



Physica D 103 (1997) 419-429

# Stability of spatio-temporal structures in a lattice model of pulse-coupled oscillators

A. Díaz-Guilera a,\*, A. Arenas b, A. Corral a, C. J. Pérez a

Departament de Física Fonamental, Facultat de Física, Universitat, de Barcelona, Diagonal 647, E-08028 Barcelona, Spain
 Departament d'Enginyeria Informática, Universitat, Rovira i Virgili, Carretera, Salou s/n, E-43006 Tarragona, Spain

#### **Abstract**

We analyze the collective behavior of a lattice model of pulse-coupled oscillators. By studying the intrinsic dynamics of each member of the population and their mutual interactions we observe the emergence of either spatio-temporal structures or synchronized regimes. We perform a linear stability analysis of these structures.

Keywords: Pulse-coupled oscillators; Lattice models; Spatio-temporal structures; Fixed points; Linear stability

## 1. Introduction

The collective behavior of large assemblies of pulse-coupled oscillators has been investigated quite often in the last years. Many physical and biological systems can be described in terms of populations of units that evolve in time according to a certain intrinsic dynamics and interact when they reach a threshold value [1]. Although it was known long time ago that the members of these systems tend to have a synchronous temporal activity, a rigorous treatment of the problem has been considered only in the last decade [2–4]. Up till now, the most important efforts have been focused on systems with long-range interactions because in this case analytical results can be derived by applying a mean-field formalism. Relevant is the work by Mirollo and Strogatz (MS) [4] who discovered under which conditions mutual synchronization emerges as the stationary configuration of the population. Later on, the study has been generalized to other situations [5–10].

When the oscillators form a finite-dimensional lattice where only short-range interactions are allowed, the spectrum of behaviors is broader. For example, under certain conditions lattice models of pulse-coupled oscillators display self-organized criticality (SOC) [11–16]. In such case the system self-organizes, due to its own dynamics, into a critical state with no characteristic time or length scales and provides some hints about the wide ocurrence of 1/f noise in nature [17]. In other cases, phase locking, synchronization, or more complex spatio-temporal structures are developed.

<sup>\*</sup> Corresponding author.

On the other hand, some efforts have been devoted recently to analyze the stability of spatio-temporal periodic structures in coupled map lattices [18]. These systems are easier to deal with, both analytically and numerically, than lattices of coupled nonlinear oscillators although they represent a less realistic view of coupled systems that appear quite often in nature.

It is precisely the purpose of the present work to study the stability of certain structures, that have been obtained recently in computer simulations in a lattice of pulse-coupled oscillators. Keeping this goal in mind the paper is organized as follows. In Section 2 we introduce the model and explain several equivalent ways to describe the time evolution of the system. These equivalent descriptions are related through well-defined transformations, which allow to study the model in terms of the most suitable dynamic variables. In Section 3, we calculate analytically the fixed points of some of the structures observed in simulations in one- and two-dimensional lattices, and in Section 4 we analyze the stability of these fixed points. Finally, Section 5 is devoted to the conclusions of this work and its future perspectives.

#### 2. The model

Let us consider a system of coupled oscillators described each one by a state variable  $E_i$ , which we can identify with a voltage-like magnitude when dealing with biological oscillators. We will assume that all the oscillators are identical and evolve in time according to the following dynamics:

$$\frac{\mathrm{d}E_i}{\mathrm{d}t} = f(E_i) + \bar{\varepsilon}(E_i) \sum_j \delta(t - t_j) \tag{1}$$

plus the reset condition for  $E_i \ge 1$ . This means that when the *i*th oscillator fires, it is reset  $(E_i \ge 1 \to 0)$ . The first terms of the RHS is the driving rate that throughout the paper will be considered a positive quantity, f(E) > 0. The second term accounts for the coupling, given in terms of a nonlinear coupling function  $\bar{\varepsilon}(E)$  that we will assume either excitatory for all  $E, \bar{\varepsilon}(E) > 0$ , or inhibitory,  $\bar{\varepsilon}(E) < 0$ ,  $\forall E$  (except at the reset point E = 0, where it could be  $\bar{\varepsilon}(0) = 0$ ).

