally have $v_{k1}^{\infty}=v_{k2}^{\infty}$, for every $k1$ and $k2$. But $v_{k1}^s=1/g_{k1}\Delta y_{k1}^s-1/g_{s+1}\Delta y_{s+1}^s$ and $v_{k2}^s=1/g_{k2}\Delta y_{k2}^s-1/g_{s+1}\Delta y_{s+1}^s$. Therefore, in the limit of a large number of firing events, $1/g_{k1}\Delta y_{k1}^{\infty}=1/g_{k2}\Delta y_{k2}^{\infty}$ for every pair of $k1$ and $k2$. Considering that at each event there is always one oscillator firing and for this one $\Delta y_k^{\infty}=0$, it turns out that after a sufficient large number of firing events, we must have $\Delta y_{k1}^{\infty}=0$ for every oscillator $k1$ in the population. This demonstrates that as long as the firing order in the dynamics is equal to that used in building the synaptic couplings, the learned trajectory is a unique attractor. Notice that for the case of identical oscillators, we have the more relaxed condition $|R_{k1}(v_{k1}^s)-R_{k2}(v_{k2}^s)|<|v_{k1}^s-v_{k2}^s|$ for any v_{k1}^s,v_{k2}^s, because in this case, we have $R_{k1}(v)=R_{k2}(v)$.

Now we turn our attention to find the conditions that ensure that the perturbed trajectory preserves the firing order. What is needed is that in the perturbed trajectory $t^{s+1}-t^s>0$, when in the learned one $t_o^{s+1}-t_o^s>0$, where the index s identifies the oscillators and the index o signals the learned trajectory. In addition, it is necessary that once an oscillator has fired, it will not fire again until the rest of the population have done it.

In what follows we find restrictions for the perturbation in the initial conditions that ensure that the order of firing is preserved in the first cycle. Then we will show that this condition is obeyed for the rest of the evolution. In fact, we have $g_{s+1}(t-t^s)+y_{s+1}^s=1$ and $g_{s+1}(t_o^{s+1}-t_o^s)+y_{s+1o}^s=1$ as the conditions for oscillator $s+1$ to fire in both the learned and perturbed trajectories, respectively. Notice that we have not given the superindex $s+1$ to the time of firing of oscillator $s+1$ in the perturbed trajectory, because we also must prove that no other oscillator fires the event $s+1$. If we subtract both equations, we obtain $t-t^s=t_o^{s+1}-t_o^s+v_s^s$, where we have used $v_s^s=-\Delta y_{s+1}^s/g_{s+1}$. Therefore, we can write the condition for $t-t^s>0$, which means that oscillator $s+1$ fires after oscillator s as

$$v_s^s>-(t_o^{s+1}-t_o^s) \tag{16}$$

for every $n\geqslant s\geqslant 1$. Below we find a condition to prevent that any other oscillator fires between oscillators s and $s+1$ and in this case we can set $t=t^{s+1}$ and $v_s^s=(t^{s+1}-t^s)-(t_o^{s+1}-t_o^s)$ above. Furthermore, we need to supplement this equation with the requirement that after the perturbation, the initial condition of oscillator $s=1$ is below threshold , ensuring that it will fire first in the cycle. This means that $t^1>0$, or equivalently $y_1^0<1$. We have $g_1t^1+y_{1o}^0+\Delta y_1^0=1$ and $g_1t_o^1+y_{1o}^0=1$ as the conditions for firing of oscillator $s=1$ in the perturbed and original trajectories, respectively. Combining these relations we conclude that if

$$\Delta y_1^0/g_1<t_o^1, \tag{17}$$

then oscillator $s=1$ fires. If the trajectory is ordered, the quantities v_s^s appearing in Eq. (16) are directly related to $v_s^0=\Delta y_s^0/g_s-\Delta y_1^0/g_1$. In effect, $v_k^k=R_k(v_k^{k-1})-R_{k+1}(v_{k+1}^{k-1})$ for every k. As we mentioned before, $v_k^{k-1}=0$ and $R(0)=0$ and therefore $v_k^k=-R_{k+1}(v_{k+1}^{k-1})$ for every k. In addition, $v_{k+1}^{k-1}=R_{k+1}(v_{k+1}^{k-2})-R_k(v_k^{k-2})=R_{k+1}(v_{k+1}^{k-2})+v_{k-1}^{k-1}$. Applying again the recursion formula to $R_{k+1}(v_{k+1}^{k-2})$, we obtain $v_k^k=-R_{k+1}(R_{k+1}(R_{k+1}(v_{k+1}^{k-3})+v_{k-2}^{k-2})+v_{k-1}^{k-1})$. We can continue the procedure to obtain finally

$$v_k^k=-R_{k+1}(((\cdots((R_{k+1}(v_{k+1}^0)+v_1^1)+v_2^2)+\cdots)+v_{k-2}^{k-2})+v_{k-1}^{k-1}).$$

In this expression the operator R_{k+1} has been applied k times. Calling $S_{k+1}(x)=[R_{k+1}(x)]^{-1}$ the inverse of $R_{k+1}(x)$, we have

$$v_{k+1}^0=S_{k+1}(S_{k+1}(\cdots(S_{k+1}(-v_k^k)-v_{k-1}^{k-1})\dots-v_2^2)-v_1^1). \tag{18}$$

This expression shows that the v_k^k determine the v_{k+1}^0, which in turn are related to the perturbations to the initial conditions of the variables y_{k+1}^0. Also, it is worth noticing that in the equation for v_k^k we can substitute the terms v_1^1 as a function of $R_2(v_2^0)$, v_2^2 as a function of $R_3(v_3^0)$ and v_1^1, and so forth, reaching the conclusion that for an ordered trajectory v_k^k depends on $v_2^0,v_3^0,\dots,v_{k+1}^0$.

