Transient oscillations in continuous-time excitatory ring neural networks with delay

K. Pakdaman,[1,2] C. P. Malta,[3] C. Grotta-Ragazzo,[4,5] O. Arino,[6] and J.-F. Vibert[1]
[1]B3E, INSERM U 444, ISARS, UPMC, Faculté de Médecine Saint-Antoine, 27, rue Chaligny, 75571 Paris Cedex 12, France
[2]Department of Biophysical Engineering, Faculty of Engineering Science, Osaka University, Toyonaka 560 Osaka, Japan
[3]Instituto de Física, Universidade de São Paulo, Caixa Postal 66318, 05389-970 São Paulo, Brazil
[4]Instituto de Matemática e Estatística, Universidade de São Paulo, Caixa Postal 66281, 05389-970 São Paulo, Brazil
[5]Mathematics Department, Princeton University, Fine Hall, Washington Road, Princeton, New Jersey 18540
[6]Laboratoire de Mathématiques Appliquées, Université de Pau et des Pays de l'Adour, IPRA, URA CNRS 1204, Avenue de l'Université, 64000 Pau, France

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A ring neural network is a closed chain in which each unit is connected unidirectionally to the next one. Numerical investigations indicate that continuous-time excitatory ring networks composed of graded-response units can generate oscillations when interunit transmission is delayed. These oscillations appear for a wide range of initial conditions. The mechanisms underlying the generation of such patterns of activity are studied. The analysis of the asymptotic behavior of the system shows that (i) trajectories of most initial conditions tend to stable equilibria, (ii) undamped oscillations are unstable, and can only exist in a narrow region forming the boundary between the basins of attraction of the stable equilibria. Therefore the analysis of the asymptotic behavior of the system is not sufficient to explain the oscillations observed numerically when interunit transmission is delayed. This analysis corroborates the hypothesis that the oscillations are transient. In fact, it is shown that the transient behavior of the system with delay follows that of the corresponding discrete-time excitatory ring network. The latter displays infinitely many nonconstant periodic oscillations that transiently attract the trajectories of the network with delay, leading to long-lasting transient oscillations. The duration of these oscillations increases exponentially with the inverse of the characteristic charge-discharge time of the neurons, indicating that they can outlast observation windows in numerical investigations. Therefore, for practical applications, these transients cannot be distinguished from stationary oscillations. It is argued that understanding the transient behavior of neural network models is an important complement to the analysis of their asymptotic behavior, since both living nervous systems and artificial neural networks may operate in changing environments where long-lasting transients are functionally indistinguishable from asymptotic regimes. [S1063-651X(97)01103-3]

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I. INTRODUCTION

Experimental studies of the behavior of self-connected single neurons have shown that the time it takes for a signal to be transmitted (referred to as delay here) from the neuron to itself can influence the discharge pattern of biological neurons [1]. The influence of delay on neural behavior has also been analyzed in theoretical and computational studies of self-connected single neuron and of recurrent neural network models [2,3]. These results indicate that the delay is an important control parameter in living nervous systems: to different ranges of delays correspond different patterns of neural activities.

In some artificial neural network (ANN) applications, such as content addressable memories, information is stored as stable equilibrium points of the system. Retrieval occurs when the system is initialized within the basin of attraction of one of the equilibria and the network is allowed to stabilize in its steady state [4,5]. Delayed interunit transmissions may render such networks more versatile, for instance, by enabling the storage and retrieval of time-varying sequences in discrete-time [6] and continuous-time networks [7]. Nevertheless, in some ANN applications, uncontrolled delay may deteriorate network performance. Such delays arise in hardware implementation of ANNs, due to finite switching and transmission times of the circuit components. They may interfere with information processing by rendering the equilibria unstable thus making the retrieval of the corresponding information impossible [8]. This problem has motivated a number of studies investigating the dynamics of networks of graded-response neurons (GRNs) in the presence of delays [8,9].

The above considerations indicate that determining the contribution of the delay to the shaping of neural dynamics is important for better understanding a variety of neural network behaviors. This work deals with the influence of delay on the behavior of networks composed of continuous-time GRNs, which have been used as models of living neuron assemblies [10] as well as in ANN applications [4].

We study the influence of the delay on the behavior of a network composed of N GRNs forming a ring where each unit is connected unidirectionally to the next one through an *excitatory* connection. Rings with an *odd number of inhibitory* connections are well known to generate sustained oscillations. For example, such rings composed of inverting gates, referred to as ring oscillators, are used to determine gate delays of complementary metal-oxide semiconductor (CMOS) circuits [11]. Systems in a ring have also been used as models for the study of feedback in living systems such as those that come in action in the control of gene expression

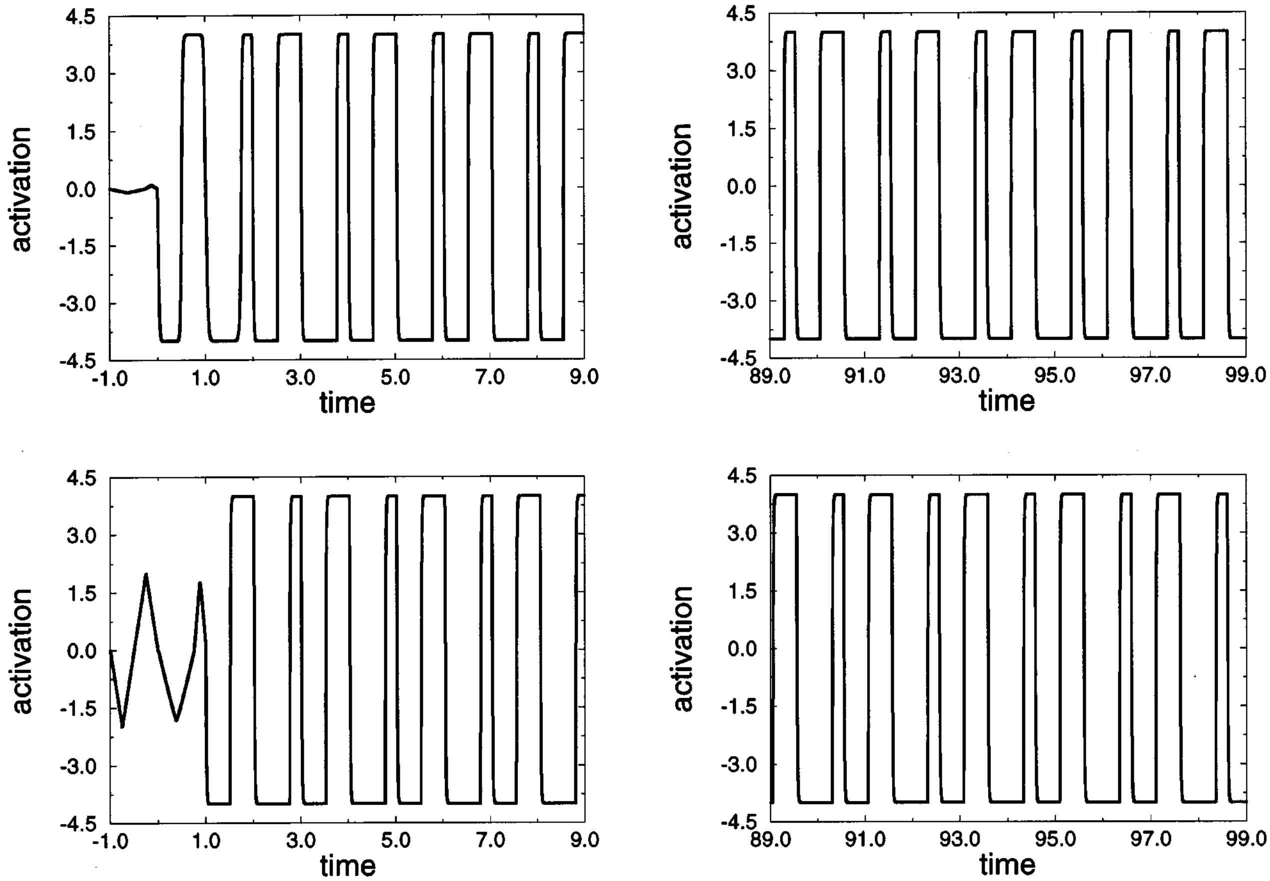

FIG. 1. Oscillations in an excitatory two-neuron ring network with delay. The panels on the left and right show the time course of the activations x_0 (upper row) and x_1 (lower row), at two different times. Parameters used: $\epsilon_0 = 0.01$, $W_0 = W_1 = 4$, $\alpha_0 = \alpha_1 = 5$, $A_0 = A_1 = 1$. Initial condition $\phi_0(\theta) = -0.267(\theta+1)$ for $-1 \leqslant \theta \leqslant -0.625$, $\phi_0(\theta) = 0.267(\theta+0.25)$ for $-0.625 \leqslant \theta \leqslant -0.25$, $\phi_0(\theta) = 0.8(\theta+1)$ for $-0.25 \leqslant \theta \leqslant -0.125$, $\phi_0(\theta) = -0.8(\theta)$ for $-0.125 \leqslant \theta \leqslant 0$, and $\phi_1(\theta) = -8(\theta+1)$ for $-1 \leqslant \theta \leqslant -0.75$, $\phi_1(\theta) = 8(\theta+0.5)$ for $-0.75 \leqslant \theta \leqslant -0.25$, $\phi_1(\theta) = -8\theta$ for $-0.25 \leqslant \theta \leqslant 0$. Abscissas: time (dimensionless, rescaled to the delay); ordinates: activation (dimensionless).

[12]. In the field of neural networks, rings are studied to gain insight into the mechanisms underlying the behavior of recurrent networks [2,13,5,14]. From the formal standpoint, ring networks belong to the class of cyclic feedback systems whose asymptotic behavior has been investigated in some detail (see [15–18], and the references therein). These theoretical results help in better understanding the system's dynamics and are important complements to experimental and numerical investigations using analog circuits and digital computers.

Ring networks are classified into positive and negative feedback systems depending on their response to a perturbation. When the effect of a perturbation (e.g., increase in one neuron's activation) is reinforced by the feedback loop (e.g., the neuron receives an excitatory feedback), the ring operates a positive feedback. Reciprocally, when the effect of a perturbation is reduced by the feedback loop (e.g., the neuron receives an inhibitory feedback), the ring operates a negative feedback. Rings may also have mixed responses, but this cannot be the case for rings of GRNs since each unit has a monotone increasing output function. A GRN ring network exerts negative feedback when it contains an odd number of inhibitory connections. All other cases, that is, when the network is excitatory or has an even number of inhibitory connections, lead to positive feedback. Schematically, this mechanism can be expressed as ''negative times negative is positive.''

