



PERGAMON

Neural Networks 12 (1999) 441–454

Neural
Networks

Contributed article

Dynamics of neural networks with a central element

Y.B. Kazanovich^a, R.M. Borisuk^{a, b,*}

^a*Institute of Mathematical Problems in Biology of the Russian Academy of Sciences, Pushchino, Russia*

^b*School of Computing, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK*

Received 29 April 1998; accepted 23 September 1998

Abstract

A neural network is considered which is designed as a system of phase oscillators and contains a central oscillator that interacts with a number of peripheral oscillators. Analytical and simulation methods are used to study the dynamics of the system that is conditioned by the interaction parameters and natural frequencies of the oscillators. The boundaries of parameter regions are found that correspond to the synchronization of the whole network or to partial synchronization between the central oscillator and a group of peripheral oscillators. For a system with two peripheral oscillators the bifurcation analysis is applied to describe the changes of synchronization modes. The implications of the results for attention modeling are discussed. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Global and partial synchronization; Phase oscillator; Central and peripheral oscillators; Dynamics; Bifurcations; Attention modeling; Attention focus formation

1. Introduction

In this work we study the synchronization modes that may appear in oscillatory neural networks. This is motivated by numerous biological data about oscillatory and synchronous activity in the brain and their role in information processing (Gray, 1994). High-frequency oscillations have been found in the visual cortex in response to stimulation by moving light bars and it has been shown that under some conditions the oscillations become coherent both in adjacent and distant groups of neurons (Eckhorn et al., 1988; Gray et al., 1989). Indirect evidence also exists for the synchronous activity of neural structures when solving psychological tasks (see, e.g., Pfirtscheller and Klimesch, 1992; Ivanitsky, 1993). According to von der Malsburg (1981), the binding of separate features of an object into an integrated image should be sought in temporally coherent phase locking of neural activity.

Recently some doubts have been put forward in relation to synchrony-binding hypothesis in perceptual organization (Kiper et al., 1996). However a new series of studies demonstrate that “human subjects are able to perform texture discrimination when texture and background elements were spatially identical but presented in a different temporal phase” (Leonards and Singer, 1998; Usher and Donnelly, 1998).

Oscillatory neural networks provide appropriate facilities to model synchronization effects in the brain (Borisuk et al., 1992). In particular, networks of phase oscillators have been found efficient when a qualitative mathematical description of synchronization is needed. A phase oscillator is described by one variable, the oscillation phase, and the interaction between oscillators is realised via phase locking. This simplifies the analysis of conditions when the synchronization of oscillators takes place (Kuramoto and Nishikawa, 1987; Daido, 1988, 1990; Strogatz and Mirollo, 1988).

The problem of reduction of the oscillatory neural networks of spiking neurones to the networks of phase oscillators has been the subject of several studies. It is known that under some conditions the average activity of interacting populations of excitatory and inhibitory spiking neurones forming a cortical column can be adequately represented by the networks of neural oscillators of Hopfield or Willson–Cowan type (Wilson and Cowan, 1973). Assuming weak coupling between neural oscillators, further reduction can be made that leads to the network of phase oscillators (Ermentrout and Kopell, 1991; Schuster and Wagner, 1990a; Kryukov, 1991). The first order approximation of the interaction function in phase equations gives the sinusoid interaction function that depends on the phase difference between interacting oscillators. In many papers such representation of the interaction between neural oscillators is postulated and used without suggesting weak coupling between oscillators. Though not quite rigorous, this

* Corresponding author.

E-mail address: borisuk@soc.plym.ac.uk (R.M. Borisuk)

approach was successfully used for modeling neurophysiological data related to the synchronization of neural activity in the cortex (Kuramoto et al., 1992; Sompolinsky et al., 1990; Schuster and Wagner, 1990b; Kammen et al., 1990).

The concept that there should be common principles of grouping the information on both preattention level (parallel processing) and attention level (serial processing) led to the application of synchronization hypothesis to explain also how the focus of attention is formed (Crick and Koch, 1990; Kryukov, 1991). The following difference has been assumed to exist between these two levels: on the low preattentional level the synchronization appears as a result of interaction between neural assemblies in the primary cortical areas, while on the higher attentional level the synchronization is controlled by some special brain structures (the thalamus, the hippocampus, the prefrontal cortex). It is presumed that these structures participate in selective synchronization of cortical areas that should be included in the attention focus. Thus, this point of view suggests a plausible and general mechanism of parallel processing on the low level and of sequential processing on the higher level.

The synchronization principle is used in several models of attention that has appeared in the last years. Horn et al. (1991) developed the idea to label the features of an object by noise. It is assumed that owing to the different locations of objects, the noise is identical for the features of a particular object, but different objects are labeled by different noise. The desynchronization between the populations of oscillators representing different objects is performed by an inhibitory neuron, which sequentially synchronizes with each of the populations. Thus, noise is used as a source of synchronization for the features of an object. A similar mechanism of desynchronization has been described in (Malsburg and Buhman, 1992). This model has been further improved in (Wang and Terman, 1995). The latter paper presents a network with a relatively small number of elements and connections that can solve the binding problem for real pictures, containing the images of several objects.

Note that all these papers have been originally directed to the solution of the binding problem but they can also be interpreted in terms of attention modeling. Such a possibility of different interpretations can already be found in the work (Malsburg and Schneider, 1986). It is well known that one of the main tasks performed by attention is to choose from the given sensory information such a part that is relevant to a prescribed object (Treisman and Gelade, 1980). Hence, attention can be described as binding applied to the features of an object, which is currently in the focus of attention.

The papers (Niebur et al., 1991; Niebur et al., 1993; Niebur and Koch, 1994) implement the search-light hypothesis of attention by Crick and Koch (1990). The first of these papers uses the oscillating noise to label the features that should be included in the attention focus. The second paper

proposes a brief and rapidly increasing signal, which is added to the main stimulus-evoked signal to simultaneously activate all attended neurons.

Also there are several models of selective attention based on traditional connectionist principles that use either serial information processing (Olshausen et al., 1993) or parallel processing (Humphreys and Muller, 1993; Grossberg et al., 1994; Usher and Niebur, 1996). Olshausen et al. (1993) developed a model of attention that gives position- and scale-invariant object representation by introducing cortical neurons to dynamically modify the synaptic strengths of intra-cortical connections. Grossberg et al. (1994) suggested a model of attentional visual search based on a clasterization algorithm similar to ART. Another grouping methods are suggested in the Humphreys and Muller (1993) model which is a bottom-up connectionist implementation of late selection theory. In the paper by Usher and Niebur (1996) the selective attention model is based on the bias originated from a working memory module. As a result of this bias, a weak additional input is added to the target object in the sensory memory by the top-down feedback projection from working memory module to the sensory memory.

In this paper a model of attention implemented as a network of phase oscillators is considered. Such a network was proposed in (Kryukov, 1991). The network was designed as a system of peripheral oscillators (PO) coupled with a central oscillator (CO) by feed forward and backward connections. It was presumed that the septo-hippocampal region might play the role of the CO, while the POs might be represented by cortical columns. Attention was interpreted as the result of the synchronization of oscillations between the septo-hippocampal region and some parts of the cortex. The POs that are phase locked by the CO were considered as forming the focus of attention. Connections between cortical columns were ignored to simplify the analysis of the model.

This model of attention is supported by many biological observations which are cited in (Kryukov, 1991). Among the most important we refer to the paper of Cowan (1988), where the concept of the central executive has been put forward in relation to selective attention. According to Cowan, the focus of attention is represented by a subset of short-term memory storage, which is controlled by the central executive. Miller (1991) formulated the theory of representation of information in the brain based on cortico-hippocampal interplay. He assumed that this representation results from the synchronization of the activity of the hippocampus and some parts of the cortex owing to a proper choice of time delays in the connections between these structures. There are many experimental works which confirm that the hippocampus is involved in the formation of attention in classical conditioning (for a review see Schmajuk and DiCarlo, 1992), though the role of the hippocampus and the mechanism of its interaction with the cortex are still under discussion.

The present work continues the study of networks with a

central unit undertaken in (Kazanovich and Borisyuk, 1994). Luzyanina (1995) have considered similar networks with time-delayed coupling. The idea of using a central unit as a global source of synchronization also appeared in Kammen et al. (1990) and Lumer and Huberman (1991) where networks of other architectures were studied.

In this work we suppose that the set of POs is divided into two groups, namely **A** and **B**, each being activated by one of two stimuli simultaneously presented to the attention system. The natural frequencies of oscillators in the groups are randomly distributed in two non-overlapping intervals. The interaction between the CO and POs is supposed to have identical strength for all oscillators of a group. We also fix the average values of natural frequencies of oscillators in each group. Thus, the dynamics of the system is controlled by three parameters: two interaction strengths between the CO and the oscillators of groups **A** and **B**, and the natural frequency of the CO.