Now let us work the condition that no oscillator fires a new pulse before the rest of the population has done it in the first cycle. We know from construction that this is the case in the learned trajectory. Assume that oscillator s has fired at $t^s<t^p$ and until t^{p-1}, the trajectory is ordered with each oscillator firing in the same order as in the learned trajectory. For the case of the first firing event it is enough to show that Eq. (17) is satisfied. Then assume that $p=2$. We need that

oscillator $p=2$ fires after $p=1$ and that no other oscillator that has already fired may fire again between $p=1$ and $p=2$. In this case the only oscillator that has fired is $s=1$. So we have to satisfy Eq. (16) with $s=1 v_1^1>-(t_o^2-t_o^1)$ and, in addition, we require that $y_1^2<1$ with $y_1^2\equiv y_1(t^2)$. Here t^2 represents the time at which oscillator 2 fires. We have therefore $y_1^2=y_1^0+g_1t^2+\Sigma_{k=1,k\neq 1}^{k=1}P_1^k-1$. The subtraction of 1 represents the fact that oscillator 1 has already fired and has been reset once. Also, in the summation we have excluded self-stimulation and used the fact that up to t^{p-1} the firing sequence is ordered. For the first oscillator the summation is null. We can obtain the time t^2 from the equation $1=y_2^0+g_2t^2+\Sigma_{k=1}^{k=1}P_2^k$ that holds for oscillator 2. After some algebra we obtain $1/g_1-y_{1o}^2/g_1>\Delta y_1^0/g_1-\Delta y_2^0/g_2+\Sigma_{k=1,k\neq 1}^{1}(P_1^k-P_{1o}^k)/g_1-\Sigma_{k=1}^{1}(P_2^k-P_{2o}^k)/g_2$. Using the fact that for ordered firing sequences, $(P_s^k-P_{so}^k)/g_s=R_s(v_s^{k-1})-v_s^{k-1}=v_s^k+v_k^k-v_s^{k-1}$, $(P_p^k-P_{po}^k)/g_p=R_p(v_p^{k-1})-v_p^{k-1}=v_p^k+v_k^k-v_p^{k-1}$, and $\Delta y_s^0/g_s-\Delta y_p^0/g_p=v_s^0-v_p^0$, we can reduce the summations, ending up with the unequality $1/g_1-y_{1o}^2/g_1>v_1^1$ as the condition that prevents oscillator $s=1$ from firing again before oscillator $p=2$. Equation (18) states that $v_2^0=S_2(-v_1^1)$; therefore, once we have chosen v_1^1 that satisfy both restrictions, we can find the variable $v_2^0=\Delta y_2^0/g_2-\Delta y_1^0/g_1$. As Eq. (17) shows, $\Delta y_1^0/g_1$ is already determined when we required that oscillator $s=1$ fired. We extend the ordered trajectory one more pulse by requiring that oscillator $p=3$ fires after oscillator $s=2$. Using relation (16) this is equivalent to requiring that $v_2^2>-(t_o^3-t_o^2)$. In addition, we need that neither oscillator $s=1$ nor $s=2$ fires its second pulse before oscillator $p=3$ fires. This means that $y_s^3<1$ for $s=1,2$ with $y_s^3=y_s(t^3)$. Here t^3 represents the time at which oscillator 3 fires. We have therefore $y_s^3=y_s^0+g_st^3+\Sigma_{k=1,k\neq s}^{k=2}P_s^k-1$. The interpretation of the terms is similar to the case $p=2$. We can obtain the time t^3 from the equation $1=y_3^0+g_3t^3+\Sigma_{k=1}^{k=2}P_3^k$ that is satisfied for oscillator $p=3$. After some algebra we obtain $1/g_s-y_{so}^3/g_s>\Delta y_s^0/g_s-\Delta y_3^0/g_3+\Sigma_{k=1,k\neq s}^{2}(P_s^k-P_{so}^k)/g_s-\Sigma_{k=1}^{2}(P_3^k-P_{3o}^k)/g_3$. Once again we apply the relations valid for ordered firing segments $(P_s^k-P_{so}^k)/g_s=v_s^k+v_k^k-v_s^{k-1}$, $(P_p^k-P_{po}^k)/g_p=v_p^k+v_k^k-v_p^{k-1}$. In addition, since $\Delta y_s^0/g_s-\Delta y_p^0/g_p=v_s^0-v_p^0$, we can reduce the summations to obtain the relation $1/g_s-y_{so}^3/g_s>v_s^2$, which prevents oscillators $s=1$ and $s=2$ from firing again before oscillator $p=3$. The procedure to extend the ordered sequence is direct we proceed one pulse at a time until $p=n$ by using relation (16) and by requiring at each new firing event the oscillators that have already fired once in the previous ordered sequence not to fire at this event. The relation that we obtain is a generalization of the cases with $p=2$ and $p=3$ and is given by

$$\frac{1}{g_s}-\frac{y_{so}^p}{g_s}>v_s^{p-1} \tag{19}$$

for every $1\leqslant s<p\leqslant n$. As the sequence is ordered by construction until $p-1$ we can express v_s^{p-1} in terms of the v_k^k as

$$v_s^{p-1}=R_s(R_s(\cdots(R_s(v_s^s)+v_{s+1}^{s+1})+\cdots)+v_{p-2}^{p-2})+v_{p-1}^{p-1},$$

where the operator R_s appears $(p-1)-s$ times.

As it has been explained, both Eqs. (16) and (19) are restrictions for the variables $v_k^k=(t^{k+1}-t^k)-(t_o^{k+1}-t_o^k)$. These variables contain the information about the shifts in the firing times along the perturbed trajectory. Then, we could take these variables as free parameters which we can choose to satisfy both set of equations. Once we have an adequate selection for them, the associated perturbations to the initial conditions can be obtained from Eqs. (18) and (17). We will show below that once the first firing cycle of n firing events is ordered the next cycles are ordered as well. Therefore, the oscillator that fires at $t=t^{n+1}$ is the oscillator with $s=1$. This consideration allows to prove that the n variables v_s^s with $1\leqslant s\leqslant n$ are not independent. Let us calculate v_n^n. We use the evolution formula (15) and obtain $v_n^n=R_n(v_n^{n-1})-R_{n+1}(v_{n+1}^{n-1})$. In the second term of the right side the subindex $n+1$ must be identified with the index of the oscillator that fires at t^{n+1}, which turns out to be $s=1$. Therefore, we have $v_n^n=R_n(v_n^{n-1})-R_1(v_1^{n-1})$. The first term on the right side is null as $v_n^{n-1}=0$, which is generally valid for any term of the form v_{s+1}^s. Thus, we have $v_n^n=-R_1(v_1^{n-1})$. Besides, using $v_1^{n-1}=R_1(v_1^{n-2})-R_n(v_n^{n-2})$ and the identity $-R_s(v_s^{s-2})=v_{s-1}^{s-1}$, valid for every s, we obtain $v_n^n=-R_1(R_1(v_1^{n-2})+v_{n-1}^{n-1})$. We continue using the relation $v_1^{n-s}=R_1(v_1^{n-s-1})+v_{n-s}^{n-s}$ for every s to obtain $v_n^n=-R_1(R_1(R_1(\cdots(R_1(v_1^1)+v_2^2)\cdots)+v_{n-2}^{n-2})+v_{n-1}^{n-1})$, where the operator R_1 is applied $n-1$ times. This relation shows that v_n^n can be determined from the $n-1$ values of the previous terms. The following identity is obtained after adding the variables v_s^s:

$$\sum_{s=1}^{n} v_s^s=\sum_{s=1}^{n}\left[(t^{s+1}-t^s)-(t_o^{s+1}-t_o^s)\right]=(t^{n+1}-t^1)-T_l\,.$$

