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Oscillations in continuous-time ring neural network models with and without delay

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Abstract: An N-ring neural network is composed of N units represented by the index i, $0 \leq i \leq N-1$, such that there is a one way connection between units i and $i+1$ (modulo N) such a network with an even number of negative weights, and formed by continuous-time nonli graded response units, the trajectory of almost all initial conditions converges to an equilibri When inter-unit transmissions are delayed, the system is still almost convergent. However, networks with and without delay can display unstable periodic trajectories. For large delays, s trajectories are transiently attracted to the unstable periodic solutions and therefore display lasting transient oscillations before converging to an equilibrium.

Keywords: Ring neural networks, cooperative system, nonlinear graded response neuron, vergence, delay, oscillation.

1 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 (Vibert *et al.*, 1979; Diez-Martínez & Segundo, 1983). The influence of delay on neural behavior has also been analyzed in theoretical and computational studies of self-connected single neuron and recurrent neural network models (an der Heiden, 1981; Plant, 1981; Pakdaman *et al.*, in press; Chapeau-Blondeau & Chauvet, 1992; Destexhe & Gaspard, 1993; Destexhe, 1994; Lourenço & Babloyantz, 1994; Vibert *et al.*, 1994; Gerstner, 1995; Houweling *et al.*, 1995). Such results indicate that the delay is an important control parameter in living nervous systems.

In artificial neural network (ANN) applications, delayed inter-unit transmissions may render the networks more versatile, for instance by allowing the storage and retrieval of time-varying sequences in discrete-time networks (Sompolinsky & Kanter, 1986; Herz *et al.*, 1988). Nevertheless, in some ANN applications, the delay may deteriorate network performance. In a continuous-time content-addressable memory network, information is stored in stable equilibrium points of the system. Retrieval occurs when the system is initialized within the basin of attraction of one the equilibria and the system is allowed to stabilize in its steady state (Hopfield, 1984; Hirsch, 1989). Delays, which arise in hardware implementation of the ANN, may interfere with information retrieval by rendering the equilibria unstable (Marcus & Westervelt, 1989).

The above examples indicate that determining the contribution of the delay in the shaping of neural dynamics is helpful 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 nonlinear graded response units, which have been used as models of living neuron assemblies (Cowan & Ermentrout, 1978) as well as in ANN applications (Hopfield, 1984).

An important issue in the study of neural network dynamics is to determine the long-term behavior of the system. Sufficient conditions have been given that ensure (almost) convergence of the continuous-time neural network (with or without delay), that is, (almost) all trajectories eventually stabilize in a steady state corresponding to one of the equilibrium points of the dynamical system (Marcus and Westervelt, 1989; Burton, 1991; Marcus *et al.*, 1991; Roska & Chua, 1992; Roska *et al.*, 1992; Bélair, 1993; Burton, 1993; Civalleri *et al.*, 1993; Roska *et al.*, 1993; Gopalsamy & He, 1994a; 1994b; Ye *et al.*, 1994; 1995; Finnochiaro & Perfetti, 1995). Such behavior allows efficient storage and retrieval of information in the network (Hirsch, 1989).

We study the influence of the delay in the behavior of a network composed of N graded response neurons forming a ring where each unit is connected unidirectionally to the next one. The asymptotic behavior of ring networks, also referred to as chain networks, have been studied in (an der Heiden, 1981; Atyia & Baldi, 1989; Hirsch, 1989; Blum & Wang, 1992; Pasemann, 1995). These studies have been concerned with the (almost) convergence of the network, and the conditions under which this property is lost due to the presence of stable non-constant periodic solutions. We suppose that the ring contains an even number of inhibitory (*i.e.* negative) connections. The behavior of such ring networks is the same as those containing only excitatory connections. Indeed, in a ring network containing an even number of inhibitory connections, the effect of a

perturbation on one unit is reinforced by the feedback, so that the global effect is similar to th of a positive feedback loop. Schematically, this mechanism can be expressed as "negative tim negative is positive".

The positive feedback constraint ensures that the network is almost convergent both with a without delay, and that no stable undamped oscillatory pattern can occur. Our analysis focus on the long-term behavior of the negligible set of the trajectories that do not eventually stabili in one of the stable equilibria of the system. We show that in ring networks with delay, the trajectories play an important role in shaping the transient regime of converging trajectories. T results presented here generalize our work on the behavior of a single self-exciting neuron and al on two-neuron networks (Pakdaman *et al.*, 1995a; 1995b; 1995c).

We present the study of the system behavior without and then with transmission delays (Section and 3). The results are discussed in (Section 4).

2 Instantaneous inter-unit transmission

In this section, the continuous-time N-ring neural network model with instantaneous inter-u transmission is presented (Section 2.1), and its asymptotic behavior analyzed (Section 2.2).

2.1 The model

The dynamics of an N-ring neural network are determined by the following system of ordina differential equations (ODEs):

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

In ODE (1), as well as in all subsequent expressions the index i is taken modulo N, so that f instance $x_N = x_0$. $x_i(t)$ represents the activation of unit i at time t, $\epsilon_i > 0$ characterizes the dec rate of the activation, W_i is the connection weight indicating the influence of unit $i-1$ on unit and σ_{α_i} is the transfer function of unit i defined by:

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

For $Y = (y_0, \cdots, y_{N-1}) \in \mathbb{R}^N$, there is a unique solution of ODE (1), denoted $z(t,Y)$ $(x_0(t,Y), \cdots, x_{N-1}(t,Y))$ and defined for all $t \in \mathbb{R}$, such that $z(0,Y) = Y$, and $z(t,Y)$ sat fies ODE (1) for $t \in \mathbb{R}$. Moreover, it can be seen that $z(t,Y)$ is bounded as $t \to +\infty$. We deno by z_t the flow associated with ODE (1), that is, $z_t(Y) = z(t,Y)$. To simplify the notations, t dependence on the initial condition Y will not be indicated unless necessary.

System (1) satisfies the positive feedback condition when $b = \alpha_0 W_0 \cdots \alpha_{N-1} W_{N-1} > 0$. Aft an appropriate change of sign of some of the activations, system (1) with the positive feedba

:ondition can be transformed into an irreducible cooperative system (Hirsch, 1989) satisfying the nore restrictive constraint C_0: $\alpha_i W_i > 0$, for all i.

'rom here on we suppose that ODE (1) satisfies C_0. Under this condition, ODE (1) preserves he order of initial conditions. That is, if an initial condition is larger than another one then the :orresponding solutions will have the same property. The activations corresponding to the larger nitial condition remain larger than the ones corresponding to the smaller initial condition. More precisely, let $Y = (y_0, \cdots, y_{N-1})$ and $Y' = (y'_0, \cdots, y'_{N-1})$ be in $\mathbb{R}^N$, we say that Y is larger (resp. trictly larger) than Y' denoted $Y \geq Y'$ (resp. $Y \gg Y'$) if for all i we have $y_i \geq y'_i$ (resp. $y_i > y'_i$). System (1) generates a strongly order preserving flow, that is:

for Y and Y' in $\mathbb{R}^N$ such that $Y \geq Y'$ and $Y \neq Y'$, we have: $z_t(Y) \gg z_t(Y')$ for all $t > 0$. (3)

!.2 The asymptotic behavior

\ constant solution of system (1) is referred to as an equilibrium point. Let $r = (a_0, \cdots, a_{N-1}) \in$ $\mathbb{R}^N$, $z(t) = r$, for $t \in \mathbb{R}$ is an equilibrium of ODE (1) if and only if r is a root of the following ystem:

$$-a_{i+1} + W_{i+1}\sigma_{\alpha_{i+1}}(a_i) = 0, \text{ for all } i. \tag{4}$$

'his system has been studied in (Blum & Wang, 1992; Pasemann, 1995). Equation (4) has the ınique root $r_0 = 0$ for $b = \alpha_0 W_0 \cdots \alpha_{N-1} W_{N-1} < 1$. For $b > 1$, equation (4) has three distinct oots denoted $r_1 = -(a_0, \cdots, a_{N-1})$, $r_2 = 0$ and $r_3 = (a_0, \cdots, a_{N-1})$, with $a_i > 0$, so that $r_1 = -r_3$ .nd $r_3 \gg r_2 = 0 \gg r_1$.

ocal analysis by linearization at the equilibria yields the following results (Selgrade, 1980; Mallet-'aret & Smith, 1990).

