ISSN 1560-3547, Regular and Chaotic Dynamics, 2015, Vol. 20, No. 6, pp. 701–715. © Pleiades Publishing, Ltd., 2015.

Sequential Dynamics in the Motif of Excitatory Coupled Elements

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Received September 04, 2015; accepted October 07, 2015

Abstract—In this article a new model of motif (small ensemble) of neuron-like elements is proposed. It is built with the use of the generalized Lotka – Volterra model with excitatory couplings. The main motivation for this work comes from the problems of neuroscience where excitatory couplings are proved to be the predominant type of interaction between neurons of the brain. In this paper it is shown that there are two modes depending on the type of coupling between the elements: the mode with a stable heteroclinic cycle and the mode with a stable limit cycle. Our second goal is to examine the chaotic dynamics of the generalized three-dimensional Lotka – Volterra model.

MSC2010 numbers: 37G35, 70K05, 70K50, 70K55

DOI: 10.1134/S1560354715060064

Keywords: Neuronal motifs, Lotka – Volterra model, heteroclinic cycle, period-doubling bifurcation, Feigenbaum scenario, strange attractor, Lyapunov exponents

1. INTRODUCTION

Many dynamical processes in motifs can be viewed as sequential switching dynamics between elements or groups of elements. These sequential dynamics could be explained by various physiological functions of the nervous system. The generation of excitation sequences and their propagation among solitary elements or among groups of neurons play a crucial role both in the brain functioning and in the functioning of the nervous system as a whole. As an illustration, this type of dynamics is an integral part of neural networks in sensory and motor systems of many animals [1]. Besides, some specific part of a bird's brain generates bursts that control glottis and enable singing [2]. There are many other examples where excitation sequences are vital [3, 4].

It seems extremely important to study sequential dynamics in motifs with regard to nonlinear dynamics. There is a hypothesis [1] that sequential dynamics in motifs can be accounted for by the existence of a stable heteroclinic circuit in the phase space of a dynamical system that models dynamics in the motifs [5–8]. The basic principle underlying sequential switching dynamics generation is the winnerless competition (WLC) principle [9]. The main idea of WLC is that there exists a stable heteroclinic circuit between the singular trajectory of saddle type in the phase space (i.e., saddle equilibrium states, saddle limit cycles etc.) and a representative point moves in the vicinity of this heteroclinic circuit [10, 11]. If the representative point is moving in the vicinity of a certain saddle trajectory, then a certain neuron-like element or group of neuron-like elements is activated. Thus, a stable heteroclinic circuit in the phase space is a mathematical representation of sequential switching dynamics in the motif of coupled neuron-like elements. A necessary condition for such behavior is the presence of inhibitory couplings between elements.

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In this article we investigate the problem of switching dynamics in the motif of *excitatory* coupled neuron-like elements.

We are also interested in finding chaotic behavior in our system. This goal is motivated by the fact that a strange attractor was found in the generalized Lotka–Volterra model. As shown in [12], a strange attractor exists even in the three-dimensional generalized Lotka–Volterra model.

2. MODEL OF A MOTIF

Following [1], we study coupled generalized Lotka–Volterra equations. Consider a motif of N elements coupled by excitatory couplings. The behavior of each element is modeled by the following equation:

$$\dot{\rho}_j = (I_j + J_j)\rho_j(-1 + I_j/M_j - {\rho_j}^2), \tag{2.1}$$

where ρ_j is the level of spike activity of the jth element (see [1]),

$$I_j = \sum_{i=1}^{N} g_{ij} F(\rho_i) \tag{2.2}$$

is the stimulus to the jth element from other elements; g_{ij} are arbitrary positive and (or) negative couplings;

$$J_j = \sum_{i=1}^{N} g_{ji} F(\rho_i) \tag{2.3}$$

is an additional parameter, which is equal to 2 if and only if the element which is to be activated after the jth element is activated.

In this work the levels of the element's activity will be calculated with the use of two functions: the Heaviside function and a continuous sigmoid function $F(x) = \frac{1}{1+\exp(-x)}$. The continuous sigmoid function will be used later, now we will use the Heaviside function.

$$F(\rho) = \begin{cases} 1, \ \rho \geqslant q \\ 0, \ \rho < q \end{cases} \tag{2.4}$$

is the Heaviside function with a threshold $q = 0.999$. Let us consider the element number i which is active if $F(\rho_i) = 1$;

$$M_j = \begin{cases} \sum\limits_{i=1, g_{ij} \neq 0}^{N} F(\rho_i), \ I_j \neq 0 \\ 1, \ I_j = 0 \end{cases} \tag{2.5}$$

are the numbers of active elements that have an impact on the jth element; if there are none, $M_j = 1$. The purpose of adding this parameter will be explained below.

3. UNIDIRECTIONAL COUPLINGS. SEQUENTIAL DYNAMICS

First of all, we consider a motif of three elements connected by reciprocal excitatory couplings. The coupling matrix for this motif is as follows:

$$G = \begin{pmatrix} 0 & 0 & 2 \\ 2 & 0 & 0 \\ 0 & 2 & 0 \end{pmatrix}.$$

The matrix describes unidirectional couplings and specifies the order of activation elements 1-2-3.

Then the system under study takes the following form (we deleted two multipliers from every equation):

$$\begin{cases} \dot\rho_1 = (F(\rho_2) + F(\rho_3))\rho_1(-1 + 2F(\rho_3) - {\rho_1}^2), \\ \dot\rho_2 = (F(\rho_3) + F(\rho_1))\rho_2(-1 + 2F(\rho_1) - {\rho_2}^2), \\ \dot\rho_3 = (F(\rho_1) + F(\rho_2))\rho_3(-1 + 2F(\rho_2) - {\rho_3}^2). \end{cases} \tag{3.1}$$

We prove that if the initial conditions belong to the cube $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$, then the corresponding phase trajectory lies in the same domain. Consider the evolution of the variable ρ_1. The proof for other variables is similar to that described below.

Suppose that the initial conditions are such that $F(\rho_2) = F(\rho_3) = 0$. Then the first equation in (3.1) is $\rho_1 = \text{const}$. If $F(\rho_2) = 1$, $F(\rho_3) = 0$, then $\dot\rho_1 = \rho_1(-1 - {\rho_1}^2)$ and ρ_1 monotonically converges to 0. If $F(\rho_2) = 0$, $F(\rho_3) = 1$, then $\dot\rho_1 = \rho_1(1 - {\rho_1}^2)$ and ρ_1 monotonically converges to 1. If $F(\rho_2) = 1$, $F(\rho_3) = 1$, then $\dot\rho_1 = 2\rho_1(1 - {\rho_1}^2)$ and ρ_1 monotonically converges to 1 again.