The main problem considered below is to describe dynamic modes that may appear in the network for various values of these parameters. Three types of network dynamics are of interest for us:

- global synchronization when all oscillators run with the same frequency (this mode is attributed to the case when the attention focus includes two stimuli);
- partial synchronization of the CO and one group of POs with their current frequencies being similar to each other while the current frequencies of the other group of POs are quite different (this mode is attributed to the case when the attention focus includes one of two competing stimuli);
- no-synchronization mode when the current frequencies of POs in both groups are far from the current frequency of the CO (this mode is attributed to the case when the attention focus is not formed).

Two limit cases are considered: first, when each group consists of one oscillator, and second, when each group consists of a large number of oscillators. Using analytical and computational methods we find the boundaries of parameter regions where the above mentioned types of dynamics take place. Biologically, the second case seems to be more realistic, but the first case is also very important. As can be seen below, the results in both cases are qualitatively similar, therefore the first case can be considered as an approximation of the second one when a group of oscillators is substituted by a single oscillator. The mathematical analysis of the first case can be made more advanced and rigorous while in the second case we have had to attract some heuristic assumptions.

Section 2 contains the formal description of the networks of phase oscillators with a central element and the formulation of the problem. In Section 3 we analyse the networks with two POs and obtain the bifurcation boundaries of various synchronization modes. This gives the possibility to control the transition from one synchronization mode to

another. Section 4 is devoted to the networks with many POs. In this case the parameter regions that correspond to various synchronization modes can be found analytically. By network simulation we describe the conditions when the final dynamics of the network depends on initial phases. In Section 5 the results obtained are interpreted and discussed in terms of attention modeling. This includes the interpretation of psychological experiments on visual selective attention, the problem of the focus of attention formation and the possibility of spontaneous attention switching.

2. Statement of the problem

Let all POs are divided into two groups with n oscillators in each group. Group **A** contains the POs whose natural frequencies ω_A^i are independently and randomly distributed in the interval $(\omega_A - l, \omega_A + l)$. The oscillators of group **B** have natural frequencies ω_B^j that are independently and randomly distributed in the interval $(\omega_B - l, \omega_B + l)$. Suppose that $\omega_B - \omega_A > 2l$, that is the intervals do not overlap. We put $l = 0$ for $n = 1$ and $l > 0$ for $n > 1$. In the latter case the value of l is taken to be by one order of magnitude lower than $\omega_B - \omega_A$.

Let $\theta_A^i(t)$ be the phases of POs of group **A**, $\theta_B^j(t)$ be the phases of POs of group **B**, $\theta_0(t)$ be the phase of the CO and ω_0 be its natural frequency. Then the dynamics of the network of phase oscillators with a central element is described by the equations

$$\frac{d\theta_0}{dt} = \omega_0 + \frac{\alpha}{n} \sum_{i=1}^n \sin(\theta_A^i - \theta_0) + \frac{\beta}{n} \sum_{j=1}^n \sin(\theta_B^j - \theta_0), \quad (1a)$$

$$\frac{d\theta_A^i}{dt} = \omega_A^i + \alpha \sin(\theta_0 - \theta_A^i), \quad i = 1, \dots, n, \quad (1b)$$

$$\frac{d\theta_B^j}{dt} = \omega_B^j + \beta \sin(\theta_0 - \theta_B^j), \quad j = 1, \dots, n, \quad (1c)$$

where α and β are parameters that determine the interaction strengths between the CO and the oscillators of groups **A** and **B**, respectively. All natural frequencies of oscillators are chosen according to their distributions and then fixed. By definition, the derivatives of the phases in the right hand side of Eq. (1) are the current frequencies of the oscillators.

Note that by changing the variables in Eq. (1) we get

$$\theta_{\text{new}} = \theta_{\text{old}} - \omega t$$

and rescaling time we can get arbitrary values of ω_A and ω_B . Hence, without loss of generality, we will restrict the consideration by a fixed pair of values ω_A , ω_B and study the dynamics of (1) as a function of three parameters ω_0 , α and β . As a result of the symmetry of the role of groups **A** and **B** in the network, the complete investigation of (1) can be restricted by the values of ω_0 satisfying the inequality

$\omega_0 \geq \frac{\omega_A + \omega_B}{2}$. The results obtained in this case can evidently be reformulated for any other values of ω_0 .

Let us say that the network is in a *global synchronization* mode if its dynamics is described by a stable solution of (1) such that all oscillators run with the same frequency Ω ,

$$\Omega = \frac{d\theta_0}{dt} = \frac{d\theta_A^j}{dt} = \frac{d\theta_B^j}{dt}, \quad i, j = 1, \dots, n.$$

In this case the difference between the phases of a PO and the CO does not vary with time. Summing the right hand sides of Eqs. (1a–c), we find that

$$\Omega = \frac{\omega_0 + \bar{\omega}_A + \bar{\omega}_B}{3}, \tag{2}$$

where $\langle \bar{\omega}_A \rangle$ and $\langle \bar{\omega}_B \rangle$ are the average values of natural frequencies of POs in groups **A** and **B**, respectively,

$$\bar{\omega}_A = \frac{1}{n} \sum_{i=1}^n \omega_A^i, \quad \bar{\omega}_B = \frac{1}{n} \sum_{j=1}^n \omega_B^j.$$

Suppose that the network is not in the global synchronization mode. Let us say that the k th PO (that can belong to any group, **A** or **B**) is partially synchronous with the CO if the dynamics of the network is described by a stable (at least locally) solution of (1) such that the difference between the phases of this PO and the CO is restricted, that is there exists such a constant C that for any moment t

$$|\theta_0(t) - \theta^k(t)| < C.$$

A group of oscillators (**A** or **B**) is called partially synchronous with the CO if all oscillators of the group are partially synchronous with the CO. In this case we say that the network is in the mode of *partial synchronization*. Note that the definition of partial synchronization in terms of phases is reasonable here because the current frequencies of partially synchronous oscillators are not equal, owing to the perturbing influence of oscillators from the other group.

According to the given definition, the partial synchronization of a group does not necessarily require that all oscillators of the other group are out of partial synchronization with the CO. If all oscillators of one group are partially synchronous while none of the oscillators of the other group is partially synchronous, we will say about *strict partial synchronization* of the former group.

If a stable dynamics of the network does not show either global or partial synchronization we say that the network is in *no-synchronization* mode.

The main problem in the study of synchronization modes can be formulated as the determination of the regions of the parameters ω_0, α, β where the network shows one of the following types of dynamics:

- Global synchronization;
- Partial synchronization of the CO and a group of POs;
- No-synchronization mode.

We study this problem for two limit cases: a small number of POs ($n = 1$) and a large number of POs ($n \rightarrow \infty$).

For a fixed value of ω_0 , let us introduce the following notation for the regions on the plane (β, α) that correspond to various dynamic modes of the network:

- *GS* is the region where global synchronization takes place for some initial phases;
- *PS_A, PS_B* are the regions where partial synchronization of groups **A** and **B** takes place for some initial phases;
- *NS* is the region where the no-synchronization mode exists.

Note that these definitions imply that the regions may overlap because different types of dynamics can be conditioned by the choice of initial phases.

3. Dynamics of a network with two peripheral oscillators

Consider a network that consists of two POs ($n = 1$), the first PO belongs to group **A** and its natural frequency is $\omega_A^1 = \omega_A$, the second PO belongs to group **B** and its natural frequency is $\omega_B^1 = \omega_B$. In this case the frequency of global synchronization is

$$\Omega = \frac{\omega_0 + \omega_A + \omega_B}{3}.$$

To study (1), it is convenient to change the variables for phase differences $\phi_1 = \theta_0 - \theta_A^1, \phi_2 = \theta_0 - \theta_B^1$. Their dynamics is described by the following system of equations on the two-dimensional torus $T = \{(\phi_1, \phi_2) : -\pi \leq \phi_1 \leq \pi, -\pi \leq \phi_2 \leq \pi\}$:

$$\begin{aligned} \frac{d\phi_1}{dt} &= (\omega_0 - \omega_A) - 2\alpha \sin\phi_1 - \beta \sin\phi_2, \\ \frac{d\phi_2}{dt} &= (\omega_0 - \omega_B) - \alpha \sin\phi_1 - 2\beta \sin\phi_2, \end{aligned} \tag{3}$$

3.1. Stationary states

Structurally stable stationary solutions of (3) can be found from the expressions

$$\sin \phi_1 = \frac{\Omega - \omega_A}{\alpha}, \quad \sin \phi_2 = \frac{\Omega - \omega_B}{\beta} \tag{4}$$

Under conditions

$$|\Omega - \omega_A| < \alpha, \quad |\Omega - \omega_B| < \beta, \tag{5}$$

there are four solutions of (4): $A_1(\xi_1, \xi_2), A_2(\xi_1, \eta_2), A_3(\eta_1, \xi_2), A_4(\eta_1, \eta_2)$, where

$$\xi_1 = \arcsin \frac{\Omega - \omega_A}{\alpha}, \quad \xi_2 = \arcsin \frac{\Omega - \omega_B}{\beta},$$

$$\eta_1 = \pi - \arcsin \frac{\Omega - \omega_B}{\alpha}, \quad \eta_2 = \pi - \arcsin \frac{\Omega - \omega_A}{\beta}.$$