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

'he basin of attraction of an equilibrium represents the set of initial conditions whose trajectories end to this equilibrium point. The monotonicity property (3) and the special form of cyclic feed-ack involved in the N-ring network imply that the asymptotic behavior of solutions of ODE (1) annot be complicated (Appendix A).

Global behavior. i) *For $b < 1$, $r_0 = 0$ is globally asymptotically stable so that the trajectories f all initial conditions tend to r_0.*
i) *For $b > 1$, the union of the basins of attraction of r_1 and r_3 is an open dense subset of $\mathbb{R}^N$. ts complementary, denoted $\mathcal{B}$, is a codimension one manifold formed by the union of the stable nanifold of $r_2 = 0$ and stable manifolds of unstable periodic solutions. Furthermore, let $Y \in \mathcal{B}$, .nd $Y' \in \mathbb{R}^N$, if $Y \geq Y'$ (resp. $Y' \geq Y$) and $Y \neq Y'$ then $z(t, Y') \to r_1$ (resp. r_3) as $t \to +\infty$.*

Conversely, let $Y' \in \mathbb{R}^N$, if $z(t, Y') \to r_1$ (resp. r_3) as $t \to +\infty$, then there is $Y \in \mathcal{B}$, such tha $Y \geq Y'$ (resp. $Y' \geq Y$) and $Y \neq Y'$.

The above result shows that ODE (1) does not admit any undamped oscillatory solution for $b <$: and $N \geq 1$, and also $b > 1$ and $N \leq 3$. In fact, for $b > 1$ and $N = 1$, we have $\mathcal{B} = \{r_2\}$, anc for $N = 2$ or $N = 3$, all solutions on the boundary tend to r_2, so that ODE (1) is convergent For $b > 1$ and $N \geq 4$, $\mathcal{B}$ may contain undamped oscillatory solutions. These are necessaril unstable and asymptotically periodic. So that in this case, solutions on the boundary $\mathcal{B}$ are eithe asymptotically periodic or damped to r_2. Solutions "below" the boundary tend to r_1, and thos "above" it, tend to r_3, while those on the boundary are unordered, in the sense that for Y and Y in $\mathcal{B}$, we have neither $Y \geq Y'$ nor $Y' \geq Y$. This leads to the following description of the solution on the boundary $\mathcal{B}$.

Let $K_+ = \{Y \in \mathbb{R}^N,\ Y \gg 0\}$ and $K_- = \{Y \in \mathbb{R}^N,\ 0 \gg Y\}$ be respectively the positive anc negative cones in $\mathbb{R}^N$. From the description of the boundary given in the previous paragraph, i can be seen that the cone K_- (resp. K_+) is in the basin of attraction of r_1 (resp. r_3). Therefore Y is in $\mathcal{B}$ if and only if $z(t, Y) \notin K_+ \bigcup K_-$, for all $t \in \mathbb{R}$. In other words, Y is in $\mathcal{B}$ if and only i for all $t \in \mathbb{R}$, there is i such that $x_i(t, Y) \times x_{i+1}(t, Y) \leq 0$. We refer to such solutions as weakl oscillating[1].

Weak oscillations. *All solutions in $\mathcal{B}$ are weakly oscillating.*

For $N = 1$, the only weakly oscillating solution is the constant solution $z(t) = r_2 = 0$. For $N = 2$ 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 sign. In general, for N even, there is always a weakly oscillating solution $z(t)$ tending t r_2 as $t \to +\infty$, and $T \in \mathbb{R}$ such that $x_0(t) \times \cdots \times x_{N-1}(t) \neq 0$ for all $t > T$. Thus none of th components of this solution takes the value 0 once t is large enough. Therefore the components of weakly oscillatory solution are not necessarily oscillating scalar functions. However, non-constan periodic solutions, whenever they exist, are strongly oscillating, that is, each of their component is a scalar oscillating function.

2.3 The transient behavior

The characteristic return (resp. escape) time to a stable (resp. from an unstable) equilibriur point, resulting from small perturbations near the equilibria is given by $1/|\mathcal{R}(\lambda)|$, where λ is th eigenvalue of the linearized system with the largest real part denoted by $\mathcal{R}(\lambda)$. For ODE (1), λ i real negative at the stable equilibria and real positive at the unstable equilibrium r_2.

The map from K_+ to $\mathbb{R}^+$ which to $E = (\epsilon_0, \cdots, \epsilon_{N-1})$ associates $1/|\lambda(E)|$, the absolute valu of the inverse of the real eigenvalue of ODE (1), with parameters ϵ_i, is strictly increasing (wit respect to the order in K_+). For $\epsilon_i = \epsilon$ for all i, $1/|\lambda(E)| = K\epsilon$, where K is a constant dependin on the equilibrium point. Hence, in general, we have $1/|\lambda(E)| \to 0$ as $E \to (0, \cdots, 0)$, $E \in K_+$

[1]This is a stronger definition than the usual one which states that a map u from $\mathbb{R}$ to $\mathbb{R}^N$ is weakly oscillatin if for all $T \in \mathbb{R}$, there is $t > T$, such that $u(t) \notin K_+ \bigcup K_-$. However, for solutions of ODE (1), the two notion coincide.

Thus close to the equilibria, the characteristic return and escape times of the system decrease and tend to zero as E decreases and tends to zero.

The local analysis presented above can be extended as follows. For a solution of ODE (1) 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.

We consider the case where $\epsilon_i = \eta_i \epsilon$, with $\eta_i > 0$ fixed for all i. Under this condition, rescaling the time to $t' = t/\epsilon$, transforms ODE (1) into a similar system, 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 (1) 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 (1). However, the speed with which the state of the system evolves along a given trajectory increases as ϵ is decreased, and for any converging solution, the transient regime duration is proportional to ϵ. Thus the transient regime duration decreases linearly to zero as $\epsilon \to 0$.

FIGURE 1 HERE

Figures 1-A1 and 1-B1 show the temporal evolutions of x_0 and x_1 and the corresponding trajectory in $\mathbb{R}^2$ for a symmetrical two-neuron ring network (*i.e.* $W_0 = W_1$, $\alpha_0 = \alpha_1$) for two values of ϵ. In figure 1-A1, it can be seen that it takes longer for solutions of the system with the larger ϵ $(= 5)$ (thin dotted line: $x_0(t)$, thick dashed line: $x_1(t)$) to stabilize at their steady state value, than for solutions with the smaller ϵ $(= 0.4)$ (thin solid line $x_0(t)$, only visible for t close to 0, is covered rapidly by the thick solid line representing $x_1(t)$). Both solutions move along the same trajectory represented by the thick solid line in figure 1-B1. For this system, the basins of attraction of r_1 and r_3 are the sets $\{Y \in \mathbb{R}^2\ y_0 + y_1 < 0\}$ and $\{Y \in \mathbb{R}^2\ y_0 + y_1 > 0\}$ respectively. The boundary separating the two basins corresponding to the stable manifold of r_2, is the negatively sloped diagonal $y_0 + y_1 = 0$. The thick line in figure 1-C shows the transient regime duration (TRD) for a given initial condition in the basin of r_3 as function of ϵ. It can be seen that the TRD increases linearly with ϵ.

3 Delayed inter-unit transmission

In this section, the continuous-time N-ring neural network model with delayed inter-unit transmission is presented (Section 3.1), and it is shown that the asymptotic behavior of most solutions is similar to that of ODE (1) (Section 3.2). The transient behavior of solutions is then analyzed (Section 3.3).

