The solution of the second Peskin conjecture and developments

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Abstract The integrate-and-fire cardiac pacemaker model of the pulse coupled oscillators was introduced by C. Peskin. Due to the function of the pacemaker, two famous synchronization conjectures for identical and not identical oscillators were formulated. The first conjecture of Peskin was solved in paper [61] by S.Strogatz and R.Mirollo. The second conjecture has been solved in paper [3] by utilizing a special map to analyze pulse-coupled biological oscillators. There are still many issues related to the nature and types of couplings. The couplings may be impulsive, continuous, delayed or advanced, and oscillators may be locally or globally connected. Consequently, it is reasonable to consider various ways of synchronization, if one wants the biological and mathematical analyses to interact productively. We investigate the integrate-and-fire model in both cases - one with identical, and another with not quite identical oscillators. A combination of continuous and pulse couplings that sustain the firing in unison is carefully constructed. Moreover, we obtain conditions on the parameters of continuous couplings that make possible a rigorous mathematical investigation of the problem. The technique developed for differential equations with discontinuities at non-fixed moments [2] and a special continuous map lie in the basis of the analysis. We consider the C. Peskin model of the cardiac pacemaker with retarded pulse-couplings and with continuous couplings. Sufficient conditions for synchronization of identical and non-identical oscillators are obtained. The bifurcation of periodic motion is observed. The results are demonstrated with numerical simulations.

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1 Introduction and preliminaries

In paper [50] C. Peskin develops the integrate-and-fire model of the cardiac pacemaker [34] to a population of identical pulse-coupled oscillators. Thus, it was proposed to consider a model of cardiac pacemaker, where signal of fire arises not from an outside stimuli, but in the population of cells itself. Well known conjectures of self-synchronization were formulated and solutions of these conjectures for *identical oscillators* [50, 47] stimulated mathematicians as well as biologists for the intensive investigations in the field [8, 17, 20, 27, 35, 38, 46, 49, 54, 60, 62, 63, 64].

A specialized bundle of about 10000 neurons located in the upper part of the right atrium of the heart is known as the sinoatrial node. It fires at regular intervals to cause the heart beat with a rhythm of about 60 to 70 beats per minute for a healthy, resting heart. The electrical impulse from the pacemaker triggers a sequence of electrical events in the heart to control the orderly sequence of muscle contractions that pump the blood out of the heart. That is why it is called the *cardiac pacemaker* in the literature. The cells of the sinoatrial node are able to depolarize spontaneously toward the threshold firing, and then recover [10]. The electrical activity of the cardiac pacemaker produces a strong pattern of voltage change. While it is the norm for nerve cells that they require a stimulus to fire, cells of the cardiac pacemaker can be considered to be “self-firing”. It repetitively goes through a depolarizing discharge and then recover to fire again. This action is analogous to a relaxation oscillator in electronics. The circuit involves a capacitor which is charged by the energy of a battery (the membranes of the sinoatrial node and the ion transport processes play the role) and a resistor which controls the flashing rate of the light. In the case of the sinoatrial node, there is an input from the physiology of the body related to oxygen demand and other factors which control the rate of firing of the sinoatrial node and hence the heart rate. The question naturally arises how the neurons organize their *firing in unison*. The simplest explanation was that the fastest neuron drives all the others bringing them to the threshold. If it were the case, then the injury of a single cell could have significantly changed the frequency of the heart beat. To avoid this important shortcoming, in paper [50] C. Peskin proposed a model of a cardiac pacemaker, where signals of fires arise not from an outside stimuli, but originate in the population of cells itself. Moreover, it was proposed that a cardiac pacemaker is a population of neurons with weak couplings such that synchrony emerges as a result of the interaction of all cells, rather than a single cell domination.

In papers [3]-[7], we have introduced a new method for investigation of biological oscillators. The method seems to be universal to analyze integrate-and-fire oscillators. In particular, we have solved the Second Peskin conjecture in [3, 5]. It was proved that an ensemble of arbitrary number of oscillators synchronizes even if they are *not quite identical*.

In the present chapter we extend the approach to the model with delayed pulse-coupling. Conditions are found, which guarantee synchronization of the model. Our system is different than that in [17], since we suppose that the pulse-coupling is instantaneous, if oscillators are close to each other and are near threshold. In next our papers, we plan to consider other models, varying types of the delay involvement, as well as inhibitory models such that analogues of results in [17] and [64] can be obtained. Moreover, we plan to develop for these systems the theory of the bifurcation of periodic solutions. Some of open problems are discussed in the conclusion part of the paper. The method of the analysis of non-identical oscillators is based on results of the theory of differential equations with discontinuities at non-fixed moments [2].

The cells that create rhythmical impulses for contraction of the cardiac muscle, and control the heart rate, are called pacemaker cells. C. Peskin developed a model of an encoding neuron [34] for a population of identical pulse-coupled oscillators [50]. The synchronization of the system, viewed as firing in unison, was proved for two [50] and more than two [47] identical oscillators. In fact, C. Peskin proposes a model, which is a hybrid of continuous and discrete equations, that admits synchrony. The suggestion was so attractive that it has been used not only for cardiac models, but also, for example, for coupled neurons [9]. The paper [47] has been the most stimulating and intensive analysis of the problem [8]-[54].

The mathematical problems connected to synchrony emerge in numerous applications - not only in a model of heart beat [34, 50], but also in models of firefly flashing [11, 25], insulin-secreting cells of the pancreas [55], neural networks [39, 53],[30]-[21], etc. There is still much uncertainty with respect to the types of coupling in population (these may be impulsive, continuous, delayed, advanced, regular or random) [47, 17, 20, 12, 11, 14, 25, 32, 37, 43, 53, 65], and with respect to the structural complexity of networks - connection may be local or global, with various quantitative characteristics and geometrical configurations [14, 59, 61]. It is clear that the larger the diversity of mathematical models, the more opportunities to tackle the biological issues.

It is natural that the problem has been considered in the more general form. In [47] the method of phase diagrams effectively is used to discuss the models. In paper [3] we suggested a special map, which helped us to solve the synchronization problem for non-identical oscillators. A version of the model is considered such that perturbations can be evaluated still to save the synchronization. Other problems of the theory are considered. Particularly, relation of synchronization and spatial structure. Nevertheless, an analysis of models with general form of dynamics has remains unconsidered. In the present chapter we are going to extend our proposals of [3] to the case suitable for various applications. They can be developed easily further such that the results have an important meaning for the theory of integrate-and-fire models of biological oscillators in both exhibitory and inhibitory cases as well as for different types of couplings: continuous; delayed, etc. Moreover, we suppose that the approach can be utilized for various types of motions of the systems: periodic, almost periodic, chaotic, since results of the discrete equations are now available for applications. To prove assertions of the present paper concerning multidimensional systems of non-identical oscillators, we need advanced comprehension of the theory of dynamical systems with discontinuities at variable moments of time [2]. This is one more reason, why we decided to write this chapter apart of [3], where only, the Peskin's model has been considered with the respectively simple theoretical methods. Oscillators considered in the present chapter are connected with each other not only at the firing moments, but permanently. That is, the differential equations are not separated as it is, for example, in papers [47, 50]. One can admit that this fact provides more biological sense to investigations. The paper consists of the main results, simulations and the discussion of the possible generalization.

The main object of our investigation in the next section is an integrate-and-fire model, which consists of n non-identical pulse-coupled oscillators, $x_i, i = 1,2,\ldots,n$. Set $x = (x_1,x_2,\ldots,x_n)$. If the system does not fire the oscillators satisfy the following equations

$$x_i' = f(x_i) + \phi_i(x), \tag{1}$$

where $0 \le x_i \le 1+\zeta_i(x), i = 1,2,\ldots,n$. When the oscillator $x_j(t), j = 1,\ldots,n$ increases its value from the zero, and meets the surface $x_j = 1+\zeta_i(x)$ at the first time, such that $x_j(t) = 1+\zeta_i(x)$ then the oscillator fires, $x_j(t+) = 0$. Firing changes the values of all oscillators with $i \ne j$, such that at the same moment t,

$$x_i(t+) = \begin{cases} 0, \text{ if } x_i(t)+\varepsilon+\varepsilon_i \ge 1+\zeta_i(x), \\ x_i(t)+\varepsilon+\varepsilon_i, \text{ otherwise.} \end{cases} \tag{2}$$

It is assumed also that there exist positive constants μ_i and ξ_i such that $|\phi_i(x)| < \mu_i$ and $|\zeta_i(x)| < \xi_i$, for all x and $i = 1,2,\ldots,n$. In what follows, we call real numbers $\varepsilon,\mu_i,\xi_i,\varepsilon_i$, *parameters*, assuming the first one is positive. Moreover, constants $\xi_i,\varepsilon_i,\mu_i$, will be called *parameters of perturbation*. If all of them are zeros one obtains the model of identical oscillators. We assume that $\varepsilon+\varepsilon_i-\xi_i > 0$ and $\varepsilon+\varepsilon_i+\xi_i < 1$, for all i, the function f is positive valued and lipschitzian. Moreover, assume that all functions involved in the discussion are continuous, and the system (1) satisfies conditions of a theorem of existence and uniqueness, and each solution of the system is continuable to the threshold's value.

We have chosen the all-to-all coupling such that each firing elicits jumps in all non-firing oscillators. If several oscillators fire simultaneously, then other oscillators react as it just one oscillator fires. In other words, any firing acts only as a signal which abruptly provokes a state change, the intensity of the signal is not important, and pulse strengths are not additive. Opposite case will also be discussed in this paper.

Two oscillators are synchronized if they firing in unison. A system of oscillators is synchronized if all of them fire in unison.

Next, in Section 3 we extend the method and these results to the model with continuous couplings. Sufficient conditions for synchronization are found. The research utilizes results and proposals from [34, 50, 24],[12]- [65]. We investigate the integrate-and-fire model for both cases - with identical and not quite identical oscillators. A combination of continuous and pulse couplings that sustain the firing in unison is carefully constructed. Moreover, we find conditions on the parameters of continuous couplings that make possible a rigorous mathematical investigation of the problem.

Let us consider, first, n identical oscillators, which are characterized by voltage state variables $x_1, x_2, \ldots, x_n$ with values in $[0,1]$. The following assumptions describe the model and its coupling style.

$(A1)$. If $x_j(t) = 1$, then the oscillator fires, and there exists a positive number ε such that

$$x_i(t+) = 0, \text{ if} x_i(t) \geq 1 - \varepsilon \tag{3}$$

for all $i \neq j$.

Fix a positive τ. If $t = s$ is a firing moment of x_j, then the interval $[s, s+\tau]$ is said to be the e^j-interval or $e-$interval for all $x_i, i \neq j$. We say that an oscillator $x_i(t)$ *is continuously excited* if t is in an $e-$interval, and $x_i(t) < 1$.

$(A2)$. When $x_i(t)$ is not continuously excited, then

$$x_i' = S - \gamma x_i. \tag{4}$$

Otherwise, there exists a positive real number η such that

$$x_i' = (S + \eta) - \gamma x_i. \tag{5}$$

$(A3)$. Positive constants S, γ, η and ε satisfy the following inequalities:

(i) $\gamma < S$;
(ii) $\eta \leq \varepsilon$;
(iii) $e^{\gamma\tau} - 1 < \min\{1, \frac{\varepsilon}{S-\gamma+\eta}\}$.