Theoretical results indicate that activations in excitatory ring networks should in general eventually stabilize, as such systems have a strong tendency to converge to stable equilibria ([19], and the references therein). Surprisingly, in numerical investigations, oscillatory behavior is easily generated in excitatory ring networks with delay. An example of such oscillatory patterns obtained with an excitatory two-neuron ring network with delay is shown in Fig. 1. The upper and lower panels represent the time course of the activations of the two neurons. The panels on the left show the behavior of the system during a short period after the network is activated, while those on the right show the dynamics at a later time. It can be seen that both activations rapidly stabilize in a periodic square-wave-like oscillation, which is maintained throughout the observation window. Such oscillations were obtained in a large number of numerical investigations using different integration schemes (Appendix A) and were robust to the reduction of the discretization time step, indicating that they were not artifacts of the numerical methods. The following two properties of the oscillatory solutions were derived from numerical investigations of the behavior of excitatory ring networks with delay: (i) When the network is initialized with oscillating activations, it displays periodic oscillations for small enough characteristic charge-discharge time of the neurons, (ii) similar oscillations do not occur in excitatory ring networks with instantaneous transmission times.

Theoretical results indicate that undamped oscillations cannot be stable in excitatory ring networks, while numerical investigations seem to indicate the opposite. Thus to examine this apparent contradiction is the main goal of this paper. We will show that the numerically observed oscillations in networks with delay are long-lasting transients.

In order to study the mechanisms underlying the generation of oscillations in excitatory ring networks, we introduce the model in Sec. II, then we analyze both the asymptotic and the transient regimes of such systems with and without delay. The study of the asymptotic regime shows the possibility of unstable periodic oscillations in excitatory rings, but these do not satisfy property (i) described above, and hence cannot explain the existence of the oscillations (Sec. III). A mechanism for the generation of long-lasting transient oscillations is then proposed which is compatible with the observed patterns (Sec. IV). The results are discussed in Sec. V.

The results presented here generalize our work on the behavior of a single self-exciting neuron [20], and on excitatory two-neuron networks [21,22].

II. THE RING NETWORK MODEL

The dynamics of an N-ring neural network is determined by the following system of delay differential equations (DDEs):

$$\epsilon_{i+1}\frac{dx_{i+1}}{dt}(t)=-x_{i+1}(t)+W_{i+1}\sigma_{\alpha_{i+1}}(x_i(t-A_{i+1})). \tag{2.1}$$

In DDE (2.1), as well as in all subsequent expressions, the index i is taken modulo N, so that, for instance, $x_N=x_0$. $x_i(t)$ represents the activation of unit i at time t, $\epsilon_i>0$ characterizes the decay rate of the activation and is referred to as the characteristic charge-discharge time of the neuron, W_i is the connection weight indicating the influence of unit $i-1$ on unit i, $A_i\geqslant 0$ is the transmission delay associated with this connection, and σ_{α_i} is the output function of unit i defined by

$$\sigma_\alpha(a)=\tanh(\alpha a)=\frac{e^{\alpha a}-e^{-\alpha a}}{e^{\alpha a}+e^{-\alpha a}}. \tag{2.2}$$

When all delays A_i are set to zero, interunit transmissions are instantaneous and DDE (2.1) becomes a set of ordinary differential equations (ODEs):

$$\epsilon_{i+1}\frac{dx_{i+1}}{dt}(t)=-x_{i+1}(t)+W_{i+1}\sigma_{\alpha_{i+1}}(x_i(t)). \tag{2.3}$$

An initial condition of DDE (2.1) is constituted by the history of the activation of each neuron i during a time interval corresponding to the delay A_{i+1}. Initial conditions for DDE (2.1) are of the form $\Phi=(\phi_0,\ldots,\phi_{N-1})$, where each ϕ_i is a continuous function defined on the interval $[-A_{i+1},0]$ of length equal to the delay A_{i+1}. Thus the phase space for DDE (2.1) is the product space $S=S_1\times\cdots\times S_{N-1}$, with $S_i=\mathcal{C}([-A_{i+1},0],\mathbb{R})$, where $\mathcal{C}(I,\mathbb{R})$ denotes the space of continuous functions from the interval I on the real line $\mathbb{R}$. Note that in cases where $A_{i+1}=0$, the corresponding initial condition ϕ_i is a real number, and S_i can be identified with $\mathbb{R}$. Thus, when $A_i=0$ for all i, we have $S=\mathbb{R}^N$, which corresponds, as expected, to the phase space of the ODE (2.3).

In the following, general results presented for DDE (2.1) hold whether interunit transmissions are delayed or not, so that no distinction is made between the two cases. When there are differences between the two, relevant to this work, they are clearly specified so that no confusion arises: systems (2.1)–(2.3) [to be read system (2.1) and system (2.3)] refer to both cases with instantaneous and delayed transmissions, DDE (2.1) refers to the cases where there is at least one delayed connection in the loop, and ODE (2.3) to the cases where all transmissions are instantaneous.

For $\Phi=(\phi_0,\ldots,\phi_{N-1})$ in S, there is a unique solution of systems (2.1)–(2.3), denoted $z(t,\Phi)=(x_0(t,\Phi),\ldots,x_{N-1}(t,\Phi))$, such that $x_i(t,\Phi)=\phi_i(t)$ for $-A_{i+1}\leqslant t\leqslant 0$, and $z(t,\Phi)$ satisfies systems (2.1)–(2.3) for $t\geqslant 0$. We denote by z_t the (semi)flow associated with systems (2.1)–(2.3), that is, $z_t(\Phi)=(x_{1t}(\Phi),\ldots,x_{N-1t}(\Phi))$ and $x_{it}(\Phi)(\theta)=x_i(t+\theta,\Phi)$ for all $-A_{i+1}\leqslant\theta\leqslant 0$. To simplify the notations, the dependence on the initial condition Φ will not be indicated unless necessary.

We say that systems (2.1)–(2.3) satisfy the positive feedback condition when $b=\alpha_0W_0\cdots\alpha_{N-1}W_{N-1}>0$. After an appropriate change of signs of some of the activations, systems (2.1)–(2.3) with the positive feedback condition can be transformed into systems satisfying the more restrictive constraint $\mathcal{C}_0$: $\alpha_i>0$ and $W_i>0$, for all i [5]. From here on we suppose that systems (2.1)–(2.3) satisfy $\mathcal{C}_0$.

A network is referred to as irreducible when there is a directed path linking any two units [5]. In a ring network any two units are connected through the directed path of connections linking consecutive units, so that ring networks are irreducible.

Besides being irreducible, systems (2.1)–(2.3) have also the property of being cooperative as defined in [19]. Let f_i from $\mathbb{R}\times\mathbb{R}$ on $\mathbb{R}$ be defined as

$$f_i(x,y)=\frac{1}{\epsilon_i}[-x+W_i\sigma_{\alpha_i}(y)]. \tag{2.4}$$

Then systems (2.1)–(2.3) can be rewritten as

$$\frac{dx_{i+1}}{dt}(t)=f_{i+1}(x_{i+1}(t),x_i(t-A_{i+1})). \tag{2.5}$$

Under $\mathcal{C}_0$, we have $(\partial f_i/\partial y)(x,y)=\alpha_iW_i[1-\sigma_{\alpha_i}^2(y)]>0$ for all x, y, and i. Thus systems (2.1)–(2.3) are cooperative systems [19].

Under condition $\mathcal{C}_0$, systems (2.1)–(2.3) preserve the order of initial conditions. That is, if an initial condition is larger than another one then the corresponding solutions will have the same property: the activations corresponding to the larger initial condition remain larger than the ones corresponding to the smaller initial condition. Thus, when plotted on the same graph, the activations of the former remain above those of the latter.

More precisely, let $\Phi=(\phi_0,\ldots,\phi_{N-1})$ and $\Phi'=(\phi'_0,\ldots,\phi'_{N-1})$ be in S, we say that Φ is larger (respectively, strictly larger) than Φ', denoted $\Phi\geqslant\Phi'$ (respectively, $\Phi\gg\Phi'$), if for all i, and for all $\theta\in[-A_{i+1},0]$, we have $\phi_i(\theta)\geqslant\phi'_i(\theta)$ [respectively, $\phi_i(\theta)>\phi'_i(\theta)$].

Monotonicity. Under condition $\mathcal{C}_0$, systems (2.1)–(2.3) generate an eventually strongly monotone semiflow, that is,

$$\text{for } \Phi \text{ and } \Phi' \text{ in } S \text{ such that } \Phi\geqslant\Phi' \text{ and } \Phi\neq\Phi',$$

$$\text{we have } z_t(\Phi)\gg z_t(\Phi') \text{ for all } t>2\max(A_i). \tag{2.6}$$

Proof. This result follows from the cooperative and irreducible properties of systems (2.1)–(2.3), and Theorem 3.4 (p. 88) in [19]. ■

III. THE ASYMPTOTIC BEHAVIOR

In the following sections we study successively the local linear stability and the global behavior of systems (2.1)–(2.3), and characterize the set of oscillating solutions of excitatory ring networks.

A. Linearization

A constant solution of systems (2.1)–(2.3) is referred to as an equilibrium point. Throughout the rest of the paper, constant functions in S are identified with their value in $\mathbb{R}^N$. Let $r=(u_0,\ldots,u_{N-1})\in\mathbb{R}^N$, then $z(t)=r$ is an equilibrium of systems (2.1)–(2.3) if and only if r is a root of the following system:

$$-u_{i+1}+W_{i+1}\sigma_{\alpha_{i+1}}(u_i)=0 \quad \text{for all } i. \tag{3.1}$$

This system has been studied in [14]. Equation (3.1) has the unique root $r_0=0$ for $b=\alpha_0W_0\cdots\alpha_{N-1}W_{N-1}<1$. For $b>1$, Eq. (3.1) has three distinct roots denoted $r_1=-(a_0,\ldots,a_{N-1})$, $r_2=0$, and $r_3=(a_0,\ldots,a_{N-1})$, with $a_i>0$, so that $r_1=-r_3$ and $r_3\gg r_2=0\gg r_1$. Note that the system has the same set of equilibria, whatever the value of the delays A_i.

Local stability. (i) For $b<1$, $r_0=0$ is locally asymptotically stable, (ii) for $b>1$, r_1 and r_3 are locally asymptotically stable while $r_2=0$ is unstable.