When some of its neighbors (labeled by index j) fire at time  $t_j$ , the ith oscillator suffers an instantaneous perturbation of its state given by the coupling function  $\bar{\varepsilon}(E_i)$ . This implies the existence of two time scales, a slow one for the driving and a fast one for the coupling. In this description both time scales appear in the same equation. This represents a quite general evolution equation, because not only the driving rate f(E) but also the coupling  $\bar{\varepsilon}(E)$  are functions of the state E.

We could also consider another two equivalent descriptions of the same model, both related to (1) by simple changes of variables. The first equivalence is obtained by applying the nonlinear transformation

$$y(E) = \varepsilon_0 \int_0^E \frac{dE'}{\bar{\varepsilon}(E')}$$
 (2)

used before in different contexts by several authors [8,19], where  $\varepsilon_0$  is defined to ensure that y(E=1)=1. By substituting into (1) we get

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = g(y_i) + \varepsilon_0 \sum_j \delta(t - t_j). \tag{3}$$

Now, the evolution of the system is described in terms of a new variable y for which the coupling is constant and whose driving rate is given by

$$g(y_i) = \varepsilon_0 \frac{f(E_i)}{\bar{\varepsilon}(E_i)}.$$
 (4)

A case of particular interest is that of a zero advance at the reset point  $(\bar{\varepsilon}(E=0)=0)$ . In such case, this transformation is well defined if the coupling is constant  $(\varepsilon_0) \forall y \neq 0$  except for y=0 where it is exactly zero. This condition plays the role of a refractory time in the fast time scale, which provokes that all the units which have fired have zero phase at the end of the interactive process.

The second equivalent description can be derived by writing (1) as a function not of the state  $E_i$  but of the phase of each oscillator  $\phi_i$ , which evolves linearly in time except when it receives a pulse from its neighbors. In this description, the driving and the coupling are integrated in a 'phase response curve' (PRC), function that gives the phase advance of the oscillator that receives the pulse [20,21],

$$\frac{\mathrm{d}\phi_i}{\mathrm{d}t} = 1 + \bar{\Delta}(\phi_i) \sum_j \delta(t - t_j). \tag{5}$$

This equation can be obtained in a straightforward manner by applying the following transformation in (1):

$$\phi(E) = \int_{0}^{E} \frac{\mathrm{d}E'}{f(E')}.$$
(6)

The fact that  $\phi(E=1)=1$  is guaranteed if the intrinsic period of the oscillators is equal to one. According to the definitions the function  $\bar{\Delta}$  is given by

$$\bar{\Delta}(\phi_i) = \frac{\bar{\varepsilon}(E_i)}{f(E_i)}.\tag{7}$$

All three descriptions are physically equivalent, but depending on the theoretical framework it is convenient to deal with one or another for specific purposes. In this paper we will use the description in terms of the phase. Finally, it is worth noting that one has to be very careful when handling with the two coexisting time scales in the system. Since they do not overlap the situation is equivalent to stopping the driving when an oscillator fires. Then, the resulting PRC  $\Delta_n(\phi)$  must be related with the function  $\bar{\Delta}(\phi)$  by

$$\int_{\phi}^{\phi+\Delta_n(\phi)} \frac{\mathrm{d}\phi'}{\bar{\Delta}(\phi')} = \sum_{j} \int_{t_j^-}^{t_j^+} \delta(t-t_j) \, \mathrm{d}t = n,$$
(8)

where we obtain a different PRC depending on the number of firings n that the oscillator receives, which will be bounded between one and the number of neighbors. This ensures that when n neighbors fire simultaneously, the ith oscillator modifies its phase as

$$\phi_i \to \phi_i + \Delta_n(\phi_i),$$
 (9)

otherwise it evolves as  $d\phi_i/dt = 1$ . In general, to go from  $\bar{\Delta}(\phi)$  to  $\Delta_n(\phi)$  is straightforward, but the inverse implies to solve an integral equation that in general can only be done numerically.