Hence, the phase trajectories are in the domain $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$.

Let us find equilibria of the system in the domain $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$. For this, we consider all possible initial conditions.

1. Suppose that the initial conditions are such that $F(\rho_1) = F(\rho_2) = F(\rho_3) = 0$. In this case, the following inequalities should be true: $0 \leqslant \rho_1, \rho_2, \rho_3 < q$. The system takes the form

$$\dot\rho_1 = \dot\rho_2 = \dot\rho_3 = 0.$$

Therefore, every point $(\rho_1,\ \rho_2,\ \rho_3) \in \{0 \leqslant \rho_1,\ \rho_2,\ \rho_3 < q\}$ is a stable steady state.

2. Suppose that the initial conditions are such that $F(\rho_1) = 1$, $F(\rho_2) = F(\rho_3) = 0$. These conditions are true in the domain $q \leqslant \rho_1 \leqslant 1$, $0 \leqslant \rho_2,\ \rho_3 < q$. The system takes the form

$$\begin{cases} \dot\rho_1 = 0 \\ \dot\rho_2 = \rho_2(1 - {\rho_2}^2) \\ \dot\rho_3 = \rho_3(-1 - {\rho_3}^2). \end{cases}$$

This system has a steady state in $(C,\ 0,\ 0)$, where $q \leqslant C \leqslant 1$ in the domain under consideration. The eigenvalues corresponding to the point $(C,\ 0,\ 0)$ are $\lambda_1 = 0$, $\lambda_2 = 1$, $\lambda_3 = -1$.

The plane $\rho_1 = C$, $q \leqslant C \leqslant 1$ is an invariant set. The point $(C, 0, 0)$ is a saddle on this plane.

3. Suppose that the initial conditions are such that $F(\rho_1) = F(\rho_2) = 1$, $F(\rho_3) = 0$. These conditions hold in the domain $q \leqslant \rho_1, \rho_2 \leqslant 1$, $0 \leqslant \rho_3 < q$. The system takes the form

$$\begin{cases} \dot\rho_1 = \rho_1(-1 - {\rho_1}^2) \\ \dot\rho_2 = \rho_2(1 - {\rho_2}^2) \\ \dot\rho_3 = 2\rho_3(1 - {\rho_3}^2). \end{cases} \tag{3.2}$$

It has the following steady states: $(0, 0, 0)$, $(0, 1, 0)$, $(0, 0, 1)$, $(0, 1, 1)$. These steady states do not belong to the domain $q \leqslant \rho_1, \rho_2 \leqslant 1$, $0 \leqslant \rho_3 < q$. The system (3.2) describes the transition process to a case similar to the previous one.

4. $F(\rho_1) = F(\rho_2) = F(\rho_3) = 1$. These conditions are satisfied in the domain $q \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$. The system takes the following form:

$$\begin{cases} \dot\rho_1 = 2\rho_1(1 - {\rho_1}^2) \\ \dot\rho_2 = 2\rho_2(1 - {\rho_2}^2) \\ \dot\rho_3 = 2\rho_3(1 - {\rho_3}^2). \end{cases}$$

It has 1 steady state $(1,\ 1,\ 1)$ with eigenvalues $\lambda_1 = -4$, $\lambda_2 = -4$, $\lambda_3 = -4$. It is a stable node.

5. The cases $F(\rho_1) = 0$, $F(\rho_2) = 1$, $F(\rho_3) = 0$ and $F(\rho_1) = F(\rho_2) = 0$, $F(\rho_3) = 1$ are similar to case 2.
6. The cases $F(\rho_1) = 1$, $F(\rho_2) = 0$, $F(\rho_3) = 1$ and $F(\rho_1) = 0$, $F(\rho_2) = F(\rho_3) = 1$ are similar to case 3.

From all this it follows that the phase space of system (3.1) is divided into 3 domains:

1. Every point from the domain $0 \leqslant \rho_1, \rho_2, \rho_3 < q$ is a nonisolated steady state;
2. Every point from the domain $q \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$ lies on the trajectory that ends in the stable node $(1, 1, 1)$;
3. Any other point in the domain $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$ lies on the trajectory on the planes $\rho_1 = C_1$, $\rho_2 = C_2$, $\rho_3 = C_3$, $q \leqslant C_1, C_2, C_3 \leqslant 1$.

Let us consider in detail the dynamics of the system. Let the initial conditions be $(0.5, 0.5, 1)$[1)].

We will denote the active state of the element by "a", the passive one by "p" (recall that the ith element is considered to be active if $\rho_i \geqslant q$). The expression (p, p, a) means that the first and the second elements are passive and the third one is active. During evolution of the system the elements change states. We will denote the process of changing states by an expression like this: $(p,\, p,\, a) \to (a,\, p,\, a)$. This expression means that the first element becomes active during evolution of the system.

1. Under initial conditions, the system takes the form

$$\begin{cases} \dot{\rho}_1 = \rho_1(1 - {\rho_1}^2) \\ \dot{\rho}_2 = \rho_2(-1 - {\rho_2}^2) \\ \dot{\rho}_3 = 0. \end{cases} \tag{3.3}$$

The phase trajectory lies on the invariant plane $\rho_3 = 1$ ending at the point $(1, 0, 1)$. Therefore, at this stage the process $(p,\, p,\, a) \to (a,\, p,\, a)$ takes place.

2. Once the first element is activated, the system takes the form

$$\begin{cases} \dot{\rho}_1 = \rho_1(1 - {\rho_1}^2) \\ \dot{\rho}_2 = 2\rho_2(1 - {\rho_2}^2) \\ \dot{\rho}_3 = \rho_3(-1 - {\rho_3}^2). \end{cases} \tag{3.4}$$

From the third equation it becomes obvious that ρ_3 converges to 0. Consequently, at this stage the process $(a,\, p,\, a) \to (a,\, p,\, p)$ takes place[2)].

3. The system is

$$\begin{cases} \dot{\rho}_1 = 0 \\ \dot{\rho}_2 = \rho_2(1 - {\rho_2}^2) \\ \dot{\rho}_3 = \rho_3(-1 - {\rho_3}^2). \end{cases}$$

At this stage, the phase trajectory comes to the point $(C, 1, 0)$ on the plane $\rho_1 = C$, $q \leqslant C \leqslant 1$. The process that takes place at this stage is $(a,\, p,\, p) \to (a,\, a,\, p)$.

[1)] The dynamics will be the same for all initial conditions from the domain $0 \leqslant \rho_i \leqslant 1$ besides the point $0 \leqslant \rho_i < q$ and $q \leqslant \rho_i \leqslant 1$.