This relation shows that the sum of v_s^s is the perturbation in the period of the firing cycle. As is evident in relation (18), it is not necessary that v_n^n determines v_s^0 with $1\leqslant s\leqslant n$, because we know by definition that $v_1^0=0$. In conclusion, to obtain an ordered perturbed firing sequence in the first cycle we determine Δy_1^0 by Eq. (17), and for $n\geqslant s>1$ we use $\Delta y_s^0=g_s(v_s^0+\Delta y_1^0/g_1)$ with v_s^0 obtained from Eq. (18) as a function of the v_s^s with $1\leqslant s<n$ that comply with Eqs. (16) and (19).

One question remains to be answered. If the first cycle of n firing events is ordered by construction, can we guarantee that the next firing cycles remain ordered as well? An affirmative answer is necessary to demonstrate the convergence to the attractor. The learned firing sequence is ordered by construction as well as the perturbed firing sequence in the first cycle. Let us look from a different perspective at the meaning of an ordered firing sequence. The phases of the n oscillators in the learned trajectory at the initial time are y_{so}^0. If there was no interaction between the oscillators, they would reach threshold at times $t_{sf}^1=(1-y_{so}^0)/g_s$. We call them "free evolution times." There is one oscillator that will have the smallest free evolution time. That one is the first to fire. This condition can be recast into the expression $(t_{sf}^1 - t_{kf}^1) < 0$ for every $k \neq s$, when oscillator s fires first. We rename this oscillator as number 1. In terms of the phases at the initial time this relation states that oscillator 1 fires first if $(y_{1o}^0/g_1 - y_{ko}^0/g_k) - (1/g_1 - 1/g_k) > 0$ for every $k \neq 1$. Once an oscillator fires, it sends an inhibitory pulse to the rest of the population, which in turn acquire a new phase: y_{ko}^1. For the oscillator that has just fired, $y_{1o}^1 = 0$. We repeat the reasoning and verify that oscillator 2 will fire next if the free evolution times satisfy $(t_{2f}^2 - t_{kf}^2) < 0$ for every $k \neq 2$. This result is translated in terms of the phases as $(y_{2o}^1/g_2 - y_{ko}^1/g_k) - (1/g_2 - 1/g_k) > 0$ for every $k \neq 2$. The procedure is iterated until the pulse emitted at t^n by oscillator n has occurred. In general, it can be stated that oscillator s fires at t_o^s if $(y_{so}^{s-1}/g_s - y_{ko}^{s-1}/g_k) - (1/g_s - 1/g_k) > 0$ for every $k \neq s$. Here y_{so}^{s-1} and y_{ko}^{s-1} are the phases of oscillators s and k just after receiving the pulse at time t_o^{s-1}, respectively. In the learned trajectory the firing order is periodic with period T_l, and therefore it is not necessary to check the identity of the firing oscillators for the following cycles. Now we repeat the procedure in a perturbed trajectory that has been constructed as ordered in the first firing cycle. We have that oscillator s fires at time t^s because $(y_s^{s-1}/g_s - y_k^{s-1}/g_k) - (1/g_s - 1/g_k) > 0$ for every $k \neq s$. If we write $y_s^{s-1}/g_s = y_{so}^{s-1}/g_s + \Delta y_s^{s-1}/g_s$ and $y_k^{s-1}/g_k = y_{ko}^{s-1}/g_k + \Delta y_k^{s-1}/g_k$ and use the equality $\Delta y_s^{s-1}/g_s - \Delta y_k^{s-1}/g_k = v_s^{s-1} - v_k^{s-1}$, we can assure that oscillator s has fired at t^s because $(y_{so}^{s-1}/g_k - y_{ko}^{s-1}/g_k) + (v_s^{s-1} - v_k^{s-1}) - (1/g_s - 1/g_k) > 0$ for every $k \neq s$. Since the firing order is preserved in the first cycle of the perturbed trajectory, this means that

$$|(v_s^{s-1} - v_k^{s-1})| < |(y_{so}^{s-1}/g_s - y_{ko}^{s-1}/g_k) - (1/g_s - 1/g_k)| \tag{20}$$

for all firing events from $s = 1$ to $s = n$ and for all $k \neq s$ in the first cycle. For the case of identical oscillators we have $|(v_s^{s-1+n} - v_k^{s-1+n})| < |(v_s^{s-1} - v_k^{s-1})|$ for segments of the trajectory already ordered and, therefore, we can use Eq. (20) to prove that the firing sequence is ordered for the next cycles as well. For the case of inhomogeneous oscillators the relation between the variables v_k^{n+p} and v_k^p involves a maximum. To ensure that the perturbed trajectory in the second and subsequent cycles is ordered we require, in this case, that the perturbations satisfy, in addition to Eqs. (16), (17), and (19), the restriction

$$\max_{k1,k2} |(v_{k1}^{s-1} - v_{k2}^{s-1})| < |(y_{so}^{s-1}/g_s - y_{ko}^{s-1}/g_k) - (1/g_s - 1/g_k)| \tag{21}$$

for all k, s with $k \neq s$ in the first cycle, where $\max_{k1,k2}$ chooses the maximum value of a function over $k1$ and $k2$. As before, we can relate v_k^{s-1} to the variables v_p^p, taking care that when $s-1 < k$ this can be achieved using Eq. (18), obtaining

$$v_k^{s-1} = R_k(S_k(\cdots S_k(S_k(-v_{k-1}^{k-1}) - v_{k-2}^{k-2}) - \cdots) - v_{s-1}^{s-1}) + v_{s-1}^{s-1}$$

for $1 \leqslant s-1 < k \leqslant n$. In this relation the operator S_k is applied $k-(s-1)$ times. In addition, we have

$$v_k^{s-1} = R_k(R_k(\cdots R_k(R_k(v_k^k) + v_{k+1}^{k+1}) + \cdots) + v_{s-2}^{s-2}) + v_{s-1}^{s-1}$$

for $n-1 \geqslant s-1 \geqslant k \geqslant 1$, where the operator R_k is applied $(s-1)-k$ times.