## 3. Fixed points

First of all, we will show that a lattice model of pulse-coupled nonlinear oscillators evolving in time following (9) with nearest-neighbor interaction and periodic boundary conditions has some periodic spatio-temporal solutions

which correspond to fixed points in a return map description. With this goal in mind, we will study initially the behavior of a system of two oscillators and after this we will generalize the analysis to one- and two-dimensional lattice models. Hereafter we will consider always refractory time in the model, i.e.,  $\Delta_n(\phi = 0) = 0$ .

#### 3.1. Two oscillators

To start the discussion we will consider a system of two oscillators. It is simple enough to allow a complete description of the dynamical evolution of the model and, additionally, to illustrate the main ideas that we want to develop later on. We present here a detailed evolution of the phase of each oscillator for half cycle. Each row corresponds to the phase of each one.

$$\begin{array}{cccc}
1 & \longrightarrow & 0 & \longrightarrow & 1 - \phi - \Delta_1(\phi) \\
\phi & \stackrel{\text{firing}}{\longrightarrow} & \phi + \Delta_1(\phi) & \stackrel{\text{driving}}{\longrightarrow} & 1
\end{array} \tag{10}$$

The fixed points of this transformation are the solutions of  $\phi^* = 1 - \phi^* - \Delta_1(\phi^*)$ . If  $\Delta_1(\phi)$  is a continuous function bounded between -1 and 1, there exists at least one fixed point. However, an important question arises about the uniqueness or multiplicity of those fixed points. It is easy to know under which sufficient conditions the fixed point is unique by simple geometrical arguments, which is  $\Delta_1'(\phi) > -2 \ \forall \phi$ . It can be proved, with our hypothesis of f(E) > 0 and  $\bar{\varepsilon}(E) \ge 0$  or  $\bar{\varepsilon}(E) \le 0 \ \forall E$ , that  $\Delta_n'(\phi) > -1 \ \forall \phi$ , verifying thus the uniqueness of the fixed point. To clarify this point, let us consider a particular example that allows to calculate the location of the fixed point, Peskin's model. It was proposed to analyze the collective behavior of an assembly of cardiac pacemaker cells [22]. In this model the intrinsic time evolution of each member of the population is given by

$$f(E) = \gamma(K - E),\tag{11}$$

where  $\gamma$  gives the slope of the driving rate and  $K = (1 - e^{-\gamma})^{-1}$ . The coupling function is for this simple case a constant  $\bar{\varepsilon}(E) = \varepsilon_0$ . Then the function  $\bar{\Delta}$  is

$$\bar{\Delta}(\phi) = \frac{\varepsilon_0}{\gamma(K - E)} = \frac{\varepsilon_0}{\gamma K} e^{\gamma \phi},\tag{12}$$

where for the last equality it is necessary to know the relation  $E(\phi)$ , substituting Eq. (11) into Eq. (6). Now it is easy to find the PRC according to (8), obtaining

$$\Delta_n(\phi) = -\frac{1}{\gamma} \ln\left(1 - \frac{n\varepsilon_0}{K} e^{\gamma \phi}\right),\tag{13}$$

It is straightforward to see from the derivative of  $\Delta_n(\phi)$  that, for a given  $\varepsilon_0 > 0$ , the PRC is an increasing function when  $\gamma > 0$ , whereas for  $\gamma < 0$  the PRC decreases monotonously. This behavior is the opposite when an inhibitory coupling is taken into account. For two oscillators the fixed point is unique and satisfies  $\Delta_1(\phi^*) = 1 - 2\phi^*$ , corresponding to

$$\phi^* = \frac{1}{2} - \frac{1}{\gamma} \sinh^{-1} \left( \varepsilon_0 \sinh \left( \frac{\gamma}{2} \right) \right). \tag{14}$$