3.1 The model

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

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

where without loss of generality the delay is set to 1 (Appendix B). The phase space of DDE is the space of continuous functions from the interval $[-1,0]$ to $\mathbb{R}^N$, denoted $S = C([-1,0],\mathbb{R}$
For $\Phi = (\phi_0,\cdots,\phi_{N-1})$, there is a unique solution of DDE (5) (Hale & Verduyn Lunel (199
denoted $z(t,\Phi) = (x_0(t,\Phi),\cdots,x_{N-1}(t,\Phi))$, defined for all $t \geq -1$, such that $z(t,\Phi) = \Phi(t)$
$-1 \leq t \leq 0$, and $z(t,\Phi)$ satisfies DDE (5) for $t \geq 0$. Moreover, $z(t,\Phi)$ is bounded as $t \to +\infty$.
denote by z_t the semi-flow associated with DDE (5), that is, $z_t(\Phi) \in S$, and $z_t(\Phi)(\theta) = z(t+\theta$
for all $-1 \leq \theta \leq 0$. To simplify the notations, the dependence on the initial condition Φ will
be indicated unless necessary.

From here on we suppose that C_0 is satisfied, that is $\alpha_i W_i > 0$ for all i, so that DDE (5) is
irreducible cooperative system. Therefore, as for the ODE (1) obtained by setting the delay
zero (Section 2.1), DDE (5) preserves the order of initial conditions. Let $\Phi = (\phi_0,\cdots,\phi_{N-1})$
$\Phi' = (\phi'_0,\cdots,\phi'_{N-1})$ be in S, we say that Φ is larger (resp. strictly larger) than Φ' noted $\Phi \geq$
(resp. $\Phi \gg \Phi'$) if for all $\theta \in [-1,0]$, and for all i we have $\phi_i(\theta) \geq \phi'_i(\theta)$ (resp. $\phi_i(\theta) > \phi'_i($
System (5) generates a strongly order preserving semiflow, that is:

for Φ and Φ' in S such that $\Phi \geq \Phi'$ and $\Phi \neq \Phi'$, we have: $z_t(\Phi) \gg z_t(\Phi')$ for all $t > 2$.

3.2 The asymptotic behavior

Throughout the rest of the paper, constant functions in S are identified with the value they t
in $\mathbb{R}^N$. $r = (a_0,\cdots,a_{N-1}) \in \mathbb{R}^N$, is an equilibrium of DDE (5) if and only if r is a root of
Therefore DDE (5) and its related ODE (1) have the same set of equilibria.

The monotonicity property (6) and the special form of cyclic feedback involved in the N-r
network imply that the asymptotic dynamics of DDE (5) and its related ODE (1) are essenti
the same (Appendix C).

Global behavior. i) *For $b < 1$, $r_0 = 0$ is globally asymptotically stable.*
ii) *For $b > 1$, the union of the basins of attraction of r_1 and r_3 is an open dense subset o*
Its complementary, denoted $\mathcal{B}$, is a codimension one manifold formed by the union of the st
manifold of $r_2 = 0$ and stable manifolds of unstable periodic solutions. Furthermore, let $\Phi \in$
and $\Phi' \in S$, if $\Phi \geq \Phi'$ (resp. $\Phi' \geq \Phi$) and $\Phi \neq \Phi'$ then $z(t,\Phi') \to r_1$ (resp. r_3) as $t \to +$
Conversely, let $\Phi' \in S$, if $z(t,\Phi') \to r_1$ (resp. r_3) as $t \to +\infty$, then there is $\Phi \in \mathcal{B}$, such t
$\Phi \geq \Phi'$ (resp. $\Phi' \geq \Phi$) and $\Phi \neq \Phi'$.

The above result presents many similarities with the description of the asymptotic behavior of
ODE. System (5) admits only damped oscillatory solution for $b < 1$. For $b > 1$, $\mathcal{B}$ may cont
undamped oscillatory solutions. These are necessarily unstable and asymptotically periodic.
that in this case, solutions on the boundary $\mathcal{B}$ are either asymptotically periodic or damped to

Solutions "below" the boundary tend to r_1, and those "above" it tend to r_3, while those on the boundary are unordered, in the sense that for Φ and Φ' in $\mathcal{B}$, we have neither $\Phi \geq \Phi'$ nor $\Phi' \geq \Phi$.

As for the ODE, the boundary $\mathcal{B}$ can also be characterized in terms of oscillating solutions. Let $K_+ = \{\Phi \in S, \ \Phi \gg 0\}$ and $K_- = \{\Phi \in S, \ 0 \gg \Phi\}$ be respectively the positive and negative cones in S. A solution $z(t)$ of DDE (5) is weakly oscillating if $z(t) \notin K_+ \bigcup K_-$, for all $t \geq 0$.

Weak oscillations. *All solutions in $\mathcal{B}$ are weakly oscillating.*

Let u be a scalar function from $\mathbb{R}^+$ to $\mathbb{R}$, u is strongly oscillating if it changes sign at arbitrarily large times, that is for all $T \geq 0$, there are times $t' > t > T$ such that $u(t) \times u(t') < 0$. This definition is extended as follows. Let $u = (u_0, \cdots, u_{N-1})$ from $\mathbb{R}^+$ to $\mathbb{R}^N$, u is strongly oscillating if each of its components u_i from $\mathbb{R}^+$ to $\mathbb{R}$ is strongly oscillating, that is for all $T \geq 0$, for all i, there are times $t_i' > t_i > T$ such that $u_i(t_i) \times u_i(t_i') < 0$. Then we have the following results (Appendix D; see also Arino & Niri, 1991):

Strong oscillations. *When the characteristic equation of DDE (5) at r_2 has no root with zero real part, all solutions in $\mathcal{B} - \{r_2\}$ are strongly oscillating.*

Therefore the components of a weakly oscillating non-constant solution are necessarily strongly oscillating scalar functions. For instance, for $N = 1$, any non-zero solution in $\mathcal{B}$, changes sign at least once in any interval of length equal to the delay (unit length).

3.3 The transient behavior

The local characteristic escape and return times for DDE (5) can be defined in a similar way as for the ODE (Section 2.3) (Brauer, 1979a; 1979b). The characteristic return (resp. escape) time to a stable (resp. from an unstable) equilibrium point, resulting from small perturbations near the equilibria is given by $1/|\mathcal{R}(\lambda)|$, where λ is the eigenvalue of the linearized system with the largest real part denoted by $\mathcal{R}(\lambda)$. For DDE (5), λ is real negative at the stable equilibria and real positive at the unstable equilibrium r_2.

The map from K_+ to $\mathbb{R}^+$ which to $E = (\epsilon_0, \cdots, \epsilon_{N-1})$ associates $1/|\lambda(E)|$, the absolute value of the inverse of the real eigenvalue of DDE (5), with parameters ϵ_i, is strictly increasing (with respect to the order in K_+). However in this case, when E decreases to zero, the characteristic return and escape times tend to a strictly positive limit $q > 0$ whose value depends on the equilibrium point: $1/|\lambda(E)| \rightarrow q$ as $E \rightarrow (0, \cdots, 0)$, $E \in K_+$. Thus close to the equilibria, the system is finitely accelerated when E tends to zero.

Globally, the transient regime of a trajectory converging to an equilibrium may drastically change as E is decreased. This illustrated in figure (1)-A2 which represents the temporal evolution of activations of a two-neuron network for $E = (5,5)$ (dashed lines) and $E = (0.4, 0.4)$ (solid lines) for a given initial condition. It can be seen that for "small" E, this solution of DDE (5) displays long-lasting transient oscillations. The difference between the transient regimes of the two solutions is also reflected in their trajectories in the (x_0, x_1)-plane as shown in figure 1-B2 ($E = (5,5)$ thick line, $E = (0.4, 0.4)$ thin line). The onset of these transient oscillations considerably increases

the TRD of the trajectories. It can be seen in figure 1-C representing the TRD as function of ($E = \epsilon, \epsilon$), that for large ϵ, the TRD of the system with delay (thin line) is close to that of t system without delay (thick line), and decreases almost linearly with ϵ. Whereas for small ϵ, t TRD of the system with delay abruptly increases due to the onset of the transient oscillations.

The change in the transient regime of some trajectories of system (5) is due to the fact that f small E, the trajectories follow transiently the trajectories of the following system of differen equations (DEs) obtained by setting $E = 0$:

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

The following result shows that the transient behavior of solutions of DDE (5), for E close $(0, \cdots, 0)$, can be obtained from the analysis of DE (7).

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

The constraint on the value of the initial condition at 0, can be relaxed. For arbitrary initi conditions in S, the solution of DDE (5) remains transiently close to the solution of DE (7 except nearby integer time values. These results are obtained by generalizing the analysis of t scalar case presented in (Sharkovsky *et al.*, 1993) to the case of systems.