We call the collection of n oscillators $x_1, x_2, \ldots, x_n$, *the integrate-and-fire model of continuously coupled identical biological oscillators*, if conditions $(A1) - (A3)$ hold.

One should emphasize that the coupling is all-to-all, and exciting strengths are not additive. The model of the present paper admits two types of coupling: the *continuous* one, which is described by $(A2)$; the *impulsive* coupling given by $(A1)$. In the first case the motion of oscillators remains continuous, if they are not near the threshold. Nevertheless, the rate of oscillators jumps to response. Otherwise, by assumption $(A1)$ oscillators are coupled impulsively.

This assumption is natural, since firing provokes other oscillators instantaneously, if they are near thresholds, and are therefore in the state ready to fire. From the proofs of this paper it will be seen that the constant η in $(A2)$ can be replaced with a function defined on the real axis, continuous and non-zero on $e-$intervals. That is why it is reasonable to say that oscillators are *continuously* coupled.

To illustrate the last remark, let us provide the following simulation. Consider three oscillators: x_1, x_2 and x_3 with initial values $0.2, 0.5$ and 0.9 respectively. They satisfy (4) and (5) with $S = 2, b = 2, \eta = 2.1, \tau = 0.05, \varepsilon = 0.15$. The motion of these oscillators is seen in Figure 1.

Couplings $\alpha^2(t - t_0)e^{\alpha(t-t_0)}$, where t_0 is the firing moment, were used in paper [64] to find that with “fast enough excitatory coupling both the fully synchronized and the asynchronous state are unstable. In this case individual units fire quasi-periodically even though the network as a whole shows a periodic firing pattern." The results of our paper are different from those of [64]. Firing in unison is achieved, and this synchrony is stable. The difference can be explained with the smallness of α functions near the firing moments. We plan to discuss the clustering phenomenon of integrate-and-fire models in [7].

Since the dynamics of systems considered in the present paper are discontinuous, we strongly believe that they can be investigated with the methods developed for differential equations with variable moments of discontinuity [2] in the future. Controllability, phase locking, frequency locking, synchrony, almost periodic solutions and even chaos can be considered in this theory.

Delays arise naturally in many biological models [48]. In particular, they were considered in firefly models [12] as delay between stimulus and response, and in continuously coupled neuronal oscillators [35]. Authors of [17] considered the phenomenon for the analysis of Mirollo and Strogatz in such a way that identical oscillators were investigated. The dynamics of two oscillators were discussed mathematically, and a multi-oscillatory system was analyzed by using computer simulations. It was found that the excitatory model of two units "can get only out-of-phase synchronization since in-phase synchronization proved to be not stable." In paper [20] a model without a leakage was discussed, that is, oscillators increase at a constant rate between moments of firing. It was found that a periodic solution is reached after a finite time. Consequently, research of integrate-and-fire models, which admit delays and fire in unison is still on the agenda. Section 4 investigates synchrony of retarded integrate-and-fire oscillators.

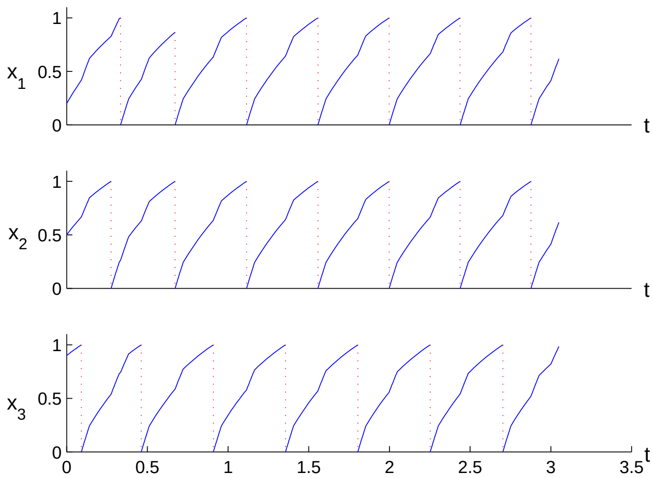

Fig. 1 The intervals where oscillators satisfy equations (4) and (5) are depicted.

2 The solution of the Peskin second conjecture

2.1 Construction of the prototype map

In this subsection we shall define the map, which is the basic instrument of our investigation. The map will be considered in a general form, such that new investigations can be done in future on its basis. Let the model of two identical oscillators, $x_1(t), x_2(t), t \geq 0$, be given such that

$$\begin{aligned} x_1' &= g(x_1, x_2), \\ x_2' &= g(x_2, x_1), \end{aligned} \tag{1}$$

where $0 \leq x_i \leq 1, i = 1, 2, \ldots, n$, the function g is positive and lipschitzian in both arguments. When the oscillator x_j fires at the moment t such that $x_j(t) = 1$, then the oscillator fires, $x_j(t+) = 0$. Firing changes the value of another oscillator with $i \neq j$, such that

$$x_i(t+) = \begin{cases} 0, \text{ if } x_i(t) + \varepsilon \geq 1, \\ x_i(t) + \varepsilon, \text{ otherwise.} \end{cases} \tag{2}$$

Denote by $u(t, t_0, u_0) = (u_1, u_2)$, the solution of (1) such that $u(t_0, t_0, u_0) = u_0$. Conditions on g imply that the solution exist, unique, and is continuable to the threshold for all t_0 and u_0. Consider the solution $u(t) = u(t, 0, (0, v + \varepsilon))$. Find the moment $t = s$ such that $u_2(s) = 1$, and define $\bar{L}(v) = u_1(s)$ on $(0, 1 - \varepsilon)$. From the conditions on g it implies that s is a strictly decreasing continuous function of v, and, then $\bar{L}$ is a strictly decreasing continuous function of v. It is clearly seen that $\lim_{v \to 1-\varepsilon} \bar{L}(v) = 0$, and there is a unique fixed point, v^*, of the function, $\bar{L}(v^*) = v^*$. Let $\eta = \lim_{v \to 0+} \bar{L}(v)$.

Now, let us define a map $L : [0, 1] \to [0, 1]$, such that

$$L(v) = \begin{cases} \bar{L}(v), \text{ if } v \in (0, 1 - \varepsilon), \\ \eta, \text{ if } v = 0, \\ 0, \text{ if } v \in [1 - \varepsilon, 1]. \end{cases} \tag{3}$$

In what follows we need the following conditions:

(A1) $\eta > 1 - \varepsilon$;
(A2) the map L^2 admits a unique fixed point v^* in $(0, 1 - \varepsilon)$.

This newly defined function is continuous on $[0, 1]$. The sketch of the graph of the function L is seen in the Figure 2.

To make the following discussion constructive consider the sequence of maps $L^k(v), k = 1, 2, \ldots$, where $L^k(v) = L(L^{k-1}(v))$. The graphs of these maps with $k = 1, 2, 3$ is shown in the Figure .

Denote $a_0 = 0, a_1 = 1 - \varepsilon, a_2 = L^{-1}(1 - \varepsilon), a_3 = (L^2)^{-1}(1 - \varepsilon), \ldots$. The sequences can be obtained also through the iterations $a_0 = L^{-1}(\eta) = 0, a_{k+1} =$

$L^{-1}(a_k), k = 0,1,2,\ldots,$ which are seen in Figure 3. It is clear that the sequences a_{2i} and a_{2i+1} are monotonic, decreasing and increasing respectively. Otherwise, one can show, by utilizing the Intermediate Value Theorem, that there exists a period-2 motion of the discrete dynamics. This contradicts the condition $(A2)$. Thus, the both sequences converge. These limits equal to v^*. Indeed, if they are different, then there exists a period-2 motion of the dynamics, and that has been excluded earlier.

Let us show the role of the map L for our research. Suppose that $t_1,t_2,t_3,$ are three successive firing moments of the system such that x_1 fires at t_1 and t_3, the oscillator x_2 fires at t_2, and the oscillators are not synchronized untill t_3. We have that $x_1(t_1+) = 0, 0 < x_2(t_1) < 1-\varepsilon$. One can see that $x_2(t) = u(t,t_1,x_2(t_1)+\varepsilon)$ for $t_1 < t \leq t_2$, and $u(t_2,t_1,x_2(t_1)+\varepsilon) = 1$. That is, $x_1(t_2) = L(x_2(t_1))$. Similarly one

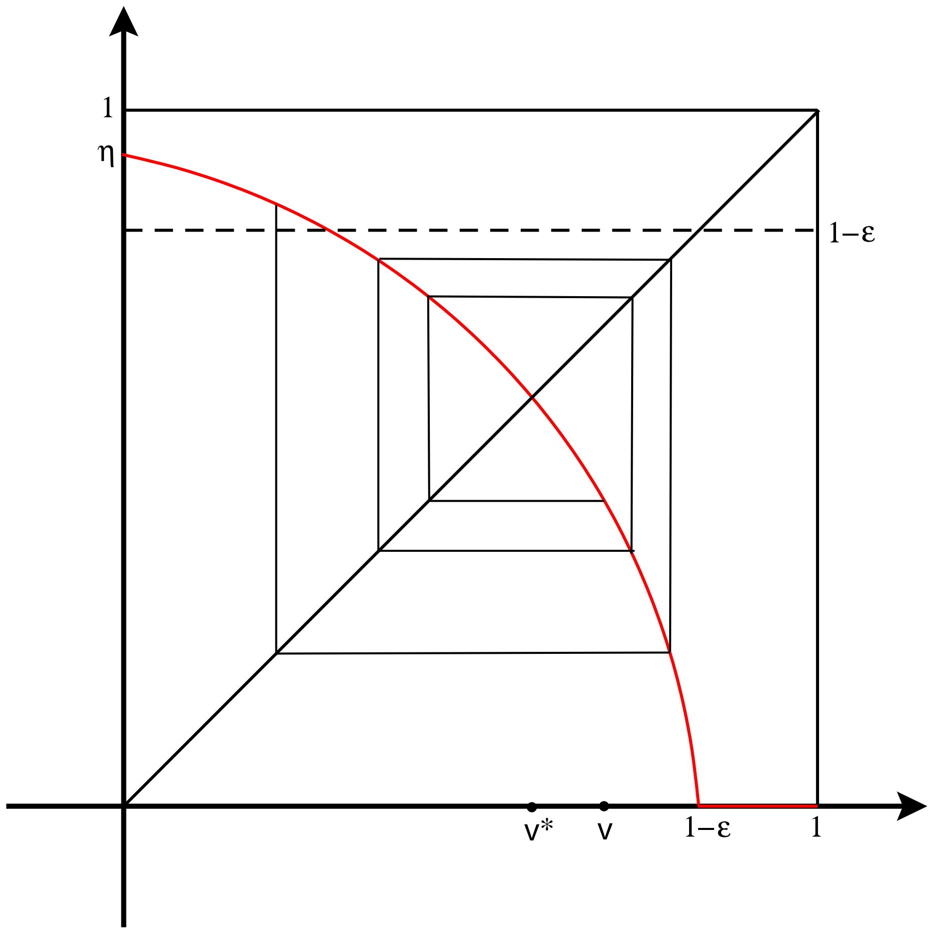

Fig. 2 The graph of the function $w = L(v)$, in red, and a stabilized trajectory.

can show that $x_2(t_3) = L(x_1(t_2))$. This demonstrates how can the map L used for the analysis of the synchronization problem.