In general for the two oscillators case we can study the global stability of the system [4]. To show this, we look at the result obtained after half a cycle assuming identical oscillators. Then for  $\Delta'_1(\phi) > 0$ , any perturbation  $\delta$  from the fixed point evolves according to (10) as

$$\phi_0 = \phi^* + \delta \longrightarrow 1 - \phi^* - \delta - \underbrace{\Delta_1(\phi^* + \delta)}_{>\Delta_1(\phi^*) = 1 - 2\phi^*} < \phi^* - \delta$$

and

$$\phi_0 = \phi^* - \delta \longrightarrow > \phi^* + \delta.$$

This behavior shows that the fixed point is a repeller of the dynamics, when the PRC is an increasing function, but due to the periodicity of the variable  $\phi$  this fact provokes synchronization between oscillators, i.e., oscillators are repelled from the fixed point and they go to phase one or zero which are the same cyclic point. The two oscillators approach each other after each cycle until they are close enough so that the firing of one of the oscillators makes the phase of the other one to reach the threshold. At this time, due to the refractory time, both oscillators fire in unison and this situation persists forever, which corresponds to the synchronized state. In the same way, if  $\Delta'_1(\phi) < 0$  we have:

$$\phi_0 = \phi^* + \delta \longrightarrow > \phi^* - \delta,$$
  
 $\phi_0 = \phi^* - \delta \longrightarrow < \phi^* + \delta.$ 

Both equations need another limit

$$\phi^* + \delta \to 1 - \phi^* - \delta - \Delta_1(\phi^* + \delta) < \phi^* + \delta,$$
  
$$\phi^* - \delta \to 1 - \phi^* + \delta - \Delta_1(\phi^* - \delta) > \phi^* - \delta,$$

where we use that  $\Delta_1(\phi) > 1 - 2\phi$  if  $\phi > \phi^*$  and  $\Delta_1(\phi) < 1 - 2\phi$  if  $\phi < \phi^*$ . Now, for a decreasing PRC, the fixed point is an attractor of the dynamics. This attractor corresponds to a phase-locked state that maintains the difference of phases between both oscillators. Note that we have assumed that the initial conditions are chosen in such a way that in the first interaction the oscillators do not synchronize. This kind of synchronization is trivial and does not depend on the slope of the PRC, only on its strength.

We have to mention, to clarify this point, that a PRC is always bounded by  $\Delta_n(\phi) < 1 - \phi$  when it is excitatory and by  $\Delta_n(\phi) > -\phi$  when inhibitory, in order to avoid phases larger than 1 or smaller than 0. However, these limits correspond to trivial synchronization of the oscillators, and will not be taken into account here. Therefore, when we say increasing or decreasing PRC we refer to the domain in which synchronization is not trivial.

#### 3.2. One-dimensional lattices

We have seen in the previous section that depending on the slope of the PRC two oscillators tend either to synchronize or to keep a phase difference between them. When generalizing this result to a periodic one-dimensional model of coupled oscillators with nearest-neighbor interaction, we can imagine the same tendency. On the one hand the strength of the coupling makes two neighboring oscillators with close phase values to synchronize. On the other hand, when they are not close enough, this coupling can make the phases to approach each other or to separate, depending on whether the slope of the PRC is positive or negative, respectively. We have observed in computer simulations, starting from a random distribution of phases, that the population reaches, after a long transient and depending on the parameters of the system, well-defined spatial structures, with concrete values of the phase differences. We have checked that these structures are limit cycles for the dynamical evolution of the lattice. When building up the return map, by looking to the system at the time that a given oscillator reaches the threshold, we obtain fixed points.

The most simple fixed point is that one in which all the oscillators have exactly the same phase. Thus all of them reach the threshold simultaneously. Having assumed that  $\Delta_n(\phi=0)=0$ , i.e. the existence of a refractory time, all the oscillators will be at zero phase after the collective firing and then a new cycle starts again. This corresponds to global synchronization of the population.



Fig. 1. General one-dimensional spatially periodic structure. Each  $\phi_l$  corresponds to a different value of the phase.

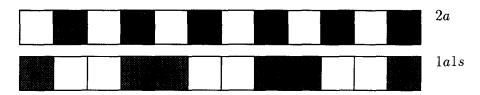


Fig. 2. One-dimensional two-phase fixed point structures: (top) chessboard-like (2a); (bottom) domino-like (1a1s).