[2)] As we see from the second equation of system (3.4), at this stage $\rho_2 \to 1$. But activation goes for a longer time than deactivation, so we do not study this process.

4. Once the second element becomes active, the system takes the form

$$\begin{cases} \dot{\rho}_1 = \rho_1(-1 - {\rho_1}^2) \\ \dot{\rho}_2 = \rho_2(1 - {\rho_2}^2) \\ \dot{\rho}_3 = 2\rho_3(1 - {\rho_3}^2). \end{cases}$$

   As can be seen from the first equation, ρ_1 converges to 0. Consequently, at this stage the process $(a,\, a,\, p) \to (p,\, a,\, p)$ is realized.

5. In the next step, by which the deactivation of the first element in the system finishes, we have

$$\begin{cases} \dot{\rho}_1 = \rho_1(-1 - {\rho_1}^2) \\ \dot{\rho}_2 = 0 \\ \dot{\rho}_3 = \rho_3(1 - {\rho_3}^2). \end{cases}$$

   The phase trajectory lies on the invariant plane, i.e., $\rho_2 = C$, to the point $(0, C, 1)$. The process $(p,\, a,\, p) \to (p,\, a,\, a)$ occurs.

6. At the end of the activation of the third element the system takes the following form:

$$\begin{cases} \dot{\rho}_1 = 2\rho_1(1 - {\rho_1}^2) \\ \dot{\rho}_2 = \rho_2(-1 - {\rho_2}^2) \\ \dot{\rho}_3 = \rho_3(1 - {\rho_3}^2). \end{cases}$$

   ρ_2 converges to 0 (which follows from the second equation). This time the process $(p,\, a,\, a) \to (p,\, p,\, a)$ takes place.

7. At the next step our system becomes identical to (3.3).

Thus, the system dynamics are a process of cyclic changes in elements' activity.

Figure 1 shows the time series for initial conditions $(1, 0.5, 0.5)$. Increase in the duration of the experiment results in the elongation of the elements' active phase. As may be remembered, a similar process occurs in motifs with unidirectional inhibitory couplings (see [1]).

Figure 2 shows the phase portrait for the same initial conditions.

We observe this type of behavior due to the fact that there exists a stable heteroclinic cycle in the phase space that consists of a sequence of saddles and connecting separatrices. Each path that connects saddles consists of two edges of the cube.

Let us find the duration of the elements' activity analytically. The activity of the ith element corresponds to the motion on the face of the cube $\rho_i = C$ $(q \leqslant C \leqslant 1)$ in the phase space. The system dynamics on this face can be described by a system of two ODE. For example, movements on the face $\rho_1 = q$ are defined by the system[3)]

$$\begin{cases} \dot{\rho}_2 = \rho_2(1 - {\rho_2}^2) \\ \dot{\rho}_3 = \rho_3(-1 - {\rho_3}^2) \end{cases}$$

with the initial conditions $\rho_2 = a$ $(0 \leqslant a < q)$, $\rho_3 = q$ when $t = 0$. We are moving on the face mentioned above, coming to the point $\rho_2 = q$, $\rho_3 = b$ when $t = \tau_1$ (at this point we move to another face of the cube).

[3)]Movements on other two faces are described by the same systems up to a cyclic permutation of the variables.

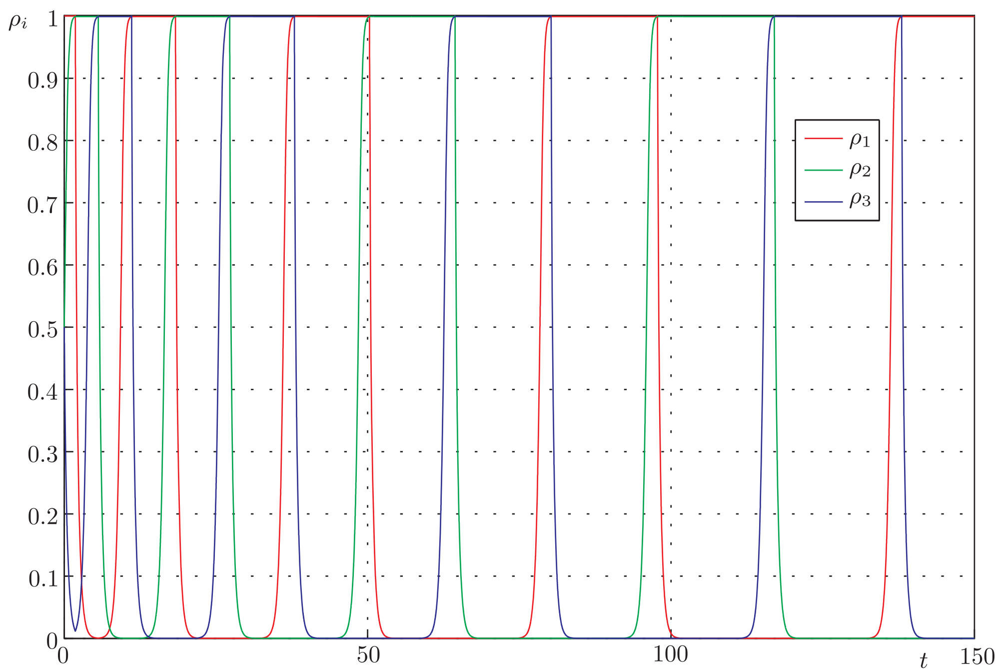

Fig. 1. Time series of the variables ρ_i. The activity time (when $\rho_i \geqslant q$) of each element increases with each subsequent activation.

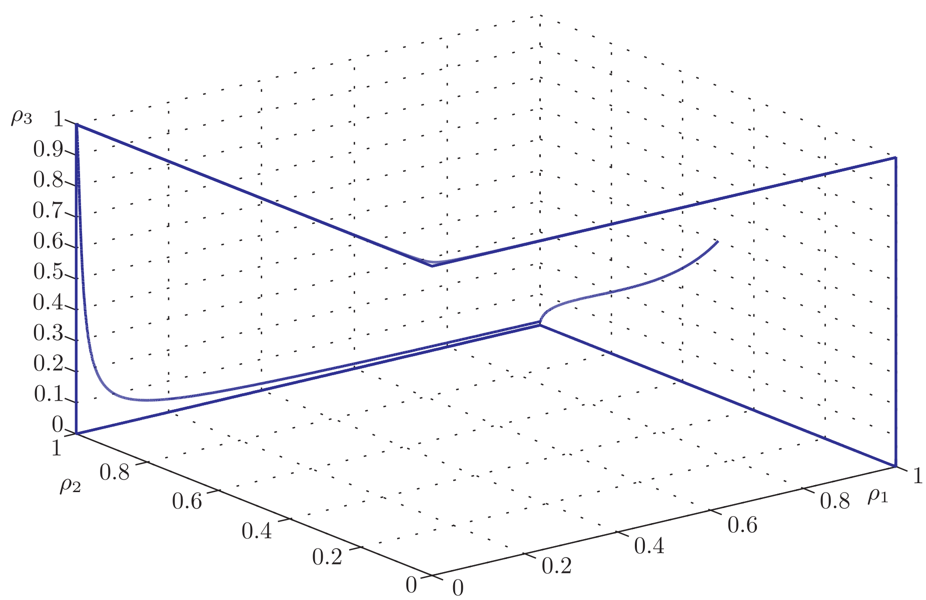

Fig. 2. Phase portrait of the system (3.1).