Next, we shall prove the synchronization and evaluate the rate of synchronization simultaneously. The rate evaluation will be done in a specific way: we shall indicate the set of initial points which synchronize after precisely k iterations of the map for each non-negative integer k. Another valuable set in this sense is collection of all points, which synchronize after no more than k iterations, is shaped. In the sequel, denote by B_k the region in $[0,1]$, where points v are synchronized after $k-$ iterations of map L. Consider the Figure 3, again.

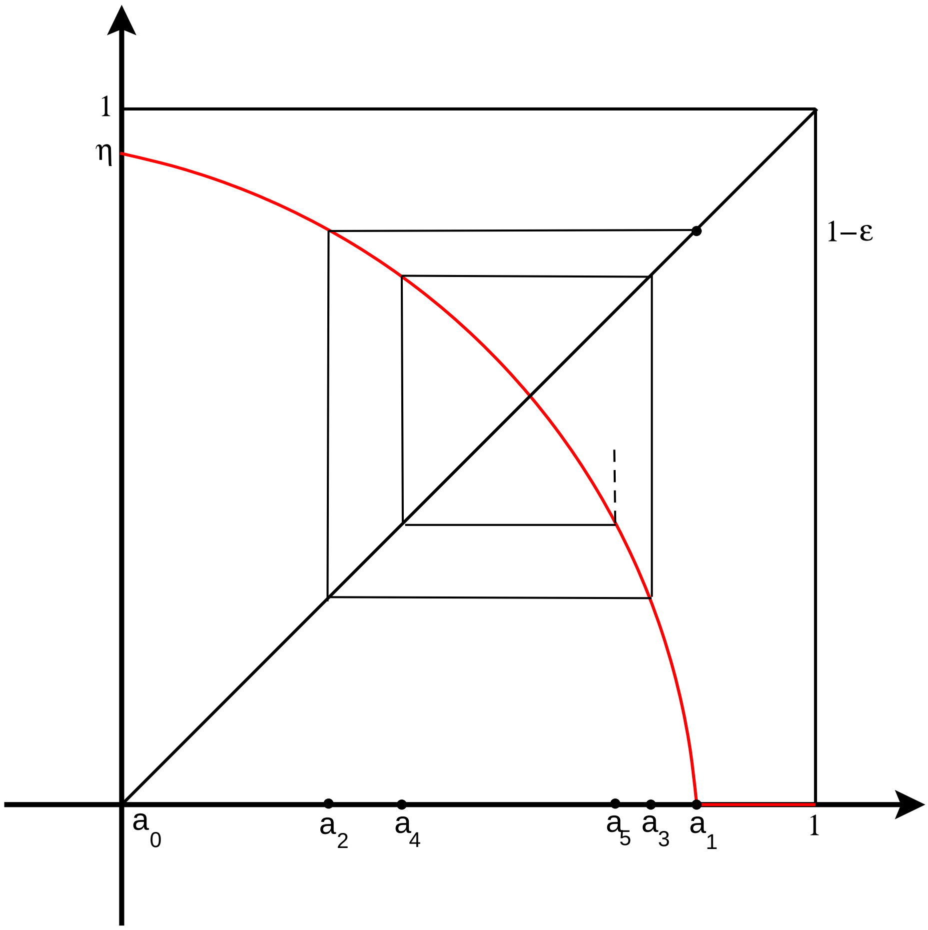

Fig. 3 The points $a_0 = L^{-1}(\eta) = 0, a_{k+1} = L^{-1}(a_k), k = 0,1,2,\dots.$

One can see that $B_0 = [1-\varepsilon, 1]$, and, consequently, $B_k = [a_{k-1}, a_{k+1}]$, if k is an odd positive integer, and $B_k = [a_{k+1}, a_{k-1}]$, if k is an even positive integer. We have that $a_k \to v^*$ as $k \to \infty$.

Denote by C_k the region of all points, which synchronize in no more than k iterations of L. One can see that $C_k = [0,1]\backslash(a_k, a_{k+1})$, if k is an even number, and it is the set $C_k = [0,1]\backslash(a_{k+1}, a_k)$, if k is an odd number. In the next section we shall use the set $C_k^c = [0,1]\backslash C_k$, that includes all points, which synchronize in no less than $k+1$ iterations of the map. From the discussion made above it follows that there is no finite time in which *all points* of the unit square synchronize. The closer v is to the equilibrium v^* the later is the moment of synchronization.

Denote by T the natural period of oscillators, that is, the period of the each of the identical units, when there is no couplings. Since each oscillator necessarily fires within an interval of length T, on the basis of the above discussion the following assertion is valid:

Theorem 1. *Assume that* $(A1)$ *and* $(A2)$ *are valid. If* $(x_1(0), x_2(0)) \in C_k \times C_m, k$ *and* m *are natural numbers, then the couple* x_l, x_r *synchronizes within the time interval* $[0, T(\max(k,m)+1)]$.

Example 1. Consider the model of two integrate-and-fire identical oscillators, which is pulse-coupled, of the form

$$
\begin{aligned}
x_1' &= S + \gamma x_1 + \beta x_2, \\
x_2' &= S + \gamma x_2 + \beta x_1,
\end{aligned}
\tag{4}
$$

where constants S and β are positive numbers, and γ negative one. One can easily see that the system is developed Peskin's model [50]. The terms with coefficient β are additional in the system. They reflect the permanent influents of the partners during the process. Eigenvalues of the correspond linear system to (4) are $\lambda_1 = \gamma + \beta$ and $\lambda_2 = \gamma - \beta$. We suppose that β is small such that both eigenvalues are negative. Moreover, it is assumed that $\kappa = S/\lambda_1 < -1$. Solution of the system (4) with value $(0, v+\varepsilon)$ at $t = 0$, is equal to

$$
u_1(t) = \frac{1}{2}[e^{\lambda_1 t} - e^{\lambda_2 t}](v+\varepsilon) + \kappa(e^{\lambda_1 t} - 1),
$$

$$
u_1(t) = \frac{1}{2}[e^{\lambda_1 t} + e^{\lambda_2 t}](v+\varepsilon) + \kappa(e^{\lambda_1 t} - 1).
$$

That is why, the needed equations have the following forms:

$$
\frac{1}{2}[e^{\lambda_1 t_2} + e^{\lambda_2 t_2}](v+\varepsilon) + \kappa(e^{\lambda_1 t_2} - 1) = 1,
\tag{5}
$$

and

$$
L(v) = \frac{1}{2}[e^{\lambda_1 t_2} - e^{\lambda_2 t_2}](v+\varepsilon) + \kappa(e^{\lambda_1 t_2} - 1).
\tag{6}
$$

Last two formulas imply that

$$L(v)=\frac{e^{\lambda_1 t_2}-e^{\lambda_2 t_2}+2\kappa e^{\lambda_2 t_2}(e^{\lambda_1 t_2}-1)}{e^{\lambda_1 t_2}+e^{\lambda_2 t_2}}.$$

Differentiating (5) one can find that

$$\frac{\partial t_2}{\partial v}=-\frac{1}{2}\frac{[e^{\lambda_1 t_2}+e^{\lambda_2 t_2}]^2}{(1+\kappa)(\lambda_1 e^{\lambda_1 t_2}+\lambda_2 e^{\lambda_2 t_2})+2\beta\kappa e^{(\lambda_1+\lambda_2)t_2}}$$

and

$$\frac{\partial^2 t_2}{\partial v^2}=-\frac{1}{2}\frac{\partial t_2}{\partial v}\frac{(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})(1+\kappa)[(\lambda_1 e^{\lambda_1 t_2}+\lambda_2 e^{\lambda_2 t_2})^2-4\beta^2 e^{(\lambda_1+\lambda_2)t_2}]}{[(1+\kappa)(\lambda_1 e^{\lambda_1 t_2}+\lambda_2 e^{\lambda_2 t_2})+2\beta\kappa e^{(\lambda_1+\lambda_2)t_2}]^2}+$$

$$\frac{2\kappa\beta e^{(\lambda_1+\lambda_2)t_2}(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})(2\lambda_1-1)(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})]}{}$$

We deliberately have written the last two formulas in the form such that it is easily seen that the both derivatives are negative if S is sufficiently large, and β is sufficiently small. Next, we evaluate the derivatives of L.

$$L'(v)=\frac{\partial t_2}{\partial v}\frac{2\kappa e^{\lambda_2 t_2}(e^{\lambda_1 t_2}-1)(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})+4\beta e^{(\lambda_1+\lambda_2)t_2}[1-\kappa(e^{\lambda_1 t_2}-1)]}{[e^{\lambda_1 t_2}+e^{\lambda_2 t_2}]^2}$$

$$L''(v)=\frac{\partial^2 t_2}{\partial v^2}\frac{2\kappa e^{\lambda_2 t_2}(e^{\lambda_1 t_2}-1)(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})+4\beta e^{(\lambda_1+\lambda_2)t_2}[1-\kappa(e^{\lambda_1 t_2}-1)]}{[e^{\lambda_1 t_2}+e^{\lambda_2 t_2}]^2}+$$

$$(\frac{\partial t_2}{\partial v})^2\frac{\kappa e^{\lambda_2 t_2}(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})[(\lambda_1^2-\lambda_1)e^{\lambda_1 t_2}-1]+}{[e^{\lambda_1 t_2}+e^{\lambda_2 t_2}]^4}$$

$$\frac{4\beta e^{(\lambda_1+\lambda_2)t_2}[1-\kappa(e^{\lambda_1 t_2}-1)]\{\lambda_1+\lambda_2-2(e^{\lambda_1 t_2}+e^{\lambda_2 t_2})(\lambda_1 e^{\lambda_1 t_2}+\lambda_2 e^{\lambda_2 t_2})]-\kappa\lambda_1 e^{\lambda_1 t_2}\}}{}$$

Again, one can find that the last derivatives both are negative if S and β are sufficiently large and small respectively. That is the function L is convex. Now, it can be easily shown that the condition $(A2)$ is fulfilled.

Consider formulas (5) and (6) with $\beta=0$ and $v=0$ to obtain that $L(0)=\kappa\frac{1-v-\varepsilon}{\kappa+v+\varepsilon}>1-\varepsilon$. That is, if β is sufficiently small, then the condition $(A1)$ is valid, and the pair synchronizes. This result of the synchronization of two identical oscillators with the right-hand side depending on both variables is a new one. In previous papers the differential equations were separated.