There are other fixed points characterized by the fact that the population is split into several subpopulations with the same number of elements. Each subpopulation is composed by oscillators with the same phase, which is different for different subpopulations. Moreover, they form periodic spatial structures and have been discussed in the context of coupled map lattices [18]. A general case is plotted in Fig. 1, where the subscripts stand for the different subpopulations.

Among these structures we will focus on the simplest ones, those having only two different phases, plotted in Fig. 2. We have introduced a notation to denote the number of synchronized (s) or phase-locked (a) neighbors of a given oscillator that will also be used for the two-dimensional models.

Without loss of generality we can assume that white sites in Fig. 2 have phase equal to one whereas black sites have a phase  $\phi$ . In these cases it is very simple to compute the value of  $\phi^*$  that correspond to the fixed points. The proof runs parallel to that for two oscillators. For the chessboard, if each row stands for a subpopulation

$$\begin{array}{cccc}
1 & \longrightarrow & 0 & \longrightarrow & 1 - \phi - \Delta_2(\phi) \\
\phi & \stackrel{\text{firing}}{\longrightarrow} & \phi + \Delta_2(\phi) & \stackrel{\text{driving}}{\longrightarrow} & 1
\end{array} \tag{15}$$

and the same for the domino writing  $\Delta_1(\phi)$  instead of  $\Delta_2(\phi)$ . Then the fixed points correspond to

chessboard: 
$$\phi^* = 1 - \phi^* - \Delta_2(\phi^*) = 1 - \phi^* - \Delta_2^*$$
,  
domino:  $\phi^* = 1 - \phi^* - \Delta_1(\phi^*) = 1 - \phi^* - \Delta_1^*$ .

In the next section we will analyze in detail the linear stability of the chessboard structure (2a) in one-dimensional and how to generalize this result to other structures.

#### 3.3. Two-dimensional lattices

In two-dimensional lattices, with periodic boundary conditions and nearest-neighbor interactions, we have also observed in computer simulations the existence of well-defined patterns that are fixed points for the discrete dynamics of the population. Some of the two-phase structures are plotted in Fig. 3, together with the unique one-phase structure, the synchronized state. The phases of the fixed points are very easily computed using the transformations for the fixed point explained in the one-dimensional case. In general we are going to have for the different possibilities

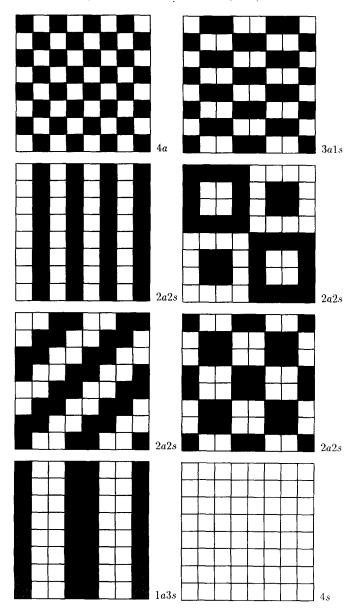


Fig. 3. Two-dimensional two-phase fixed point structures and the synchronized state (4s).

between phase-locked (a) or synchronized (s) neighbors in a two-dimensional square lattice, the following fixed point equations:

$$4a \phi^* = 1 - \phi^* - \Delta_4^*,$$

$$3a1s \phi^* = 1 - \phi^* - \Delta_3^*,$$

$$2a2s \phi^* = 1 - \phi^* - \Delta_2^*,$$

$$1a3s \phi^* = 1 - \phi^* - \Delta_1^*.$$
(16)

In our computer simulations we have observed that these structures have different basins of attraction depending on the values of the parameters as well as on the size of the lattice. Nevertheless, the chessboard (4a) seems to be the most stable in two senses: it has the largest basin of attraction and it is the most robust to different sources of dynamical noise. In Section 4 we will briefly discuss the linear stability of these patterns.

### 4. Stability of the periodic structures

Now we will analyze the stability of the fixed points discussed in Section 3. We will discuss in detail the onedimensional chessboard, and later on we will explain how to generalize this to other structures.