Let us start the second cycle. At t^n the phases of the oscillators are y_s^n. The next oscillator s in firing is that having $(y_{so}^n/g_s - y_{ko}^n/g_k) + (v_s^n - v_k^n) - (1/g_s - 1/g_k) > 0$ for every $k \neq s$. In this expression we can replace $y_{so}^n = y_{so}^0$ and $y_{ko}^n = y_{ko}^0$ because the learned trajectory is periodic with period T_l. Since the first cycle of the perturbed trajectory is ordered, we can relate the v_p^n to the values they had in previous firings. In particular, we know the important relations for every s and k $|v_s^n - v_k^n| < \max_{s,k}|v_s^0 - v_k^0|$ for the case of nonequal oscillators and $|v_s^n - v_k^n| < |v_s^0 - v_k^0|$ for identical oscillators. These inequalities together with Eqs. (21) and (20) allow us to write that $|(v_1^n - v_k^n)| < |(y_{1o}^0/g_1 - y_{ko}^0/g_k) - (1/g_1 - 1/g_k)|$ for every $k \neq 1$. This inequality shows that, for oscillator $s = 1$, the condition to fire first at t^{n+1} in the second cycle is satisfied.

The ordered trajectory now extends from $t = 0$ to $t = t^{n+1}$. To decide which oscillator will fire next we proceed again to look for the oscillator s that has $(y_{so}^{n+1}/g_s - y_{ko}^{n+1}/g_k) + (v_s^{n+1} - v_k^{n+1}) - (1/g_s - 1/g_k) = (y_{so}^1/g_s - y_{ko}^1/g_k) + (v_s^{n+1} - v_k^{n+1}) - (1/g_s - 1/g_k) > 0$ for every $k \neq s$. In this relation we have used $y_{po}^{n+1} = y_{po}^1$ for every p and we know that there is an ordered trajectory up to time t^{n+1}. For the case of nonequal oscillators we have $|(v_2^{n+1} - v_k^{n+1})| < \max_{s,k}|v_s^1 - v_k^1| < |(y_{2o}^1/g_2 - y_{ko}^1/g_k) - (1/g_2 - 1/g_k)|$ and for the case of identical oscillators the condition is $|(v_2^{n+1} - v_k^{n+1})| < |v_2^1 - v_k^1| < |(y_{2o}^1/g_2 - y_{ko}^1/g_k) - (1/g_2 - 1/g_k)|$. These relations are valid for every $k \neq 2$. Therefore, we have that the inequality that decides which oscillator fires is satisfied for $s = 2$. This implies that the next oscillator to fire at t^{n+2} must be $s = 2$. It is clear that we can extend the argument to the rest of the second cycle to demonstrate that it is also an ordered firing sequence. This procedure can be repeated to the next firing cycles as well, because as the perturbations get smaller from one cycle to the next, they are unable to modify the results of the inequalities that determine the firing order in one cycle as compared with the previous one. In conclusion, if the perturbations are such that Eqs. (16),(17), and (19) are satisfied, the firing sequence will keep the order set in the first firing cycle. For the case of identical oscillators this condition is sufficient to have an ordered firing sequence in subsequent cycles as well. For the case of inhomogeneous oscillators, Eq. (21) must also be satisfied to guarantee an ordered firing sequence in posterior cycles.

IV. APPLICATION TO PESKIN'S NEURONS

In this section we apply the results discussed in previous sections to the special, but important, case of Peskin's model [35], where $F_i(x_i)=I_i-\gamma_i x_i$ and $G_i(x_i)=1$ for every oscillator. The integration of Eq. (2) gives the phase variable $y_i=g_i/\gamma_i \ln(I_i/[I_i-\gamma_i x_i(t)])$ and its inverse $x_i=(I_i/\gamma_i)[1-\exp(-\gamma_i/g_i y_i)]$. If the firing threshold is $x_i=\theta_i$, we obtain the natural frequency $g_i=\gamma_i(\ln[I_i/(I_i-\gamma_i\theta_i)])^{-1}$. In addition, from Eq. (4) we obtain $H_{ij}(y_i(t))=-g_i/\gamma_i \ln(1-\gamma_i J_{ij}/I_i \exp[\gamma_i/g_i y_i(t)])$. If we require that $H_{ij}(y_i(t))=(1-g_i T_l)/(n-1)$, the synaptic coupling coefficient adopts the form

$$J_{ij}=\left\{1-\exp\left[\frac{-\gamma_i}{g_i}\left(\frac{1-g_i T_l}{n-1}\right)\right]\right\}\frac{I_i}{\gamma_i}\exp\left[\frac{-\gamma_i}{g_i}y_i^j\right].$$

This expression can be rewritten using the x variable:

$$J_{ij}=\left\{1-\exp\left[\frac{-\gamma_i}{g_i}\left(\frac{1-g_i T_l}{n-1}\right)\right]\right\}\frac{1}{\gamma_i}\frac{dx_i(t^{j-})}{dt}. \tag{22}$$

As is shown in Eq. (22) for Peskin's model, the synaptic coupling is proportional to the temporal derivative of the membrane potential at all orders in J. For this case the value of the pulse $P_k(z)$ is given by

$$P_k(z)=-\lambda_k \ln\left\{1-\exp\left[\frac{z}{\lambda_k}\right]\left[1-\exp\left(\frac{-P_{ko}}{\lambda_k}\right)\right]\right\} \tag{23}$$

and the value for $R_k(z)$ is

$$R_k(z)=\frac{z}{g_k}+\frac{P_k(z)}{g_k}-\frac{P_{ko}}{g_k}, \tag{24}$$

with $\lambda_k=g_k/\gamma_k$ and $P_{ko}=(1-g_k T_l)/(n-1)$. When we take the derivative with respect to z, we have $dR_k/dz=1/[1+b_k(z)]$, with $b_k(z)=\exp(z/\lambda_k)(\exp[-P_{ko}/\lambda_k]-1)$. Since $P_{ko}<0$, because $T_l>1/g_k$ for every g_k, we have that $b_k(z)>0$. We verify that $0<dR_k/dz<1$ and also $R_k(0)=0$. According to Sec. III these are necessary conditions for the stored firing sequence to be an attractor.