Proof. Local stability of any of the equilibria, denoted by $r_j=(u_1,\ldots,u_N)$ with $j\in\{0,1,2,3\}$ is derived from the study of the roots of the characteristic equation:

$$P(\lambda)=\prod_{i=0}^{N-1}(1+\epsilon_i\lambda)-be^{-\lambda\tau}\prod_{i=0}^{N-1}\sigma'_1(\alpha_iu_{i-1})=0, \tag{3.2}$$

where $\tau=A_0+\cdots+A_{N-1}$.

Local stability is ensured when all the eigenvalues of the above characteristic equation (3.2), associated with systems (2.1)–(2.3) at r_j, have strictly negative real parts [23].When there is at least one delayed transmission, i.e., there is j such that $A_j>0$, the characteristic equation (3.2) is a transcendental equation with infinitely many solutions. However, the monotonicity property implies that all of its solutions have negative real parts if and only if the same holds when $A_i=0$ for all i [Corollary 5.2 (p. 93) [19]]. In other words, DDE (2.1) and its associated ODE (2.3) have exactly the same set of locally asymptotically stable equilibria. Therefore, in the following, we consider the roots of the polynomial $P(\lambda)$ for $\tau=0$.

ODE (2.3) is an irreducible cooperative system, thus the root of the characteristic equation (3.2) with the largest real part is indeed a real number [Corollary 3.2 (p. 60) in [19]]. Therefore, for the stability analysis, it is sufficient to determine the sign of the largest real root of $P(\lambda)$. The equilibrium point is unstable if $P(\lambda)$ has a strictly positive root. $P(\lambda)$ is strictly increasing for $\lambda\geqslant0$, therefore it has a real strictly positive root if and only if $P(0)<0$, that is,

$$1-b\prod_{i=0}^{N-1}\sigma'_1(\alpha_iu_{i-1})<0. \tag{3.3}$$

At the point $r_j=0$ we have $\sigma'_1(0)=1$ so that inequality (3.3) is equivalent to $1<b$, thus proving the statements concerning the stability and lack of stability of r_0 and r_2, respectively. At r_1 and r_3 the study of the solutions of Eq. (3.1) shows that $b\prod_{i=0}^{N-1}\sigma'_1(\alpha_iu_{i-1})<1$, which proves the statements concerning the stability of these two points. ■

B. Global analysis

Thanks to the monotonicity of the system it is also possible to draw a picture of the global behavior of the trajectories in the phase space. We first verify that systems (2.1)–(2.3) satisfy a boundedness condition.

Lemma: boundedness. (i) For $\Phi=(\phi_0,\ldots,\phi_{N-1})$, we define

$$F(\Phi)=(f_0(\phi_0(0),\phi_{N-1}(-A_0)),\ldots,f_{N-1}(\phi_{N-1}(0),\phi_{N-2}(-A_{N-1}))) \text{ in } \mathbb{R}^N, \tag{3.4}$$

then, F maps bounded subsets of S to bounded subsets of $\mathbb{R}^N$. (ii) There is a bounded subset D of S such that for all Φ in S, there is $T>0$ such that $z_t(\Phi)\in D$ for all $t>T$.

Proof. (i) This point stems from the fact that each f_i maps bounded subsets of $\mathbb{R}^2$ to bounded subsets of $\mathbb{R}$. (ii) We first remark that for $\Phi=(\phi_0,\ldots,\phi_{N-1})$ and $\Psi=(\psi_0,\ldots,\psi_{N-1})$ in S such that $\Phi\leqslant\Psi$ and $\phi_j(0)=\psi_j(0)$ for some $j\in\{0,\ldots,N-1\}$ we have $f_j(\phi_j(0),\phi_{j-1}(-A_j))\leqslant f_j(\psi_j(0),\psi_{j-1}(-A_j))$. Moreover, since $-1\leqslant\sigma_{\alpha_i}(a)\leqslant1$, we have the following inequalities:

$$\frac{1}{\epsilon_i}(-x-W_i)\leqslant f_i(x,y)\leqslant\frac{1}{\epsilon_i}(-x+W_i). \tag{3.5}$$

Therefore for all $\Phi \in S$ we have

$$\mathcal{L}^{-}(\Phi) \leqslant F(\Phi) \leqslant \mathcal{L}^{+}(\Phi), \tag{3.6}$$

where

$$\mathcal{L}^{-}(\Phi) = \left(\frac{1}{\epsilon_0}[-\phi_0(0) - W_0], \ldots, \frac{1}{\epsilon_{N-1}}[-\phi_{N-1}(0) - W_{N-1}] \right)$$

and

$$\mathcal{L}^{+}(\Phi) = \left(\frac{1}{\epsilon_0}[-\phi_0(0) + W_0], \ldots, \frac{1}{\epsilon_{N-1}}[-\phi_{N-1}(0) + W_{N-1}] \right).$$

We denote by z_t^- and z_t^+ the semiflows associated with the DDEs $dz^-/dt = \mathcal{L}^-(z_t^-)$ and $dz^+/dt = \mathcal{L}^+(z_t^+)$, respectively. Then, from Theorem 1.1 (p. 78) in [19], we obtain $z_t^-(\Phi) \leqslant z_t(\Phi) \leqslant z_t^+(\Phi)$ for all $t \geqslant 0$. Since $z_t^-(\Phi) \to -W = -(W_0, \ldots, W_{N-1})$ and $z_t^+(\Phi) \to W = (W_0, \ldots, W_{N-1})$ as $t \to +\infty$, for $\eta = (\eta_0, \ldots, \eta_{N-1}) \geqslant 0$, and T sufficiently large, we have $-W - \eta \leqslant z_t(\Phi) \leqslant W + \eta$ for all $t > T$. ■

The fact that systems (2.1)–(2.3) are cooperative and irreducible together with the previous lemma imply that, when they have a unique equilibrium point, all trajectories converge to this point [Proposition 4.2 (p. 90) [19]], as follows.

Global asymptotic stability. For $b < 1$, the equilibrium $r_0 = 0$ is globally asymptotically stable, that is, $z(t, \Phi) \to r_0$ as $t \to +\infty$ for all $\Phi \in S$.

From this point on and throughout the rest of the paper we suppose $b > 1$, so that the system is bistable, i.e., it has two locally asymptotically stable equilibrium points r_1 and r_3.

Again, the fact that the system is cooperative and irreducible implies that the trajectory of most initial conditions converges to either r_1 or r_3 [Theorem 4.1 (p. 90) [19]].

Almost convergence. For $b > 1$, the union of the basins of attraction of r_1 and r_3 contains an open dense subset of S.

We recall that the set of solutions that tend to an equilibrium point is referred to as its basin of attraction.

The complement of the union of the basins of attraction of the two stable equilibria is a negligible set denoted $\mathcal{B}$. Any neighborhood of $\mathcal{B}$ intersects the union of the two basins. Thus $\mathcal{B}$ is the boundary of the two basins. This is described more precisely as follows.

The basin boundary. (i) $\mathcal{B}$ divides the phase space S into two regions in the same way a plane divides a three-dimensional space: Points ''below'' and ''above'' $\mathcal{B}$ form the basins of attraction of r_1 and r_3, respectively. More precisely, let $\Phi \in \mathcal{B}$, and $\Phi' \in S$, if $\Phi \geqslant \Phi'$ (respectively, $\Phi' \geqslant \Phi$) and $\Phi \neq \Phi'$ then $z(t, \Phi') \to r_1$ (respectively, r_3) as $t \to +\infty$. Conversely, let $\Phi' \in S$, if $z(t, \Phi') \to r_1$ (respectively, r_3) as $t \to +\infty$, then there is $\Phi \in \mathcal{B}$, such that $\Phi \geqslant \Phi'$ (respectively, $\Phi' \geqslant \Phi$) and $\Phi \neq \Phi'$.

(ii) $\mathcal{B}$ is the boundary separating the two basins of attraction, that is, every neighborhood of $\mathcal{B}$ intersects both attraction basins.

(iii) $\mathcal{B}$ is unordered in the sense that for two different points Φ and Φ' in $\mathcal{B}$, we have neither $\Phi \geqslant \Phi'$ nor $\Phi' \geqslant \Phi$. Moreover, $\mathcal{B}$ is positively invariant under the semiflow z_t, i.e., if Φ is in $\mathcal{B}$, then so is $z_t(\Phi)$ for all $t \geqslant 0$.

(iv) $\mathcal{B}$ is a codimension one locally Lipschitz manifold containing the unstable equilibrium point $r_2 = 0$ and its stable manifold.

Proof. We only sketch the proof of statement (i) since general results on invariant sets can be found in [24,25] and a detailed proof for two-neuron networks is given in [21]. Let u be in S, such that $u \geqslant 0$. There exists a continuous, strictly decreasing (with respect to the order defined on S) map, b_u, from S to $\mathbb{R}$ such that (1) for all Φ in S, $\Phi + b_u(\Phi)u$ is the unique intersection between the line going through Φ and directed by u (i.e., the set $\{\Phi + \lambda u, \lambda \in \mathbb{R}\}$) with the boundary separating the two basins of attraction; (2) the set $B(r_1) = \{\Phi \in S, b_u(\Phi) > 0\}$ is exactly the basin of attraction of r_1; (3) the set $B(r_3) = \{\Phi \in S, b_u(\Phi) < 0\}$ is exactly the basin of attraction of r_3; and (4) the set $\mathcal{B} = \{\Phi \in S, b_u(\Phi) = 0\}$ is exactly the boundary separating the two basins of attraction.

Statement (i) is implied by the above characterization of the attraction basins and the basin boundary in terms of the zeros of the map b_u, with appropriately selected u.

Statement (ii) is a direct implication of (i).

Statements (iii) and (iv) result from [25]. ■

C. Oscillations on the boundary

We define the notions of weak and strong oscillations for scalar and vectorial functions as in [26].

Definition 1. Let $a:[t_0, +\infty) \to \mathbb{R}$ be a continuous function. We say that a is strictly oscillatory if for every $T \geqslant t_0$ there exist $T' \geqslant T$ and $T'' \geqslant T$ such that $a(T')a(T'') < 0$.

Definition 2. Weak oscillations. A solution $z(t) = (x_0(t), \ldots, x_{N-1}(t))$ of systems (2.1)–(2.3) is weakly oscillating if there exists T_0 such that for all $T \geqslant T_0$

$$\inf\{x_i(s): s \geqslant T, 0 \leqslant i \leqslant N-1\} \leqslant 0 \leqslant \sup\{x_i(s): s \geqslant T, 0 \leqslant i \leqslant N-1\}. \tag{3.7}$$

The components of a weakly oscillating solution are not necessarily strictly oscillating scalar functions. In fact, if after some time, the different neuron activations are not all of the same sign, then the corresponding solution is weakly oscillating, even if none of the activations is strictly oscillating.