Example 2. Consider the system of two identical oscillators with the differential equations

$$\begin{aligned} x_1' &= x_1^2 + c, \\ x_2' &= x_2^2 + c, \end{aligned} \tag{7}$$

where c is a positive constant. It is known that the canonical type I phase model [15] can be reduced by a transformation [21] to the form

$$u' = u^2 + c. \tag{8}$$

That is, to the quadratic integrate-and-fire model. This time we have added to the model the pulse-coupling, which has been described in the begin of the section, and investigate the synchronization problem by using the last result. We can assume, without loss of generality, that $t_1 = 0$. Since the two equations of are identical, we consider a solution $u(t)$ of the equation (8) for the construction of the map L. We have that $u(t,0,v+\varepsilon) = \sqrt{c}\tan(\sqrt{c}t + \arctan(\frac{v+\varepsilon}{\sqrt{c}}))$ and

$$\sqrt{c}\tan(\sqrt{c}t_2 + \arctan(\frac{v+\varepsilon}{\sqrt{c}})) = 1. \tag{9}$$

Next, $u(t_2,0,0) = \sqrt{c}\tan(\sqrt{c}t_2)$, and by applying (8) and (9) we find that

$$L(v) = \sqrt{c}\frac{1-(v+\varepsilon)}{\sqrt{c}+(v+\varepsilon)},$$

if $v \in (0, 1-\varepsilon)$, and the fixed point is $v^* = \sqrt{c+\sqrt{c}+\varepsilon^2/4} - (\sqrt{c}+\varepsilon/2)$. Evaluate

$$L(0) = \sqrt{c}\frac{1-\varepsilon}{\sqrt{c}+\varepsilon}$$

to see that $\eta = L(0) > 1-\varepsilon$, if $c < 1$ and ε is sufficiently small such that

$$\sqrt{c} + \varepsilon < 1. \tag{10}$$

Moreover, one can verify that v^* is a unique fixed point of L^2. Thus, we obtain that if (10) is valid then all conditions of the Theorem 1 fulfilled, and, consequently, the couple synchronizes, if only $v \neq v^*$.

Example 3. Consider the pair of identical oscillators, when $f(u) = S - \gamma u, \kappa = \frac{S}{\gamma} > 1$. That is, the Peskin's model [50]. Assume again that $t_1 = 0$. One can find that $u(t,0,v+\varepsilon) = (v+\varepsilon)\mathrm{e}^{-\gamma t} + \kappa(1-\mathrm{e}^{-\gamma t})$ and

$$(v+\varepsilon)\mathrm{e}^{-\gamma t_2} + \kappa(1-\mathrm{e}^{-\gamma t_2} = 1,$$

We have that

$$\mathrm{e}^{-\gamma t_2} = \frac{\kappa - 1}{\kappa - (v+\varepsilon)}. \tag{11}$$

Substituting the last expresion in $u(t_2,0,0)=\kappa(1-\mathrm{e}^{-\gamma t_2})$, one obtains that

$$L(v)=\kappa\frac{1-(v+\varepsilon)}{\kappa-(v+\varepsilon)}, \tag{12}$$

where $0<v<1-\varepsilon$.

There is a unique fixed point of L and L^2, and it is equal to

$$v^*=(\kappa-\frac{\varepsilon}{2})-\sqrt{\kappa^2-\kappa+\frac{\varepsilon^2}{4}}. \tag{13}$$

Finally, $L(0)=\kappa\frac{1-\varepsilon}{\kappa-\varepsilon}>1-\varepsilon$. That is, all conditions of the last theorem are valid. Thus, we have proved the assertion in [50].

2.2 *The general case: the multidimensional system of non-identical oscillators.*

In this section we shall discuss the main object of investigation. First, we apply the result of the last section and analyze the motion of a pair of oscillators in the multi-oscillatory ensemble, and find that the couple synchronizes if the parameters are close to zero. Next, the main theorem will be proved.

Consider a model of n non-identical oscillators given by relations (1) and (2). Fix two of the oscillators, let say, x_l and x_r. Denote $\mathscr{C}_j^k=[0,1+\xi_j]\backslash C_k^c$, $j=1,2,\dots,n$, where $C_k^c=[0,1]\backslash C_k$, as defined in the last section, is the set which consists of all points of the unit section, that synchronize after no less than $k+1$ iterations of L.

Lemma 1. *Assume that conditions* $(A1)$ *and* $(A2)$ *valid. If* $(x_l(0),x_r(0))\in\mathscr{C}_l^k\times\mathscr{C}_r^m$, *$k$ and m are natural numbers, then the couple x_l,x_r synchronizes within the time interval* $[0,T(\max(k,m)+3)]$, *if parameters are sufficiently close to zero, and absolute values of the parameters of perturbation sufficiently small with respect to* ε.

Proof. Denote by $x(t)=(x_1(t),x_2(t),\dots,x_n(t))$, a motion of the oscillator, $u(t)=(u_1,u_2,\dots,u_n)$, the solution of the equation (1) with $u_i(t_0,t_0,u_0)=u_0^i, u_0=(u_0^1,u_0^2,\dots,u_0^n)$. Suppose, without loss of generality, that $k\geq m$ and $t=0$ is a moment of firing such that $x_l(0)=1+\zeta_l(x(0)),x_l(0+)=0$. We will show that the couple x_l,x_r synchronizes at some moment $0\leq t<(k+2)T$, if the parameters are close to zero. If $1+\zeta_r(x(0))-\varepsilon-\varepsilon_r\leq x_r(0)\leq 1+\zeta_r(x(0))$, then these two oscillators fire simultaneously, and we only need to prove the persistence of synchrony, which will be done later. So, fix another oscillator $x_r(t)$ such that $0\leq x_r(0)<1+\zeta_r(x(0))-\varepsilon-\varepsilon_r$.

We shall divide the proof into two parts. First, we will show that the couple synchronizes eventually and then keeps the synchrony state permanently. In the second part the time of synchronization will be evaluated.

Assume that the pair does not synchronize. Then, there is a sequence of firing moments, t_i, such that $0=t_0<t_1<t_2<\dots$, the oscillator x_l fires at t_i with even i, and x_r fires at t_i with odd i. For the sake of brevity let $u_i = x_r(t_i), i = 2j, j \geq 0, u_i = x_l(t_i), i = 2j+1, j \geq 0$.

Let's fix an even i. If the parameters are sufficiently small, then there are $m \leq n-2$ distinct firing moments of the motion $x(t)$ on the interval (t_i, t_{i+1}). Denote by $t_i < \theta_1 < \theta_2 < \ldots < \theta_m < t_{i+1}$, the moments of firing, when at least one of the coordinates of $x(t)$ fires. We have that

$$x_r(\theta_1) = x_r(t_i) + \varepsilon + \int_{t_i}^{\theta_1} f(x_r(s))ds + \int_{t_i}^{\theta_1} \phi_r(s)ds, \tag{14}$$

where $x(t) = u(t, t_i, x(t_i+))$, is the solution of (1),

$$x_r(\theta_2) = x_r(\theta_1) + \varepsilon + \int_{\theta_1}^{\theta_2} f(x_r(s))ds + \int_{\theta_1}^{\theta_2} \phi_r(s)ds, \tag{15}$$

where $x(t) = u(t, \theta_1, x(\theta_1+))$,

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

$$x_r(t_{i+1}) = x_r(\theta_m) + \varepsilon + \int_{\theta_m}^{t_{i+1}} f(x_r(s))ds + \int_{\theta_m}^{t_{i+1}} \phi_r(s)ds. \tag{16}$$

The moment t_{i+1} satisfies

$$1 + \zeta_r(x(t_{i+1})) - \varepsilon - \varepsilon_r \leq x_r(t_{i+1}) \leq 1 + \zeta_r(x(t_{i+1})). \tag{17}$$

Similarly to the expressions for x_r we have that

$$\begin{aligned}
x_l(\theta_1) &= \int_{t_i}^{\theta_1} f(x_l(s))ds + \int_{t_i}^{\theta_1} \phi_l(s)ds, \\
x_l(\theta_2) &= x_l(\theta_1) + \varepsilon + \int_{\theta_1}^{\theta_2} f(x_l(s))ds + \int_{\theta_1}^{\theta_2} \phi_l(s)ds, \\
&\ldots \\
x_l(t_{i+1}) &= x_l(\theta_m) + \varepsilon + \int_{\theta_m}^{t_{i+1}} f(x_l(s))ds + \int_{\theta_m}^{t_{i+1}} \phi_l(s)ds.
\end{aligned} \tag{18}$$

One can see that formulas (14) to (18) completely define a relation $u_{i+1} = K_i(u_i) = x_l(t_{i+1})$. A similar one can be found for odd i.

Let us construct the value of $L(u_i, \varepsilon)$, now. With this aim, evaluate

$$\phi(\overline{t_{i+1}}) = x_r(t_i) + \varepsilon + \int_{t_i}^{\overline{t_{i+1}}} f(\phi(s))ds, \tag{19}$$

where $\overline{t_{i+1}}$ satisfies

$$\phi(\overline{t_{i+1}}) = 1, \tag{20}$$

and

$$\psi(\overline{t_{i+1}}) = \int_{t_i}^{\overline{t_{i+1}}} f(\psi(s))ds, \tag{21}$$

to find that $L(u_i, \varepsilon) = \psi(\overline{t_{i+1}})$. Next, we will show that the difference $K_i(u_i) - L(u_i, \varepsilon)$ is small if the parameters are small.

First, we have that for $t \in [t_i, \theta_1]$, it is true that

$$\phi(t) - x_r(t) = \int_{t_i}^{t} [f(\phi(s)) - f(x_r(s))]ds - \int_{t_i}^{t} \phi_r(s)ds. \tag{22}$$

Then, by applying the Gronwell-Bellman Lemma one can find easily that

$$|\phi(\theta_1) - x_r(\theta_1)| \leq \mu_r(\theta_1 - t_i)\mathrm{e}^{\ell(\theta_1 - t_i)}, \tag{23}$$

where T is the natural period defined in the first section for the identical oscillators. Next, similarly, we have that if $t \in [\theta_1, \theta_2]$, then

$$|\phi(\theta_2) - x_r(\theta_2)| \leq [\mu_r(\theta_1 - t_i)\mathrm{e}^{\ell(\theta_1 - t_i)} + \varepsilon]\mathrm{e}^{\ell(\theta_2 - \theta_1)}. \tag{24}$$

Without loss of generality assume that $t_{i+1} > \overline{t_{i+1}}$. Continue evaluations made above, we can obtain that $|1 - x_r(t_{i+1})| = |\phi(t_{i+1}) - x_r(t_{i+1})| = \Phi(\varepsilon, \mu_r)$, where Φ is of the order $O(\varepsilon, \mu_r, \xi_r)$. There are two positive numbers m, M such that $m \leq f(s) \leq M$, if $0 \leq s \leq 1 + \max_i \xi_i$. We have that $|x_r(t_{i+1}) - x_r(\overline{t_{i+1}})| \leq |1 - x_r(t_{i+1})| + |1 - x_r(\overline{t_{i+1}})| \leq \Phi(\varepsilon, \mu_r) + \xi_r$. Consequently,

$$|t_{i+1} - \overline{t_{i+1}}| < \frac{\Phi(\varepsilon, \mu_r) + \xi_r}{m - \mu_r}.$$

By applying the last inequality, (18) and (21) to evaluate the difference $|\psi(\overline{t_{i+1}}) - x_l(t_{i+1})|$, one can find that $K_i(u_i) - L(u_i, \varepsilon)$ can be made arbitrarily small if the parameters are sufficiently close to zero the parameters of perturbation are small, in absolute values, with respect to ε. This convergence is uniform with respect to $u_0 \in \mathscr{C}_r^k$. We can also vary the number of points θ_i and their location in the intervals (t_j, t_{j+1}) between 0 and $n-1$. The convergence is indifferent with respect to these variations, too.