The analysis of stability of these solutions shows that A_1

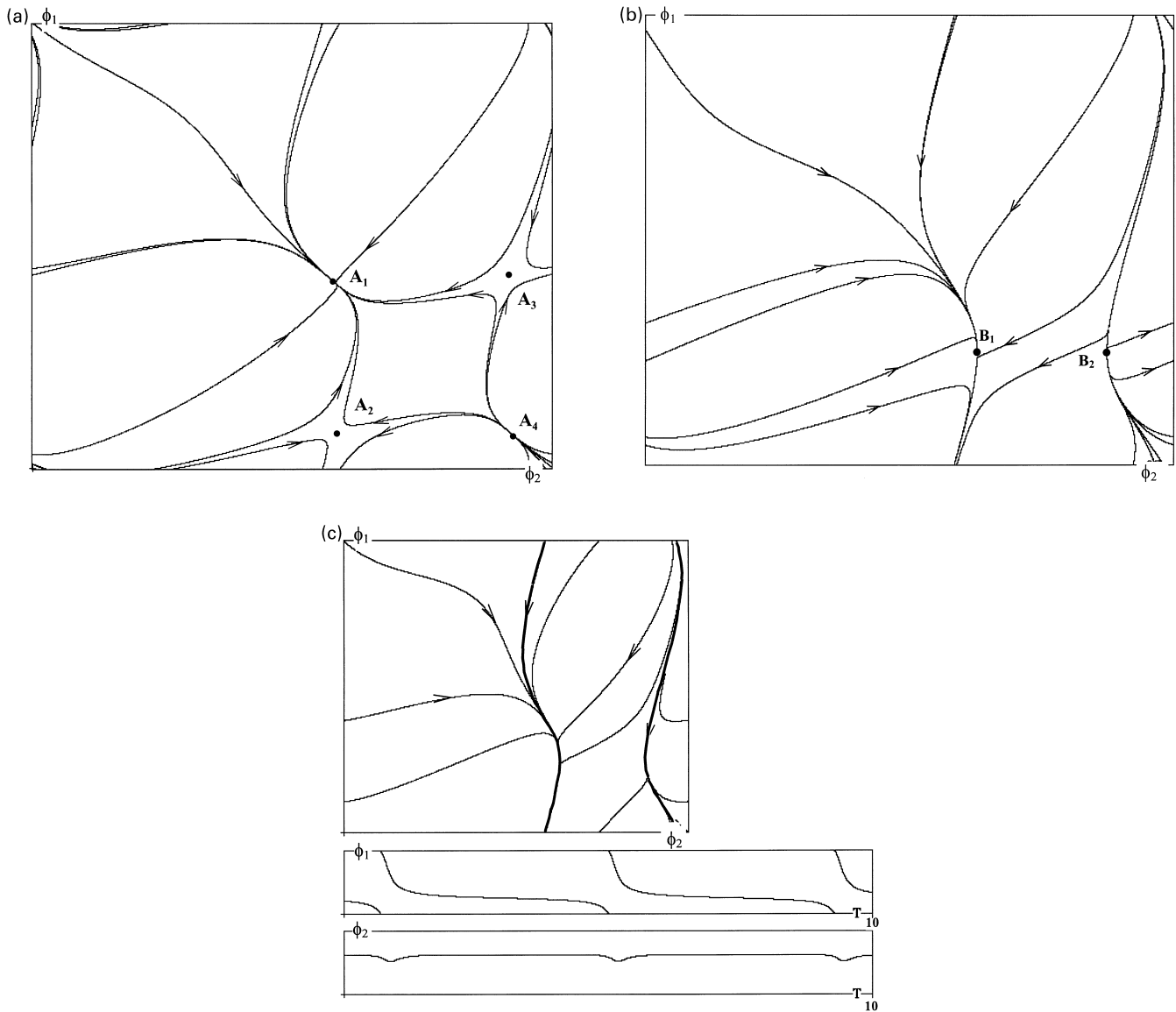


Fig. 1. (a) Phase diagram of the system in the mode of global synchronization, $\omega_0 = 5, \alpha = \beta = 10$; (b) Phase diagram of the system on the boundary of the region of global synchronization (saddle-nodes formation), $\omega_0 = 5, \alpha = 7, \beta = 5$; (c) Phase diagram of the system in the mode of partial synchronization (a stable and an unstable limit cycles of the homotopy type (1,0)), $\omega_0 = 5, \alpha = 7, \beta = 4.8$.

is a stable node, A_2 and A_3 are saddle points, and A_4 is an unstable node. The phase diagram is shown in Fig. 1.

The global synchronization is represented by a stable stationary solution of (3). Fig. 1 shows the case where there is a unique stable solution. It will be seen later that this is not always true.

For several values of the natural frequency of the CO, Fig. 2 shows parameter regions on the plane (β, α) that correspond to various dynamic modes. The global synchronization region (region *GS*) given by (5) has the form of a right angle with the boundaries being parallel to co-ordinate axes. Fig. 2d represents a special case where $\Omega = \omega_B = 10$ ($\omega_0 = 20$). In this case the vertical boundary of *GS* goes along the ordinate axis, therefore the global synchronization can be reached here for an arbitrary weak

interaction between the CO and the second PO, though the natural frequencies of these oscillators are different.

For any fixed value of ω_0 , there exist such interaction parameters α, β that formula (5) is true. The bifurcation of stationary solutions (3) takes place when at least one of conditions (5) is broken. For example, let α be equal to the critical value $\alpha = \Omega - \omega_A$ that turns the first condition of (5) into equality (the violation of the second condition can be considered similarly). Then $\xi_1 = \eta_1 = \pi/2$, and at the moment of bifurcation two saddle-nodes appear as a result of collision of the points A_1 with A_3 and A_2 with A_4 , respectively. The phase diagram of the system at the moment of bifurcation is given in Fig. 1b. When an interaction parameter becomes lower than critical, a limit cycle is born from a separatrix of the saddle-node. Two limit

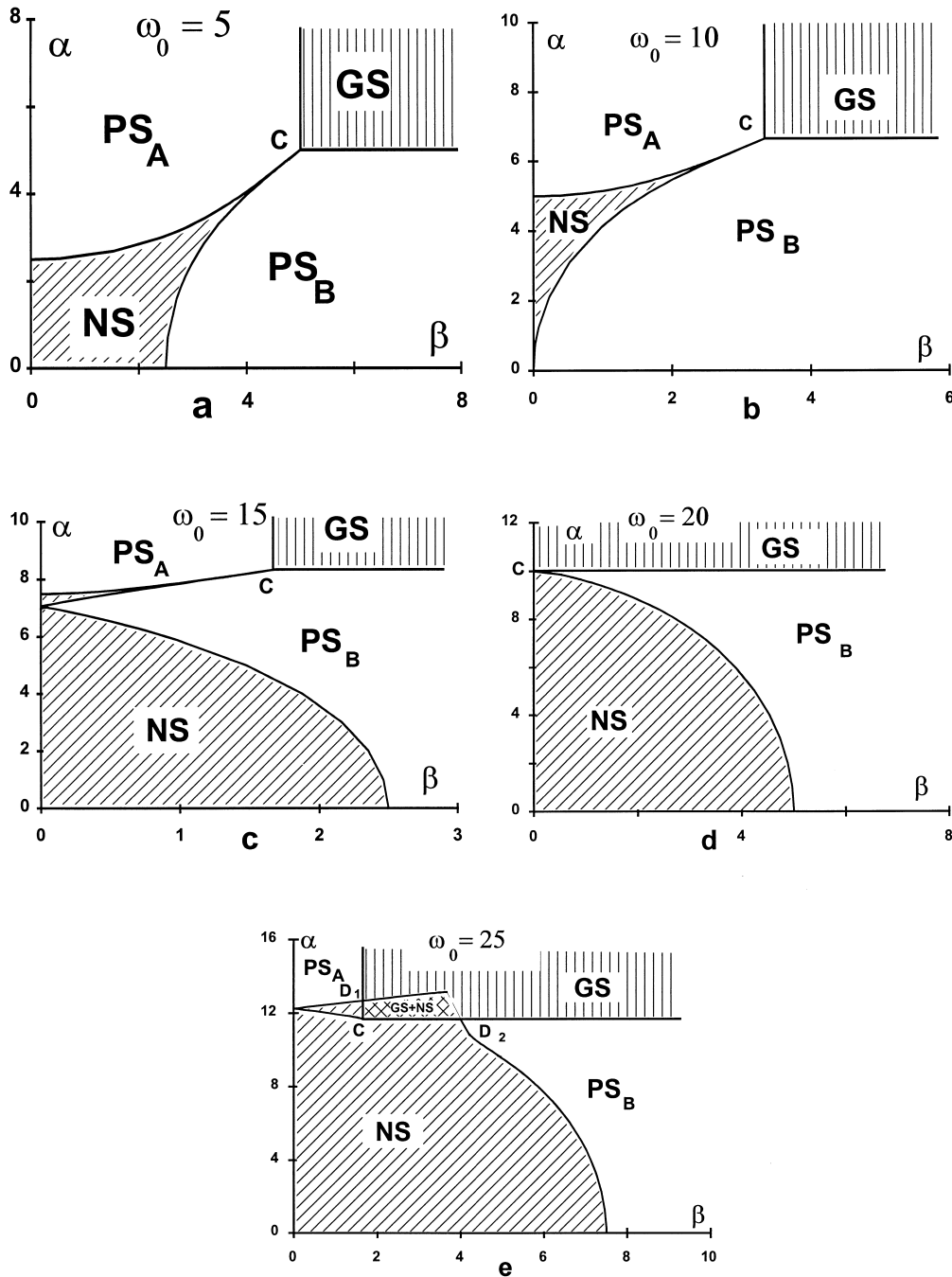


Fig. 2. Bifurcation diagrams on the plane (β, α) for various values of the natural frequency of the CO in the case of two POs.

cycles, stable C_1 and unstable C_2 , that appear in this case are shown in Fig. 1c.