The solution of the system is as follows:

$$\begin{cases} \dfrac{\sqrt{1-a^2}}{\sqrt{1-\rho_2^2}} \cdot \dfrac{\rho_2}{a} = e^t, \\ \dfrac{\sqrt{1+\rho_3^2}}{\sqrt{1+q^2}} \cdot \dfrac{q}{\rho_3} = e^t. \end{cases} \tag{3.5}$$

From the first equation of (3.5) we find τ_1:

$$e^{\tau_1} = \frac{\sqrt{1-a^2}}{\sqrt{1-q^2}} \cdot \frac{q}{a}.$$

From the condition $\rho_3(\tau_1) = b$ we obtain the equation

$$e^{\tau_1} = \frac{\sqrt{1+b^2}}{\sqrt{1+q^2}} \cdot \frac{q}{b}.$$

As a result, we find the dependence of b on a:

$$b = \sqrt{\frac{a^2(1-q^2)}{1+q^2-2a^2}}. \tag{3.6}$$

Time τ_2 when the next element is active can be defined by the expression below:

$$e^{\tau_2} = \frac{\sqrt{1-b^2}}{\sqrt{1-q^2}} \cdot \frac{q}{b}.$$

The time difference between two successive activations is

$$\tau_2 - \tau_1 = \ln \frac{a\sqrt{1-b^2}}{b\sqrt{1-a^2}}.$$

In view of (3.6), this formula takes the form

$$\tau_2 - \tau_1 = \ln \sqrt{1 + \frac{2}{1-q^2} - \frac{2}{1-a^2}}.$$

If a is small enough, then the last formula takes the following form:

$$\tau_2 - \tau_1 \approx \ln \sqrt{\frac{2}{1-q^2} - 1}.$$

Therefore, the period of activity increases to infinity. If a is small enough, then the activity period increases linearly.

4. SYSTEM WITH MUTUAL EXCITATORY COUPLINGS

Let us now consider a system with the following coupling matrix:

$$G = \begin{pmatrix} 0 & \varepsilon & 2 \\ 2 & 0 & \varepsilon \\ \varepsilon & 2 & 0 \end{pmatrix},$$

where $0 < \varepsilon \leqslant 2$.

The system takes the form

$$\begin{cases} \dot{\rho}_1 = F(\rho_2, \rho_3)\rho_1(-1 + \Phi(\rho_2, \rho_3)/M_1 - {\rho_1}^2) \\ \dot{\rho}_2 = F(\rho_3, \rho_1)\rho_2(-1 + \Phi(\rho_3, \rho_1)/M_2 - {\rho_2}^2) \\ \dot{\rho}_3 = F(\rho_1, \rho_2)\rho_3(-1 + \Phi(\rho_1, \rho_2)/M_3 - {\rho_3}^2), \end{cases}$$

where $F(x, y) = (2 + \varepsilon)(F(x) + F(y))$, $\Phi(x, y) = \varepsilon F(x) + 2F(y)$.

Let us find equilibria in the domain $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$. As it was done previously, we split this domain into several parts so that in each of them the condition $F(\rho_i) = \text{const}$, $i \in \{1, 2, 3\}$ is satisfied.

1. $F(\rho_1) = F(\rho_2) = F(\rho_3) = 0$. Steady states must be placed in the cube $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant q$. The system takes the form

$$\dot{\rho}_1 = \dot{\rho}_2 = \dot{\rho}_3 = 0.$$

It follows that any point $(\rho_1, \rho_2, \rho_3) \in \{0 \leqslant \rho_1, \rho_2, \rho_3 < q\}$ is a stable steady state.

2. $F(\rho_1) = 1$, $F(\rho_2) = F(\rho_3) = 0$. These conditions are satisfied in the domain $q \leqslant \rho_1 \leqslant 1$, $0 \leqslant \rho_2, \rho_3 < q$. So we rewrite the system as follows:

$$\begin{cases} \dot{\rho}_1 = 0 \\ \dot{\rho}_2 = (2+\varepsilon)\rho_2(1-{\rho_2}^2) \\ \dot{\rho}_3 = (2+\varepsilon)\rho_3(\varepsilon - 1 - {\rho_3}^2). \end{cases} \tag{4.1}$$

In the current domain this system has a steady state $(C, 0, 0)$, where $q \leqslant C \leqslant 1$. When the condition $1 < \varepsilon < q^2 + 1$ is satisfied, there is another steady state $(C, 0, \sqrt{\varepsilon - 1})$. For the point $(C, 0, 0)$ the corresponding eigenvalues are $\lambda_1 = 0$, $\lambda_2 = 2 + \varepsilon$, $\lambda_3 = (2+\varepsilon)(\varepsilon - 1)$. For the point $(C, 0, \sqrt{\varepsilon - 1})$ the eigenvalues are $\lambda_1 = 0$, $\lambda_2 = 2 + \varepsilon$, $\lambda_3 = -2(2+\varepsilon)(\varepsilon - 1) < 0$. Thus, $\varepsilon = 1$ and $\varepsilon = q^2 + 1$ are bifurcation values of the parameter.

The plane $\rho_1 = \mathrm{const}$ is an invariant manifold. When $1 < \varepsilon < q^2 + 1$, the point $(0, 0)$ on this plane is an unstable node, and the point $(0, \sqrt{\varepsilon - 1})$ is a saddle. When $0 < \varepsilon \leqslant 1$, $(0, 0)$ is a saddle.