In contrast with DDE (5), which does not have any stable non-constant periodic solution, DE (has infinitely many periodic solutions with non negligible basins of attraction (Appendix E). F DDE (5) with small enough E, trajectories of initial conditions within one of these basins a transiently attracted to the corresponding non-constant periodic solution, before escaping to o of the stable equilibria, and therefore they display transient oscillations.

4 Discussion

We have studied the dynamics of ring GRN networks, with an even number of inhibitory conne tions in the loop, with and without delay. The analysis of the behavior of this system allows point out the similarities and the differences between the system with and without delay.

4.1 Similarities

There are two main similarities between the behavior of the ring GRN network with and witho delays. These are both due to the fact that we deal with a positive feedback system, whi generates a strongly order preserving (semi-) flow (Hirsch, 1988; Smith, 1987; Roska *et al.*, 199

The first similarity between the two systems is that the local stability of the stable equilibria not affected by the delay. In other words, the ring networks with and without delay have exac the same set of locally stable equilibria, and hence also the same set of unstable equilibria.

The second similarity is that both the system with and without delay are almost convergent, in the sense that almost all trajectories converge to one of the locally stable equilibria. This is a remarkable property because the system without delay evolves in a finite dimensional phase space, whereas the one with delay is defined over an infinite dimensional phase space. In fact, there are examples of GRN networks with delay, which display stable asymptotic behavior that have no counter-part in the corresponding network without delay (Gilli, 1993; 1995).

4.2 Differences

The dynamics on the basin boundary.

One difference between the cases with and without delay resides in the fact that in the latter the boundary $\mathcal{B}$ has a finite dimension whereas in the former it is "infinite dimensional". For this reason, for rings made of less than three neurons ($N \leq 3$), there are no undamped oscillatory solutions in the system without delay. Whereas for the system with delay, it is known that even scalar delay equations generating an order preserving semi-flow can display undamped periodic solutions (Arino & Séguier, 1979; 1980; Arino & Benkhalti, 1988; Arino, 1993). Such periodic solutions have been shown to exist in scalar equations (an der Heiden & Mackey, 1982; Sharkovsky *et al.*, 1993) and also in two-variable systems (Pakdaman *et al.*, 1995b) of delay differential equations similar to DDE (5).

The transient regime.

Small perturbations displace a system stabilized at one of the equilibrium points. The characteristic return time indicates how fast the system will stabilize again at the equilibrium. For the ring network without delay, this quantity tends linearly to zero with the parameter E. At the limit $E = 0$, stabilization is instantaneous (the system is infinitely accelerated). A similar local analysis for the ring network with delay indicates that in this case, the return to the equilibrium point is never instantaneous: the system is at most finitely accelerated. This is an "expected" consequence of the presence of delay, which slows down the feedback, and hence the return to the equilibrium, as compared with the system without delay.

A global analysis shows that when the parameter E tends to zero, along an appropriate direction, the phase portrait of the system without delay does not depend on E. Only the speed of evolution of the system along the trajectories is linearly accelerated. This is in accord with the local analysis yielding the characteristic return times to an equilibrium point. For the system with delay, decreasing E causes some trajectories to display transient oscillations that have no counterpart in the system without delay. These oscillations induce a considerable lengthening of the transient regime duration in the corresponding trajectories. Solutions of the initial conditions that are prone to display such oscillations were determined by the analysis of the asymptotic behavior of the difference equation obtained by setting $E = 0$. 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.

4.3 General considerations

Transient regimes have received little attention compared to steady states in theoretical st of neural network model behaviors. Nervous system operation can be described as a succe transients between steady states. Experimentalists have long recognized the importance of sients in neural behavior as a means to convey information about environmental as well as int changes (e.g. (Segundo *et al.*, 1994). The information contained in the transient regime is a more important when the system evolves in rapidly changing environments such that the n networks involved in information processing does not dispose of the time lapse necessary to a steady regime.

Determining the different parameters that shape the transient behavior of neural network m is thus important for understanding how nervous systems operate. The study of the dynam GRN ring networks shows that converging neuronal networks may display oscillating trans during extremely long time intervals. In fact these transients can be so long that, practicall system will not reach its steady state during the observation window.

Overall oscillatory patterns are frequently observed in the activity of nervous systems; their are either clear as in respiration or obscure as in the electroencephalogram. Overall oscill patterns are observed when units discharge periodically and synchronously. It has been pro that these latter patterns could be important in a number of functions such as respiration information processing (e.g. Cohen *et al.*,1992; Skarda and Freeman, 1987; Gray *et al.*, 1989). long-lasting transient oscillations in the GRN ring network arise thanks to the presence of i unit transmission delays, and are also expected to occur in other network architectures. In l nervous systems, delays are ubiquitous, ranging from a few to several hundreds of millisec They are due to action potential propagation along axons, synaptic delay etc. Delay-ind 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 ove transient regime is also an important issue. Large increase in the transient regime duratio those observed in the networks studied here, can seriously deteriorate the network's perform by slowing down the system.

5 Conclusion

We have studied the behavior of ring GRN networks containing an even number of neg weights. We have shown that for instantaneous as well as delayed inter-unit transmission, trajectories tend to equilibrium points, and that the remaining ones tend to unstable per solutions. For the system with delay, the presence of such non-constant periodic solutions, inc long-lasting transient oscillations, which can be analyzed through the study of the behavior o corresponding discrete-time network.

6 References

Arino, O. (1993). A note on "the discrete Lyapunov function ...". *Journal of Differential Equations*, **104**, 169–181.

Arino, O., & Benkhalti, R. (1988). Periodic solutions for $\dot{x} = \lambda f(x(t), x(t-1))$. *Proceedings of the Royal Society of Edinburgh*, **109A**, 245–260.

Arino, O., & Niri, K. (1991). Oscillations in vector spaces: a comparison result for monotone delay differential systems. *Journal of Mathematical Analysis and Applications*, **160**, 267–283.

Arino, O. & Séguier, P. (1979). Existence of oscillating solutions for certain differential equations with delay. in H.O. Peitgen & H.-O. Walther (Eds.), *Functional Differential Equations and Approximation of Fixed Points, Lecture Notes in Mathematics vol. 730* (pp. 46–63). Berlin: Springer-Verlag.

Arino, O. & Séguier, P. (1980). Contribution à l'étude des comportements des solutions d'équations différentielles à retard par des méthodes de monotonie et de bifurcation. Thèses d'État, Bordeaux I, Pau, 1980.

Atyia, A. & Baldi, P. (1989). Oscillations and synchronizations in neural networks: an exploration of the labeling hypothesis. *International Journal of Neural Systems*, **1**, 103–124.

Bélair, J. (1993). Stability in a model of a delayed neural network. *Journal of Dynamics and Differential Equations*, **5**, 607–623.

Blum, E.K. & Wang, X. (1992). Stability of fixed points and periodic orbits and bifurcations in analog neural networks. *Neural Networks*, **5**, 577–587.

Brauer, F. (1979a). Characteristic return times for harvested population models with time lag. *Mathematical Biosciences*, **45**, 295–311.

Brauer, F. (1979b). Decay rate for solutions of a class of differential-difference equations. *SIAM Journal of Mathematical Analysis*, **10**, 783–788.

Burton, T.A. (1991). Neural networks with memory. *Journal of Applied Mathematics and Stochastic Analysis*, **4**, 313–332.

Burton, T.A. (1993). Averaged neural networks. *Neural Networks*, **6**, 677–680.

Cao, Y. (1990). The discrete Lyapunov function for scalar differential delay equations. *Journal of Differential Equations*, **87**, 365–390.

Chapeau-Blondeau, F. & Chauvet, G. (1992). Stable, oscillatory and chaotic regimes in the dynamics of small neural networks, with delay. *Neural Networks*, **5**, 735–743.

Chiang, H.-D., Hirsch, M.W. & Wu, F.F. (1988). Stability regions of nonlinear dynamical systems. *IEEE Transactions on Automatic Control*, **33**, 16–26.