3.2. Limit cycles

A limit cycle of (3) can be characterised by its homotopy type (m, k) , where m and k are the numbers of rotations made during one period of the cycle by ϕ_1 and ϕ_2 , respectively. Evidently, a PO is partially synchronous with the CO if the dynamics of (3) is a limit cycle of the type $(0,1)$ (for the oscillator A) or of the type $(1,0)$ (for the oscillator B).

The bifurcation of stationary solutions described in Section 3.1 gives rise to limit cycles of the type $(1,0)$ or $(0,1)$, hence it leads to partial synchronization. Partial synchronization disappears when both interaction parameters become small enough and the limit cycles C_1 and C_2 merge and disappear. So, the boundary of the region of partial synchronization on the plane (β, α) that separates it from the region of no-synchronization mode is the curve of the fold bifurcation of limit cycles. To find this curve, we used the program LOCBIF (Khibnik et al., 1993). The results of computations of the boundaries are presented in Fig. 2.

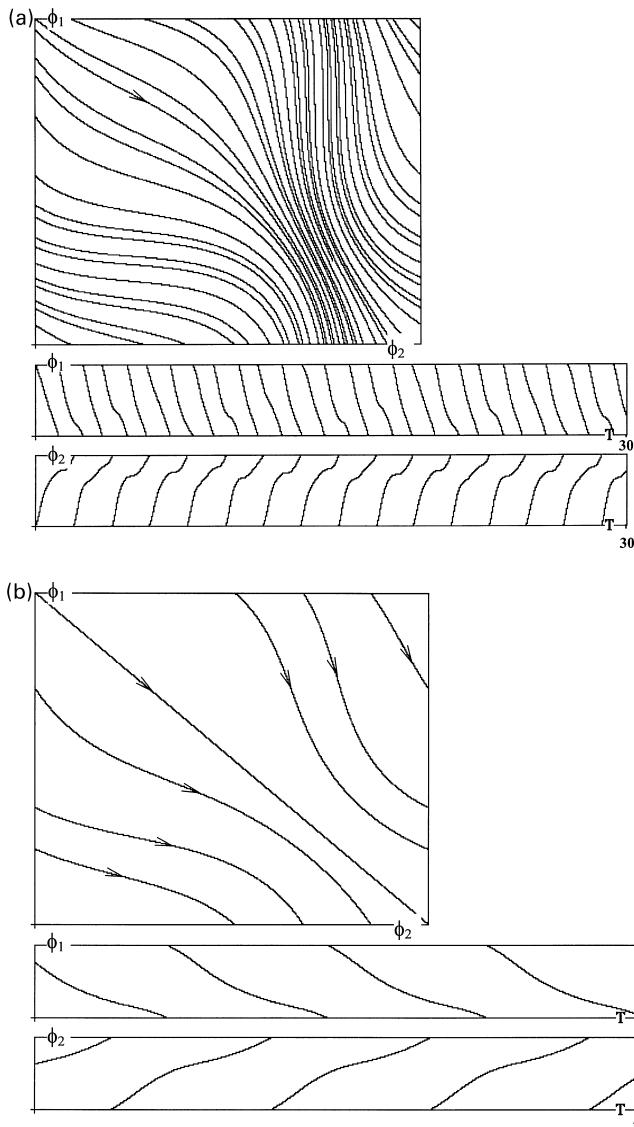


Fig. 3. Examples of phase diagrams for the no-synchronization mode: (a) $\omega_0 = 5, \alpha = 2, \beta = 1$, (b) $\omega_0 = 5, \alpha = 1, \beta = 1$.

Fig. 2a shows a typical bifurcation diagram for $5 \leq \omega_0 < 10$. In this case, crossing the boundary from the region of partial synchronization to the region *NS* implies that quasiperiodic oscillations (torus **T**) appear in the phase space (the exception is represented by the “symmetric” case when $\omega_0 = 5$ and $\alpha = \beta$, in this case the phase diagram consists of closed trajectories). Examples of phase diagrams for *NS* are given in Fig. 3.

Fig. 2b ($\omega_0 = 10$) shows a unique case when the boundary between *PS_B* and *NS* originates from zero.

If $10 < \omega_0 < 20$ (Fig. 2c), the region *NS* breaks up into two parts with a single common point between them. It is interesting to see how the synchronization modes are changing with the increase of α . Let, e.g., $\omega_0 = 15, \beta = 1$ and α be gradually increasing up from zero. This results in gradual decrease of the average value of the current frequency of the

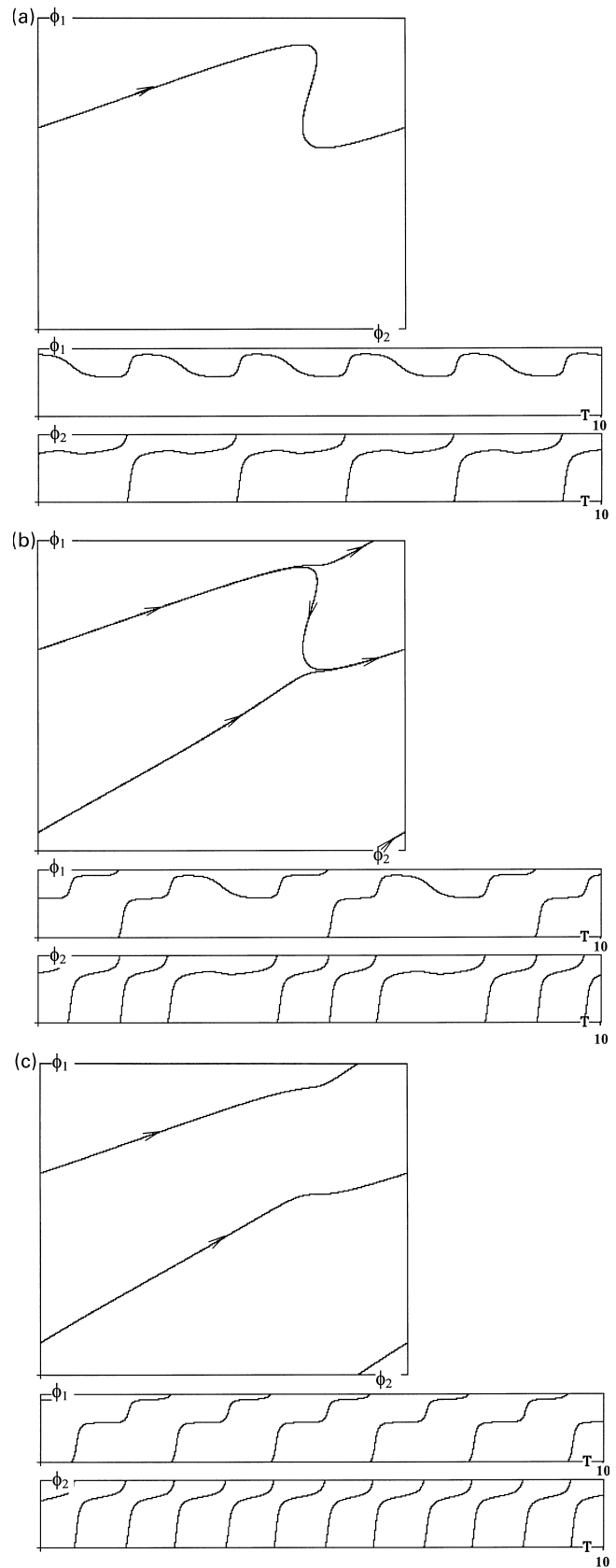


Fig. 4. Examples of limit cycles near the saddle mode loop bifurcation: (a) $\omega_0 = 25, \alpha = 11, \beta = 4.15$, (b) $\omega_0 = 25, \alpha = 11, \beta = 4.14$, (c) $\omega_0 = 25, \alpha = 11, \beta = 4.13$.