Consider now the sequence $L^i(u_0)$. It is true that $L^k(u_0) \in [1 - \varepsilon, 1]$ for some $k \geq 0$. Assume, without loss of generality, that k is an even number. Since L is a continuous function, we can conclude that either $1 + \xi_r - \varepsilon - \varepsilon_r \leq u_k < 1 + \xi_r$ or $1 + \xi_l - \varepsilon - \varepsilon_l \leq u_{k+1} < 1 + \xi_l$, if the parameters are sufficiently close to zero, and absolute values of the parameters of perturbation are sufficiently small with respect to ε.

Both of these inequalities bring the system to synchronization.

In Figure 4 one can see the sequence of maps K_i, and the synchronizing sequence u_i is constructed. In the figure we show not only u_i, but also the graphs of functions $w = K_i(u), u_{i+1} = K_i(u_i)$, in the neighborhood of u_i, to give a better geometrical visualization of the convergence.

To evaluate the time of synchronization we should consider the general case, when $t = 0$ is not necessarily the firing moment. Then either x_l or x_r fires within the interval $I = [0, \bar{T}]$, where $\bar{T}$ is close to T, the natural period of the identical oscillators, as ξ_i, ζ_i and μ_i are close to zero. Since each of the iterations of map L happens within an interval with the length of no more than T, we obtain now that the couple x_l, x_r is synchronized no later than $t = (k+3)T$.

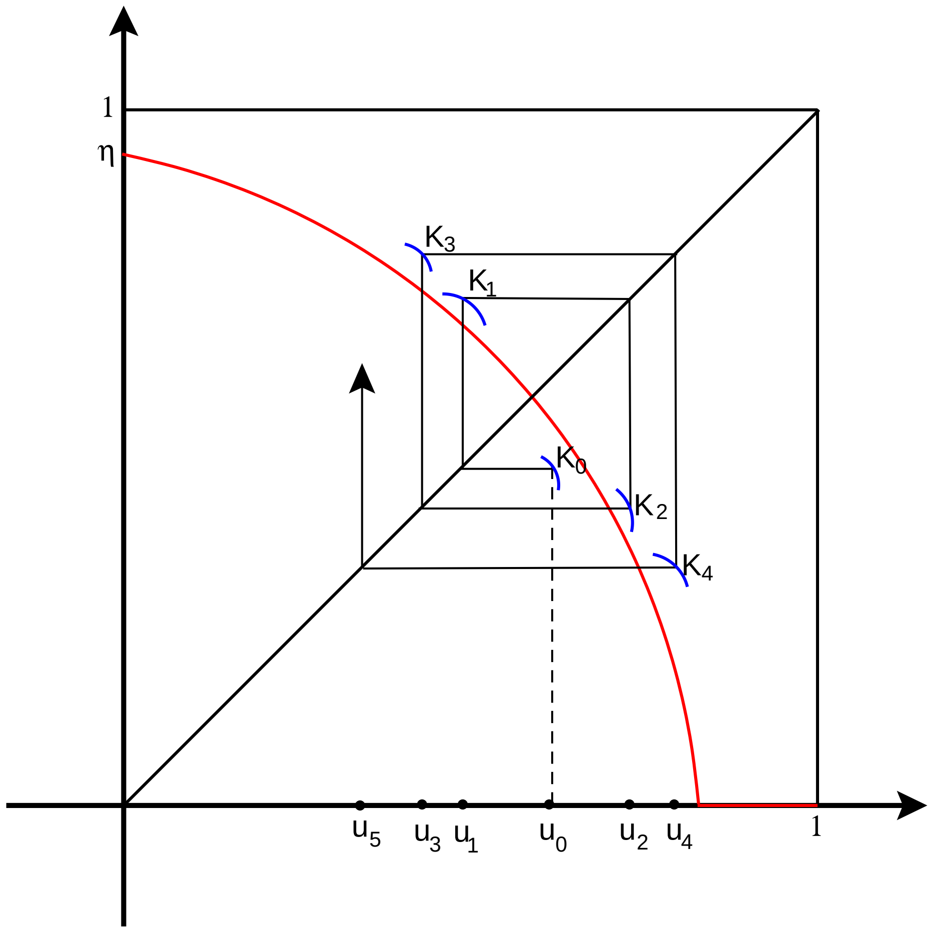

Fig. 4 The dynamics of a pair of oscillators from the system. The graphs of functions $w = K_i(u)$ are shown.

If two oscillators x_l and x_r are non-identical and fire simultaneously at a moment $t = \theta$, how will they retain the state of firing in unison, despite being different? To find the required conditions, let us denote by $\tau > \theta$ a moment when one of the two oscillators, let's say x_r, fires. We have that $x_l(\theta+) = x_r(\theta+) = 0$. Then $x_l(t) = x_r(t), \theta \leq t \leq \tau$. It is clear that to satisfy $x_l(\tau+) = x_r(\tau+) = 0$, we need $1+\xi_l - \varepsilon - \varepsilon_l \leq x_l(\tau)$. By applying formula (18) again, this time with $t_i = \theta, t_{i+1} = \tau$, one can easily obtain that the inequality is correct if parameters are close to zero. Thus, one can conclude that if a couple of oscillators is synchronized at some moment of time then it persistently continues to fire in unison. The lemma is proved.

Remark 1. The last lemma not only plays an auxiliary role for next main theorem, but can also be considered as a synchronization result for the model of two non-identical oscillators.

Let us extend the result of the lemma for the whole ensemble.

Theorem 2. *Assume that a motion $x(t)$ of the system satisfies $x(0) \in \Pi_{i=1}^{n} \mathscr{C}_i^{k_i}$. If parameters are sufficiently close to zero, and absolute values of the parameters of perturbation are sufficiently small with respect to ε, then the motion synchronizes within the time interval $[0, (\max_i k_i + 3)T]$.*

Proof. Fix one of the oscillators, let say, x_1, and consider the collection of couples $(x_1, x_j), j = 2, \ldots, n$. Applying the last lemma, we can say that each pair of oscillators synchronizes within $[0, (\max_i k_i + 3)T]$. The theorem is proved.

To illustrate the last theorem, we consider a group of oscillators, $x_i, i = 1, 2, \ldots, 100$, with random uniform distributed start values in $[0, 1]$. It is supposed that they satisfy the equations $x_i' = (3 + 0.01\bar{\mu}_i) - (2 + 0.01\bar{\zeta}_i)x_i$. The constants $\bar{\mu}_i, \bar{\zeta}_i$, as well as ξ_i in the thresholds $1 + 0.005\xi_i, i = 1, 2, \ldots, 100$, are uniform random distributed numbers from $[0, 1]$. In Figure 5 one can see the result of simulation with $\varepsilon = 0.08$, where the state of the system is shown before the first, twenty first, forty second and sixty third firing of the system. So, it is obvious that eventually the model states in the synchrony.

Let us describe a more general system of oscillators such that Theorem 2 is still true. A system of n oscillators is given, such that if $i-$th oscillator does not fire or jump up, it satisfies the $i-$th equation of system (1). If several oscillators $x_{i_s}, s = 1, 2, \ldots, k$, fire so that $x_{i_s}(t) = 1 + \xi_{i_s}$ and $x_{i_s}(t+) = 0$, then all other oscillators $x_{i_p}, p = k+1, k+1, \ldots, n$, change their coordinates by the law

$$x_{i_p}(t+) = \begin{cases} 0, \text{ if } x_{i_p}(t) + \varepsilon + \sum_{s=1}^{k} \varepsilon_{i_p i_s} \geq 1 + \xi_{i_p}, \\ x_{i_p}(t) + \varepsilon + \sum_{s=1}^{k} \varepsilon_{i_p i_s}, \text{ otherwise.} \end{cases} \tag{25}$$

One can easily see that the last theorem is correct for the model just described, if $\varepsilon + \sum_{s=1}^{k} \varepsilon_{i_p i_s} > 0$, for all possible k, i_p and i_s.

Remark 2. Since the length of C_k^c diminishes to zero as $k \to \infty$, one can say that our results are consistent with conjecture $(C2)$. Indeed, it was said in the beginning that all initial points must synchronize. Then, the fixed point was excluded [50]. In [47] the condition is weekend to the exception of a set with the Lebesgue measure null. In the present paper we just analyze another kind of smallness of the set.

Remark 3. Our preliminary analysis shows that the dynamics in the neighborhood of v^* can be very complex. We would not exclude the possibility of chaos appearance and the belongings of trajectories to a fractal, if parameters are not small [62]. It does not contradict to the zero Lebesgue measure of non-synchronized points set. The analysis of non-identical oscillators with non-small parameters may shed light on the investigation of arrhythmias, chaotic flashing of fireflies, etc.

Remark 4. The time of synchronization for a given initial point does not change much with the number of oscillators increasing (but the parameters need to be closer to zero!). This property can be viewed as a small-world phenomenon.

2.3 Possible generalization.

Next, it is natural to extend the result for the system of the following form

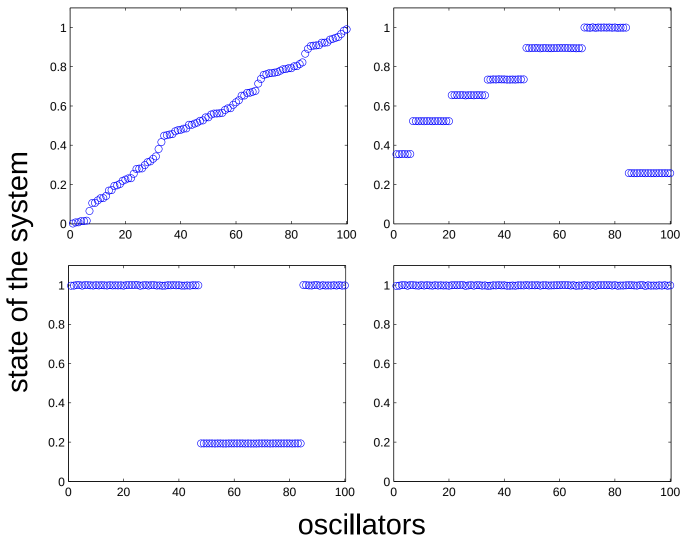

Fig. 5 The state of the model before the first, twenty first, forty second and sixty third firing of the system. The flat sections of the graph are groups of synchronized oscillators.

$$
\begin{aligned}
&x_1' = g(x_1, x_2, \ldots, x_n),\\
&x_2' = g(x_2, x_1, \ldots, x_n),\\
&\ldots,\\
&x_n' = g(x_1, x_2, \ldots, x_{n-1}),
\end{aligned}
\tag{26}
$$

considered with the condition (2). One can say that the coupling is now not only pulse, but is continuous also. We assume that the function g is continuous and positive again. If one suppose that the scalar-valued function g is indifferent with respect to permutations of the variables second to the last, then we can use the map L constructed in this section in the same way as it is done for the system (1). It is natural to accept some conditions of smallness with respect to the variables second to the last, to obtain synchronization of the system. Nevertheless, it seems that conditions can be found except the smallness to have still the system synchronized?

3 Integrate-and-fire models with continuous couplings

3.1 The model of two identical oscillators

Start the investigation with the simplest model of two identical oscillators. That is, assume that $n = 2$ in the description of the last section.