## 4.1. Linear stability analysis of the one-dimensional chessboard

To perform the stability analysis in the one-dimensional model we are going to deal with the most simple configuration of two phases (black and white) slightly perturbed at random from its fixed point  $(..., 1, \phi^*, 1, \phi^*, ...)$ . Suppose without loss of generality we have the subpopulation of white sites distributed slightly below phase one, and the subpopulation of black sites with phases around  $\phi^*$ , that is

White sites (W) 
$$\begin{cases} 1, & \text{first,} \\ 1 - \delta_1, & \text{last,} \end{cases}$$
 (17)

where the top row stands for the first oscillator that will reach the threshold and the bottom row for the last one, after a first driving of amount  $\delta_1$ . On the other hand we have for black sites

Black sites (B) 
$$\begin{cases} \phi^* + \delta_2, & \text{first,} \\ \phi^* + \delta_3, & \text{last,} \end{cases}$$
 (18)

where the two rows have the same meaning as for the white sites. Nevertheless, this does not mean that these oscillators have the largest and smallest phases, in contrast to the white oscillators. Since during the driving  $\delta_1$  the black sites will receive pulses from their white neighbors at unknown phases, the order is not maintained and the black oscillators can overtake each other. Then the two oscillators shown in (18) are those that after receiving the two pulses have the maximum and minimum phases, respectively.

As we have stated before, the first step is to wait for a driving  $\delta_1$ ; at this point all the white sites have fired and the new configuration becomes, if in order to simplify we call  $\Delta$  to  $\Delta_1$ :

$$W \begin{cases} \delta_{1}, \\ 0, \end{cases}$$

$$B \begin{cases} \phi^{*} + \delta_{2} + \delta_{1} + \Delta(\phi^{*} + \delta_{2} + \alpha_{1}\delta_{1}) + \Delta(\phi^{*} + \delta_{2} + \alpha_{2}\delta_{1} + \Delta(\phi^{*} + \delta_{2} + \alpha_{1}\delta_{1})), \\ \phi^{*} + \delta_{3} + \delta_{1} + \Delta(\phi^{*} + \delta_{3} + \beta_{1}\delta_{1}) + \Delta(\phi^{*} + \delta_{3} + \beta_{2}\delta_{1} + \Delta(\phi^{*} + \delta_{3} + \beta_{1}\delta_{1})), \end{cases}$$

where  $\alpha_1$ ,  $\alpha_2$ ,  $\beta_1$ ,  $\beta_2$  are the unknown fractions of the driving  $\delta_1$  the oscillators have run at the moment they receive the pulses from the white neighboring sites. At this point we linearize  $\Delta$  around  $\phi^*$ :

$$\Delta(\phi^* + \delta_2 + \alpha_1 \delta_1) = \underbrace{\Delta(\phi^*)}_{\Delta^*} + (\delta_2 + \alpha_1 \delta_1) \underbrace{\Delta'(\phi^*)}_{\Delta'^*},$$

$$\Delta(\phi^* + \delta_2 + \alpha_2 \delta_1 + \Delta(\phi^* + \delta_2 + \alpha_1 \delta_1)) = \underbrace{\Delta(\phi^* + \Delta^*)}_{\Delta^{**}} + (\delta_2 + \alpha_2 \delta_1 + (\delta_2 + \alpha_1 \delta_1) \Delta'^*) \underbrace{\Delta'(\phi^* + \Delta^*)}_{\Delta'^{**}}.$$

With this linearization, the previous structure can be written for the black oscillators as

$$\mathbf{B} \begin{cases} \phi^* + \Delta^* + \Delta^{**} + C\delta_2 + A\delta_1, \\ \phi^* + \Delta^* + \Delta^{**} + C\delta_3 + B\delta_1, \end{cases}$$
(19)

where A, B, and C have the following expressions:

$$A = 1 + \alpha_1 \Delta'^* (1 + \Delta'^{**}) + \alpha_2 \Delta'^{**},$$

$$B = 1 + \beta_1 \Delta'^* (1 + \Delta'^{**}) + \beta_2 \Delta'^{**},$$

$$C = \Delta'^* + 1 + \Delta'^{**} + \Delta'^{**} \Delta'^{**} = (1 + \Delta'^{*})(1 + \Delta'^{**}).$$
(20)