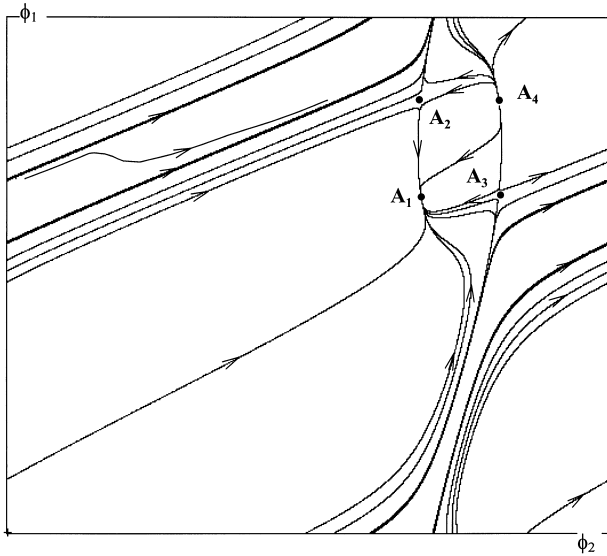


Fig. 5. Phase diagram of the system when a stable node (global synchronization) co-exists with a stable limit cycle of the homotopy type (1,1) (synchronization is absent), $\omega_0 = 25$, $\alpha = 12.7$, $\beta = 2$.

CO (Kazanovich and Borisjuk, 1994). If α is small enough, the average frequency of the CO is much greater than $\omega_B = 10$ and β is too small to synchronize the CO with B . For greater values of α , the average frequency of the CO is drawn nearer ω_B and therefore the partial synchronization between the CO and B becomes possible. If α is increased even more, this leads to further decrease of the average frequency of the CO, the gap between this frequency and ω_B becomes too large and again the partial synchronization between the CO and B becomes impossible. If α is large enough, the partial synchronization of A arises.

A new topological transformation of the bifurcation diagram takes place for $\omega_0 < 20$ (Fig. 2d). Now only the oscillator B can be in partial synchronization with the CO. Note that for $\omega_0 < 20$ the left boundary of GS has been moving to the left with the increase of ω_0 , further increase of ω_0 ($\omega_0 < 20$) changes the direction of this movement to the right.

For $\omega_0 > 20$ a new peculiarity of the phase diagram appears (a typical diagram in this case is shown in Fig. 2e): now the boundary between GS and NS is no longer a single point but a curve connecting a point D_1 on the vertical boundary region (5) and a point D_2 on the horizontal boundary of this region.

For $\omega_0 < 20$ the bifurcations considered above give a comprehensive description of the transformations of phase diagrams which are related to the changes of dynamics of (3). If $\omega_0 > 20$, the transition between the regions GS , PS and NS can be accompanied by more complex bifurcations. For example, consider a neighbourhood of the point D_2 (a neighbourhood of the point D_1 is arranged similarly). Crossing the boundary of the region GS on the right of D_2 gives rise to a pair of limit cycles (stable and unstable) of the homotopy type (1,0), in other words, the partial

synchronization of B appears. However, if crossing of the boundary takes place on the left of D_2 , there appears a pair of limit cycles of the type (1,2). This is explained by the fact that the point D_2 is located on the saddle-node curve and the bifurcation of co-dimension 2 takes place at this point. At the moment of bifurcation the separatrix that goes out from a saddle-node with the stable node part comes to a saddle-node with the unstable saddle part. We do not know the exact diagram for this bifurcation, similar bifurcations on the torus have been considered in (Baesens et al., 1991). It seems that the curve of fold bifurcation of limit cycles of the homotopy type (0,1) has the end at the point D_2 ; in a neighborhood of this point one can find limit cycles of various homotopy types. Examples of such cycles are shown in Fig. 4. Note that this part of the region NS is not homogeneous. It contains both the points that correspond to limit cycles of the type different from (0,1) and (1,0) and the points that correspond to quasiperiodic oscillations.

For $\omega_0 > 20$ limit cycles of the type not equal to (1,0) and (0,1) can also be found in the region GS , co-existing with stationary solutions (the region $GS + NS$ in Fig. 2e). In this case the choice between the global synchronization and no-synchronization modes is conditioned by initial phases (see Fig. 5).

4. Dynamics of a network with many peripheral oscillators

Consider a network with a large number n of oscillators in groups A and B . To determine the boundaries of the regions GS , PS_A , PS_B , NS in this case, we use analytical methods and computer simulation of the network.

Again, as in the case $n = 1$ studied above, global synchronization implies that there exists a stable stationary solution of the system of equations for the phase differences between the CO and POs. The necessary condition for global synchronization is

$$|\Omega - \omega_A^i| \leq \alpha, \quad |\Omega - \omega_B^j| \leq \beta, \quad i, j = 1, \dots, n, \quad (6)$$

where Ω is determined by (2). The corresponding boundary on the plane (β, α) is the right angle with the vertex $C = (\max_j |\Omega - \omega_A^j|, \max_i |\Omega - \omega_B^i|)$ and with arms parallel to co-ordinate axes. Condition (6) is not sufficient because the region of parameters (β, α) defined by it may include subregions, where a stable stationary state is formed for special values of initial phases only.

Consider the boundary between the region of the no-synchronization mode and a region of partial synchronization. For definiteness, let it be the boundary between NS and PS_B . In fact, as computer experiments show, these regions are overlapping, but the overlapping takes place in a narrow strip whose width will be neglected in our approximation formulas. The following formulas are derived to approximate the boundary between NS and some subregion of PS_B , where strict partial synchronization takes place. It will be

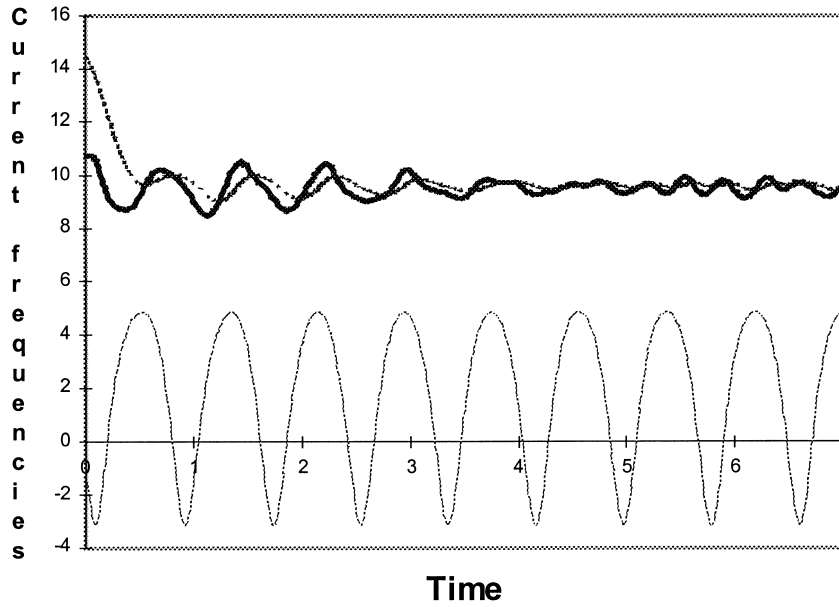


Fig. 6. Example of time evolution of current frequencies of the CO (1) and two POs from groups **A** (3) and **B** (2), $\omega_0 = 10, \alpha = 4, \beta = 5, n = 50$.

seen later that this boundary constitutes some part of the boundary between NS and PS_B . The determination of this boundary is based on an equation that describes the time average of the current frequency of the CO as a function of interaction parameters. Denote this average value by

$$\langle \omega \rangle = \frac{1}{T} \int_{t_0}^{t_0+T} \frac{d\theta_0}{dt}(\tau) d\tau,$$

where the time interval $(t_0, t_0 + T)$ is supposed to be large enough. The averaging is based on the additional assumption that if n is large and l is not too small relative to $\langle \omega \rangle$, the deviation of the current frequency of the CO from $\langle \omega \rangle$ under strict partial synchronization (after some moment t_0) is relatively small. This gives us the possibility to substitute $\langle \omega \rangle$ for the current frequency of the CO when deriving the average values of the current frequencies of POs.

The assumption is based upon the results of computer modeling of the network dynamics. An example showing the time evolution of the current frequencies of the CO and POs is given in Fig. 6. As computer experiments show, under the formulated conditions the current frequencies of the oscillators from **A** vary more or less independently from each other (this independence is lost if l is small). Therefore, their integral influence on the CO is averaged and changes only a little with time. The oscillators from **B** have current frequencies, which are quite near the frequency of the CO; hence these frequencies also change little.

Thus, we can suppose that $d\theta_0/dt$ is approximately constant and is equal to $\langle \omega \rangle$. This assumption gives the possibility to consider a pair interaction of each PO with the CO independently from other POs. Then the strict partial synchronization condition for group **B** becomes

equivalent to

$$|\langle \omega \rangle - \omega_B^j| \leq \beta, \quad j = 1, \dots, n, \quad (7)$$

$$|\langle \omega \rangle - \omega_A^i| > \alpha, \quad i = 1, \dots, n. \quad (8)$$

In Appendix A, Eq. (15) for $\langle \omega \rangle$ is derived (a slightly different approximation formula for $\langle \omega \rangle$ can also be found in Kazanovich and Borisyuk, 1994). From this equation we find $\langle \omega \rangle$ as a function of α by using a continuation technique implemented in the program LOCIBIF (Khibnik et al., 1993).