Let $[s, s+\tau]$ be $e-$interval for $x_i(s)$. Then, one can easily find that

$$x_i(t) = x_i(s)\mathrm{e}^{-\gamma(t-s)} + \int_s^t \mathrm{e}^{-\gamma(t-u)}(S+\eta)du, \tag{1}$$

for $t > s$.

Set $\kappa = \frac{S}{\gamma} > 1$. By integrating in (1), we have that

$$x_i(s+\tau) = x_i(s)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1 - \mathrm{e}^{-\gamma\tau}).$$

From $(A3), (iii)$, it follows, that $x_i(t) < 1$ for all $t \in [s, s+\tau]$. That is, x_i does not fire in the $e-$interval, if $x_i(s) < 1 - \varepsilon$. Consequently, the domain of any oscillator contains only disjoint $e-$intervals.

Denote by t_1, t_2, t_3 three successive firing moments of the system such that x_1 fires at t_1 and t_3, the oscillator x_2 fires at t_2, and the oscillators are not synchronized until t_3. We have that $0 < x_2(t_1) < 1 - \varepsilon$, and $x_2(t_1 + \tau) < 1$. From $x_2(t_2) = 1$ or $[x_2(t_1)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1 - \mathrm{e}^{-\gamma\tau})]\mathrm{e}^{-\gamma(t_2 - t_1 - \tau)} + \kappa[1 - \mathrm{e}^{-\gamma(t_2 - t_1 - \tau)}] = 1$, it follows that

$$\mathrm{e}^{-\gamma(t_2 - t_1)} = \frac{\kappa - 1}{\kappa - x_2(t_1) - \eta_1}, \tag{2}$$

where $\eta_1 = \frac{\eta}{\gamma}(\mathrm{e}^{\gamma\tau} - 1) < \eta$.

Apply (2) in

$$x_1(t_2) = \int_{t_1}^{t_2} \mathrm{e}^{-\gamma(t-u)} S du = \kappa[1 - \mathrm{e}^{-\gamma(t_2-t_1)}]$$

to obtain $x_1(t_2) = L_C(x_2(t_1))$, where

$$L_C(v) = \kappa \frac{1-v-\eta_1}{\kappa - v - \eta_1} \tag{3}$$

is a map defined for $0 < v < 1-\eta_1$. Similarly, by using the identity of oscillators, one can find that $x_2(t_3) = L_C(x_1(t_2))$. That is, the map L_C evaluates the sequence of coordinates of the model interchanging at firing moments. Its derivatives satisfy

$$L_C'(v) = \kappa \frac{1-\kappa}{(\kappa - (v+\eta_1))^2} < 0,$$

and

$$L_C''(v) = 2\kappa \frac{1-\kappa}{(\kappa - (v+\eta_1))^3} < 0.$$

in $(0, 1-\eta_1)$. There is a fixed point of L_C, and it is equal to $v^* = (\kappa - \frac{\eta_1}{2}) - \sqrt{\kappa^2 - \kappa + \frac{\eta_1^2}{4}}$.

Moreover, we have that

$$L_C'(v^*) = \kappa \frac{1-\kappa}{(\sqrt{\kappa^2 - \kappa + \frac{\eta_1^2}{4}} - \frac{\eta_1}{2})^2} < -1. \tag{4}$$

That is, v^* is a repellor.

Next, we extend the map on $[0,1]$ in the following way. Set $L_C(0) = \omega$, where $\omega = \kappa \frac{1-\eta_1}{\kappa-\eta_1}$. It is easy to check that $1-\varepsilon < \omega < 1$. Moreover, we define $L_C(v) = 0$, if $1-\eta_1 \leq v \leq 1$. On the basis of the analysis above, one finds that this newly introduced map is continuous and monotonic, and $[0,1]$ is an invariant set. Hence, $L_C(v)$ is very appropriate for iteration analysis. The graph of the function $w = L_C(v)$ is seen in Figure 6.

Let us show how synchronization can be investigated by analyzing iterations of L_C. Fix $t_1 \geq 0$, a firing moment, $x_1(t_1) = 1, x_1(t_1+) = 0$. While the couple x_1, x_2 does not synchronize, there exists a sequence of moments $t_1 < t_2 < t_3 < \ldots$ such that x_1 fires at t_i with odd i and x_2 - at t_i with even i. Set $u_i = x_1(t_i)$, if i is even, and $u_i = x_2(t_i)$, if i is odd. Then $u_{i+1} = L_C(u_i), i \geq 1$. The pair synchronizes if and only if there exists $j \geq 1$ such that $x_1(t) \neq x_2(t)$, if $t \leq t_j$, and $x_1(t) = x_2(t)$, for $t > t_j$. In particular, both oscillators have to fire at t_j. That is, inequalities $1-\varepsilon \leq u_j < 1$ hold, which is possible if $0 \leq u_{j-1} \leq L^{-1}(1-\varepsilon)$. We have that $L_C(0) = \omega$ satisfies this condition.

If $1-\varepsilon \leq x_2(t_1) \leq 1$, then we have that t_1 is a common firing moment of both x_1 and x_2, and it is the synchronization moment. Moreover, $1-\varepsilon < L_C^2(x_2(t_1)) = \eta < 1$. That is, the map L_C brings us to synchrony, with two steps of delay. Summarizing, if there exists an integer $k \geq 0$ such that $1-\varepsilon \leq L_C^k(v) \leq 1$, then a motion

$(x_1(t), x_2(t))$ with $x_1(t_1+) = v, x_2(t_1+) = 0$, synchronizes. Conversely, if a motion $(x_1(t), x_2(t))$ synchronizes, then one can find a firing moment, t_1, such that $x_1(t_1+) = v, v \in [0,1], x_2(t_1+) = 0$, and a number k such that $1 - \varepsilon \leq L_C^k(v) \leq 1$. Thus, it is verified that the constructed map is in full correspondence with the synchronization goal.

Analyzing maps $L_C^k, k \geq 0$, one can easily obtain that they all have only one non-zero fixed point v^*, and $|[L_C^k(v^*)]'| > 1$. Consequently, there is no $k-$periodic motion, $k > 1$, of the map, and a motion stabilizes, if its initial point $v \neq v^*$ (See Figure 6).

Our next goal is to locate, for each non-negative integer k, the set of initial points such that their motions synchronize in precisely k iterations of the map. In the sequel, denote by S_k the region in $[0,1]$, where points v are synchronized after precisely

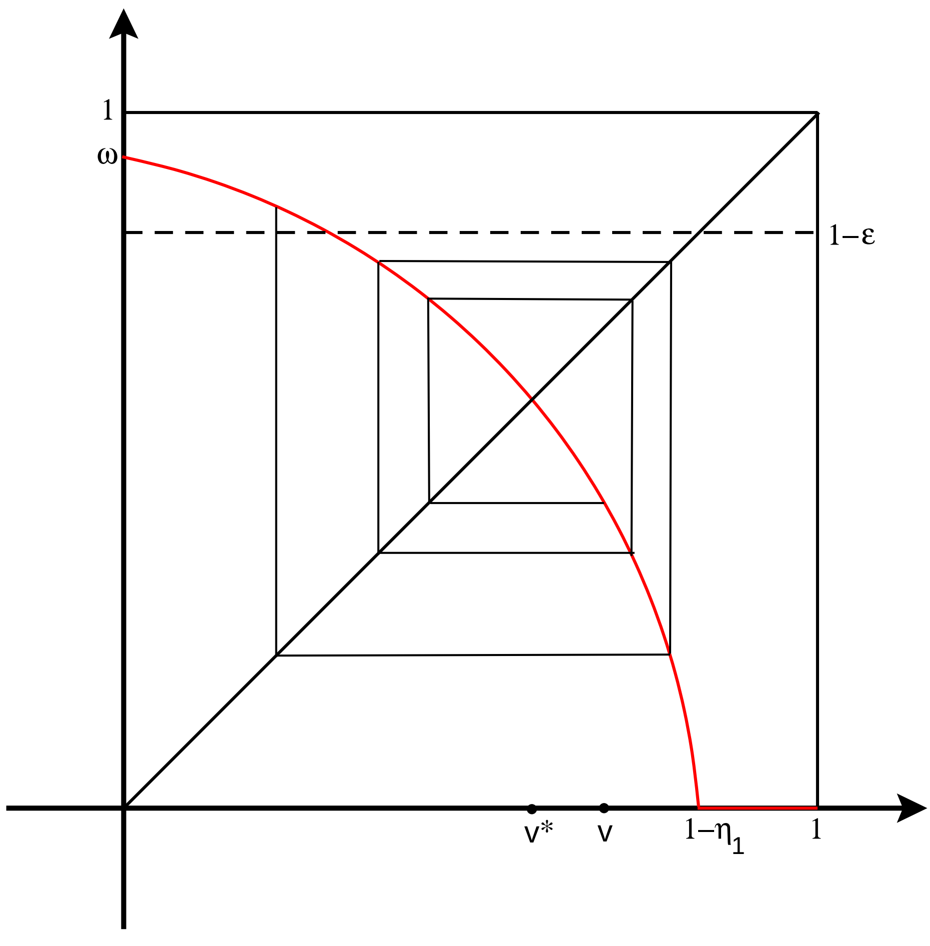

Fig. 6 A sketch of the map L_C, in red, and a stabilized trajectory.

$k-$ iterations of L_C. Let $a_0 = L_C^{-1}(\eta) = 0, a_{k+1} = L_C^{-1}(a_k), k = 0,1,2,\ldots.$ The points are pictured in Figure 7.

One can see that $S_0 = [1-\varepsilon,1], S_1 = [a_0,a_2]$ and $S_k = (a_{k-1},a_{k+1}]$, if $k \geq 3$ is an odd positive integer, and $S_k = [a_{k+1},a_{k-1})$, if $k \geq 2$ is an even positive integer. We have that $a_k \to v^*$ as $k \to \infty$. We shall call $S_k, k \geq 0$, as the rate intervals.

From the discussion above it follows that there is no finite time in which *all points* of the unit square synchronize. The closer v is to the equilibrium v^*, the later is the moment of synchronization.