We can get an estimation for the speed of convergence by considering the case when n is large; i.e., $|P_{ko}|\ll 1$. In this condition we can linearize Eqs. (23) and (24) to obtain $R_k(v_k^p)=v_k^p(1+P_{ko}/\lambda_k)$. The iteration of the operator R_k in terms of the number of full cycles N_c, made of n pulses, gives

$$(R_k)^{N_c}(v_k^p)=\exp\left(-\frac{N_c}{\mu_k}\right)(v_k^p)^{N_c n} \tag{25}$$

with $\mu_k=(g_k/\gamma_k)1/|1-g_k T_l|$. For example, for values $T_l=0.1$ s, $g_k=25$ Hz, $\gamma=70\ \mathrm{s}^{-1}$, and $v_k^p=1$ we obtain $\mu=0.23$ cycles. This simple estimate suggests that in less than a cycle a perturbed firing sequence can converge to the stored one.

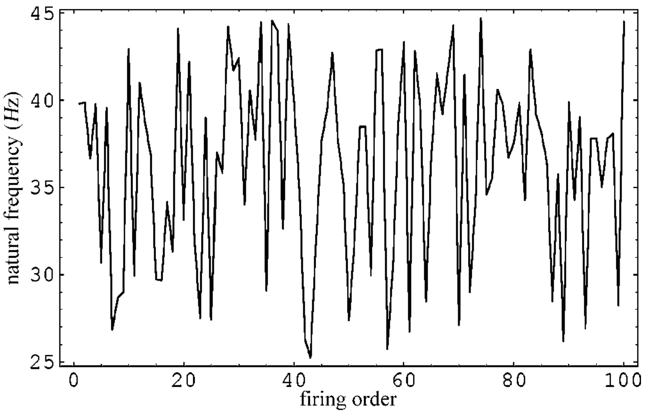

FIG. 1. Oscillator natural frequencies. The natural frequencies of the oscillators are chosen randomly in the range from 25 Hz to 45 Hz. The index on the horizontal axis corresponds to the firing order.

To illustrate the theory we present results from numerical simulations. We have chosen 100 Peskin's neurons with natural frequencies distributed randomly in the interval 25 Hz to 45 Hz. In Fig. 1 we present the frequencies asigned to each unit. All units have a decay constant $\gamma=70\ \mathrm{s}^{-1}$ and the threshold to fire is $\theta=1$ for every oscillator. The firing configuration to be learned will result from the chosen initial conditions for the variables x of each unit. These values are obtained from the phases y_{so}^0 that satisfy the constraints given by Eq. (9) and after the application of the relation that links each x and y. The values for y_{so}^0 have been selected recursively from y_n^0 to y_1^0 as follows: $y_p^0=g_p[(1-r)R_S(p)+rL_S(p)]$, where $R_S(p)=\min_{s,s>p}[R_S(p,s)+y_s^0/g_s]$ and $L_S(p)=\max_{s,s>p}[L_S(p,s)+y_s^0/g_s]$, starting with $y_n^0=0$. Here $\min_{s,s>p}[f(s)]$ and $\max_{s,s>p}[f(s)]$ means the minimum and maximum values for the function $f(s)$ inside the brackets for values of s such that $s>p$. The constant r is chosen so that $y_1^0<1$. In our simulations a value of r around $r=0.95$ has proved to be effective in generating initial values for x that cover most of the interval $[0,1)$. Analogously, the perturbed firing configuration is the result of perturbations on the initial values for the variables x. In the simulation, these perturbations obey the restrictions imposed by Eqs. (16), (17), and (19) on the associated initial phase shifts to achieve an ordered firing sequence. Note that we have not imposed the restriction given by equation Eq. (21) for inhomogeneous oscillators and nevertheless obtain an ordered firing sequence. We have chosen $v_s^s=\kappa[1+\rho(s)](t_o^{s+1}-t_o^s)$ with $\rho(s)$ being a random variable between -0.9 and 0.9 and κ negative, with values around -0.001 to -0.003. In addition, for this simulation we have chosen $\Delta y_n^0=0$ which forces $\Delta y_1^0=-g_1 v_n^n$. Both, the learned and perturbed distributions of initial values for x are shown in Fig. 2 as a function of the firing order.

As was mentioned before, in this experiment we obtain an ordered firing sequence even though relation (21) is not strictly satisfied. We can explain this result considering that, in general, $|v_{k1}^s-v_{k2}^s|=|R_{k1}(v_{k1}^{s-1})-R_{k2}(v_{k2}^{s-1})|$. When the functions R_k satisfy additionally that $R_k''\neq 0$, they have a first derivative that grows or decreases monotonical. In this case we can write $|R_{k1}(v_{k1}^{s-1})-R_{k2}(v_{k2}^{s-1})|<\max_{k,i,j}[|R_k(q_{k,i,j}|v_i^{s-1}-v_j^{s-1}|)|]$, where $\max_{k,i,j}(x)$ takes

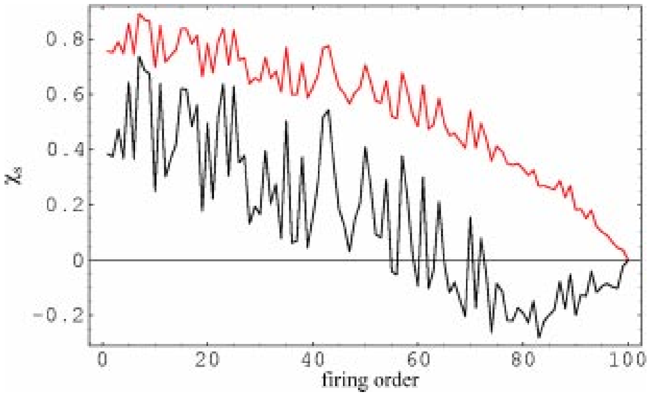

FIG. 2. x_s^0 and x_{so}^0. The top curve represents the stored distribution of values of the variable x for 100 different oscillators at the initial time. This distribution was chosen to satisfy the ordering relations for the phases given by Eq. (9). The lower curve represents the perturbed initial distribution of values for x for the same population. This distribution satisfies the constraints given for the phase shifts Δy_s^0 by Eqs. (16) and (19) and restriction (26). The numbers on the horizontal axis correspond to the order of firing in each cycle. We used oscillators with natural frequencies as in Fig. 1, randomly chosen between 25 Hz and 45 Hz. The values for γ and θ for all the population were $\gamma=70\ \mathrm{s}^{-1}$ and $\theta=1$ and used $T_l=0.1125$ s.