Definition 3. Strong oscillations. A solution $z(t)=(x_0(t),\ldots,x_{N-1}(t))$ of systems (2.1)–(2.3) is strongly oscillating if each of its components x_i is strictly oscillating in the sense of definition 1.

Strong oscillation implies weak oscillations.

Definition 4. Damped oscillations. A solution $z(t)=(x_0(t),\ldots,x_{N-1}(t))$ of systems (2.1)–(2.3) is said to display damped oscillations if it is weakly oscillating and $z(t)\to 0$ as $t\to+\infty$.

Weak or strong oscillations that are not damped are referred to as undamped oscillations. The following result is deduced from the fact that systems (2.1)–(2.3) are almost convergent.

Undamped oscillations. Undamped oscillatory solutions of systems (2.1)–(2.3), if they exist, are necessarily unstable.

We have the following characterization of the dynamics of solutions on the boundary $\mathcal{B}$.

Weak oscillations. A solution of systems (2.1)–(2.3) is in $\mathcal{B}$ if, and only if, it is weakly oscillating.

Proof. A weakly oscillating solution is not converging to either r_1 or r_3, and belongs therefore to the boundary $\mathcal{B}$. To prove the reciprocal we define $K_+=\{\Phi\in S,\Phi\geqslant 0\}$ and $K_-=\{\Phi\in S,\ 0\geqslant\Phi\}$ as the positive and negative cones in S, respectively. A given Φ is in the basin of attraction of r_1 (respectively, r_3) if, and only if, there is $t\geqslant 0$ such that $z_t(\Phi)\in K_-$ [respectively, $z_t(\Phi)\in K_+$]. Conversely, Φ is in $\mathcal{B}$, if and only if $z_t(\Phi)\notin K_+\cup K_-$ for any $t\geqslant 0$. That is, Φ is in $\mathcal{B}$ if and only if, for all $t\geqslant 0$, there are two integers k and k' in $\{0,\ldots,N-1\}$ and two real numbers θ and θ' in $[-A_k,0]$ and $[-A_{k'},0]$, respectively, such that $x_k(t+\theta)\leqslant 0\leqslant x_{k'}(t+\theta')$. Hence $z(t,\Phi)$ satisfies the inequalities (3.7). ■

We present the following examples of weak oscillations. For $N=1$ and $A_0=0$, the only weakly oscillating solution is the constant solution $z(t)=r_2=0$. For $N=2$, with $A_0=A_1=0$, if $z(t)\neq r_2$ is weakly oscillating then $x_0(t)\times x_1(t)<0$ for all $t\in\mathbb{R}$, so that neither $x_0(t)$ nor $x_1(t)$ change signs. Hence the solution $z(t)$ is not strongly oscillating. However, for delayed interunit transmission times, using [26], we have the following result (the proof is given in Appendix C).

Strong oscillations. Assume that there is j such that $A_j>0$, that the characteristic equation of DDE (2.1) at r_2 has no root with zero real part, and that $\epsilon_i<\theta$ for all i, where θ is the unique solution of

$$1+\frac{N}{\tau}\theta\left[1-\ln\left(\frac{N}{\tau b^{1/N}}\theta\right)\right]=0, \tag{3.8}$$

then all solutions in $\mathcal{B}-\{r_2\}$ are strongly oscillating.

Therefore, when interunit transmissions are delayed, and the characteristic charge-discharge times of the neurons are small enough, the components of a weakly oscillating nonconstant solution are necessarily strictly oscillating scalar functions. For instance, for $N=1$, any nonzero solution of DDE (2.1) in $\mathcal{B}$ changes signs at least once in any interval of length equal to the delay.

The condition $\epsilon_i<\theta$ on the characteristic charge-discharge time is important to ensure strong oscillations. This is illustrated in Fig. 2 showing the activations of an excitatory ring network composed of two identical neurons

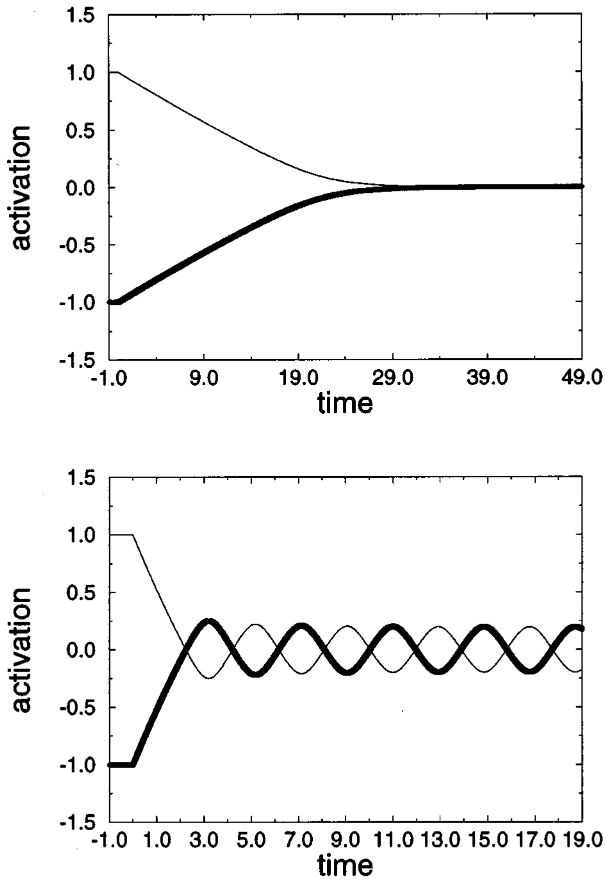

FIG. 2. Weak and strong oscillations. Examples of weakly (upper panel) and strongly (lower panel) oscillating solutions, for an excitatory two-neuron ring network. Parameters: $\epsilon=100$ (upper panel), $\epsilon=10$ (lower panel), $W_0=W_1=4$, $\alpha_0=\alpha_1=5$, $A_0=A_1=1$. Initial conditions $\phi_0(\theta)=-\phi_1(\theta)=-1$ for $-1\leqslant\theta\leqslant 0$. Abscissas: time (dimensionless, rescaled to the delay); ordinates: activation (dimensionless).

($\epsilon_0=\epsilon_1$, $\alpha_0=\alpha_1=5$) connected through symmetrical weights and delays ($W_0=W_1=4$, $A_0=A_1=1$) for the initial condition $\Phi=(\phi_0,\phi_1)$, with $\phi_0(\theta)=-\phi_1(\theta)=-1$. The corresponding solution $z(t,\Phi)$ is in $\mathcal{B}$, since the system is invariant under the transformation $x_0\to x_1$, $x_1\to x_0$, implying that initial conditions $\Psi=(\psi_0,\psi_1)$ such that $\psi_0=-\psi_1$ lie on the boundary $\mathcal{B}$, giving rise to weakly oscillating solutions. The upper panel shows the time course of the activations for $\epsilon_0=\epsilon_1=100$ larger than $\theta\simeq 55$. It can be seen that the two activations x_0 and x_1 are of opposite signs, so that $z(t)$ is weakly oscillating. Yet neither x_0 nor x_1 is strictly oscillating, hence $z(t)$ is not strongly oscillating. However, in the lower panel of Fig. 2, it is shown that, as predicted by the result stated above, when ϵ is small enough ($\epsilon_0=\epsilon_1=10$ smaller than $\theta\simeq 55$), the solution of the same initial condition is strongly oscillating.

We have seen that the solutions on the boundary are oscillating either weakly or strongly. These can be damped to the unstable equilibrium point r_2 as shown, for example, in the upper panel of Fig. 2. The following result concerns undamped oscillations (the proof is given in Appendix D).

Periodic oscillations. We assume the same conditions as the statement ‘‘Strong oscillations.’’ Then, undamped oscil-

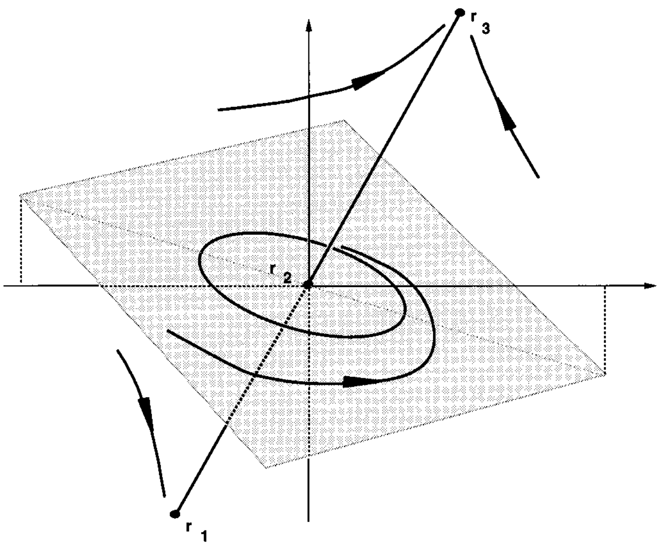

FIG. 3. Schematic phase portrait of an excitatory ring network. The phase space of a ring network is represented by a three-dimensional space, in which the three equilibria r_1, r_2, and r_3 are positioned. The gray surface represents the boundary separating the basins of attraction of r_1 and r_3. This boundary contains the unstable point r_2 together with an unstable closed orbit.

lations, when they exist, are asymptotically periodic.

This result shows that $\mathcal{B}$ is exactly the union of the stable manifold of $r_2=0$ with those of unstable periodic orbits when they exist. This is schematically illustrated in Fig. 3. The phase space of the system is represented by the three-dimensional space, the gray surface that divides the plane into two regions is $\mathcal{B}$, which contains r_2, an unstable periodic orbit (the closed curve), to which some solutions on the boundary tend. The regions below and above the gray surface are the basins of attraction of the stable equilibria r_1 and r_3, respectively.

As the output functions σ_{α_i} are odd, the periodic solutions of the system, when they exist, are symmetrical in the following sense [18]: let z be a periodic solution of Eq. (2.1) with period T, then $z(t+T/2)=-z(t)$ for all $t\geqslant 0$. Clearly this is not the case for the solution presented in Fig. 1. Therefore the presence of oscillations of the type displayed in Fig. 1 cannot be explained by the analysis of the asymptotic behavior of the system. Such oscillations can only be transients lasting longer than the experimental and numerical observation window. This point is addressed in the following section.

IV. THE TRANSIENT BEHAVIOR

In the following sections we study the transient dynamics of solutions of systems (2.1)–(2.3). We show that, in contrast with the asymptotic behavior which did not depend on the delay, the transient regime of the system with instantaneous interunit transmission [ODE (2.3)] greatly differs from that of the system with delayed interunit transmission [DDE (2.1)].