Civalleri, P.P., Gilli, M. & Pandolfi, L. (1993). On stability of cellular neural network delay. *IEEE Transactions on Circuits and Systems_I: Fundamental Theory and Applica* **40**, 157–165.

Cohen, M.I., Miller, A.D., Barnhardt, B., and Shaw C. (1992). Weakness of short-terr chronization among respiratory nerve activities during fictive vomiting. *American Jo of Physiology, 263(Regulatory Integrative Comparative Physiology. 32)*, R339-R347.

Cowan, J. & Ermentrout G.B. (1978). Some aspects of the 'eigenbehavior' of neural In S.A. Levin (Ed.) *Studies in Mathematical Biology, part I*, 67–117, The Mathem Association of America.

Destexhe, A. (1994). Oscillations, complex spatiotemporal behavior, and information t port in networks of excitatory and inhibitory neurons. *Physical Review E*, **50**, 1594–1(

Destexhe, A. & Gaspard, P. (1993). Bursting oscillations from a homoclinic tangency time delay system. *Physics Letters A*, **173**, 386-391.

Diez-Martínez, O. & Segundo, J.P. (1983). Behavior of a single neuron in a recu excitatory loop. *Biological Cybernetics*, **47**, 33–41.

Finnochiaro, M. & Perfetti, R. (1995). Relation between template spectrum and stabil cellular neural networks with delay. *Electronics Letters*. **31**, 2024–2026.

Gerstner, W. (1995). Time structure of the activity in neural network models. *Ph Review E*, **51**, 738–758.

Gilli, M. (1993). Strange attractors in delayed cellular neural networks. *IEEE Transac on Circuits and Systems_I: Fundamental Theory and Applications*, **40**, 849–853.

Gilli, M. (1995). A spectral approach for chaos prediction in delayed cellular neural netw *International Journal of Bifurcation and Chaos*, **5**, 869–875.

Gopalsamy, K. & He, X.-Z. (1994a). Stability in asymmetric Hopfield nets with transmi delays. *Physica D*, **76**, 344–358.

Gopalsamy, K. & He, X.-Z. (1994b). Delay-independent stability in bidirectional associ memory networks. *IEEE Transactions on Neural Networks*, **5**, 998–1002.

Gray, C.M., König, P., Engel, A.K. & Singer, W. (1989). Oscillatory responses in ca sual cortex exhibit inter-columnar synchronization which reflects global stimulus proper *Nature*, **338**, 334–337.

Hale, J.K. & Verduyn Lunel, S.M. (1993). Introduction to Functional Differential Equat Applied Mathematical Sciences vol. **99**. New-York: Springer-Verlag.

an der Heiden, U. (1981). *Analysis of neural networks, Lecture Notes in Biomathem vol. 35*. Berlin; New York: Springer-Verlag.

an der Heiden, U. & Mackey, M. C. (1982). The dynamics of production and destruction: analytic insight into complex behavior. *Journal of Mathematical Biology*, **16**, 75-101.

Herz, A., Sulzer, B., Kühn, R. & Van Hemmen, J.L. (1988). The Hebb rule: storing static and dynamic objects in an associative neural network. *Europhysics Letters*, **7**, 663–669.

Hirsch, M.W. (1982). Systems of differential equations which are competitive or cooperative. I: limit sets. *SIAM Journal of Mathematical Analysis*, **13**, 167–179.

Hirsch, M.W. (1985). Systems of differential equations which are competitive or cooperative. II: convergence almost everywhere. *SIAM Journal of Mathematical Analysis*, **16**, 423–439.

Hirsch, M.W. (1988). Stability and convergence in strongly monotone dynamical systems. *Journal für die reine und angewandte Mathematik*, **383**, 1–53.

Hirsch, M.W. (1989). Convergent activation dynamics in continuous time networks. *Neural Networks*, **2**, 331–349.

Hopfield, J.J. (1984). Neurons with graded response have collective computational properties like those of two-state neurons, *Proceedings National Academy of Science USA*, **81**, 3088–3092.

Houweling, A.R., Van Ooyen, A. & Van Pelt, J. (1995). Effects of transmission delays in a leaky integrator two-neuron network. Personal communication.

Lourenço, C. & Babloyantz, A. (1994). Control of chaos in networks with delay: a model for synchronization of cortical tissue. *Neural Computation*, **6**, 1141–1154.

Mallet-Paret, J. & Sell, G.R. (1994a). "Systems of differential delay equations I: Floquet multipliers and discrete Lyapunov functions," *Technical Report*, LCDS #94-13. Providence, USA: Brown University.

Mallet-Paret, J. & Sell, G.R. (1994b). The Poincaré Bendixson theorem for monotone cyclic feedback systems with delay, *Technical Report*, LCDS #94-14. Providence, USA: Brown University, 1994.

Mallet-Paret, J. & Smith, H.L. (1990). The Poincaré Bendixson theorem for monotone cyclic feedback systems. *Journal of Dynamics and Differential Equations*, **2**, 367–421.

Marcus, C.M., Waugh, F.R. & Westervelt, R.M. (1991). Nonlinear dynamics and stability of analog neural networks. *Physica D*, **51**, 234–247.

Marcus, C.M. & Westervelt, R.M. (1989). Stability of analog neural networks with delay. *Physical Review A*, **39**, 347–359.

Pakdaman, K., Grotta-Ragazzo, C., Malta, C.P. & Vibert, J.-F. (1995a). Effect of delay on the boundary of the basin of attraction in a system of two neurons. *Technical report IFUSP/P-1169, Instituto de Física, Universidade de São Paulo, Brasil.*

Pakdaman, K., Grotta-Ragazzo, C., Malta, C.P. & Vibert, J.-F. (1995b). Delay-induce transient oscillations in a two-neuron network. *Technical report IFUSP/P-1181, Institut de Física, Universidade de São Paulo, Brasil.*

Pakdaman, K., Malta, C.P., Grotta-Ragazzo, C. & Vibert, J.-F. (1995c). Effect of dela on the boundary of the basin of attraction in a self-excited single neuron. *Technical repo IFUSP/P-1164, Instituto de Física, Universidade de São Paulo, Brasil.*

Pakdaman, K., Vibert, J.-F., Boussard, E. & Azmy, N. Single neuron with recurrent exci tation: effect of the transmission delay. *Neural Networks*. in press.

Pasemann, F. (1995). Characterization of periodic attractors in neural ring networks. *Neura Networks*, **8**, 421–429.

Plant, R.E. (1981). A FitzHugh differential-difference equation modeling recurrent neura feedback. *SIAM Journal of Applied Mathematics*, **40**, 150–162.

Roska, T. & Chua, L.O. (1992). Cellular neural networks with non-linear and delay-type template elements and non-uniform grids. *International Journal of Circuit Theory an Applications*, **20**, 469–481.

Roska, T., Wu, C.F., Balsi, M. & Chua, L.O. (1992). Stability and dynamics of delay-type general and cellular neural networks. *IEEE Transactions on Circuits and Systems_I: Fundamental Theory and Applications*, **39**, 487–490.

Roska, T., Wu, C.F. & Chua, L.O. (1993). Stability of cellular neural networks with dominant nonlinear and delay-type templates. *IEEE Transactions on Circuits and Systems_I: Fundamental Theory and Applications*, **40**, 270–272.

Segundo, J.P., Stiber, M., Altshuler, E. & Vibert, J.-F. (1994). Transients in the inhibitory driving of neurons and their postsynaptic consequences. *Neuroscience*, **62**, 459–480.

Selgrade, J.F. (1980). Asymptotic behavior of solutions to single loop positive feedback systems. *Journal of Differential Equations*, **38**, 80–103.

Sharkovsky, A.N., Maistrenko, Yu.L. & Romanenko, E.Yu. (1993). Difference Equations and Their Applications. Dordrecht: Kluwer Academic Publishers.

Skarda, C.A., & Freeman, W.J. (1987). How brains make chaos in order to make sense of the world. *Behavioral and Brain Sciences*, **10**, 161–195.

Smith, H. (1987). Monotone semiflows generated by functional differential equations. *Journal of Differential Equations*, **66**, 420–442.

Smith, H. (1988). Systems of ordinary differential equations which generate an order preserving flow: a survey os results. *SIAM Review* **30**, 87-113.