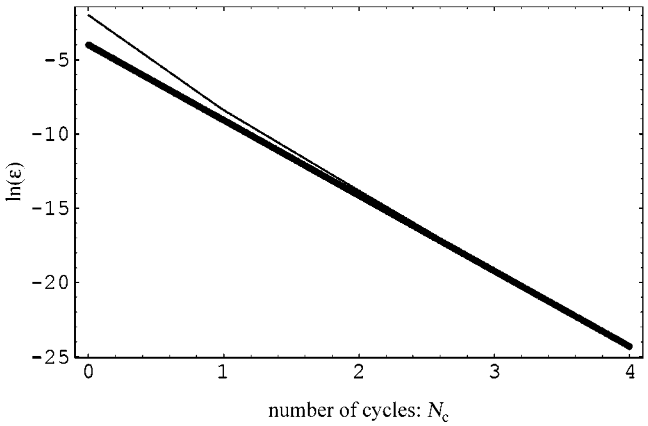

FIG. 3. Convergence rate. The thin curve represents $\ln[\epsilon(N_c)]$ as a function of the number N_c of full cycles. $\epsilon(N_c)=\sqrt{[1/(n-1)\Sigma_{s=1}^{s=n}(x_s^{(nN_c)}-x_{so}^{(nN_c)})^2]}$. The slope of the thick curve is $1/\mu_m=(1-g_mT_l)\gamma/g_m$, with g_m the maximum natural frequency, and is a good estimation of the limit rate of convergence. The data are the same as used in Figs. 1 and 2.

the maximum value of its argument with $1\leqslant k,i,j\leqslant n$, and $q_{k,i,j}$ takes the values 1 or -1 depending on the concavity of the function R_k. We can continue the recursion and write for an ordered trajectory

$$|v_{k1}^{s-1+n}-v_{k2}^{s-1+n}|$$
$$<\max(|R(q\max(|R(q\max(\cdots\max(|R(q|v_i^{s-1}-v_j^{s-1}|)|)\cdots))|))|),$$

where we have omitted the subindexes of the functions R, max and q and these functions are applied n times. This relation shows that we can guarantee that the second cycle is ordered if

$$\max(|R(q\cdots\max(|R(q|v_i^{s-1}-v_j^{s-1}|)|)\cdots)|)$$
$$<\min_j|(y_{so}^{s-1}/g_s-y_{jo}^{s-1}/g_j)-(1/g_s-1/g_j)|$$

for $1\leqslant s\leqslant n$. In the case of Peskin's neurons $R_k''(z)=-1/\lambda_k b_k(z)/[1+b_k(z)]<0$ for all k and we can chose the function R_M that has the maximum first derivative for negative arguments and write the condensed form

$$\max_{i,j}|(R_M)^n(-|v_i^{s-1}-v_j^{s-1}|)|<\min_j|(y_{so}^{s-1}/g_s-y_{jo}^{s-1}/g_j)-(1/g_s-1/g_j)| \tag{26}$$

as the restriction to obtain ordered trajectories in the second and following cycles. Here $\max_{i,j}$ and $\min_j$ take the maximum and minimum values for $1\leqslant i,j\leqslant n$ and $1\leqslant s\leqslant n$. This restriction turns out to be more relaxed than Eq. (21) and in our simulations is satisfied even though relation (21) is not. We observe that the convergence is very fast to the learned sequence. This is illustrated in Fig. 3, where we plot the logarithm of the average shifts $\epsilon(N_c)=\sqrt{1/(n-1)\Sigma_{s=1}^{s=n}(x_s^{nN_c}-x_{so}^{nN_c})^2}$. Here $x_s^{nN_c}=x_s(t^{(nN_c)})$ and $x_{so}^{nN_c}=x_{so}(t_o^{(nN_c)})$ are the values for x for the oscillator that fires in the order s evaluated at the firing time of oscillator that fires at order n, in different cycles. The subindex o distinguish between the perturbed and learned firing sequences. In this figure it should be remarked that the rate of convergence agrees well with the estimate given by Eq. (25).

We have performed a series of experiments with frequencies randomly chosen in the range [25,30] Hz. In Fig. 4 we show the initial distributions for x in both the learned and perturbed trajectories. Both distributions satisfy the ordering relations of the theory with the exception of relation (21) but obeying (26). We note that the perturbed trajectory converges to the attractor very fast, as it is shown in part (b) of the figure.

We have repeated the experiment with the same learned sequence as in Fig. 5 but, in this case, the perturbed sequence starts from initial conditions that are a scaled version of the learned ones. The plot of convergence shows that after a short transient, where the firing order may be upset, the dynamics find eventually a path to the attractor. This suggest that the valley of attraction is larger than the set of trajectories complying strictly with the ordering relations. For comparison we have repeated the experiment but now the perturbed sequence starts from completely random initial conditions. In Fig. 6 it is shown that in this case the attractor is never reached. We end the series with an experiment carried out with identical oscillators having a natural frequency equal to 25 Hz. In this case we intentionally distort the perturbed sequence, without disobeying the ordering equations. In Fig. 7 we show the results that confirm that the dynamics flows directly to the attractor right from the beginning.

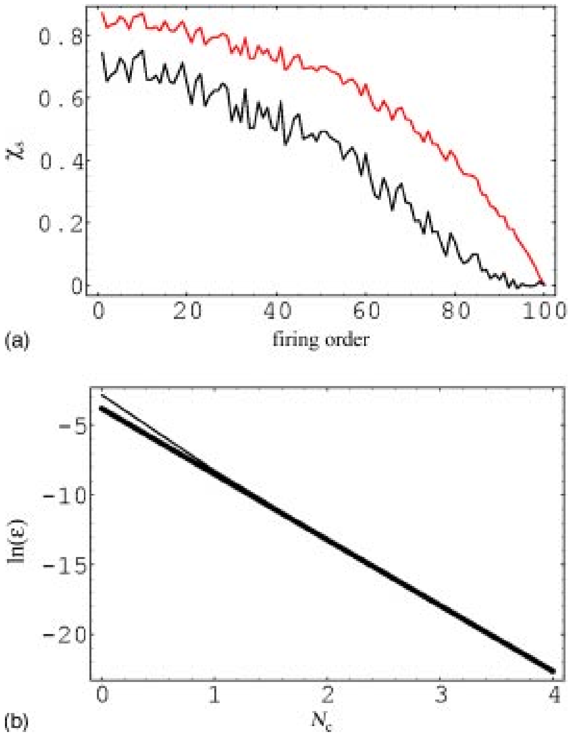

FIG. 4. x_s^0 and x_{so}^0 and rate of convergence. In (a) each curve represents the stored distribution of values of the variable x for 100 different oscillators at the initial time. The top curve of this figure contains the distribution chosen to satisfy the ordering relations for the phases given by Eq. (9). The lower curve represents the perturbed initial distribution of values for x for the same population. This distribution is calculated to satisfy the ordering restrictions with relation (26) instead of Eq. (21). In (b) we have plotted the shifts $\ln[\epsilon(N_c)]$ (light curve) vs the number of cycles and the theoretical convergence rate (dark curve). We used oscillators with natural frequencies randomly chosen between 25 Hz and 30 Hz. The values for γ and θ for the whole population were $\gamma = 70\ \mathrm{s}^{-1}$ and $\theta = 1$ with $T_l = 0.1072$ s.