3. $F(\rho_1) = F(\rho_2) = 1$, $F(\rho_3) = 0$. These conditions are satisfied in the domain $q \leqslant \rho_1, \rho_2 \leqslant 1$, $0 \leqslant \rho_3 < q$. The system takes the following form:

$$\begin{cases} \dot{\rho}_1 = (2+\varepsilon)\rho_1(\varepsilon - 1 - {\rho_1}^2) \\ \dot{\rho}_2 = (2+\varepsilon)\rho_2(1-{\rho_2}^2) \\ \dot{\rho}_3 = 2(2+\varepsilon)\rho_3(\varepsilon/2 - {\rho_3}^2). \end{cases} \tag{4.2}$$

When the condition $q^2 + 1 \leqslant \varepsilon < 2 \cdot q^2$ is satisfied, the system has one steady state $(\sqrt{\varepsilon - 1}, 1, \sqrt{\varepsilon/2})$. The corresponding eigenvalues are $\lambda_1 = -2(\varepsilon - 1)$, $\lambda_2 = -2$, $\lambda_3 = -\varepsilon$. Consequently, the state is a stable node. The system (4.2) describes a transient response leading to a situation similar to the previous one.

4. $F(\rho_1) = F(\rho_2) = F(\rho_3) = 1$. These conditions hold in the domain $q \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$. The system is as follows:

$$\begin{cases} \dot{\rho}_1 = 2(2+\varepsilon)\rho_1(\varepsilon/2 - {\rho_1}^2) \\ \dot{\rho}_2 = 2(2+\varepsilon)\rho_2(\varepsilon/2 - {\rho_2}^2) \\ \dot{\rho}_3 = 2(2+\varepsilon)\rho_3(\varepsilon/2 - {\rho_3}^2). \end{cases}$$

When $\sqrt{\varepsilon/2} \geqslant q$ is satisfied, the system has one steady state $(\sqrt{\varepsilon/2}, \sqrt{\varepsilon/2}, \sqrt{\varepsilon/2})$. The corresponding eigenvalues are $\lambda_1 = -\varepsilon$, $\lambda_2 = -\varepsilon$, $\lambda_3 = -\varepsilon$. This steady state is a stable node[4)].

5. The cases $F(\rho_1) = 0$, $F(\rho_2) = 1$, $F(\rho_3) = 0$ and $F(\rho_1) = F(\rho_2) = 0$, $F(\rho_3) = 1$ are studied similarly to case 2.

6. The cases $F(\rho_1) = 1$, $F(\rho_2) = 0$, $F(\rho_3) = 1$ and $F(\rho_1) = 0$, $F(\rho_2) = F(\rho_3) = 1$ are studied similarly to case 3.

Let us consider the process of switching dynamics of the motif when $\sqrt{\varepsilon - 1} < q$ and assume that the initial conditions are $(q, 0.1, 0.1)$. Then the system takes the form (4.1). From the second equation of the system it follows that $\rho_2 \to 1$. Once ρ_2 reaches the threshold of the Heaviside

[4)] Here the parameter M_i is significant. Since all elements are active, $M_1 = M_2 = M_3 = 2$, which means that the stable node has coordinates $(\sqrt{\varepsilon/2}, \sqrt{\varepsilon/2}, \sqrt{\varepsilon/2})$. If the parameter M_i is omitted, then the stable node has coordinates $(\sqrt{\varepsilon}, \sqrt{\varepsilon}, \sqrt{\varepsilon})$, and when $\varepsilon > 1$, the representative point leaves the cube $0 \leqslant \rho_1, \rho_2, \rho_3 \leqslant 1$.

function, the system takes the form (4.2). As can be seen from the first equation of this system, ρ_1 starts to decrease, converging to $\sqrt{\varepsilon-1}$. But once ρ_1 is less than the threshold, the system takes the form

$$\begin{cases} \dot\rho_1 = (2+\varepsilon)\rho_1(\varepsilon-1-{\rho_1}^2) \\ \dot\rho_2 = 0 \\ \dot\rho_3 = (2+\varepsilon)\rho_3(1-{\rho_3}^2). \end{cases}$$

Therefore, $\rho_3 \to 1$ and $\rho_1 \to \sqrt{\varepsilon-1}$. After ρ_3 exceeds the threshold, we can write

$$\begin{cases} \dot\rho_1 = 2(2+\varepsilon)\rho_1(\varepsilon/2-{\rho_1}^2) \\ \dot\rho_2 = (2+\varepsilon)\rho_2(\varepsilon-1-{\rho_2}^2) \\ \dot\rho_3 = (2+\varepsilon)\rho_3(1-{\rho_3}^2). \end{cases}$$

The variable ρ_2 starts to decrease, converging to $\sqrt{\varepsilon-1}$. After it becomes less than the threshold value, the system takes the form

$$\begin{cases} \dot\rho_1 = (2+\varepsilon)\rho_1(1-{\rho_1}^2) \\ \dot\rho_2 = (2+\varepsilon)\rho_2(\varepsilon-1-{\rho_2}^2) \\ \dot\rho_3 = 0. \end{cases} \tag{4.3}$$

As can be seen from the first equation of (4.3), $\rho_1 \to 1$. When ρ_1 becomes equal to the threshold,

$$\begin{cases} \dot\rho_1 = (2+\varepsilon)\rho_1(\varepsilon-1-{\rho_1}^2) \\ \dot\rho_2 = 2(2+\varepsilon)\rho_2(\varepsilon/2-{\rho_2}^2) \\ \dot\rho_3 = (2+\varepsilon)\rho_3(\varepsilon-1-{\rho_3}^2). \end{cases}$$

The variable ρ_3 begins to decrease after it no longer exceeds the threshold value; the system takes its original form and the whole process repeats.

It follows from the above that the elements will be oscillating in the range $(\sqrt{\varepsilon-1}, q]$. The time series is presented in Figure 3.

Now consider the case where the motif is such that $q^2+1 \leqslant \varepsilon \leqslant 2$.

If there are no active elements, i.e., $F(\rho_1) = F(\rho_2) = F(\rho_3) = 0$, then $\dot\rho_1 = \dot\rho_2 = \dot\rho_3 = 0$.

If there is only 1 active element, for example, the first (i.e., $F(\rho_1) = 1$, $F(\rho_2) = F(\rho_3) = 0$), then the system takes the following form:

$$\begin{cases} \dot\rho_1 = 0 \\ \dot\rho_2 = (2+\varepsilon)\rho_2(1-{\rho_2}^2) \\ \dot\rho_3 = (2+\varepsilon)\rho_3(\varepsilon-1-{\rho_3}^2). \end{cases}$$

In this case all the elements are active for a period of time.

If there are 2 active elements, for example, the first and the third (i.e., $F(\rho_1) = 1$, $F(\rho_2) = 0$, $F(\rho_3) = 1$), then we can write

$$\begin{cases} \dot\rho_1 = (2+\varepsilon)\rho_1(1-{\rho_1}^2) \\ \dot\rho_2 = 2(2+\varepsilon)\rho_2(\varepsilon/2-{\rho_2}^2) \\ \dot\rho_3 = (2+\varepsilon)\rho_3(\varepsilon-1-{\rho_3}^2). \end{cases}$$

Since $\sqrt{\varepsilon/2} \geqslant \sqrt{\varepsilon-1} \geqslant q$, all the elements become active.