It follows from (15) that if α increases, $\langle \omega \rangle$ monotonically approaches ω_A and

$$\langle \omega \rangle = \frac{\omega_0 + \omega_B}{2}$$

for $\alpha = 0$. Let $\tilde{\alpha}$ be the maximal value of α for which the inequality $|\langle \omega \rangle - \omega_A| \geq l + \alpha$ holds. For $\tilde{\alpha}$, (8) is fulfilled. Under this condition the equation for the boundary between NS and PS_B follows from (7) and has the form

$$\beta = \max_j |\langle \omega \rangle - \omega_B^j|, \quad j = 1, \dots, n, \quad (9)$$

where $\langle \omega \rangle$ is given by (15). If $\alpha \tilde{\alpha}$, (15) cannot be used because partial synchronization involves oscillators of both groups **A** and **B**. The boundaries of the regions of strict partial synchronization found according to the described procedure are shown in Fig. 7 by solid curves.

Now let us describe how the boundaries of the regions of various synchronization modes have been determined by computer simulation. The integration of (1) has been made according to a Runge–Kutta method with an adaptive time step and the integration error lower than 10^{-5} . In computations we put $n = 50$ and choose the initial phases

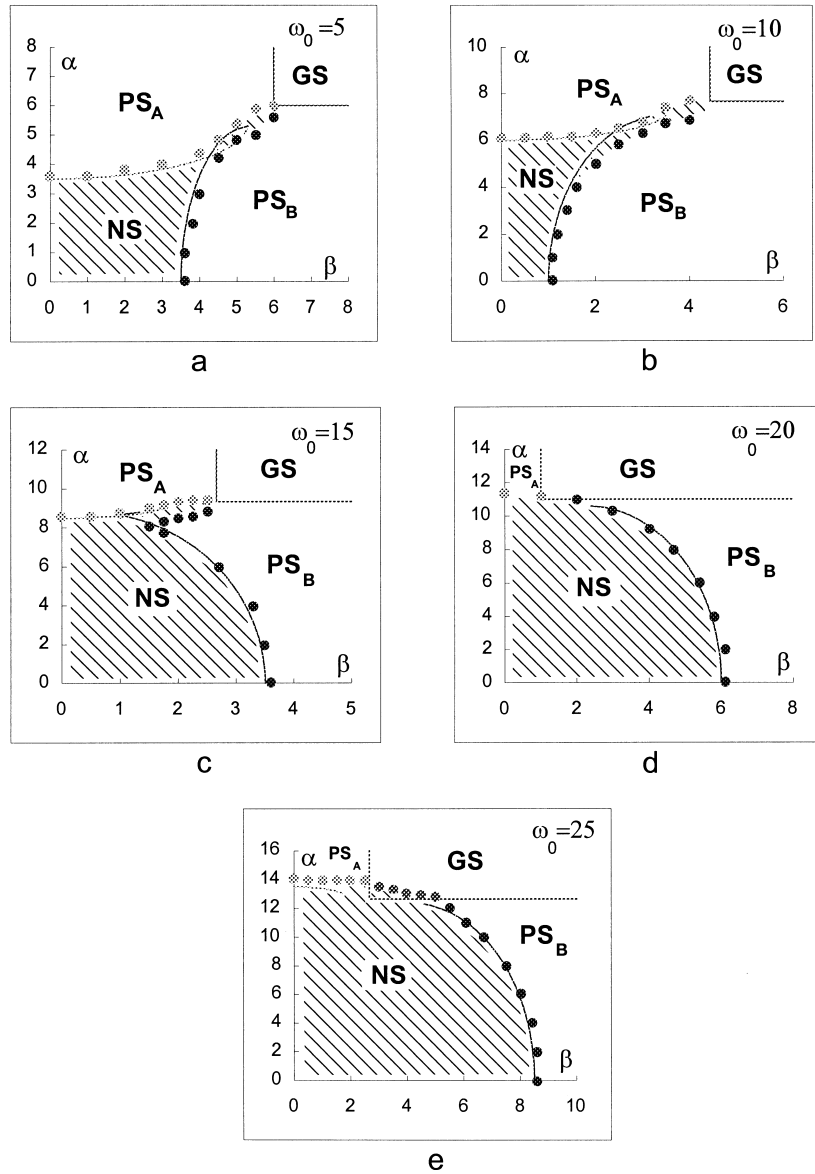


Fig. 7. Regions of interaction parameters corresponding to various types of dynamic modes in a network with 100 POs. Analytical approximation of the boundaries between the regions are shown by solid lines. Filled circles show the boundaries obtained by computer simulation of the network dynamics. (a)–(e) correspond to different values of the natural frequency of the CO.

of oscillators to be randomly and uniformly distributed in the range $(0, 2\pi)$. During simulation a track has been kept of the phase differences between the CO and POs. The following types of network behavior have been found in the computer experiments:

- For all POs the phase difference between the CO and PO is gradually stabilizing. This corresponds to global synchronization.
- After some time the phase difference between the CO and a PO changes in a range of the width not greater than 2π . This corresponds to the partial synchronization of this PO with the CO.
- The absolute value of the phase difference of the CO and a PO is gradually increasing. This increase can

be either permanent or stepwise. In the latter case the difference is oscillating for some time around a fixed value, then it abruptly changes as a result of phase slipping and oscillates around another value, which is shifted by 2π relative to the previous one. This implies that there is no synchronization between the CO and the PO.

The dynamic modes were determined for fixed values of α and β in 50 identical experiments, which only differed by a random choice of natural frequencies and initial phases of the oscillators. By 50 iterations, the boundaries of the regions can be determined reproducibly with the accuracy not less than 0.1.

Filled circles show the computed boundary of NS in

Fig. 7. The boundaries of the regions PS_A and PS_B are located inside the region NS close to its boundary. Thus, the regions of partial synchronization and the region of no-synchronization mode overlap over narrow strips of multistability. In particular, in the “narrow” parts of NS (such “narrow” parts can be seen in Fig. 7a,b,c) where the regions PS_A and PS_B come close to each other, the partial synchronization of both groups A and B as well as no-synchronization mode can be found under the same values of network parameters.

As can be seen from Fig. 7, for $\omega_0 \leq 20$ the boundary between GS and NS consists of a single point C . If $\omega_0 > 20$, some region near the point C simultaneously belongs to NS and GS (Fig. 7e). This region also overlaps with PS_A and PS_B . No other overlapping of PS_A , PS_B and NS has been found.

Fig. 7 shows that analytically obtained boundaries between the regions of strict partial synchronization and no-synchronization region are in good agreement with the results of computer simulation of the network. For those values of interaction parameters, which make (15) sensible, the computer experiments show that the boundaries of the regions of partial synchronization and strict partial synchronization are identical. Relatively poor results in analytical determination of the boundary can be seen for $\omega_0 = 25$ in the boundary of PS_A .

This inaccuracy is caused by the fact that for the given parameter values the variance of the natural frequencies of the oscillators from A becomes too small when compared to $\langle \omega \rangle$, and this results in the violation of our assumption about the independent influence of the oscillators from A on the CO.

5. Discussion

Our analysis of the attention model fully describes the necessary for various types of synchronization, global or partial, between the central oscillator and peripheral oscillators if the natural frequencies of POs form two non-overlapping clusters. The main results are presented in Fig. 2 for the case when each group is represented by a single oscillator and in Fig. 7 for the case when the groups contain many oscillators. The comparison of the regions of interaction parameters that correspond to various types of synchronization in these two figures shows that they have similar forms. In particular, in both cases the transition from GS to NS is possible in one point if the natural frequency of the CO is relatively low, and the boundary curve appears between these regions in both cases if the natural frequency of the CO becomes greater than a critical value (Figs. 2e and 7e).

This fact is unexpected to some extent. For $n = 1$, the CO and POs are equally “strong” in their mutual interaction, but for large n the network contains a “strong” central element and many “weak” peripheral elements. The

qualitative similarity of these two cases means that in some sense a group of peripheral oscillators with similar natural frequencies can be approximately considered as one “large” oscillator.

The main difference between these two cases is related to the conditions of multistability, when depending on initial phases the network can demonstrate various types of synchronization or its absence. In the first case ($n = 1$), the multistability appears for relatively large values of the natural frequency of the CO in a small region of the interaction parameters (the region $GS + NS$ in Fig. 2e). In this region, depending on initial phases, the network will be either in the global synchronization or in no-synchronization mode. In the second case ($n \rightarrow \infty$), the multistability takes place everywhere near the boundaries of NS with the regions GS , PS_A and PS_B .