Sompolinsky, H. & Kanter, I. (1986). Temporal association in asymmetric neural network. *Physical Review Letter*, **57**, 2861–2864.

Takáč, P. (1991). Domains of attraction of generic omega-limit sets for strongly monotone semi-flows. *Zeitschrift fur Analysis und ihre Anwendungen.* **10**, 275–317.

Vibert, J.-F., Davis, M. & Segundo, J.P. (1979). Recurrent inhibition: its influence upon transduction and afferent discharges in slowly adapting stretch receptor organs. *Biological Cybernetics*, **3**, 167–178.

Vibert, J.-F., Pakdaman, K. & Azmy, N. (1994). Inter-neural delay modification synchronizes biologically plausible neurons. *Neural Networks*, **7**, 589–607.

Ye, H., Michel, A.N. & Wang, K. (1994). Global stability and local stability of Hopfield neural networks with delays. *Physical Review E*, **50**, 4206–4213.

Ye, H., Michel, A.N. & Wang, K. (1995). Qualitative analysis of Cohen-Grossberg neural networks with multiple delays. *Physical Review E*, **51**, 2611–2618.

A Asymptotic behavior of the N-ring network without delay

Global behavior. i) *For $b < 1$, $r_0 = 0$ is globally asymptotically stable so that the trajectories of all initial conditions tend to r_0.*
ii-a) *For $b > 1$, the union of the basins of attraction of r_1 and r_3 is an open dense subset of $\mathbb{R}^N$.*
ii-b) *Its complementary, denoted $\mathcal{B}$, is a codimension one manifold formed by the union of the stable manifold of $r_2 = 0$ and stable manifolds of unstable periodic solutions.* ii-c) *Furthermore, let $Y \in \mathcal{B}$, and $Y' \in \mathbb{R}^N$, if $Y \geq Y'$ (resp. $Y' \geq Y$) and $Y \neq Y'$ then $z(t, Y') \to r_1$ (resp. r_3) as $t \to +\infty$. Conversely, let $Y' \in \mathbb{R}^N$, if $z(t, Y') \to r_1$ (resp. r_3) as $t \to +\infty$, then there is $Y \in \mathcal{B}$, such that $Y \geq Y'$ (resp. $Y' \geq Y$) and $Y \neq Y'$.*

Proof
i) and *ii-a)*. System (1) is an irreducible cooperative system (Hirsch, 1988; Smith, 1988), this implies that for $b < 1$, the equilibrium point r_0 is globally asymptotically stable and for $b > 1$, the two equilibrium points r_1 and r_3 are locally asymptotically stable, while r_2 is unstable, moreover, trajectories of most initial conditions tend to the stable equilibria in the sense that the union of the basins of attraction of r_1 and r_3 is a dense open subset of $\mathbb{R}^N$, whose complementary, denoted $\mathcal{B}$ has measure zero.

ii-c). This point is deduced from the properties of of cooperative irreducible systems given in (Hirsch, 1982; 1985) Let u be in $\mathbb{R}^N$, such that $u \gg 0$. There exists a continuous, strictly decreasing (with respect to the order defined on $\mathbb{R}^N$) map, b_u, from $\mathbb{R}^N$ to $\mathbb{R}$ such that:
1) For all Y in $\mathbb{R}^N$, $Y + b_u(Y).u$ is the unique intersection between the line going through Y and directed by u (i.e. the set $\{Y + \lambda u,\ \lambda \in \mathbb{R}\}$) with the boundary separating the two basins of attraction.
2) the set $\{Y \in \mathbb{R}^N, b_u(Y) > 0\}$ is exactly the basin of attraction of r_1;
3) the set $\{Y \in \mathbb{R}^N, b_u(Y) < 0\}$ is exactly the basin of attraction of r_3;
4) the set $\{Y \in \mathbb{R}^N, b_u(Y) = 0\}$ is exactly the boundary separating the two basins of attraction.

ii-b). From the characterization given above, we can deduce that the boundary has a "regula structure. Indeed, let $u \gg 0$ be in $\mathbb{R}^N$, and H be a hyperplane supplementary to u. So that f all Y in $\mathbb{R}^N$, we can write in a unique way: $Y = h + \lambda u$, where $h \in H$ and $\lambda \in \mathbb{R}$. λu is t projection of Y onto the line $\mathbb{R}u$ along the direction H. We denote $p_u(Y) = -\lambda$. Then, $p_u(Y)$ the unique real number such that $Y + p_u(Y)u$ belongs to H.

Let Y belong to the boundary $\mathcal{B}$, we can write $Y = h - p_u(Y)u$. From the definition of b_u, we knc that $b_u(h)$ is the unique real number such that $h + b_u(h)u$ belongs to $\mathcal{B}$, so that we have necessaril $p_u(Y) = -b_u(h)$. Therefore, the map $Y \to Y + p_u(Y)u$ from $\mathcal{B}$ to H is a homeomorphism wi inverse: $h \to h + b_u(h)u$ from H to $\mathcal{B}$. Hence $\mathcal{B}$ is homeomorphic to the linear hyperplane H.

We remark that $\mathcal{B}$ contains necessarily the stable manifolds of r_2 as well as those of unstable pe odic solutions (if they exist). There are no other solutions in $\mathcal{B}$. To prove this result, we show th there are no homoclinic orbits through r_2 (see the lemma below). Thus the Poincaré-Bendixso theorem for feedback systems similar to ODE (1) (Mallet-Paret & Smith, 1990) yields that f $Y \in \mathcal{B}$, one of the following holds: 1) $z(t, Y)$ is damped to r_2, 2) $Z(t, Y)$ tends asymptotical to a non-constant periodic solution. This shows that Y is either in the stable manifold of r_2, in that of an unstable periodic solution. The description of the basin boundary in terms of t stable manifold of neighboring unstable points and limit cycles is in fact valid for a wide class systems (Chiang *et al.*, 1988).

Lemma. *There are no homoclinic orbits through r_2.*

proof. We follow the strategy described in (Arino & Séguier, 1979; 1980; Cao, 1990; Arino, 1993 System (1) admits an integer valued Lyapunov function V. That is, $V(z(t))$ is non-increasing alo solutions *i.e.* $V(z(t)) \leq V(z(t'))$ for all $t \geq t'$ (Mallet-Paret & Smith, 1990).
Let $z(t)$ and $z'(t)$ be two non constant solutions of ODE (1), tending to r_2 as $t \to +\infty$ ar $t \to -\infty$ respectively. We suppose that the linearization of system (1) at r_2 does not have ar eigenvalue with zero real part. Then:

$$z(t) = t^m e^{\mu t} p(t) + \mathcal{O}(t^{m-1} e^{\mu t}) \quad \text{as } t \to +\infty;$$
$$z'(t) = t^n e^{\nu t} q(t) + \mathcal{O}(t^{n-1} e^{\nu t}) \quad \text{as } t \to -\infty; \qquad (\text{8}$$

where $t^m e^{\mu t} p(t)$ and $t^n e^{\nu t} q(t)$ represent solutions of the ODE obtained by linearizing ODE (1) r_2, with $\mu < 0$ and $\nu > 0$. The Lyapunov function is constant along such solutions of the line equation, and we have $V_+ = V(t^m e^{\mu t} p(t)) > V_- = V(t^n e^{\nu t} q(t))$ (Mallet-Paret & Smith, 1990 This inequality and the fact that $V(z(t) \to V_+$ as $t \to +\infty$ and $V(z'(t)) \to V_-$ as $t \to -\infty$ show that there can be no non-constant solution of ODE (1) tending to r_2 at both $t \to +\infty$ an $t \to -\infty$.

B Rescaling the delays

We consider the following system of delay differential equations (DDEs):

$$\epsilon'_{i+1} \frac{dy_{i+1}}{dt'}(t') = -y_{i+1}(t') + W_{i+1}\sigma_{\alpha_{i+1}}(y_i(t' - A_{i+1})) \qquad (\text{9}$$

with $A_0 \geq A_1 \geq \cdots \geq A_{N-1} > 0$. Let $A = (A_0 + \cdots + A_{N-1})/N$, $K_0 = 0$, $K_p = pA - (A_1 + \cdots + A_p)$ for $1 \leq p \leq N-1$ and $u_i(t') = y_i(t' - K_i)$. Then the variables u_i satisfy DDE (9) 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 $x_i(t) = u_i(t'/A)$ satisfy DDE (5).