If all the elements are active ($F(\rho_1) = F(\rho_2) = F(\rho_3) = 1$), the system takes the form

$$\begin{cases} \dot{\rho}_1 = 2(2+\varepsilon)\rho_1(\varepsilon/2 - {\rho_1}^2) \\ \dot{\rho}_2 = 2(2+\varepsilon)\rho_2(\varepsilon/2 - {\rho_2}^2) \\ \dot{\rho}_3 = 2(2+\varepsilon)\rho_3(\varepsilon/2 - {\rho_3}^2). \end{cases}$$

In this case, the representative point comes to a stable node ($\sqrt{\varepsilon/2}, \sqrt{\varepsilon/2}, \sqrt{\varepsilon/2}$), and all the elements remain active.

From the foregoing it follows that for such values of ε there exist two modes in the system: when all the elements are passive and when all the elements are active ($\rho_1 = \rho_2 = \rho_3 = \sqrt{\varepsilon/2}$). Switching sequential dynamics are absent here.

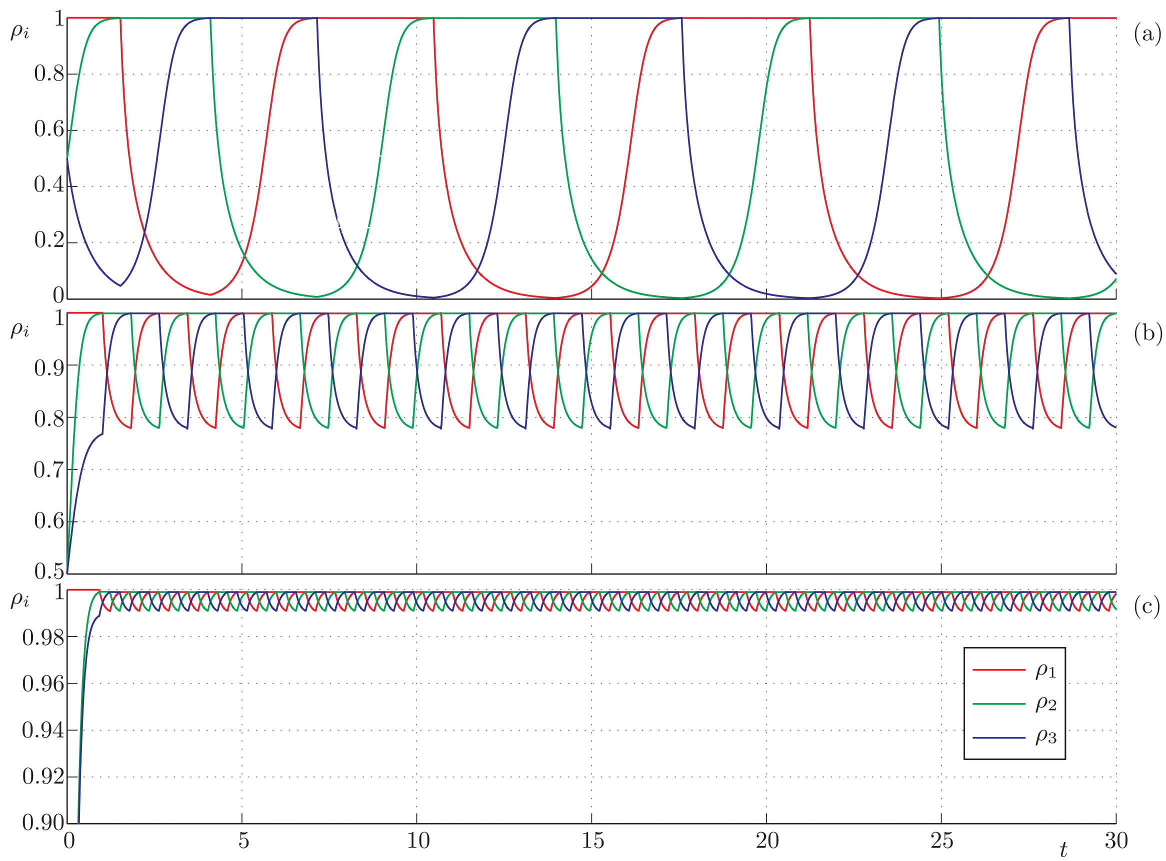

Fig. 3. Time series of the variables ρ_i for different values of ε ((a) $\varepsilon = 0.4$, (b) $\varepsilon = 1.6$, (c) $\varepsilon = 1.98$). When ε increases, the oscillation amplitude decreases to zero.

Let us determine possible types of motion in the phase space depending on ε ($0 < \varepsilon < q^2 + 1$). Let the initial conditions be (q, a, q)[5]. Then we construct a map from the cube edge $\rho_1 = \rho_3 = q$, $0 \leqslant \rho_2 \leqslant q$ to the edge $\rho_1 = \rho_2 = q$, $0 \leqslant \rho_3 \leqslant q$. The dynamics of the system on the invariant plane $\rho_1 = q$ are defined by

$$\begin{cases} \dot{\rho}_2 = \rho_2(1 - {\rho_2}^2) \\ \dot{\rho}_3 = \rho_3(\varepsilon - 1 - {\rho_3}^2). \end{cases} \tag{4.4}$$

[5] We consider initial conditions of this type only because for any other set of initial conditions that allows the existence of one active element only the representative point acquires a similar type of behavior after a while.

If $\varepsilon = 1$, the solution of (4.4) that satisfies the initial conditions is

$$\begin{cases} \dfrac{\rho_2\sqrt{1-a^2}}{a\sqrt{1-{\rho_2}^2}} = e^t \\ \dfrac{1}{2{\rho_3}^2} - \dfrac{1}{2\cdot q^2} = t. \end{cases}$$

The final point to which we come has coordinates $\rho_2 = q$, $\rho_3 = b$[6]. The dependence $b(a)$ is given by the formula

$$b = \sqrt{\frac{1}{\dfrac{1}{q^2} + \ln\dfrac{q^2(1-a^2)}{a^2(1-q^2)}}}.$$

This function has 3 points of intersection with the line $b = a$: at the endpoints of $[0, q]$ and at the interior point of this interval that corresponds to a stable limit cycle[7].