To simplify mathematical analysis, we restricted our consideration by the networks activated by two stimuli. Therefore our network represents only a small part of the cortex activated by these stimuli. In the above, the term “global synchronization” was used in a specific sense, meaning the synchronization of the whole network but certainly not the whole cortex or some large area in it. In reality, there are many regions of the cortex that are simultaneously active owing to external or internal stimulation and only some of these areas participate in attention focus formation. Our results can be easily generalized for this case. The formation of the attention focus in this situation can be described in terms of partial synchronization. Moreover, we think that partial synchronization is the type of brain dynamics that is most suitable for information processing.

Another simplification was that we studied stable modes like limit cycles or quasiperiodic oscillations though in the brain the synchronization is not a long-lasting phenomenon. This is a general approach in neurophysiological modeling by dynamical systems when analytical results are to be obtained.

Finally, let us discuss the possible implications of the results obtained for attention modeling. Suppose that two stimuli are inputted to the attention system. The stimuli are represented by their features that elicit the activity of peripheral oscillators associated with these features. We suppose that each stimulus is represented by a group of oscillators (groups A and B) whose natural frequencies form a cluster. The stimulation of the attention system also activates a central oscillator. The natural frequency of the CO is conditioned by the earlier evolution of the attention system and the interaction parameters between the CO and POs are assumed to be formed in previous learning.

In terms of the model, the formation of the attention focus is related to the synchronization between the CO and some groups of POs. As the model shows, the focus of attention can combine both stimuli in a complex pattern (the global synchronization mode), or the focus can be formed by the features of one of two competing stimuli, one of them

representing a target and the other representing a distracting object (the partial synchronization mode), or the stimuli can be ignored by the attention system (the no-synchronization mode).

The model predicts that depending on the relations between natural frequencies of the CO and POs a distracting stimulus can improve or deteriorate attention focusing on the target stimulus. Suppose that \mathbf{B} represents a target stimulus and \mathbf{A} represents a distracting stimulus, that is the interaction parameters are chosen to provide the partial synchronization of \mathbf{B} . If $\omega_A < \omega_0 < \omega_B$ (this case is represented by Figs. 2a and 7a), the partial synchronization of \mathbf{B} can be achieved for a smaller value of the interaction parameter β when \mathbf{A} is silent ($\alpha = 0$) than when it is active ($\alpha > 0$). If $\omega_A < \omega_0 < \omega_B$ (this case is represented by Fig. 2c–e and 7c–e), there is an interval of the values of β such that if we gradually increase α starting from 0, the system will be in the no-synchronization mode for the low values of α but will get in the region of partial synchronization with \mathbf{B} if α becomes large enough. Thus, the presence of \mathbf{A} gives the possibility to use smaller values of β to get the partial synchronization of \mathbf{B} .

We think that the difference between these two cases can be used to explain the results of psychological experiments which revealed the significance of a cue for attention focusing on a target (Posner, 1988). A typical experiment of this kind is organized in the following way. A person is trying to focus attention in the middle point of the visual field and should react to target stimuli, which randomly appear in the left or in the right part of the visual field. A target stimulus can be preceded by a cue (a flash of light) in the left or in the right part of the visual field. The difficulty of the task is measured by the reaction time. It has been shown that the reaction time is lower (greater) than in the experiments without a cue if the cue appears in the same (in the opposite) part of the visual field relative to the target. In terms of the model we consider the cue as a distracting stimulus. Our hypothesis is that different locations of the cue correspond to different relations between natural frequencies of oscillators representing the stimuli and the central executive. Suppose that concentration of attention in the central portion of the visual field makes the central oscillator natural frequency equal to Ω_0 . Suppose also that the natural frequencies of the POs are distributed so that those activated by a stimulus in the left part of the field have natural frequencies lower than Ω_0 , and those activated by a stimulus in the right part of the visual field have natural frequencies greater than Ω_0 . Note that, as a result of a short time lag between the cue and the target, there is a period of simultaneous activity of both groups of POs representing the cue and the target in the cortex. Then, the presentation of the cue in the same, or in the opposite, part of the field corresponds to one of the above-mentioned cases when an additional stimulus can improve attention focusing on the other stimulus or make it more difficult.

Another important consequence of the result of modeling

is illustrated by Figs. 2e and 7e and states that decreasing the interaction of the CO with the oscillators representing one of two stimuli that form the attention focus may lead not to focusing attention on the other stimulus but to complete destruction of the attention focus. In this case the boundary between GS and NS has such a form that the transition between these regions can be realized by changing only one of the interaction parameters α or β .

The dependence of the dynamics of the model on initial conditions that is found for some parameter values can be interpreted as the possibility of a spontaneous shift of the focus of attention. Such abrupt change of dynamics can be achieved in the model if we presume that the spontaneous shift of attention is caused by an internal signal or noise that change the relations between the current phases. Then, as the analysis of the model shows, a spontaneous shift of attention from one stimulus to another can be realized if only each stimulus is represented by the activity of not one but many oscillators.

The results obtained for attention modeling are of qualitative nature. The network of phase oscillators is suitable for modeling how the attention focus is formed or changed but it is too simple to model reaction times. The latter modeling can be made basing on the same ideas (that is the idea of a central element as a source of synchronization and the idea of partial synchronization as the criterion of attention focus formation), yet more sophisticated network elements and network architecture should be used to include into analysis the amplitude patterns of neural activity. An improved model can be built using special organization of amplitude information exchange between synchronized and not synchronized areas. The model should also combine attention focusing with short-term memory. This will be the subject of our further research.

Acknowledgements

We are grateful to E.E. Schnoll for careful reading of the manuscript and valuable comments. This work was supported by grants 93-9 from the James S McDonnell Foundation, RMQ000 from the International Science Foundation, RMQ300 from the International Science Foundation and Russian Government, and 94-01-01270-a from the Russian Foundation of Fundamental Research.

Appendix A. Average frequency of the central oscillator

We present the derivation of the equation for the average frequency $\langle \omega \rangle$ of the CO in the mode of strict partial synchronization with the oscillators of group \mathbf{B} . It is assumed that the current frequency of the CO does not deviate much from $\langle \omega \rangle$ and can be approximately changed for it. We suppose that $\langle \omega \rangle$ satisfies Eqs. (7), (8). Moreover, our consideration is restricted by the case when $\langle \omega \rangle$ is out of the range $(\omega_A - l, \omega_A + l)$ which guarantee that (8) is

fulfilled for any sample of natural frequencies of the oscillators in **A**. Let

$$\langle \omega \rangle - \omega_A^i > \alpha, \quad i = 1, \dots, n$$

(the case $(\omega_A^i - \langle \omega \rangle) > \alpha$, $i = l, \dots, n$, is considered in a similar way). By (7), the oscillators of **B** are running synchronously with the CO at the frequency $\langle \omega \rangle$, hence

$$\left\langle \frac{d\theta_B^j}{dt} \right\rangle = \langle \omega \rangle, \quad j = 1, \dots, n. \quad (10)$$

Consider an oscillator from group **A** (with the number i) and put $\phi = \theta_0 - \theta_A^i$. Then it follows from (1b) that

$$\frac{d\phi}{dt} = \langle \omega \rangle - \omega_A^i - \alpha \sin \phi. \quad (11)$$

Integrating (11) we find that the derivative of the solution of (11) $d\phi/dt$ is a periodic function of time and that its average value (over the period) is ¹

$$\left\langle \frac{d\phi}{dt} \right\rangle = (\langle \omega \rangle - \omega_A^i) \sqrt{1 - \frac{\alpha^2}{(\langle \omega \rangle - \omega_A^i)^2}} = \sqrt{(\langle \omega \rangle - \omega_A^i)^2 - \alpha^2} \quad (12)$$

(in the last equality of (12) we took into account that $(\langle \omega \rangle - \omega_A^i) > 0$). It follows from (12) that

$$\left\langle \frac{d\theta_A^i}{dt} \right\rangle = \langle \omega \rangle - \sqrt{(\langle \omega \rangle - \omega_A^i)^2 - \alpha^2}. \quad (13)$$

Using (1b) and (1c), (1a) can be written as

$$\frac{d\theta_0}{dt} \omega_0 - \frac{1}{n} \sum_{i=1}^n \left(\frac{d\theta_A^i}{dt} - \omega_A^i \right) - \frac{1}{n} \sum_{j=1}^n \left(\frac{d\theta_B^j}{dt} - \omega_B^j \right).$$

Substituting into this expression the results of (10) and (13), we obtain for $\langle \omega \rangle$ the equation

$$\begin{aligned} \langle \omega \rangle = \omega_0 - \frac{1}{n} \sum_{i=1}^n \left(\langle \omega \rangle - \omega_A^i - \sqrt{(\langle \omega \rangle - \omega_A^i)^2 - \alpha^2} \right) \\ - \frac{1}{n} \sum_{j=1}^n \left(\langle \omega \rangle - \omega_B^j \right). \end{aligned} \quad (14)$$