C Asymptotic behavior of the N-ring network with delay

Global behavior. i) *For $b < 1$, $r_0 = 0$ is globally asymptotically stable.*
ii-a) *For $b > 1$, the union of the basins of attraction of r_1 and r_3 is an open dense subset of S.*
ii-b) *Its complementary, denoted $\mathcal{B}$, is a codimension one manifold formed by the union of the stable manifold of $r_2 = 0$ and stable manifolds of unstable periodic solutions.* ii-c) *Furthermore, let $\Phi \in \mathcal{B}$, and $\Phi' \in S$, if $\Phi \geq \Phi'$ (resp. $\Phi' \geq \Phi$) and $\Phi \neq \Phi'$ then $z(t, \Phi') \to r_1$ (resp. r_3) as $t \to +\infty$. Conversely, let $\Phi' \in S$, if $z(t, \Phi') \to r_1$ (resp. r_3) as $t \to +\infty$, then there is $\Phi \in \mathcal{B}$, such that $\Phi \geq \Phi'$ (resp. $\Phi' \geq \Phi$) and $\Phi \neq \Phi'$.*

Proof.
i) and *ii-a)*. System (5) is an irreducible cooperative system (Smith, 1987), so that the asymptotic behavior of DDE (5) and ODE (1) are essentially the same in the following sense. **(P1)** The equilibrium r_k of DDE (5) is locally asymptotically stable if, and only if, the same is true of the related ODE (1); **(P2)** the union of the basins of attraction of the stable equilibria of DDE (5) is an open and dense set in the phase space S.

ii-c). A result identical to that for the ODE (Appendix A) holds for the system of delay differential equations.

ii-b). The boundary $\mathcal{B}$ is a positively invariant unordered codimension one Lipschitz manifold containing r_2 (Takáč, 1991). The proof of the remaining results is similar to that for the ODE (appendix A). The boundary $\mathcal{B}$ contains the stable manifolds of r_2 and that of any unstable periodic solution. The Poincaré-Bendixson theorem (Mallet-Paret & Sell, 1994b) and the fact that there are no homoclinic orbits through r_2 (see the lemma below), show that there are no other solutions in $\mathcal{B}$.

Lemma. *There are no homoclinic orbits through r_2.*

Proof. The proof goes along the same line as for the ODE. Mallet-Paret and Sell (1994a) have extended the integer-valued Lyapunov function V to systems with delay, and they have estimated the value taken by V on solutions of linear systems. Therefore, we only need to establish that an approximation similar to (8) holds for the solutions of DDE (5) tending to r_2 as $t \to +\infty$. Sufficient conditions for this have been given by Arino and Niri (1991).

We rewrite DDE (5) as:

$$\frac{dz}{dt} = L z_t + f(z_t) \qquad (10)$$

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:

$$M = \begin{pmatrix} 0 & & \cdots & & 0 & \frac{\alpha_0 W_0}{\epsilon_0} \\ \frac{\alpha_1 W_1}{\epsilon_1} & 0 & \cdots & & & 0 \\ 0 & \frac{\alpha_2 W_2}{\epsilon_2} & 0 & \cdots & & 0 \\ & & & \cdots & & \\ 0 & & & \cdots & \frac{\alpha_{N-1} W_{N-1}}{\epsilon_{N-1}} & 0 \end{pmatrix} \quad \text{and} \quad M' = \begin{pmatrix} \frac{-1}{\epsilon_0} & 0 & & \cdots & & 0 \\ 0 & \frac{-1}{\epsilon_1} & 0 & \cdots & & 0 \\ & & & \cdots & & 0 \\ 0 & & & \cdots & 0 & \frac{-1}{\epsilon_{N-1}} \end{pmatrix} \qquad (1$$

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

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

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

$$g(u) = NW(\alpha u - \sigma_\alpha(u)) \qquad (1$$

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

$$||f(\Phi)|| \leq g(||\Phi(-1)||). \qquad (1$$

Thus proposition 5 in (Arino & Niri, 1991) stating that system (10) does not have any super ponential solutions can be applied.

D Strong oscillations

Strong oscillations. *When the characteristic equation of DDE (5) at zero has no root with z real part, all solutions in $\mathcal{B} - \{r_2\}$ are strongly oscillating.*

Proof. All solutions in $\mathcal{B} - \{r_2\}$ are weakly oscillating, so that we prove that in fact all weal oscillating solutions are strongly oscillating by showing that DDE (5) satisfies all the hypotheses theorem 3 in (Arino & Niri, 1991). The first three hypotheses are deduced from the fact that t DDE (5) is an irreducible cooperative system, and that the image of a bounded set by the rig hand side of DDE (5) is a bounded set (Smith, 1987). Hypothesis 5 regarding the non-existe of superexponential solutions tending to r_2 has been checked in appendix C. From (14) we dedu that:

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

So we need only to check hypothesis 4, that is:

Lemma. *Let $z(t)$ be a weakly oscillating solution, if there is $T \geq 0$, such that $x_i(t) \neq 0$, for all $t \geq T$, then $z(t) \to 0$ as $t \to +\infty$.*

Proof. Let $z = (x_0, \cdots, x_{N-1})$ be a weakly oscillating solution of DDE (5) such that $x_i(t) \neq 0$, for all $t \geq T$ and all i. There is necessarily j, such that $x_j(t) < 0$ and $x_{j+1}(t) > 0$ for all $t \geq T$. Thus $x_{j+1}(t)$ is a strictly decreasing bounded function, and we have $x_{j+1}(t) \to l_{j+1}$ with $l_{j+1} \geq 0$, as $t \to +\infty$. From this we derive that for all k:

$$x_{j+k}(t) \to l_{j+k} \text{ as } t \to +\infty, \text{ where } l_{j+k} = W_{j+k}\sigma_{a_{j+k}}(W_{j+k-1}\sigma_{a_{j+k-1}}(\cdots W_{j+2}\sigma_{a_{j+2}}(l_{j+1}))) \geq 0. \quad (16)$$

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

Finally, when the characteristic equation of DDE (5) at 0 does not have any roots with zero real part, theorem 3 ((Arino & Niri, 1991), p.281) yields that at least one of the components $x_i(t)$ is oscillating. For the special case of DDE (5) this implies that all are oscillating. In fact, let $x_i(t)$ be oscillating for some i, then for all $T > 0$, there are $t_2 > t_1 > t_0 > T+1$ such that: $x_i(t_0) > 0$, $x_i(t_1) < 0$ and $x_i(t_2) > 0$. Let t' and t'' such that $t_0 < t' < t_1 < t'' < t_2$, $x_i(t') = x_i(t'') = 0$ and $x_i(t) < 0$ for all $t' < t < t_1$ and $x_i(t) > 0$ for all $t'' < t < t_2$. There are θ and θ' such that $t' < \theta < t_1$ and $t'' < \theta' < t_2$ such that $\frac{dx_i}{dt}(\theta) = \frac{x_i(t_1)}{t_1 - t'} < 0$ and $\frac{dx_i}{dt}(\theta') = \frac{x_i(t_2)}{t_2 - t''} > 0$ Thus $-x_i(\theta) + W_i\sigma_{a_i}(x_{i-1}(\theta - 1) < 0$ and $-x_i(\theta') + W_i\sigma_{a_i}(x_{i-1}(\theta' - 1)) > 0$, so that: $x_{i-1}(\theta - 1) < 0$ and $x_{i-1}(\theta' - 1) > 0$. This shows that x_{i-1} is oscillating and we can apply a similar method to $i-2$, etc.

E Asymptotic behavior of the discrete-time N-ring network

We denote by $z(E, t, \Phi)$ the solution of DDE (5) with parameters $E = (\epsilon_0, \cdots, \epsilon_{N-1}) \gg (0, \cdots, 0)$, and $z(0, t, \Phi)$ the solution of DE (7) obtained by setting $\epsilon_i = 0$ for all i.