For a solution of systems (2.1)–(2.3) converging to an equilibrium point, the transient regime refers to the dynamics before the system reaches a state that cannot be distinguished from the equilibrium point, within some given precision. Once the system is in the neighborhood of one of the stable equilibria, its convergence speed is determined by the characteristic return time defined as $1/|\mathcal{R}(\lambda)|$, where λ is the root of the characteristic equation (3.2) with the largest real part denoted by $\mathcal{R}(\lambda)$ [27]. For systems (2.1)–(2.3), λ is real negative at the stable equilibria.

The map from K_+ to $\mathbb{R}^+$, that to $E=(\epsilon_0,\ldots,\epsilon_{N-1})$ associates $1/|\lambda(E)|$, the absolute value of the inverse of the real eigenvalue of characteristic equation (3.2), is strictly increasing (with respect to the order in K_+). As E decreases to zero, the characteristic return (or escape) time decreases to a positive limit, $q\geqslant 0$, whose value depends on the equilibrium point. In other words,

$$1/|\lambda(E)|\to q\geqslant 0 \quad \text{as} \quad E\to(0,\ldots,0), \qquad E\in K_+ .$$

Therefore, close to the equilibria, the return and escape times decrease and the system is accelerated when E tends to zero. When interunit transmissions are instantaneous (i.e., $A_i=0$ for all i) $q=0$, whereas when at least one of the transmissions is delayed (i.e., there is j such that $A_j>0$), we have $q>0$. This shows that the system without delay [ODE (2.3)] responds instantaneously to a small perturbation near an equilibrium, as $E\to 0$, whereas in the presence of delay, the system [DDE (2.1)] responds in a finite time, no matter how small E is.

The local analysis presented above is extended to the global transient behavior of the system in the following sections. Cases without and with interunit transmission delays are treated separately, because they present important differences.

A. Instantaneous interunit transmission

We consider the case where $A_i=0$, and $\epsilon_i=\eta_i\epsilon$, with $\eta_i>0$ fixed for all i. Under this condition, rescaling the time to $t'=t/\epsilon$ transforms ODE (2.3) into a similar ring network, with the same weights W_i and gains α_i. Only all ϵ_i are set to η_i. This shows that the trajectories of solutions of ODE (2.3) in the phase space $\mathbb{R}^N$ are independent of the parameter ϵ. Therefore this parameter does not affect the geometrical aspect of the phase portrait of ODE (2.3). However, the speed with which the state of the system evolves along a given trajectory increases as ϵ is decreased. This is illustrated in Fig. 4(A), which shows the temporal evolutions of x_0 and x_1 in its left-hand side panel, and the corresponding trajectory in $\mathbb{R}^2$ in its right-hand side panel, for a symmetrical two-neuron ring network (i.e., $\eta_0=\eta_1=1$, $W_0=W_1=4$, $\alpha_0=\alpha_1=5$) for two values of ϵ (5 and 0.4). The solutions with $\epsilon=5$ take longer to reach their steady states than those with $\epsilon=0.4$ (panel on the left). Nevertheless, both solutions move along the same trajectory in the phase space (panel on the right).

B. Delayed interunit transmission

When there is j such that $A_j>0$, the transient regime of a trajectory converging to an equilibrium may drastically change as $E=(\epsilon_0,\ldots,\epsilon_{N-1})$ is decreased to 0. This is illustrated in Figs. 4(B)–4(D), which represent the time course

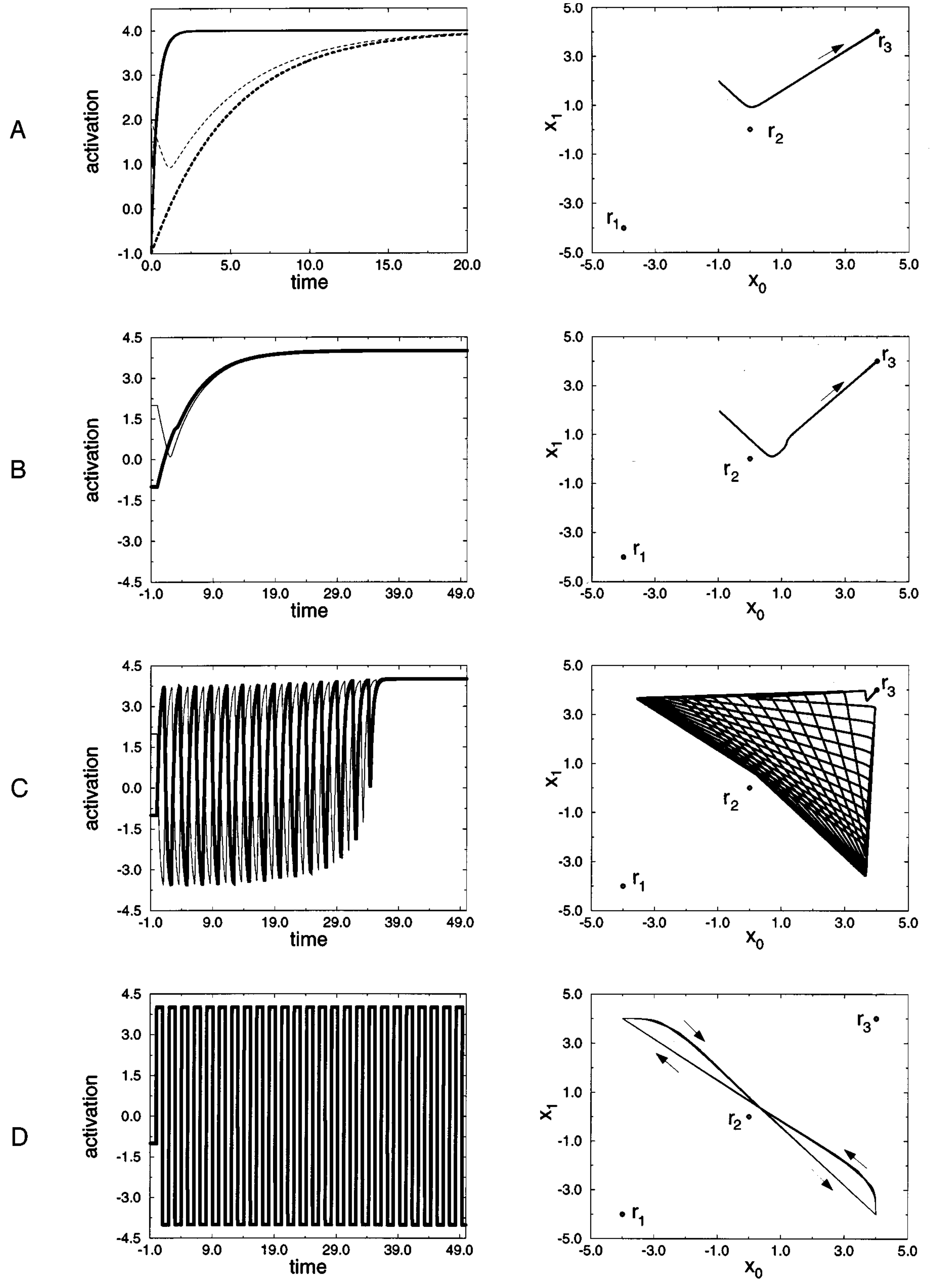

FIG. 4. Transient behavior. Time course (panels on the left) and trajectories in the x_0,x_1 plane (panels on the right) for an excitatory two-neuron ring network, without (A) and with delay (B), (C), (D), for different values of the characteristic charge-discharge time ϵ. (A) Dashed lines $\epsilon_0=\epsilon_1=5$, solid lines $\epsilon_0=\epsilon_1=0.4$, (B) $\epsilon_0=\epsilon_1=5$, (C) $\epsilon_0=\epsilon_1=0.4$, (D) $\epsilon_0=\epsilon_1=0.01$. In the panels on the left, thick and thin lines represent x_0 and x_1, respectively. In (D) only x_0 is represented. Parameters: $W_0=W_1=4$, $\alpha_0=\alpha_1=5$; uppermost panels, $A_0=A_1=0$, other panels $A_0=A_1=1$. Initial conditions: uppermost panels $(\phi_0,\phi_1)=(-1,2)$, other panels, $(\phi_0(\theta),\phi_1(\theta))=(-1,2)$ for $-1\leqslant\theta\leqslant0$. Panels on the left, abscissae: time (dimensionless, rescaled to the delay); ordinates: activation (dimensionless). Panels on the right, abscissa: activation x_0; ordinates: activation x_1, both dimensionless.

of activations of a two-neuron network for $E=(5,5)$ [Fig. 4(B)], $E=(0.4,0.4)$ [Fig. 4(C)], and $E=(0.01,0.01)$ [Fig. 4(D)] for the same initial condition $[(\phi_0(\theta),\phi_1(\theta))=(-1,2)]$. We are dealing with the same two-neuron network as in Fig. 2, described in Sec. III C. Thus considerations on the symmetry of the system show that this initial condition lies in the basin of attraction of r_3, so that its trajectory will eventually tend to this equilibrium point. It can be seen that, for large E, this solution of DDE (2.1) resembles the corresponding solution of ODE (2.3) and converges rapidly [compare Fig. 4(A) and Fig. 4(B)]. As E is decreased, it displays, first, transient oscillations during a short time [Fig. 4(C)], and, then, square-wave-like oscillations that outlast the observation window [Fig. 4(D)], only x_0 is shown]. Only the *a priori* knowledge that the point is in the basin of attraction of r_3 allows us to state that these oscillations are transient. The change of behavior, as E is decreased, is also reflected in the trajectories in the (x_0,x_1) plane as shown in the panels on the right in Figs. 4(B)–4(D), where the lowest panel is reminiscent of the projection of a closed orbit, even though the corresponding trajectory will eventually converge to r_3.