Now, we drive the population until the first black oscillator arrives to the threshold, that will be a driving  $1 - (\phi^* + \Delta^* + \Delta^{**} + C\delta_2 + A\delta_1)$ , equal to  $\phi^* - A\delta_1 - B\delta_2$ , due to the fixed point condition. The new configuration is thus

$$W \begin{cases} \phi^* + (1 - A)\delta_1 - C\delta_2, \\ \phi^* - A\delta_1 - C\delta_2, \end{cases}$$

$$B \begin{cases} 1. \\ 1 - ((A - B)\delta_1 + C(\delta_2 - \delta_3)). \end{cases}$$

These steps explain exactly half a cycle of the process. Then we can define a new set of perturbations as

$$\delta_1' = -C(\delta_3 - \delta_2) - (B - A)\delta_1, \qquad \delta_2' = \delta_1 - C\delta_2 - A\delta_1, \qquad \delta_3' = -C\delta_2 - A\delta_1. \tag{21}$$

Now we can compare with the initial configuration. The white oscillators are bounded between  $\phi^* + \delta_3'$  and  $\phi^* + \delta_2'$ , whereas the black ones are between  $1 - \delta_1'$  and 1. Then the transformation matrix for the perturbations  $\delta_1$ ,  $\delta_2$ ,  $\delta_3$  is

$$\begin{pmatrix} A - B & C & -C \\ 1 - A & -C & 0 \\ -A & -C & 0 \end{pmatrix}. \tag{22}$$

The eigenvalues of (22) give the information about the linear stability of the fixed points. They are:

$$\lambda_1 = -C, \qquad \lambda_{2,3} = \frac{1}{2}(A - B \pm \sqrt{(A - B)^2 + 4C}).$$
 (23)

Now we use that  $\Delta'(\phi) > -1$  always, and then C > 0. The absolute value of the eigenvalues will be

$$|\lambda_1| = C, \qquad |\lambda_{2,3}| < \frac{1}{2}(|A - B| + \sqrt{|A - B|^2 + 4C}).$$
 (24)

Due to the fact that  $0 < \alpha_i, \beta_i < 1$  (by definition), we have, for a decreasing PRC and using Eq. (20), that C < A, B < 1, that is, |A - B| < 1 - C. This yields

$$|\lambda_1| = C < 1, \qquad |\lambda_{2,3}| < \frac{1}{2}(1 - C + \sqrt{(1 - C)^2 + 4C}) = 1.$$
 (25)

The fact that the three eigenvalues are less than one, in absolute value, ensures the stability of the fixed point, when the PRC is a decreasing function.

On the other hand, for  $\Delta'(\phi) > 0$  and using again that  $0 < \alpha_i$ ,  $\beta_i < 1$  and Eq. (20), we have 1 < A, B < C, which implies |A - B| < C - 1, and then  $|\lambda_1| = C > 1$ ,  $|\lambda_{2,3}| < C$ . The fact of having at least one eigenvalue with absolute value larger than one ensures that the fixed point is unstable if the PRC is an increasing function.

#### 4.2. Generalization to other structures

The analysis of the 'domino' structure in one-dimensional follows the same ideas developed for the chessboard structure if an excitatory coupling is assumed. The only difference is that a given unit receives always a pulse from another unit of the same color, and a further pulse from a unit of different color. This fact introduces new values for A, B, and C in the transformation matrix (22). In particular, the value of C is given by  $C = (1 + \Delta^{*})$ . The analysis of the transformation matrix of the perturbations shows that all the eigenvalues  $\lambda_i$  satisfy  $|\lambda_i| < 1$  provided  $\Delta'(\phi) < 0$ . As this transformation is iterated n times  $(n \to \infty)$  the perturbations will tend to zero, ensuring the linear stability of the structure.

A generalization of the results for the one-dimensional lattice to the two-dimensional is also easy to carry out and can be applied to any structure shown in Fig. 3. In these cases, the value of C depends on the number of phase-locked neighbors (a) as

$$C = \underbrace{(1 + \Delta'^*)(1 + \Delta'^{**}) \cdots}_{a \text{ times}}.$$
 (26)

Again, following the same formalism it is easy to prove that the new structures satisfy the same stability criteria as those in one dimension.