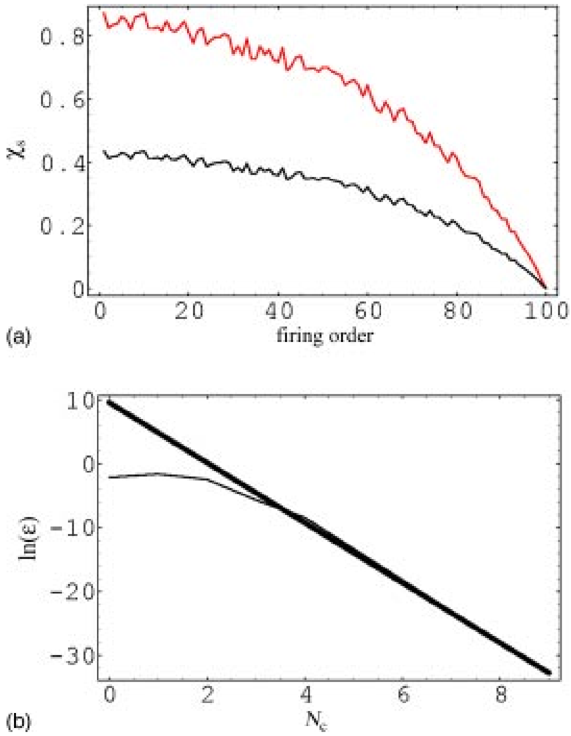

FIG. 5. x_s^0 and x_{so}^0 and rate of convergence. (a) each curve represents the stored distribution of values of the variable x for 100 different oscillators at the initial time. The top curve of this figure contains the distribution chosen to satisfy the ordering relations for the phases given by Eq. (9). The lower curve represents the perturbed initial distribution of values for x for the same population. For this experiment this distribution is simply a scaled version of the learned distribution $x_s^0 = 0.5 x_{so}^0$. In (b) we have plotted the shifts $\ln[\epsilon(N_c)]$ vs the number of cycles and superposed for comparison the theoretical rate close to the attractor. We used oscillators with natural frequencies randomly chosen between 25 Hz and 30 Hz. The value for γ and θ for all the population were $\gamma = 70\ \mathrm{s}^{-1}$ and $\theta = 1$ and used $T_l = 0.1072$ s.

V. DISCUSSION

In the present work we have developed a procedure to store simple periodic firing sequences in a fully connected set of IF neurons that communicate via instantaneous and inhibitory synapses. The type of neurons are quite general; however, they need to satisfy certain criteria about the concavity of the leak function. In particular, the method is applicable to Peskin's neurons with arbitrary natural frequencies. We have proved that the stored firing sequence is a unique attractor for the dynamics, with an attraction valley that is constituted by firing patterns with a similar firing order as the stored sequence. We have provided restrictions to the extent of the perturbations in the initial conditions of the different units, which guarantee that the firing order is preserved at all times during the evolution to the attractor. The stored firing sequences have precise time relations between the firing events of different units. For a model with no time delays, as that we have discussed in this paper, this means that the oscillators are not synchronized in the attractor. We explicitly show a method to use structured inhibitory synapses to get stable and general firing sequences in which each neuron fires once per cycle. In addition, the prescription to obtain the synaptic values can be implemented using the first firing cycle. An interesting aspect of the procedure is that the calculation of the synapses is related to the evaluation of the temporal derivative of the state variable of each unit at the moment of the reception of a pulse. An important point that is necessary to remark is that in common approaches, the synaptic couplings are chosen as negative and equal. In these cases, systems of fully connected homogeneous IF neurons with instantaneous communication reach a periodic solution after a transient. A characteristic of this solution is that the firing times are equally distributed along the firing cycle. This necessarily means that when a neuron fires, the others receive the pulse with a different phase. Otherwise, they would fire the next pulse simultaneously as they have the same natural frequency. These solutions, whose stability have been the subject of many studies by others, are radically different from the attractor we have discussed in this paper, because it is impossible to get equal values for the J_{ij} with neurons that have different values for their phases at the moment of the reception of the pulses. The *ab initio*

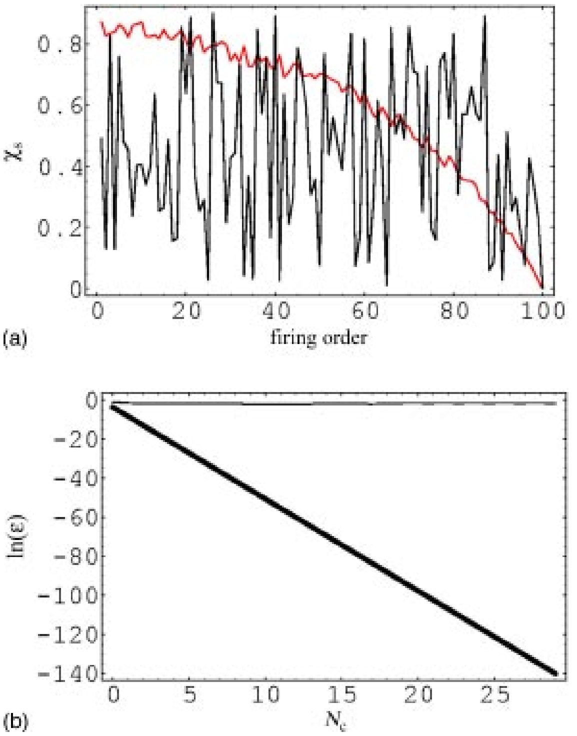

FIG. 6. x_s^0 and x_{so}^0 and rate of convergence . In (a) each curve represents the stored distribution of values of the variable x for 100 different oscillators at the initial time. The top curve of this figure contains the distribution chosen to satisfy the ordering relations for the phases given by Eq. (9). The lower curve represents the perturbed initial distribution of values for x for the same population. For this experiment this distribution has values for x_s^0 randomly chosen in the interval [0,0.9]. In (b) we have plotted the shifts $\ln[\epsilon(N_c)]$ vs the number of cycles and superposed for comparison the theoretical rate close to the attractor. We used oscillators with natural frequencies randomly chosen between 25 Hz and 30 Hz. The values for γ and θ for the whole population were $\gamma=70\ \mathrm{s}^{-1}$ and $\theta=1$ with $T_l=0.1072$ s.