The following analysis provides a heuristic explanation for the delay-induced transient oscillations. The two-neuron network of the example above is described by

$$\epsilon \frac{d}{dt} x_0(t)=-x_0(t)+W\sigma_\alpha(x_1(t-1)),$$

$$\epsilon \frac{d}{dt} x_1(t)=-x_1(t)+W\sigma_\alpha(x_0(t-1)), \tag{4.1}$$

where $\epsilon>0$, $b=(\alpha W)^2>1$. In the limit $\epsilon\to 0$ the dynamics of this system is formally described by the following system of difference equations (DE):

$$x_0(t)=W\sigma_\alpha(x_1(t-1)),$$

$$x_1(t)=W\sigma_\alpha(x_0(t-1)), \tag{4.2}$$

or its discrete-time version,

$$x_0(n)=W\sigma_\alpha(x_1(n-1)),$$

$$x_1(n)=W\sigma_\alpha(x_0(n-1)), \tag{4.3}$$

where $n=1,2,\ldots$. The global dynamics of Eq. (4.3) can be easily analyzed. Let us denote by a the positive root of the equation $a-W\sigma_\alpha(a)=0$. As $b>1$, the map (4.3) has three fixed points $r_1=(-a,-a)$, $r_2=(0,0)$, and $r_3=(a,a)$. The fixed points r_1 and r_3 are stable and attract all initial conditions (x_0,x_1) satisfying $x_0<0,x_1<0$ and $x_0>0,x_1>0$, respectively. Using the fact that σ_α is an odd function, it can be shown that Eq. (4.3) has a stable periodic orbit of period 2 given by the points $(-a,a)$ and $(a,-a)$. This periodic orbit attracts all initial conditions (x_0,x_1) that satisfy $x_0x_1<0$ [to see this, notice that $x_0(n+2)=W\sigma_\alpha(W\sigma_\alpha(x_0(n)))$, $x_1(n+2)=W\sigma_\alpha(W\sigma_\alpha(x_1(n)))$]. Now, let us consider DDE (4.1) with ϵ small. For an initial condition $\Phi=(\phi_0,\phi_1)$ that is sufficiently smooth (namely, $|d\phi_0/dt|,|d\phi_1/dt|$ are much smaller than ϵ) the left-hand side of Eq. (4.1) can be neglected so that the dynamics of Eq. (4.1) is approximated by the dynamics of Eq. (4.2). This approximation is valid provided the absolute values of the derivatives of the solution $z(t,\Phi)$ of Eq. (4.1) remain much smaller than ϵ. The dynamical properties of map (4.3) imply that if the initial condition Φ satisfies $\Phi\ll 0$ ($\Phi\gg 0$) then the solution of the DE (4.2) tends to r_1 (r_3). This is in perfect agreement with the asymptotic behavior of DDE (4.1). So, for initial conditions that satisfy either $\Phi\ll 0$ or $\Phi\gg 0$, the transient regime of $z(t,\Phi)$ is essentially determined by the map (4.3) and is independent of ϵ.

Now, consider an initial condition $\Phi=(\phi_0,\phi_1)$ such that $\phi_0<0$ and $\phi_1>0$, such as the one used in Fig. 4. In this case, as can be seen in Fig. 4(D) which shows the time course of x_0, the solution $z(t,\Phi)$ of the DDE (4.1) is initially attracted to the period-2 square-wave solution of the DE (4.2) given by

$$x_0(t)=a,\quad x_1(t)=-a,\quad t\in(2n,2n+1),\quad n=0,1,2,\ldots$$

$$x_0(t)=-a,\quad x_1(t)=a,\quad t\in(2n+1,2n+2),\quad n=0,1,2,\ldots.$$

Since this square wave is discontinuous at integer times, there will be values of t [the zeros of $z(t,\Phi)$] where the derivatives of $z(t,\Phi)$ will be large. Close to these points (and only close to them) the approximation of the DDE (4.1) by the DE (4.2) breaks down. Due to the existence of these points, the effect of the right-hand side of DDE (4.1) will be, for most initial conditions, to eliminate very slowly the zeros of $z(t,\Phi)$. So $z(t,\Phi)$ will eventually tend to either r_1 or r_3. We can summarize this argument by saying that the long transient behavior observed in $z(t,\Phi)$ is due to the competition between the two antagonistic asymptotic behaviors of the DDE (4.1) and of its formal limit, the DE (4.2), as ϵ tends to zero. More general oscillatory initial conditions will display the same behavior.

The following mathematical result corroborates the heuristic analysis presented above. It constitutes a generalization of the analysis of the scalar DDE presented in [28] to the case of systems of DDEs. In order to present this result we introduce the system of DEs that is obtained from DDE (2.1) by rescaling the delays (Appendix B), and setting $E=0$:

$$x_{i+1}(t)=W_{i+1}\sigma_{\alpha_{i+1}}(x_i(t-1)). \tag{4.4}$$

We denote by $z(E,t,\Phi)$ the solution of DDE (2.1), rescaled such that all $A_i=1$ (Appendix B), with $E=(\epsilon_0,\ldots,\epsilon_{N-1})\gg(0,\ldots,0)$, and $z(0,t,\Phi)$ the solution of DE (4.4), obtained by setting $\epsilon_i=0$ for all i. The solutions of Eq. (4.4) are double valued at integer times unless the initial condition Φ satisfies $\phi_{i+1}(0)=W_{i+1}\sigma_{\alpha_{i+1}}(\phi_i(-1))$. Then we have the following result.

Transient behavior. For $T>0$, $\eta>0$, and $\Phi\in S$ such that $\phi_{i+1}(0)=W_{i+1}\sigma_{\alpha_{i+1}}(\phi_i(-1))$, there exists $E_0\gg 0$ such that for all $0\leqslant E\leqslant E_0$, $||z(E,t,\Phi)-z(0,t,\Phi)||<\eta$ for all $0\leqslant t\leqslant T$.

The constraint on the value of the initial condition at 0 can be relaxed. For arbitrary initial conditions in S, the solution of DDE (2.1) remains transiently close to the solution of DE (4.4), except nearby integer time values.

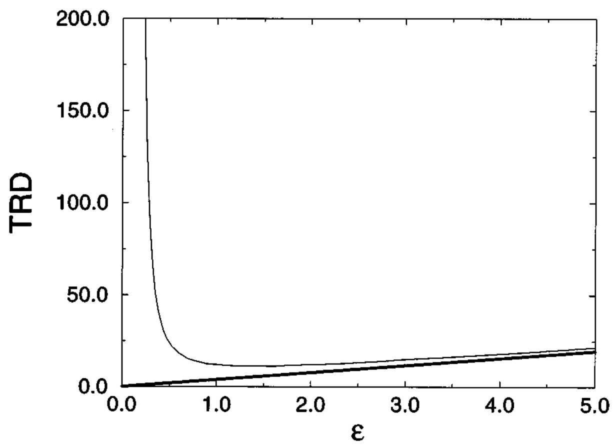

FIG. 5. Transient regime duration. Transient regime duration for the system without delay (thick line) and the system with delay (thin line) as a function of the characteristic charge-discharge time ϵ for an excitatory two-neuron network. Parameters: $W_0 = W_1 = 4$, $\alpha_0 = \alpha_1 = 5$, $A_0 = A_1 = 0$ for the system without delay and $A_0 = A_1 = 1$ for the system with delay. Initial conditions $(\phi_0, \phi_1) = (-1,2)$, for the system without delay, and $(\phi_0(\theta), \phi_1(\theta)) = (-1,2)$, for $-1 \leqslant \theta \leqslant 0$ for the system with delay. Abscissa: charge-discharge time of the neurons ϵ (dimensionless, rescaled to the delay); ordinates: transient regime duration (dimensionless, rescaled to the delay).

This result indicates that, for small enough E, the solutions of Eq. (2.1) remain close to those of Eq. (4.4) for some transient time whose length depends on the initial condition.

In contrast with DDE (2.1), which does not have any stable nonconstant periodic solution, DE (4.4) has infinitely many periodic solutions with non-negligible basins of attraction (Appendix E). For these initial conditions, each activation tends to a periodic square-wave-like oscillation, the jumps between lower and upper parts of the wave appearing at integer multiples of the period added to the times of sign changes in the initial condition. Thus the basins of attraction of the periodic oscillations and their boundaries cover the set of weakly oscillating initial conditions, so that, for any such initial condition, and for small enough E, the corresponding solution of DDE (2.1) displays transient oscillations reminiscent of those of DE (4.4).

C. Transient regime duration

For excitatory ring networks with instantaneous transmission times, the transient regime duration (TRD) of any converging trajectory is proportional to ϵ (where the characteristic charge-discharge time are $\epsilon_i = \epsilon \eta_i$ as defined in Sec. IV A). Thus the TRD decreases linearly to zero as $\epsilon \to 0$. This is illustrated by the thick straight line in Fig. 5 that shows the TRD as a function of ϵ, for the two-neuron network and initial condition used in Fig. 4(A).

For the same network with delayed interunit transmission, the TRD (thin line in Fig. 5) is close to that of the system without delay (thick straight line) for large ϵ. The TRD is in fact almost linear for ϵ large enough. This is in accord with the fact that the trajectories of the networks with and without delay are similar for large ϵ [Figs. 4(A) and 4(B)]. However, for small ϵ, the TRD of the system with delay increases abruptly as ϵ is decreased towards zero. For ϵ small enough, the curve representing the TRD as a function of ϵ can be fitted by an exponential function of $1/\epsilon$. The sharp increase in the TRD corresponds to the onset of transient oscillations. It indicates the time interval during which the solution of DDE (2.1) remains close to the corresponding solution of the discrete-time network given by DE (4.4).

The above numerical results are in accord with analytical results obtained for two-neuron networks with piecewise constant output functions [22].

V. DISCUSSION

We have studied the asymptotic and the transient dynamics of excitatory ring networks of GRNs in order to better understand the mechanisms underlying the onset of oscillations in such networks with delay.

Excitatory ring networks may display unstable, nonconstant, periodic orbits. These have been reported for rings with five units [29] or more (i.e., $N \geqslant 5$), with instantaneous transmission times, and for scalar DDEs with delay [30–32] (i.e., $N \geqslant 1$). Yet, as argued in Sec. III, the existence of these periodic orbits does not explain the presence of oscillations such as those displayed in Fig. 1, providing strong support for the hypothesis that the observed oscillations are transient. We argue in the following that the proposed mechanism according to which the system with delay behaves transiently as a discrete-time network, and asymptotically as a continuous-time network without delay, accounts for the properties of the oscillations observed numerically. We will focus on the two main characteristics of such oscillations, already mentioned in the Introduction, and we show how each one is compatible with the proposed mechanism.

(i) When the network is initialized with oscillating activations, it displays periodic oscillations for small enough characteristic charge-discharge time of the neurons.

According to our analysis, these periodic oscillations correspond to trajectories of the continuous-time network with delay transiently attracted to periodic orbits of the discrete-time network. The trajectories susceptible to displaying such behavior lie in the basin of attraction (for the discrete-time network) of periodic orbits. The union of these basins of attraction, and their boundaries, corresponds exactly to the set of oscillating initial conditions.