When $\varepsilon \neq 1$, the system has the following solution:

$$\begin{cases} \dfrac{\rho_2\sqrt{1-a^2}}{a\sqrt{1-{\rho_2}^2}} = e^t, \\ \dfrac{\rho_3\sqrt{|q^2-\varepsilon+1|}}{q\sqrt{|{\rho_3}^2-\varepsilon+1|}} = e^{(\varepsilon-1)t}. \end{cases} \tag{4.5}$$

Hence, we obtain the expression for b:

$$b = \sqrt{\frac{q^2(\varepsilon-1)}{q^2 - |q^2-\varepsilon+1|\left(\dfrac{a^2(1-q^2)}{q^2(1-a^2)}\right)^{\varepsilon-1}}}. \tag{4.6}$$

The function $b(a)$ is increasing. It intersects the y-axis in $\sqrt{\varepsilon-1}$ when $1 \leqslant \varepsilon < q^2+1$ and in 0 when $0 < \varepsilon \leqslant 1$. It also passes through the point (q, q) and has another intersection with the line $b = a$ in (a^*, b^*) (i.e., $a^* = b^*$) when $0 < a^* < q$. This point corresponds to a stable limit cycle. The dependence $b(a)$ is shown in Figure 4.

Thus, in the phase space of the system for $0 < \varepsilon < q^2+1$ there is a stable limit cycle, and b^* is the minimum level of spike activity.

The duration of the elements' activity can be found from the first equation of system (4.5) and formula (4.6). To do this, we set the initial value of a_0 and use the formulas

$$\Delta t_{i+1} = \ln\frac{q\sqrt{1-{a_i}^2}}{a_i\sqrt{1-q^2}}$$
$$a_{i+1} = \sqrt{\frac{q^2(\varepsilon-1)}{q^2 - |q^2-\varepsilon+1|\left(\dfrac{{a_i}^2(1-q^2)}{q^2(1-{a_i}^2)}\right)^{\varepsilon-1}}}.$$

---

[6] a and b are the coordinates of intersection points where the phase trajectory crosses the cube edges.

[7] To determine if we have a limit cycle, it is not necessary to consider all three invariant planes $\rho_i = q$ because the dynamics are exactly the same on all of them.

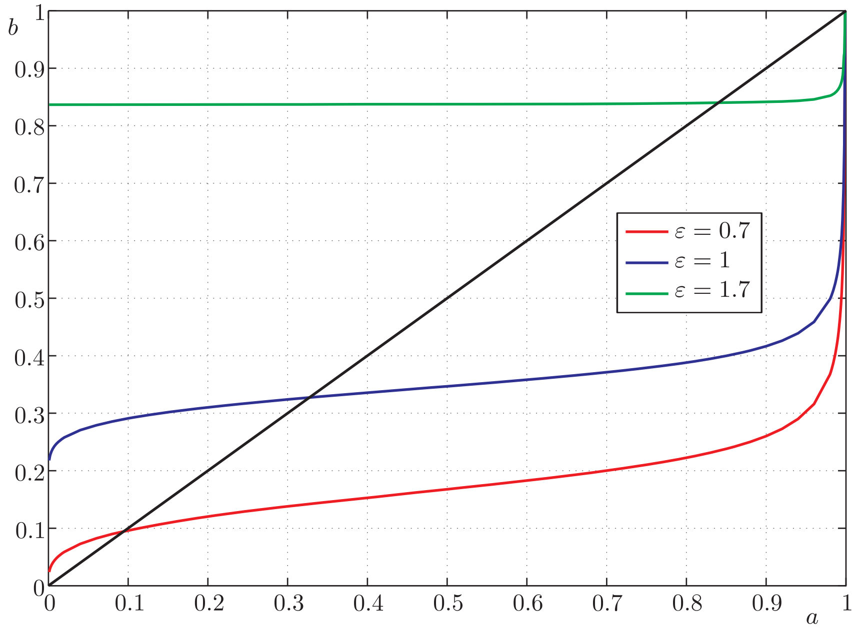

Fig. 4. The dependence $b(a)$ for various values of ε.

5. IMPACT OF A SMALL PARAMETER ON THE SYSTEM

In real situations the behavior of neural networks is affected by external perturbations. Let us add a small parameter μ to the system and consider its effect on the dynamics of the original system with unidirectional couplings.

The perturbed system is

$$\begin{cases} \dot{\rho}_1 = F(\rho_2, \rho_3)(\rho_1(-1 + 2F(\rho_3) - {\rho_1}^2) + \mu), \\ \dot{\rho}_2 = F(\rho_3, \rho_1)(\rho_2(-1 + 2F(\rho_1) - {\rho_2}^2) + \mu), \\ \dot{\rho}_3 = F(\rho_1, \rho_2)(\rho_3(-1 + 2F(\rho_2) - {\rho_3}^2) + \mu), \end{cases}$$

where $F(x, y) = F(x) + F(y)$.

Numerical calculations show that in this case there is no increase in time that the phase point spends in the vicinity of the saddles.

Thus, the introduction of a small parameter μ destroys the heteroclinic cycle and leads to the creation of a stable limit cycle.

6. CHAOTIC DYNAMICS OF MOTIF

The generalized Lotka–Volterra model has been the subject of many studies. For example, as shown in [13], if we assume that there is interspecific competition, a strange attractor can exist in 4- and higher dimensional systems. Thus, a strange attractor was found in a 4-dimensional system [14, 15]. It is also proved in some works ([12]) that without interspecific competition a strange attractor can exist even in a 3-dimensional system. The above-mentioned study gives us an example of a Henon strange attractor that appears after a sequence of period-doubling bifurcations. In this paper, we aimed to find strange attractors in system (3.1) with some changes. We will not use normalization, i.e., all coefficients M_i from formula (2.5) are equal to 1. Also, we will use the continuous sigmoid function

$$F(x) = \frac{1}{1 + \exp(10(0.999 - x))}$$

instead of the Heaviside function as it was mentioned in Section 2. In order to find strange attractors, we will fix the values of some parameters of the system and will only vary the parameter g_{21}. The coupling matrix is as follows:

$$G = \begin{pmatrix} 0 & 2 & -10 \\ g_{21} & 0 & 2 \\ 2 & 3 & 0 \end{pmatrix}. \tag{6.1}$$

Figures 5 show phase portraits of the system. Figure 5a shows the system with a limit cycle. When parameter g_{21} decreases to 8.245, the period-doubling bifurcation occurs, resulting in the creation of a limit cycle with doubled period (see Fig. 5b). As g_{21} decreases even further and reaches the value of 6.795, we observe another period-doubling bifurcation and the limit cycle doubles again (see Fig. 5c). We suppose that with a further decrease of g_{21} the limit cycle undergoes an endless cascade of period-doubling bifurcations. As a result, when $g_{21} < 5.7$, the system has a strange attractor of Feigenbaum type ([16], see Fig. 5d). To support this hypothesis, we calculated the spectrum of Lyapunov exponents of our system depending on g_{21} in the range $[5.5, 8.5]$. Figure 6 shows the graph of dependence of three Lyapunov exponents λ_1, λ_2 and λ_3 on g_{21}. At the moment of period-doubling bifurcation the second highest exponent becomes 0, and when $g_{21} < 5.75$, the maximum of the Lyapunov exponent is greater than 0, which corresponds to the emergence of chaotic behavior in the system (birth of a strange attractor).