Denote by $T = \frac{1}{\gamma}\ln\frac{\kappa}{\kappa-1}$ the natural period of oscillators, that is, the period of motion without couplings, and denote by $\tilde{T}$ the time needed for solution $u(t,0,v^*)$ of the equation $u' = S - \gamma u$, to achieve threshold. Since both oscillators fire within

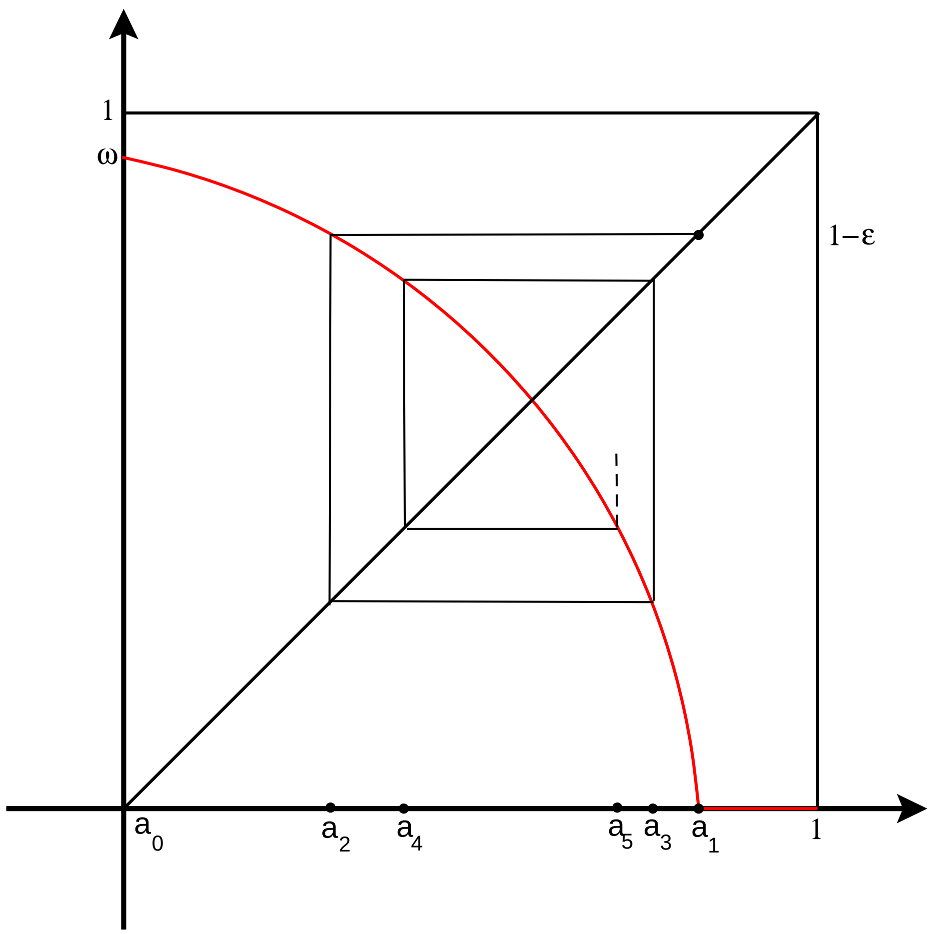

Fig. 7 The points $a_0 = L^{-1}(\eta) = 0, a_{k+1} = L^{-1}(a_k), k = 0,1,2,\ldots.$

an interval of length T and the distance between two firing moments of an oscillator is not less than $\tilde{T}$, the following assertion is valid.

Theorem 3. *Assume that* $t_1 \geq 0$ *is a firing moment,* $x_1(t_1) = 1, x_1(t_1+) = 0$*. If* $x_2(t_1) \in S_m$ *for some natural number* m*, then the couple* x_1, x_2 *of continuously coupled identical biological oscillators synchronizes within the time interval* $[t_0 + \frac{m}{2}\tilde{T}, t_0 + Tm]$.

3.2 Synchronization of an ensemble of identical oscillators.

Consider the integrate-and-fire model of continuously coupled identical biological oscillators $x_1, x_2, \ldots, x_n$. We intend to apply the map L_C defined in the last section to this model. Let us start with the synchronization of a pair of oscillators in the multi-oscillatory ensemble, and prove that the synchrony occurs for this couple, if the parameters are close to zero. Next, we prove the phenomenon for the whole model. Fix two of the oscillators, let us say x_l and x_r.

Lemma 2. *If* $t_0 \geq 0$ *is a firing moment,* $x_l(t_0) = 1, x_l(t_0+) = 0$*. If parameter* η *is sufficiently small, then the couple* x_l, x_r *synchronizes within the time interval* $[t_0, t_0 + T]$ *if* $x_r(t_0) \notin [a_0, a_1)$ *and within the time interval* $[t_0 + \frac{m-1}{2}\tilde{T}, t_0 + (m+1)T]$*, if* $x_r(t_0) \in S_m, m \geq 1$.

Proof. While the pair does not synchronize, there exists a sequence of firing moments, t_i, such that $0 \leq t_0 < t_1 < \ldots$, the oscillator x_l fires at t_i with even i, and x_r fires at t_i with odd i. For the sake of brevity let $u_i = x_l(t_i), i = 2j+1, j \geq 0, u_i = x_r(t_i), i = 2j, j \geq 0$.

Let us fix an even i. There are $k, k \leq n-2$ distinct firing moments of the motion $x(t)$ on the interval (t_i, t_{i+1}). Denote by $t_i < \theta_1 < \theta_2 < \ldots < \theta_k < t_{i+1}$, the moments of firing, when at least one of the coordinates of $x(t)$ fires. We assume, without loss of generality, that the length of intervals $(t_i, \theta_1), (\theta_1, \theta_2), \ldots, (\theta_k, t_{i+1})$ is more than τ. Other cases can be considered similarly.

We have that

$$
\begin{aligned}
&x_r(t_i+\tau) = x_r(t_i)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),\\
&x_r(\theta_1) = x_r(t_i+\tau)\mathrm{e}^{-\gamma(\theta_1-t_i-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(\theta_1-t_i-\tau)}),\\
&x_r(\theta_1+\tau) = x_r(\theta_1)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),\\
&x_r(\theta_2) = x_r(\theta_1+\tau)\mathrm{e}^{-\gamma(\theta_2-\theta_1-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(\theta_2-\theta_1-\tau)}),\\
&\ldots\ldots\\
&x_r(\theta_j) = x_r(\theta_{j-1}+\tau)\mathrm{e}^{-\gamma(\theta_j-\theta_{j-1}-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(\theta_j-\theta_{j-1}-\tau)}),\\
&x_r(\theta_j+\tau) = x_r(\theta_j)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),\\
&\ldots\ldots\\
&x_r(t_{i+1}) = x_r(\theta_k+\tau)\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)}).
\end{aligned}
\tag{5}
$$

The moment t_{i+1} satisfies

$$
1-\varepsilon \le x_r(t_{i+1}) \le 1. \tag{6}
$$

We also have that

$$
\begin{aligned}
&x_l(\theta_1) = \kappa(1-\mathrm{e}^{-\gamma(\theta_1-t_i)}),\\
&x_l(\theta_1+\tau) = x_l(\theta_1)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),\\
&\ldots\ldots\\
&x_l(\theta_k+\tau) = x_l(\theta_k)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),\\
&x_l(t_{i+1}) = x_l(\theta_k)\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)}).
\end{aligned}
\tag{7}
$$

The last three formulas determine the relation $u_{i+1} = K_i(u_i)$. A similar one can be found if i is odd. Evaluations in (5) and (7) bring us to expressions

$$
\begin{aligned}
&x_r(t_{i+1}) = x_r(t_i)\mathrm{e}^{-\gamma(t_{i+1}-t_i)} + \kappa(1-\mathrm{e}^{-\gamma(t_{i+1}-t_i)}) +\\
&\frac{\eta}{\gamma}(1-\mathrm{e}^{-\gamma\tau})(\mathrm{e}^{-\gamma(t_{i+1}-t_i-\tau)} + \sum_{j=1}^{k}\mathrm{e}^{-\gamma(t_{i+1}-\theta_j-\tau)})
\end{aligned}
\tag{8}
$$

and

$$
\begin{aligned}
&x_l(t_{i+1}) = \kappa(1-\mathrm{e}^{-\gamma(t_{i+1}-t_i)}) +\\
&\frac{\eta}{\gamma}\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)}(1-\mathrm{e}^{-\gamma\tau})\sum_{j=1}^{k}\mathrm{e}^{-\gamma(\theta_k-\theta_j)}.
\end{aligned}
\tag{9}
$$

Recall map L_C defined in the last section. We have

$$
\phi(t_i+\tau) = x_r(t_i)\mathrm{e}^{-\gamma\tau} + (\kappa + \frac{\eta}{\gamma})(1-\mathrm{e}^{-\gamma\tau}),
$$

$$\phi(\overline{t_{i+1}}) = \phi(t_i+\tau)\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i-\tau)} + \kappa(1-\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i-\tau)}),$$

or

$$\begin{aligned}\phi(\overline{t_{i+1}}) = x_t(t_i)\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i)} + \\ \kappa(1-\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i)}) + \frac{\eta}{\gamma}\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i-\tau)}(1-\mathrm{e}^{-\gamma\tau}),\end{aligned} \tag{10}$$

where $\overline{t_{i+1}}$ satisfies

$$\phi(\overline{t_{i+1}}) = 1, \tag{11}$$

and

$$\psi(\overline{t_{i+1}}) = \kappa(1-\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i)}), \tag{12}$$

to evaluate $L_C(u_i) = \psi(\overline{t_{i+1}})$.

We assume, without loss of generality, that $\overline{t_{i+1}} \leq t_{i+1}$. Then one can find that

$$x_r(\overline{t_{i+1}}) - \phi(\overline{t_{i+1}}) = x_r(\overline{t_{i+1}}) - 1 = \Phi(\eta,\gamma,\tau), \tag{13}$$

where

$$\Phi(\eta,\gamma,\tau) = \frac{\eta}{\gamma}(1-\mathrm{e}^{-\gamma\tau})\sum_{j=1}^{k}\mathrm{e}^{-\gamma(\overline{t_{i+1}}-\theta_j-\tau)},$$

and the last expression tends to zero as $\eta \to 0$. Next, by applying (6) and (13) we have that

$$t_{i+1} - \overline{t_{i+1}} \leq \frac{|\Phi(\eta,\gamma,\tau)|}{S+\eta-\gamma}.$$

Now, consider

$$K_i(u_i) - L_C(u_i,\varepsilon) = x_l(t_{i+1}) - \psi(\overline{t_{i+1}}) = \frac{\eta}{\gamma}\mathrm{e}^{-\gamma(t_{i+1}-\theta_k-\tau)}(1-\mathrm{e}^{-\gamma\tau})\sum_{j=1}^{k}\mathrm{e}^{-\gamma(\theta_k-\theta_j)} +$$

$$\kappa\big(\mathrm{e}^{-\gamma(\overline{t_{i+1}}-t_i)} - \mathrm{e}^{-\gamma(t_{i+1}-t_i)}\big)$$

to see that $K_i(u_i) - L_C(u_i,\varepsilon)$ can be made arbitrarily small if η is sufficiently small. This convergence is uniform with respect to u_0. We can also vary the number of points θ_i between 0 and $n-1$, as well as the distance between them. The convergence is indifferent with respect to these variations. Remember that the exciting strengths are not additive. Consider now the sequence $L_C^i(u_0,\varepsilon)$. We have that $1-\varepsilon \leq L_C^m(u_0,\varepsilon) \leq 1$. Now, since L_C is a continuous function, we can discuss recurrently inequalities

$$|u_i - L_C^i(u_0,\varepsilon)| \leq |K_{i-1}(u_{i-1}) - L_C^i(u_{i-1},\varepsilon)| +$$

$$|L_C^i(u_{i-1},\varepsilon) - L_C(L_C^{i-1}(u_0,\varepsilon))|, i = 1,2,\ldots,$$

to conclude that either $1-\varepsilon \le u_m \le 1$ or $1-\varepsilon \le u_{m+1} \le 1$, if the parameters are sufficiently small. Both of these inequalities confirm synchronization.

In Figure 8 one can see the sequence of maps K_i, and the synchronizing sequence u_i is constructed. In the figure we show not only u_i, but also the graphs of functions $w = K_i(u), u_{i+1} = K_i(u_i)$, in the neighborhood of u_i, to give a better geometrical visualization of the convergence.