The main point is that the oscillations constitute long-lasting transients. The time interval during which the trajectory of a given oscillating initial condition displays oscillations is also the time during which it remains close to the orbit of the corresponding trajectory of the discrete-time network. This time interval depends on the initial condition and also on the parameter E, representing the charge-discharge time of the neurons. As E is decreased, the duration of the oscillation increases exponentially. In other words, the solution of an oscillating initial condition displays transient oscillations, whose duration increases exponentially as E tends to zero. Thus, for small enough E, any reasonable observation window is shorter than the duration of these transient oscillations, making them indistinguishable from stationary oscillations.

(ii) Similar oscillations do not occur in excitatory ring networks with instantaneous transmission times.

For special ranges of parameters an excitatory ring network without delay displays unstable periodic orbits. By selecting an initial condition close to the stable manifold of such a periodic solution, it is possible to observe a long-lasting transient oscillation followed by the convergence of the solution to one of the stable equilibria. So, for the system without delay, there is a set of initial conditions with transient oscillatory trajectories. Yet, this set does not depend on the value of the parameter E. Moreover, even for such initial conditions, the duration of the transient regime tends linearly to zero as E is decreased. Clearly, excitatory ring networks without delay, no matter the number of units they contain, do not display long-lasting transient oscillations for oscillating initial conditions as the characteristic charge-discharge time is decreased.

General considerations

Transient regimes have received little attention compared to steady states in theoretical studies of neural network models. The description of the asymptotic behavior of the system provides invaluable information about the transients but, as shown in our work, this is not always sufficient to account for some of the important aspects in the system's dynamics. Theoretical studies of transients can help in better understanding nervous system operation. Experimentalists have long recognized the importance of transients in neural behavior as a means to convey information about environmental as well as internal changes (e.g., [33]). The information contained in the transient regime is all the more important when the system evolves in rapidly changing environments where the neural networks involved in information processing do not dispose of the time lapse necessary to reach a stationary regime.

Living neurons act collectively on target neurons, muscles, etc. The output of such assemblies is a graded response observed, for instance, when recording the action potential of nervous trunks (neurogram). GRNs model the activity of such neuron assemblies [10]. Determining the different parameters that shape the transient behavior of such neural network models is thus important for understanding how nervous systems operate. The study of the dynamics of GRN ring networks shows that converging neuronal networks may display oscillating transients during extremely long time intervals. In fact, these transients can be so long that, practically, the system will not reach its stationary regime during the observation window.

Overall oscillatory patterns are frequently observed in the activity of nervous systems. Their roles are either clear as in respiration, where they control motor activity, or unexplained as in the electroencephalogram where they are apparently related to the brain information processing in a still obscure way. Overall oscillatory patterns are observed when units discharge periodically and synchronously. It has been proposed that the latter could be important in a number of functions such as in coordination of motor acts and information processing (e.g., [34]). The long-lasting transient oscillations in excitatory rings of GRNs arise thanks to the presence of interunit transmission delays, and are also expected to occur in other network architectures. In living nervous systems, delays are ubiquitous, ranging from a few to several hundreds of milliseconds. They are due to action potential propagation along axons, synaptic delay, etc. Delay-induced long-lasting transient oscillations could thus take part in various nervous system operations.

In ANN applications relying on the convergence of the network to a steady state, control over the transient regime is also an important issue. Large increase in the transient regime duration, such as those observed in the networks studied here, can seriously deteriorate the network's performance by slowing down the system. Our analysis shows that the presence of delay-induced long-lasting transients can be predicted by the analysis of the dynamics of the associated discrete-time network.

VI. CONCLUSION

We have studied the behavior of excitatory GRN ring networks. We have shown that for instantaneous as well as delayed interunit transmission, most trajectories tend to equilibrium points, and that the remaining ones oscillate around an unstable equilibrium point. When interunit transmissions are delayed, the system may display long-lasting transient oscillations, which can be analyzed through the study of the behavior of the corresponding discrete-time network. In this sense, the behavior of the ring network with delay is intermediate between the behavior of the system without delay and that of the discrete-time network. These theoretical results are important to complement the experimental and numerical observations made in circuits and digital computers, in order to better understand the mechanisms underlying the system's dynamics.

Note added in proof Theoretical analysis of the effect of delay on neural network dynamics is currently an active field of study, and recently some additional results have been published that we would like to mention.

The two following references deal with the influence of delay on the asymptoic behavior in a model of a single neuron and a network of spiking neurons with delayed recurrent excitatory connection [J. Foss, A. Longtin, B. Mensour, and J. Milton, Phys. Rev. Lett. **76**, 708 (1996); W. Gerstner, J. L. Van Hemmen, and J. D. Cowan, Neural Comput. **8**, 1653 (1996)]. They are complementary to the publications cited in [3].

Results concerning the asymptotic behavior of continuous-time GNRs in the presence of delay are also presented [Y. J. Cao and Q. H. Wu, IEEE Trans. Neural Netw. **7**, 1533 (1996); Y. Zhang, Int. J. Syst. Sci. **27**, 227 (1996); Y. Zhang, S. M. Zhong, and Z. L. Li, *ibid.* **27**, 895 (1996); L. Olien and J. Bélair, Physica D (to be published)]. These are complementary to the publications cited in [9]. We became aware that a result, concerning the asymtotic behavior of continuous-time excitatory ring neural netowrks with delay, similiar to the statement *Almost convergence* in our paper, was independently, and prior to our work, proven [P. Baldi and A. Atyia, IEEE Trans. Neural Netw. **5**, 612 (1994)]. They also mentioned the existence of transient oscillations based on numerical investigations. Our analysis takes these results further by providing a description of the basin boundary (statement, *The basin boundary*) and unstable oscillations (Sec. III C), as well as elucidating the mechanisms underlying transient oscillations (Sec. IV).

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APPENDIX A: NUMERICAL INTEGRATION METHODS

Two numerical integration methods were used to investigate the dynamics of DDE (2.1). Both methods were applied to the system after rescaling all delays to one (Appendix B).

The first method is the Gear predictor-corrector formula [35] adapted for the special case of DDE (2.1) for which the nonlinear term is delayed. In this particular case only the corrector formula is required.

The second method consists in writing solutions of DDE (2.1) in integral form, and then evaluating the integral using a trapezoidal approximation (e.g., [36]).

For both methods, the time steps used depended on both the system parameters and the initial conditions. The convergence of the solutions was checked.

APPENDIX B: RESCALING THE DELAYS

We consider Eq. (2.1) with delayed interunit transmission. It is possible to reindex the variables so that $A_0>0$ and $A_0\geqslant A_1\geqslant\cdots\geqslant A_{N-1}\geqslant 0$. Let $A=(A_0+\cdots+A_{N-1})/N$, $K_0=0$, $K_p=pA-(A_1+\cdots+A_p)$ for $1\leqslant p\leqslant N-1$, and $u_i(t)=x_i(t-K_i)$. Then the variables u_i satisfy DDE (2.1) with $A_i=A$ for all i. By rescaling the time unit to the delay A that is $t'=t/A$, $\epsilon_i'=\epsilon_i/A$, the new variables $y_i(t')=u_i(t/A)$ satisfy the following system of delay differential equations:

$$\epsilon_{i+1}'\frac{dy_{i+1}}{dt'}(t')=-y_{i+1}(t')+W_{i+1}\sigma_{\alpha_{i+1}}(y_i(t'-1)). \tag{B1}$$

APPENDIX C: PROOF THAT WEAK OSCILLATIONS IMPLY STRONG OSCILLATIONS

In order to prove that weak oscillations imply strong oscillations, we show that DDE (2.1) satisfies the hypotheses (H1)–(H5) given below [26]. Without loss of generality we can consider that all delays equal one, that is, $A_i=1$ for all i in DDE (2.1) (see Appendix B).

We rewrite DDE (2.1) as

$$dz_t/dt=F(z_t), \tag{C1}$$

where F from S to $\mathbb{R}^N$ is defined by $F(\Phi)=(f_0(\Phi),\ldots,f_{N-1}(\Phi))$, with

$$f_i(\Phi)=-\phi_i(0)+W_i\sigma_{\alpha_i}(\phi_{i-1}(-1))/\epsilon_i .$$

F satisfies the following hypothesis.

Hypothesis (H1). F is continuous on its domain, sends bounded sets of S into bounded sets of $\mathbb{R}^N$, and is such that DDE (2.1) has one and only one solution starting from any given data $\Phi\in S$. For every pair Φ, Ψ in S, such that $\Phi\leqslant\Psi$ and $\Phi(0)=\Psi(0)$, we have $F(\Phi)\leqslant F(\Psi)$.

In Sec. II, statement *monotonicity* shows that the following hypothesis is satisfied.

Hypothesis (H2). DDE (2.1) is strongly monotone, in the sense that it verifies (H1) and for $\Phi\leqslant\Psi$ and $\Phi\neq\Psi$, there is $t_1\geqslant 0$ such that $z_t(\Phi)\ll z_t(\Psi)$ for all $t\geqslant t_1$.

We assume that $\epsilon_i<\theta$ for all i, where θ is the unique solution of

$$-1+\frac{N}{\tau}\theta\left[1-\ln\left(\frac{N}{\tau b^{1/N}}\theta\right)\right]=0.$$

Then, the analysis of the real roots of the characteristic equation (3.2) leads to Hypothesis (H3).

Hypothesis (H3). The characteristic equation (3.2) has one and only one real root. This root has multiplicity one.

Hypothesis (H4). Let z be a solution of DDE (2.1) such that z oscillates weakly and does not oscillate strongly, then $z(t)\to 0$, as $t\to+\infty$.