The asymptotic behavior of DE (7) for initial conditions in S is derived from the description given in (Blum & Wang, 1992; Pasemann, 1995). We introduce the following notations. For $\delta = (\delta_0, \cdots, \delta_{N-1})$ such that $\delta_i \in \{-1, 0, +1\}$, we define the shift of order i by $s_i(\delta) = (\delta_i, \delta_{i+1}, \cdots, \delta_{i-1})$, 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 $K_\delta = \{x = (x_0, \cdots, x_{N-1}) \in \mathbb{R}^N \ : \ \delta_i.x_i > 0 \ 0 \leq i \leq N-1\}$, 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 complementary of the union of the wedges is formed by the union H of N hyperplanes H_i in $\mathbb{R}^N$ defined by $H_i = \{x = (x_0, \cdots, x_{N-1}) \in \mathbb{R}^N \ : \ x_i = 0\}$.

We remind that the equilibria of DDE (5) are denoted by $r_1 = -(a_0, \cdots, a_{N-1})$, $r_2 = 0$ and $r_3 = (a_0, \cdots, a_{N-1})$, with $a_i > 0$. These are also the equilibria of DE (7). Let δ be defined as above, then the solution $z(0, t, P_\delta)$ of DE (7) with initial condition $P_\delta \in S$ defined by $P_i(\theta) = \delta_i a_i$.

is $k(\delta)$ periodic with $z(0, t, P_\delta) = (\delta_i a_0, \delta_{i+1} a_1, \cdots, \delta_{i-1} a_{N-1})$ for all $i - 1 + n.k(\delta) \leq t \leq i + n.$ with $0 \leq i < k(\delta)$ and $n \geq 0$.

Asymptotic behavior of solutions of DE (7). *Let $\Phi \in S$,*

1. if $\Phi(\theta) \in W$ for all $-1 \leq \theta \leq 0$, then there is δ with $\delta_i > 0$ for all i, such that $z(0, t, \Phi$ $K_{s_i(\delta)}$ for all $i - 1 + n.k(\delta) \leq t \leq i + n.k(\delta)$ with $0 \leq i < k(\delta)$ and $n \geq 0$, moreover, 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 $-1 \leq \theta \leq 0$, there is δ with $\delta_j = 0$, such $z(0, t, \Phi) \in H_{j+i}$ for all $i - 1 + n.k(\delta) \leq t \leq i + n.k(\delta)$ with $0 \leq i < k(\delta)$ and n moreover, as t increases to infinity, $z(0, t, \Phi)$ tends to the $k(\delta)$ periodic solution $z(0, t,$
3. for arbitrary $\Phi \in S$, we have $\Phi^{-1}(W) = \bigcup_{i \in I}(l_i, l'_i)$, and $\Phi^{-1}(H) = \bigcup_{j \in J}[m_j, m'_j]$, $\Phi((l_i, l'_i)) \subset K_\delta$, for some δ with $\delta_i \neq 0$, and $\Phi((m_i, m'_i)) \subset H_k$ for some $k \in \{0, \cdots,$ $1\}$. The analysis performed in the two previous cases, shows that for $\theta \in (m_i.m'_i)$ (r $\theta \in (l_i.l'_i))$, $z(0, \theta + n, \Phi)$ tends to the periodic sequence $P_\delta(\theta + n)$ as $n \to \infty$.

FIGURE LEGENDS

and

FIGURES

Figure 1: *Transient behavior.*

A1: Temporal evolution of $x_0(t)$ *(thin solid line and dotted line) and* $x_1(t)$ *(thick solid line a thick dashed line) for a two neuron ring network without delay, for* $\epsilon_0 = \epsilon_1 = 0.4$ *(solid lin and* $\epsilon_0 = \epsilon_1 = 5$ *(dashed and dotted lines). Abscissa: time; ordinates: neuron activation. Trajectory in the* x_0, x_1 *plane of the solutions presented in A1. Abscissa: activation* x_0*, ordinat activation* x_1*. A2: Temporal evolution of* $x_0(t)$ *(thin solid line and dotted line) and* $x_1(t)$ *(th solid line and thick dashed line) for a two neuron ring network with delay, for* $\epsilon_0 = \epsilon_1 = 0.4$ *(s lines) and* $\epsilon_0 = \epsilon_1 = 5$ *(dashed and dotted lines). Abscissa: time; ordinates: neuron activation. Trajectories in the* x_0, x_1 *plane of the solutions presented in A1. Thin solid line for* $\epsilon_0 = \epsilon_1 =$ *and thick solid line for* $\epsilon_0 = \epsilon_1 = 5$*. Abscissa: activation* x_0*, ordinates: activation* x_1*. C: transi regime duration for the system without delay (thick line) and the system with delay (thin li as function of* ϵ*, for the same systems and initial condition considered in A and B. Absci* ϵ*, ordinates: transient regime duration, TRD. Parameters used for the figures:* $W_0 = W_1 =$ $\alpha_0 = \alpha_1 = 5$*. Initial condition of the solutions* $(-1, 2)$*.*

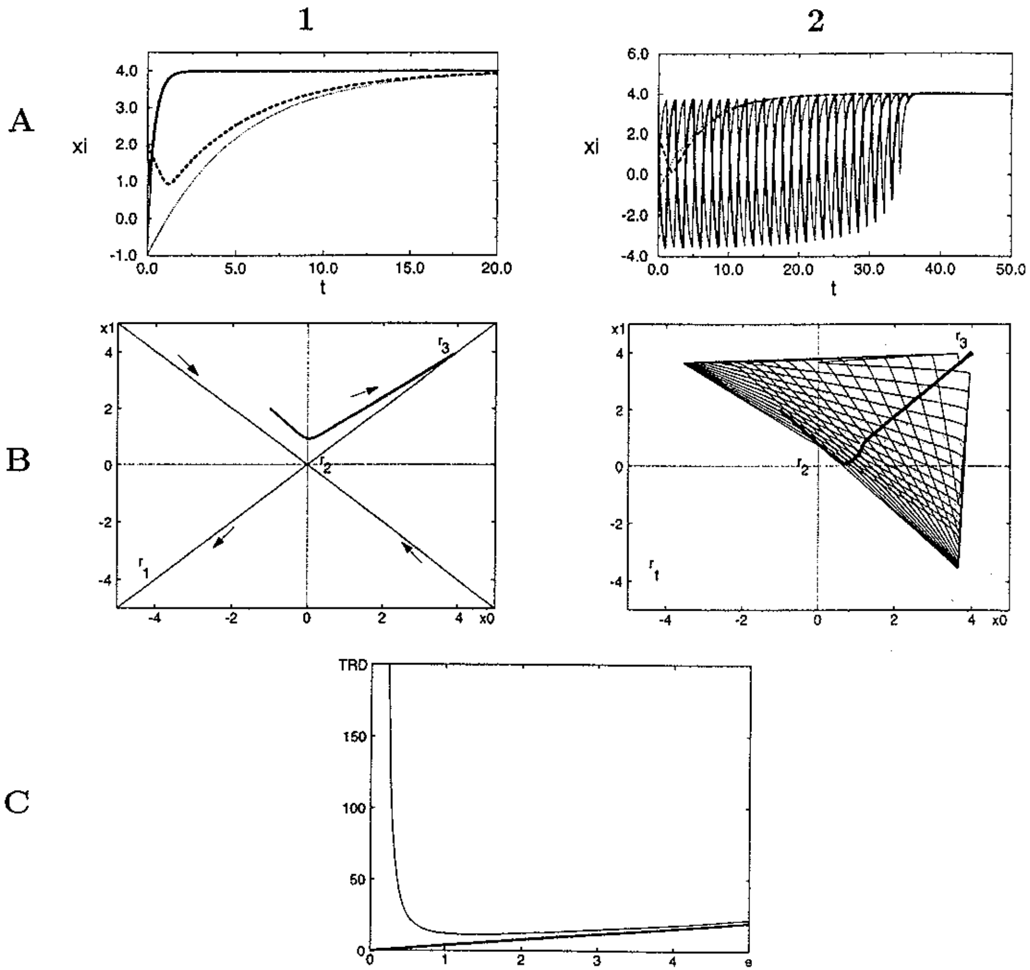

Figure 1