#### 5. Conclusions

In this paper we have studied the collective behavior of a lattice model of pulse-coupled nonlinear oscillators. Each single unit has its own intrinsic dynamics and interacts instantaneously with its neighbors when it reaches a threshold value. At this moment the oscillator is reset. The response of an oscillator at the reset point plays a relevant role when considering the dynamical properties of the model. The existence of a refractory time is assumed throughout the paper.

The continuous dynamical evolution of each unit can be transformed into a discrete one by looking at the system when a fixed oscillator reaches the threshold. This picture is appropriate to describe the features of spatially periodic patterns which are fixed points of the discrete dynamics, and whose linear stability has been analyzed. Our main result is that a monotonously decreasing (increasing) phase response curve makes these structures to be linearly stable (unstable). However, a detailed analysis of their basins of attraction is still missing and deserves future attention.

#### Acknowledgements

The authors are indebted to L.F. Abbott and A.V.M. Herz for very fruitful discussions and to S. Bottani for sending us a copy of [14] prior to publication. This work has been supported by CICyT of the Spanish Government, grant #PB94-0897.

#### References

- [1] J.J. Hopfield, Phys. Today 47 (1994) 40; S.H. Strogatz and I. Stewart, Sci. Amer. 269 (1993) 68.
- [2] A.T. Winfree, The Geometry of Biological Time (Springer, New York, 1980).
- [3] G.B. Ermentrout, J. Math. Biol. 22 (1985) 1.

- [4] R.E. Mirollo and S.H. Strogatz, SIAM J. Appl. Math. 50 (1990) 1645.
- [5] Y. Kuramoto, Physica D50 (1991) 15.
- [6] C.C. Chen, Phys. Rev. E 49 (1994) 2668.
- [7] C. Van Vreeswijk and L.F. Abbott, SIAM J. Appl. Math. 53 (1993) 253.
- [8] C. Van Vreeswijk and L.F. Abbott, Phys. Rev. E 48 (1993) 1483.
- [9] U. Ernst, K. Pawelzik and T. Geisel, Phys. Rev. Lett. 74 (1995) 1570.
- [10] A. Corral, C.J. Pérez, A. Díaz-Guilera and A. Arenas, Phys. Rev. Lett. 75 (1995) 3697.
- [11] K. Christensen, Ph.D. thesis, University of Aarhus, Denmark (1992).
- [12] A. Corral, C.J. Pérez, A. Díaz-Guilera and A. Arenas, Phys. Rev. Lett. 74 (1995) 118.
- [13] A.A. Middleton and C. Tang, Phys. Rev. Lett. 74 (1995) 742.
- [14] S. Bottani, Phys. Rev. Lett. 74 (1995) 4189.
- [15] A.V.M. Herz and J.J. Hopfield, Phys. Rev. Lett. 75 (1995) 1222; J.J. Hopfield and A.V.M. Herz, Proc. Natl. Acad. Sci. USA 92 (1995) 6655.
- [16] C.J. Pérez, A. Corral, A. Díaz-Guilera, K. Christensen and A. Arenas, Int. J. Mod. Phys. B 10 (1996) 1111.
- [17] P. Bak, C. Tang and K. Wiesenfeld, Phys. Rev. A 38 (1988) 364.
- [18] Q. Zhilin, H. Gang, M. Benkun and T. Gang, Phys. Rev. E 50 (1994) 163.
- [19] W. Gerstner, Phys. Rev. E 51 (1995) 738.
- [20] J.P. Keener, F.L. Hoppensteadt and J. Rinzel, SIAM J. Appl. Math 41 (1981) 503; N. Ikeda, Biol. Cybern. 43 (1982) 157.
- [21] C. Torras, J. Math. Biol. 24 (1986) 291; J.P. Segundo and A.F. Kohn, Biol. Cybern. 40 (1981) 113.
- [22] C.S. Peskin, Mathematical Aspects of Heart Physiology, Courant Institute of Mathematical Sciences (New York University, New York, 1975).