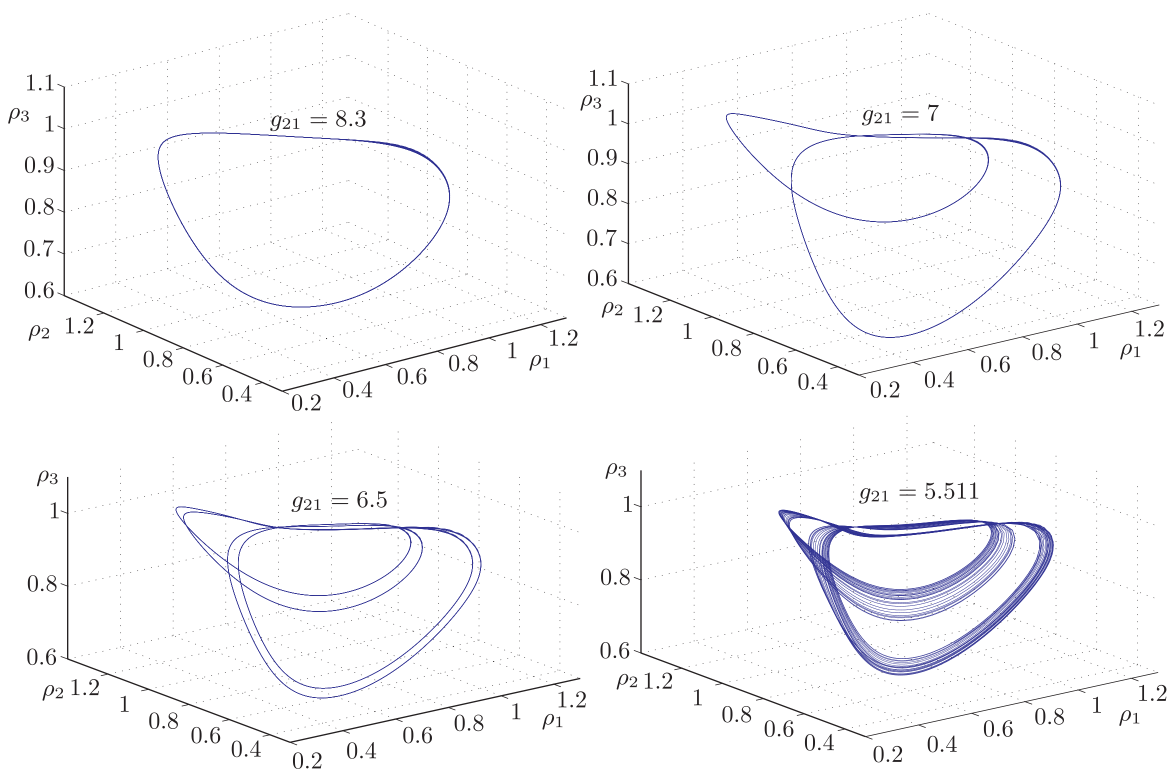

Fig. 5. Phase portraits of the system (2.1)–(2.5) with the coupling matrix (6.1). A cascade of period-doubling bifurcation leads to the birth of a strange attractor of Feigenbaum type.

7. CONCLUSION

In this paper we have proposed and studied a new model of a motif. The elements were connected with each other by excitatory couplings. We studied models with both mutual and unidirectional couplings. It was found that if an asymmetric coupling takes place, then there appears a stable

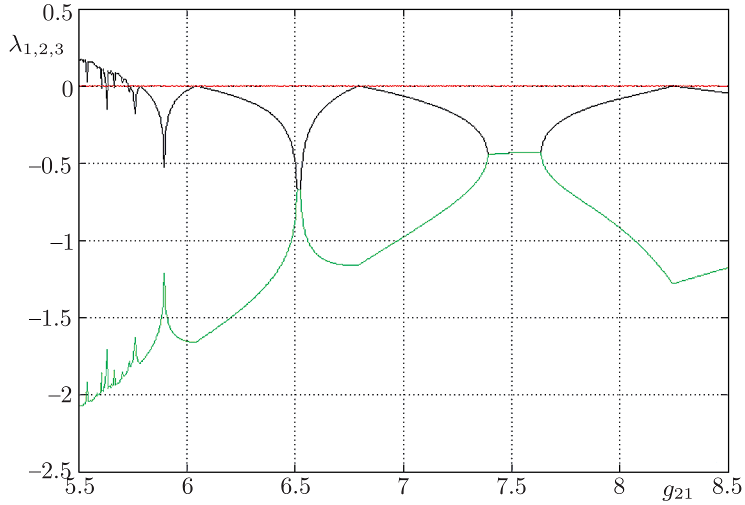

Fig. 6. The Lyapunov exponents of the system (2.1)–(2.5) with the coupling matrix (6.1).

heteroclinic cycle in the phase space of the system. A stable heteroclinic cycle also exists in the motif of inhibitorily coupled neuron-like elements. However, the motif with mutual couplings does not have a stable heteroclinic cycle but has a stable limit cycle. In addition, we studied the perturbed system. It was discovered that this system also has a stable limit cycle instead of a stable heteroclinic one.

We studied our system (with small changes) in order to examine its chaotic behavior and found a strange attractor. This attractor is born via the Feigenbaum scenario. Recall that strange attractors were found in the classical generalized Lotka – Volterra model and were born via a cascade of period-doubling bifurcations. Although our system is not a classical one, the birth of a strange attractor also happens via a cascade of period-doubling bifurcations.

ACKNOWLEDGMENTS

The authors thank I. R. Sataev for help with numerics.

The research for this paper was supported by the following grants: the results from Sections 1–3 were supported by the Russian Science Foundation under Contract No. 14-12-00811, those from Sections 4, 5 were supported by the Russian Science Foundation under Contract No. 14-11-00693, and the results from Section 6, 7 were supported by by the Basic Research Program at the National Research University Higher School of Economics (project 138) in 2015 and by LATNA Laboratory, NRU HSE, RF government grant 11.G34.31.0057.

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