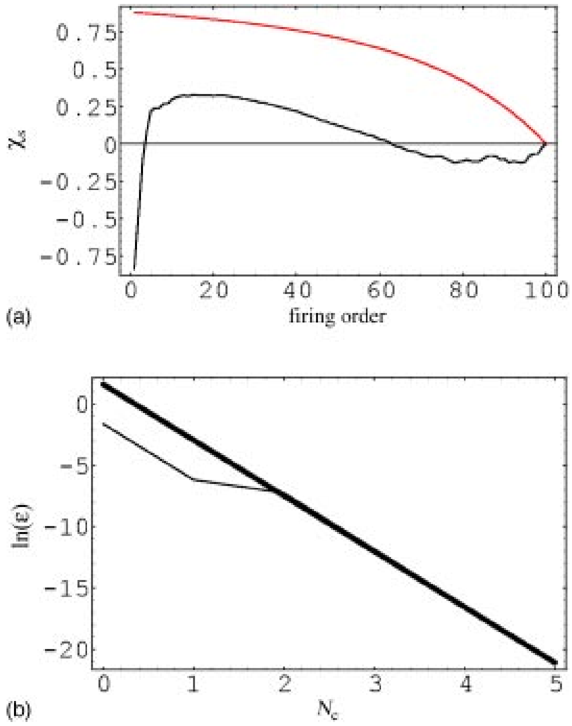

FIG. 7. x_s^0 and x_{so}^0 and rate of convergence. In (a) each curve represents the stored distribution of values of the variable x for 100 different oscillators at the initial time. The top curve of this figure contains the distribution chosen to satisfy the ordering relations for the phases given by Eq. (9). The lower curve represents the perturbed initial distribution of values for x for the same population. In this experiment we achieve a very distorted initial distribution that nevertheless satisfies the restrictions of the theory to give an ordered firing sequence. In (b) we have plotted the shifts $\ln[\epsilon(N_c)]$ vs the number of cycles and superposed for comparison the theoretical rate close to the attractor. We used oscillators with natural frequencies of 25 Hz. The values for γ and θ for the whole population were $\gamma=70\ \mathrm{s}^{-1}$ and $\theta=1$ with $T_l=0.1048$ s.

fixation of the values for the J_{ij} is normally done in most of the work on the subject and therefore might conceal interesting phenomena.

For the case of Peskin's neurons we have provided estimates for the speed of convergence to the attractor, which suggests a very fast convergence with rates of less than one pulse per neuron—a full firing cycle — to almost reach the attractor. This observation is relevant if we were to employ a model like that proposed for a pattern recognition task. If this were the case we could get full recognition with one firing event per neuron. This result is interesting from a neurobiological perspective because it supports experimental observations in which behavioral responses are reached after very few pulses per neuron [36]. We can think of generalizations of the model to include at least two other aspects (i) communication delay and pulses of finite width and (ii) a non-fully-connected system. In work not presented in this paper we have explored successfully both aspects. It is possible to incorporate synaptic delays if we keep computing the synapses at the moment of reception of the pulse. For the case of pulses with finite width the theory leads to synapses with efficiencies that depend on time, and the effect of each pulse turns out to be convolutions of the products of these synaptic efficiencies and the pulse profile. The cases of sparse connectivity are easily dealt with if we replace $1/(n-1)(1-g_sT_l)$ with $1/c_s(1-g_sT_l)$, where c_s is the connectivity of each neuron with the rest. In numerical simulations not shown in this work, we have used with success networks of Peskin's neurons in which each member is connected only to a second one. Some modifications are necessary to the ordering preservation relations, though.

One interesting observation is that a perturbed firing sequence that preserves the firing order usually is the result of initial conditions in the membrane potential that are approximately a scaled version of the initial conditions used to generate the learned firing sequence. In the language of the variables v_s^s they can be obtained when we use $v_s^s=(\kappa-1)\times(t_o^{s+1}-t_o^s)$ with $\kappa>0$, and then the new firing interval is $(t^{s+1}-t^s)=\kappa(t_o^{s+1}-t_o^s)$. The example presented in Fig. 5 was obtained by making this type of selection. Thus, it is conceivable that we could use the proposed system to store the information of external signals in the values of the initial conditions of the membrane potentials. The preservation of the firing order, when the initial conditions of the perturbed state are a scaled version of those used in the learning stage, assures a recovery of the stored signal, as the dynamics of the network converges to the attractor. A direct application could be in the recognition of images under different levels of illumination.

A further step to make a model of these IF neurons more realistic is to incorporate a refractory period after the emission of a pulse. As we are working with inhibitory synapses and the final firing frequencies become smaller than the natural values, an incorporation of a refractory period appears that will not modify substantially the main results. On the other hand, the refractory period is a manifestation of the true dynamics of the membrane potential and an acceptable inclusion may require the use of a more sophisticated model for the neuron. Consequently, we have performed simulations with oscillators made of patches of Hodgkin-Huxley membranes [37] and we have been able to force the membrane to fire periodically with a lower period when stimulated with an external periodic inhibitory signal, and with synapses calculated according to the prescription of this paper, as long as the pulses arrive at times when the main nonlinearities that are responsible for the pulse generation and recovery of the membrane potential have died out. In other words, as long as the membrane potential has an evolution closer to a leaky capacitor, the synaptic prescription that uses only the membrane potential appears to be effective. This observation clearly imposes some restrictions on the connectivity of the network. A satisfactory periodic solution can be obtained if each neuron receives pulses within time windows located away from the extremes of the firing period. This in turn may require that each neuron receive only a few pulses per cycle. In this respect it is important to point out that a reduced connectivity can also improve noise immunity related to random shifts in the firing times. As the average time differences between two firing events involving connected neurons increases with reduced connectivity, the noncontrolled time shifts are less likely to upset the firing order, which is crucial to the convergence to the attractor.

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