Owing to large n , $(1/n) \sum_{i=1}^n \omega_A^i$ and $(1/n) \sum_{j=1}^n \omega_B^j$ can be changed for ω_A and ω_B , respectively. Then (14) takes the form

$$3\langle \omega \rangle = h(\langle \omega \rangle, \alpha) + \omega_0 + \omega_A + \omega_B, \quad (15)$$

where

$$h(\langle \omega \rangle, \alpha) = \frac{1}{n} \sum_{i=1}^n \sqrt{(\langle \omega \rangle - \omega_A^i)^2 - \alpha^2}.$$

Again taking into account that n is large, the function $h(\langle \omega \rangle, \alpha)$ can be evaluated as the expectation of the random

variable $\sqrt{(\langle \omega \rangle - \omega_A^i)^2 - \alpha^2}$. The result is

$$h(\langle \omega \rangle, \alpha) = g(\langle \omega \rangle - \omega_A + l) - g(\langle \omega \rangle - \omega_A - l),$$

where

$$g(x) = \frac{1}{4l} \left[x\sqrt{x^2 - \alpha^2} - \alpha^2 \ln \left(x + \sqrt{x^2 - \alpha^2} \right) \right].$$

References

- Baesens, C., Guckenheimer, J., Kim, S., & MacKay, R. S. (1991). Three coupled oscillators: mode-locking, global bifurcations and toroidal chaos. *Physica D*, 49, 387–475.
- Borisyuk, N., Borisyuk, M., Kazanovich, B., Luzyanina, B., Turova, S., & Cymbalyuk, G. S. (1992). Oscillatory neural networks: Mathematics and applications. *Math. Modeling*, 4, 3–43 (in Russian).
- Cowan, N. (1988). Evolving conceptions of memory storage, selective attention and their mutual constraints within the human information-processing system. *Psychol. Bull.*, 104, 163–191.
- Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, 2, 263–275.
- Daido, H. (1988). Lower critical dimension for populations of oscillators with randomly distributed frequencies: a renormalization-group analysis. *Phys. Rev. Lett.*, 61, 231–234.
- Daido, H. (1990). Intrinsic fluctuations and a phase transition in a class of large populations of interacting oscillators. *J. Stat. Phys.*, 60, 753–800.
- Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., & Munk, M. (1988). Reitboeck, H.J., Coherent oscillations: a mechanism of feature linking in the visual cortex?. *Biol. Cybern.*, 60, 121–130.
- Ermentrout, B., & Kopell, N. (1991). Multiple pulse interactions and averaging in systems of coupled neural oscillators. *Math. Biol.*, 29, 195–217.
- Gray, C. M. (1994). Synchronous oscillations in neuronal systems: Mechanisms and functions. *J. Comput. Neurosci.*, 1, 11–38.
- Gray, C. M., Konig, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, 338, 334–337.
- Grossberg, S., Mingolla, E., & Ross, W. (1994). A neural theory of attentive visual search interactions at boundary searfice, spatial and object recognition. *Psychological Review*, 101, 470–489.
- Horn, D., Sagi, D., Usher, M., & Segmentation, binding (1991). illusory conjunctions. *Neural Computations*, 3, 510–525.
- Humphreys, G., & Muller, H. (1993). Search via recursive rejection (SERR). A connectionist model of visual search. *Cognitive Psychology*, 25, 43–110.
- Ivanitsky, M. (1993). Interaction foci. *informational synthesis and mental processes. J. Higher Nervous Activity*, 43, 219–227 (in Russian).
- Kammen, M., Holmes, P. J., & Koch, C. (1990). Origin of oscillations in visual cortex: feedback versus local coupling. In R. M. J. Cotterill (Ed.), *Models of Brain Function*, (pp. 273). Cambridge: Cambridge Univ. Press.
- Kazanovich, Y. B., & Borisyuk, R. M. (1994). Synchronization in a neural network of phase oscillators with the central element. *Biol. Cybern.*, 71, 177–185.
- Khibnik, A. I., Kuznetsov, Yu. A., Levitin, V. V., & Nikolaev, E. V. (1993). Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps. *Physica D*, 62, 360–371.
- Kiper, D. C., Gegenfurtner, K. R., & Movshon, J. A. (1996). Cortical oscillatory responses do not affect visual segmentation. *Vision Research*, 36, 529–544.
- Kryukov, V. I. (1991). An attention model based on the principle of dominance. In A. V. Holden & V. I. Kryukov (Eds.), *Neurocomputers and Attention I. Neurobiology, Synchronization and Chaos*, (pp. 319). Manchester: Manchester University Press.

¹ If in the equation $d\phi/dt = g(\phi)$ the function g is periodic with the period 2π and $g(\phi) \geq \varepsilon > 0$, then $d\phi/dt$ is periodic function of t and $d\phi/dt \geq 2\pi \{ \int_0^{2\pi} ds/g(s) \}$.

- Kuramoto, Y., & Nishikawa, I. (1987). Statistical macrodynamics of large dynamical systems. Case of a phase transition in oscillator communities. *J. Stat. Phys.*, *49*, 605.
- Kuramoto, Y., Aoyagi, T., Nishikawa, I., Chawanya, T., & Okuda, I. (1992). Neural network model carrying phase information. *Progr. Theor. Phys.*, *87*, 1119–1126.
- Leonards, U., & Singer, W. (1998). Two segmentation mechanisms with differential sensitivity for colour and luminance contrast. *Vision Research*, *38*, 101–109.
- Lumer, E. D., & Huberman, B. A. (1991). Hierarchical dynamics in large assemblies of interacting oscillators. *Phys. Lett. A*, *160*, 227–232.
- Luzyanina, T. B. (1995). Synchronization in an oscillator neural network model with time delayed coupling. *Network: Computation in Neural Systems*, *6*, 43–59.
- Malsburg, von der (1981). The correlation theory of brain function. Internal Report 81-2. Göttingen: Max-Planck-Institute for Biophysical Chemistry.
- Malsburg, C. von der, & Schneider, W. (1986). A neural cocktail-party processor. *Biol. Cybern.*, *54*, 29–40.
- Malsburg, C. von der, & Buhman, J. (1992). Sensory segmentation with coupled neural oscillators. *Biol. Cybern.*, *67*, 233–242.
- Miller, R. (1991). Cortico-Hippocampal Interplay and the Representation of Contexts in the Brain. Berlin: Springer-Verlag.
- Niebur, E., & Koch, C. (1994). A model for the neuronal implementation of selective visual attention based on temporal correlation among neurons. *J. Neurosci.*, *1*, 141–158.
- Niebur, E., Kammen, D. M., & Koch, C. (1991). Phase-locking in 1-D and 2-D networks of oscillating neurons. In W. Singer & H. G. Schuster (Eds.), *Non-Linear Dynamics and Neuronal Networks*, Weinheim: VCW Verlag.
- Niebur, E., Koch, C., & Rosin, C. (1993). An oscillation based model for the neuronal basis of attention. *Vision Research*, *33*, 2789–2802.
- Olshausen, B. A., Anderson, C. H., & Van Essen, D. C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *J. Neurosci.*, *13*, 4700–4719.
- Pfurtscheller, G., & Klimesch, W. (1992). Event-related synchronization and desynchronization of alpha and beta waves in a cognitive task. In E. Basar & T. Bullock (Eds.), *Induced Rhythms in the Brain*, (pp. 117). Boston: Birkhauser.
- Posner, M. (1988). Structures and functions of selective attention. In T. Boll & B. Bryant (Eds.), *Master Lectures in Clinical Neurophysiology*, (pp. 173). Washington DC: Am. Psych. Assoc.
- Schmajuk, N., & DiCarlo, J. (1992). Stimulus configuration, classical conditioning and hippocampal function. *Psychol. Rev.*, *99*, 268–305.
- Schuster, H. G., & Wagner, P. (1990a). A model for neuronal oscillations in the visual cortex. 1. Mean-field theory and derivation of the phase equations. *Biol. Cybern.*, *64*, 83–85.
- Schuster, H. G., & Wagner, P. (1990b). A model for neuronal oscillations in the visual cortex. 2. Phase description of the feature dependent synchronization. *Biol. Cybern.*, *64*, 83–85.
- Sompolinsky, H., Golomb, D., & Kleinfeld, D. (1990). Global processing of visual stimuli in a neural network of coupled oscillators. *Proc. Natl. Acad. Sci. (USA)*, *87*, 7200–7204.
- Strogatz, S. H., & Mirollo, R. E. (1988). Phase-locking and critical phenomena of coupled nonlinear oscillators with random intrinsic frequencies. *Physica D*, *31*, 143–168.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive psychology*, *12*, 97–136.
- Usher, M., & Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. *Nature*, *394*, 179–182.
- Usher, M., & Niebur, E. (1996). Modeling the temporal dynamics of IT neurons in visual search: a mechanism for top-down selective attention. *J. Cognitive Neuroscience*, *8*, 311–327.
- Wang, D.-L., & Terman, D. (1995). Locally excitatory globally inhibitory oscillator network. *IEEE Transactions on Neural Networks*, *6*, 283–286.
- Wilson, H., & Cowan, J. (1973). A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. *Kybernetik*, *13*, 55–80.