Proof. Let us verify that DDE (2.1) satisfies (H4). Let $z=(x_0,\ldots,x_{N-1})$ be a weakly oscillating solution of DDE (2.1) such that $x_i(t)\neq 0$, for all $t\geqslant T$ and all i. There is necessarily j, such that $x_j(t)<0$ and $x_{j+1}(t)>0$ for all $t\geqslant T$. Thus $x_{j+1}(t)$ is a strictly decreasing bounded function, and we have $x_{j+1}(t)\to l_{j+1}$ with $l_{j+1}\geqslant 0$, as $t\to+\infty$. From this we derive that for all k

$$x_{j+k}(t)\to l_{j+k}\ \text{ as }\ t\to+\infty,\ \text{ where }\ l_{j+k}=W_{j+k}\sigma_{\alpha_{j+k}}(W_{j+k-1}\sigma_{\alpha_{j+k-1}}(\cdots W_{j+2}\sigma_{\alpha_{j+2}}(l_{j+1})))\geqslant 0. \tag{C2}$$

In particular, for $k=N-1$, we get $x_j(t)\to l_j\geqslant 0$, hence $l_j=0$, and consequently $l_i=0$ for all i. Thus $z(t)\to 0$, as $t\to+\infty$. ■

We rewrite Eq. (2.1) as

$$\frac{dz}{dt}=Lz_t+f(z_t), \tag{C3}$$

where $L:S\to\mathbb{R}^N$ is the linear map defined by $L(\Phi)=M\Phi(-1)+M'\Phi(0)$, with M and M', two $N\times N$ matrices defined as

$$M=\begin{pmatrix} 0 & & & \cdots & 0 & \dfrac{\alpha_0 W_0}{\epsilon_0} \\ \dfrac{\alpha_1 W_1}{\epsilon_1} & 0 & & \cdots & & 0 \\ 0 & \dfrac{\alpha_2 W_2}{\epsilon_2} & 0 & \cdots & & 0 \\ \vdots & & & \cdots & & \vdots \\ 0 & & & \cdots & \dfrac{\alpha_{N-1} W_{N-1}}{\epsilon_{N-1}} & 0 \end{pmatrix}, \quad M'=\mathrm{diag}\left(\frac{-1}{\epsilon_0},\ldots,\frac{-1}{\epsilon_{N-1}}\right) \tag{C4}$$

and $f=(f_0,\ldots,f_{N-1}):S\to\mathbb{R}^N$ is the map defined by

$$f_{i+1}(\Phi)=\frac{W_{i+1}}{\epsilon_{i+1}}[\sigma_{\alpha_{i+1}}(\phi_i(-1))-\alpha_{i+1}\phi_i(-1)]. \tag{C5}$$

For $Y=(y_0,\ldots,y_{N-1})\in\mathbb{R}^N$, we denote by $||Y||=|y_0|+\cdots+|y_{N-1}|$. Let $W=\max_i(|W_i/\epsilon_i|)$ and $\alpha=\max_i(|\alpha_i|)$ and $g:\mathbb{R}\to\mathbb{R}$ the real function defined by

$$g(u)=NW(\alpha u-\sigma_\alpha(u)). \tag{C6}$$

We have $g(u)/u\to 0$ as $u\to 0$ and

$$||f(\Phi)||\leq g(||\Phi(-1)||). \tag{C7}$$

The linear part L satisfies the following hypothesis.

Hypothesis (H5′). $L(\Phi)=M\Phi(-1)+\int_{-1^+}^{0}d\eta(\theta)\Phi(\theta)$, where M is nonsingular, and $\int_{-1^+}^{0}d\eta(\theta)\Phi(\theta)=N\Phi(0)$.

The nonlinear part f satisfies the following hypothesis.

Hypothesis (H5″). For the nonlinear part f of DDE (2.1), there exists a function g defined from $\mathbb{R}^+$ into $\mathbb{R}^+$ such that $g(u)/u\to 0$ as $u\to 0$ and $||f(\Phi)||\leq g(||\Phi(-1)||)$.

Thus Proposition 5 (p. 278) in [26], implies that DDE (2.1) satisfies the following hypothesis.

Hypothesis (H5). DDE (2.1) does not have any solution z such that each component of z is $\neq 0$ for each t large enough and $z(t)\to 0$ faster than any exponential as $t\to+\infty$.

Moreover, from Eq. (C7) we deduce that

$$||f(\Phi)||=O(||\Phi||_\infty^3). \tag{C8}$$

We have thus checked all the hypotheses of Theorem 3 (p. 281) in [26] showing that the notions of weak and strong oscillations coincide.

APPENDIX D: PERIODIC OSCILLATIONS

Monotone cyclic feedback systems such as systems (2.1)–(2.3) admit a discrete Lyapunov function, denoted V [15,17,18]. We present some of the properties of this function that are useful in the following. Rigorous definitions and analyses can be found in the original papers cited above. This Lyapunov function counts the number of sign changes of the activations during an interval of length equal to the delay plus those between activations. Therefore it is integer valued. It decreases along trajectories of systems (2.1)–(2.3), hence the reference to Lyapunov functions, which are usually continuous valued energy functions decreasing along trajectories of many physical systems.

One important implication of the existence of the function V is that the Poincaré-Bendixson theorem holds for systems (2.1)–(2.3) [15,18]. In other words, the dynamics of ring networks cannot be more complex than that of two-dimensional systems. More precisely, this implies that trajectories on the boundary $\mathcal{B}$ tend either to the unstable equilibrium point r_2, are asymptotically periodic, or ''approach'' an orbit homoclinic to r_2, that is, an orbit that starts at r_2 and moves back to the same point. Therefore, to show that all undamped solutions on the boundary are asymptotically periodic, we need to prove that there are no homoclinic orbits through r_2. This result has been proved for scalar DDEs with monotone feedback [37]. We use the same method as in those papers, which was also applied in [30,31]. It consists in showing that the value of the discrete Lyapunov function for any nontrivial solution tending to r_2 as $t\to+\infty$ is larger than its value for any nontrivial solution tending to r_2 as $t\to-\infty$. Thus if there is a nontrivial solution connecting r_2 to itself, the discrete Lyapunov function V would be increasing along this solution, which contradicts the fact that V is decreasing along any trajectory.

We consider the cases of $z(t)\to r_2$ as $t\to-\infty$ and as $t\to\infty$ separately.

Let us assume that $z(t)$ is a solution of DDE (2.1) tending to r_2 as $t\to-\infty$. Then, by definition, $z(t)$ is in the unstable manifold of r_2. In the vicinity of r_2, this manifold is finite dimensional and can be approximated by the unstable manifold of the linearized equation at r_2. Thus for t negative with $|t|$ large enough, $z(t)$ is close to a fundamental solution of the DDE (2.1) linearized at r_2. For such solutions, the discrete Lyapunov function has been estimated in Corollary 3.3 (p. 404) in [17]. It should be noted that the fundamental solution associated to z as $t\to-\infty$ corresponds to an eigenvalue λ of the characteristic equation with strictly positive real part.

A solution $z'(t)$ of DDE (2.1) tending to r_2 as $t\to+\infty$ is within the stable manifold of r_2. The associated manifold of the linearized equation at r_2 is infinite dimensional so that z' may tend to r_2 faster than any exponential. Yet, thanks to Hypothesis (H5) in Appendix C, we know that this is not the case and that z' is close to a fundamental solution of the DDE (2.1) linearized at r_2. Thus $V(z'(t))$ as $t \to +\infty$ is also estimated thanks to Corollary 3.3 (p. 404) in [17].

The important difference between the two cases is that for z' the real part of the eigenvalue λ' of the characteristic equation is strictly negative. Hence we have necessarily $\lambda' < \lambda$, which from the estimates in [17] implies that $V(z) < V(z')$, which finishes the proof that there are no homoclinic orbits through r_2.

APPENDIX E: ASYMPTOTIC BEHAVIOR OF THE DISCRETE-TIME *N*-RING NETWORK

The asymptotic behavior of DE (4.4) for initial conditions in S is derived from the description given in [14]. We introduce the following notations. For $\delta = (\delta_0, \ldots, \delta_{N-1})$ such that $\delta_i \in \{-1, 0, +1\}$, we define the shift of order i by $s_i(\delta) = (\delta_i, \delta_{i+1}, \ldots, \delta_{i-1})$, and $k(\delta) > 0$ the lowest strictly positive integer such that $s_{k(\delta)} = \delta$. For δ such that $\delta_i \neq 0$, for all i, we denote by K_δ the cone in $\mathbb{R}^N$ defined by $K_\delta = \{x = (x_0, \ldots, x_{N-1}) \in \mathbb{R}^N : \delta_i x_i > 0 \;\; 0 \leqslant i \leqslant N-1\}$, and by W_δ the wedge in $\mathbb{R}^N$ defined by $W_\delta = K_\delta \cup K_{-\delta}$. There are 2^N such cones and 2^{N-1} wedges. We denote by W the union of the wedges. The complement of the union of the wedges is formed by the union H of N hyperplanes H_i in $\mathbb{R}^N$ defined by $H_i = \{x = (x_0, \ldots, x_{N-1}) \in \mathbb{R}^N : x_i = 0\}$.

We recall that the equilibria of DDE (2.1) are denoted by $r_1 = -(a_0, \ldots, a_{N-1})$, $r_2 = 0$, and $r_3 = (a_0, \ldots, a_{N-1})$, with $a_i > 0$. These are also the equilibria of DE (4.4). Let δ be defined as above, then the solution $z(0,t,P_\delta)$ of DE (4.4) with initial condition $P_\delta \in S$ defined by $P_i(\theta) = \delta_i a_i$ is $k(\delta)$ periodic with $z(0,t,P_\delta) = (\delta_i a_0, \delta_{i+1} a_1, \ldots, \delta_{i-1} a_{N-1})$ for all $i-1+nk(\delta) \leqslant t \leqslant i+nk(\delta)$ with $0 \leqslant i < k(\delta)$ and $n \geqslant 0$.

Asymptotic behavior of solutions of DE (4.4). Let $\Phi \in S$, (1) If $\Phi(\theta) \in W$ for all $-1 \leqslant \theta \leqslant 0$, then there is δ with $\delta_i \neq 0$ for all i, such that $z(0,t,\Phi) \in K_{s_i(\delta)}$ for all $i-1+nk(\delta) \leqslant t \leqslant i+nk(\delta)$ with $0 \leqslant i < k(\delta)$ and $n \geqslant 0$, moreover, as t increases to infinity, $z(0,t,\Phi)$ tends to the $k(\delta)$ periodic solution $z(0,t,P_\delta)$; (2) in the same way if $\Phi(\theta) \in H_j$ for all $-1 \leqslant \theta \leqslant 0$, there is δ with $\delta_j = 0$, such that $z(0,t,\Phi) \in H_{j+i}$ for all $i-1+nk(\delta) \leqslant t \leqslant i+nk(\delta)$ with $0 \leqslant i < k(\delta)$ and $n \geqslant 0$, moreover, as t increases to infinity, $z(0,t,\Phi)$ tends to the $k(\delta)$ periodic solution $z(0,t,P_\delta)$; and (3) for arbitrary $\Phi \in S$, we have $\Phi^{-1}(W) = \cup_{i \in I}(l_i, l_i')$, and $\Phi^{-1}(H) = {}_{j \in J}[m_j, m_j']$, with $\Phi[(l_i, l_i')] \subset K_\delta$, for some δ with $\delta_i \neq 0$, and $\Phi[(m_i, m_i')] \subset H_k$ for some $k \in \{0, \ldots, N-1\}$. The analysis performed in the two previous cases shows that for $\theta \in (m_i, m_i')$ [respectively, $\theta \in (l_i, l_i')$], $z(0, \theta+n, \Phi)$ tends to the periodic sequence $P_\delta(\theta+n)$ as $n \to \infty$.

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