Since each of the iterations of the map L_C happens within an interval of length not more than T, and the distance between two firing moments of an oscillator is not smaller than $\tilde{T}$, we obtain that the couple x_l, x_r is synchronized no earlier than $t = t_0 + \frac{m-1}{2}\tilde{T}$, and no later than $t = t_0 + (m+1)T$.

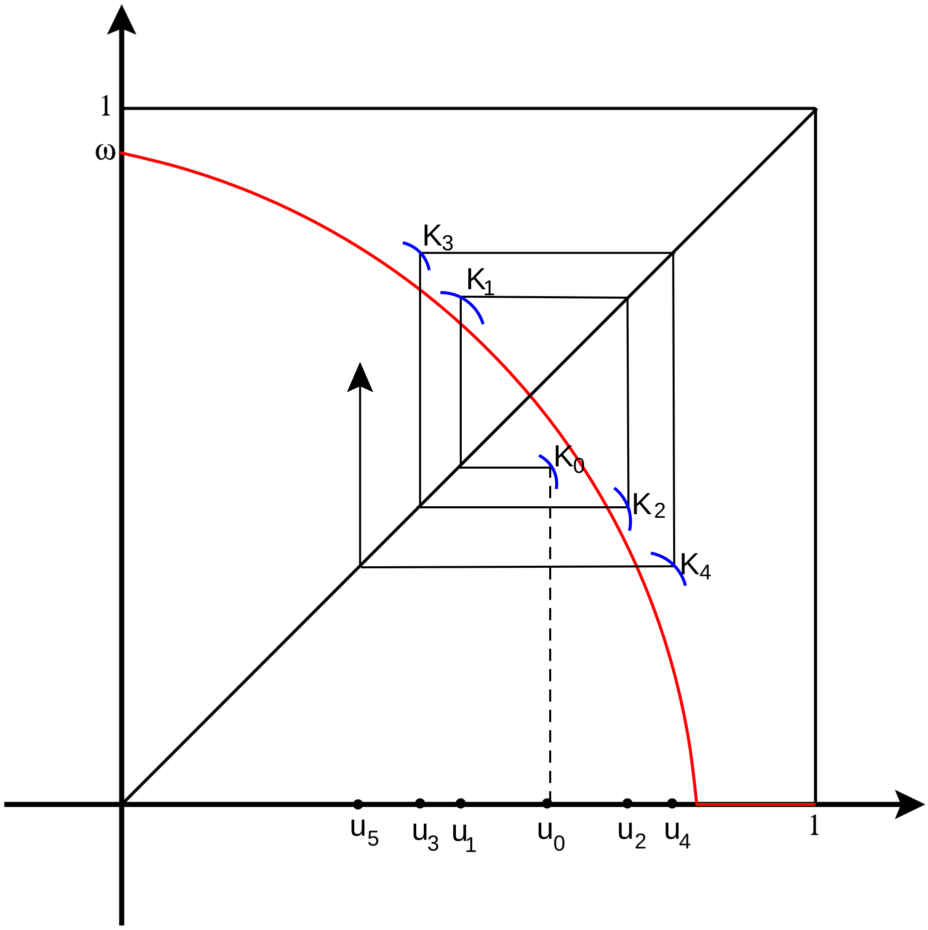

Fig. 8 The dynamics of the couple (x_l, x_r).

Thus, one can conclude that if a couple of oscillators is synchronized at some moment of time then, since the oscillators are identical, it persistently continues to fire in unison.

The lemma is proved.

Let us apply the last lemma to the entire ensemble.

Theorem 4. *Let $t_0 \geq 0$ be a firing moment such that $x_j(t_0) = 1, x_j(t_0+) = 0$. If parameter η is sufficiently small, then the motion $x(t)$ of the system synchronizes within the time interval $[t_0, t_0 + T]$, if $x_i(t_0) \notin [a_0, a_1), i \neq j$, and within the time interval $[t_0 + \frac{\max_{i\neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i\neq j} k_i + 1)T]$, if there exist $x_s(t_0) \in [a_0, a_1)$ for some $s \neq j$ and $x_i(t_0) \in S_{k_i}, i \neq j$.*

Proof. Apply the last lemma to each pair $(x_j, x_i), i \neq j$ to obtain that it synchronizes within the time interval. The theorem is proved.

On the basis of the last proof and the analysis of formulas (10)-(12) with (8),(6) and (9), one can conclude that the following assertion, which can be useful in applications and theory, is valid.

Theorem 5. *Assume that $t_0 \geq 0$ is a firing moment, $x_j(t_0) = 1, x_j(t_0+) = 0$. The motion $x(t)$ of the integrate-and-fire model of identical continuously coupled biological oscillators synchronizes within the time interval $[t_0, t_0 + T]$, if $x_i(t_0+) \notin [a_0, a_1), i \neq j$, and within the time interval $[t_0 + \frac{\max_{i\neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i\neq j} k_i + 1)T]$, if there exist $x_s(t_0) \in [a_0, a_1)$ for some $s \neq j$ and $x_i(t_0) \in S_{k_i}, i \neq j$, and if the delay τ is sufficiently small.*

3.3 Non-identical oscillators

Let us describe a more general system of oscillators such that the synchronization is still true.

Consider a system of n non-identical oscillators $x_i, i = 1, 2, \ldots, n$, whose values are in $[0, 1 + \xi_i]$. We assume that the following conditions are valid:

$B1)$. If several oscillators $x_{i_m}, m = 1, 2, \ldots, k$, fire at a moment $t = s$, such that $x_{i_m}(s) = 1 + \xi_{i_m}$, and $x_{i_m}(s+) = 0$, then all other oscillators $x_{i_p}, p = k+1, k+1, \ldots, n$, exhibit the following behavior near the moment of firing:

- If $x_{i_p}(s) + \varepsilon + \varepsilon_{i_p} \geq 1 + \xi_{i_p}$, then $x_{i_p}(s+) = 0$.
- Otherwise,

$$x'_{i_p} = (S + s_{i_p} + \eta + \sum_{m=1}^{k} s_{i_p i_m}(t - \theta_{i_p i_m}(t))) - (\gamma + \gamma_{i_p})x_{i_p}, \tag{14}$$

for all $t \in [s, s + \tau + \tau_{i_p}]$ that belong to the same continuity interval of x_{i_p} as s. Functions s_{ij} are piecewise continuous and $\theta_{i_p i_m}(t) > 0$ are bounded delays. There exist positive constants η_{ij} such that $|s_{ij}(t)| < \eta_{ij}$ for all i, j.

If x_j fires at a moment $t = s$, we name the interval $[s, s+\tau]$ as an e^j-interval. An oscillator x_i *is excited* at a moment t, if the moment belongs to an e^j-interval with $j \neq i$, or $x_i(t) = 1+\xi_i$.

$B2)$. When $i-$th oscillator is not excited

$$x_i' = (S+s_i)-(\gamma+\gamma_i)x_i. \tag{15}$$

In $(B1)$ and $(B2)$ constants $S,\gamma,\varepsilon,\eta$ are the same as in $(A1)-(A4)$, parameters $s_i,\gamma_i,\xi_i,\eta_{ij},\tau_{i,j}, i,j = 1,2,\ldots,n$, are fixed real numbers. Additionally we require that

$B3)$. $\tau+\tau_{i_p} > 0, \eta-\sum_{s=1}^{k}\eta_{i_p i_s} > 0$, for all possible k, i_p and i_s.

We shall call the system of n oscillators with conditions $(B1)-(B3),(A3)$ *the integrate-and-fire model of continuously coupled non-identical biological oscillators*.

Theorem 6. *Let $t_0 \geq 0$ be a firing moment such that $x_j(t_0) = 1, x_j(t_0+) = 0$. If parameters $s_i,\gamma_i,\zeta_i,\eta_{ij},\tau_{ij}$ and η are sufficiently small, then the motion $x(t)$ of the integrate-and-fire model of continuously coupled non-identical biological oscillators synchronizes within the time interval $[t_0, t_0+T]$, if $x_i(t_0) \notin [a_0,a_1), i \neq j$, and within the time interval $[t_0 + \frac{\max_{i\neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i\neq j} k_i + 1)T]$, if there exist $x_s(t_0) \in [a_0,a_1)$ for some $s \neq j$ and $x_i(t_0) \in S_{k_i}, i \neq j$.*

We decided to omit the proof of the last theorem, since it is very similar to that of Theorem 4 with slight changes caused by newly introduced parameters. Still, one point in the proof deserves special attention. If two oscillators x_l and x_r are non-identical and fire simultaneously at a moment $t = \theta$, how will they retain the state of firing in unison, despite being different? To find the required conditions, let us denote by $\tau, \tau > \theta$ a moment when one of them, let us say x_l, fires. We have that $x_l(\theta+) = x_r(\theta+) = 0$. This time it is not necessary to have $x_l(t) = x_r(t), \theta \leq t \leq \tau$. It is clear that to satisfy $x_l(\tau+) = x_r(\tau+) = 0$, we need $x_r(\tau)+\varepsilon+\varepsilon_r \geq 1+\xi_r$. By applying formulas similar to (5) and (6), this time with $t_i = \theta, t_{i+1} = \tau, x_r(\theta) = 0$, one can easily obtain that the inequality is correct if the parameters are sufficiently small. Thus, one can conclude that if a couple of oscillators is synchronized at some moment of time then it persistently continues to fire in unison.

Remark 5. We do not impose any restriction on the delay functions $\theta_{i_p i_m}(t)$ in (14), except that they are bounded functions. Oscillators with delayed excitatory interaction, without leakage, and their applications are discussed in [20]. Similarly to the way it is done for pulse-coupled models in [3], all results can be extended to systems, when the coupling is not all-to-all, and general types of thresholds and differential equations are considered. Parameter η is chosen as the main one to establish synchronization. It is obvious that the choice of the control can be varied, for example, by choosing τ, or both of them, instead.

3.4 Simulations

To illustrate the theory consider a system of oscillators, $x_1, x_2, \ldots, x_{100}$, with random start values in $[0,1]$. Choose, also randomly, numbers $\xi_i, \alpha_i, \beta_i, i = 1,2,\ldots,100$, from the interval $[0,1]$. Assume that if $x_j(s) = 1 + 0.005\xi_j$ at some moment $t = s$, then the oscillator fires, $x_j(s+) = 0$, and other oscillators $x_i, i \neq j$, change their behavior near the firing moment in the following way: if $x_i(s) + 0.03 \geq 1 + \xi_i$, then $x_i(s+) = 0$; otherwise,

$$x_i' = (13 + 0.01\alpha_i) - (2 + 0.01\beta_i)x_i, \tag{16}$$

for all $t \in [s, s+0.01]$, till x_i fires.

If x_j fires at a moment $t = s$, then an oscillator x_i is excited at the moment t, if either the moment belongs to the interval $[s, s+0.01]$ with $j \neq i$, or $x_i(t) = 1 + 0.005\xi_i$.

When $x_i, i = 1,2,\ldots,n$, is not excited then

$$x_i' = (3 + 0.01\alpha_i) - (2 + 0.01\beta_i)x_i. \tag{17}$$

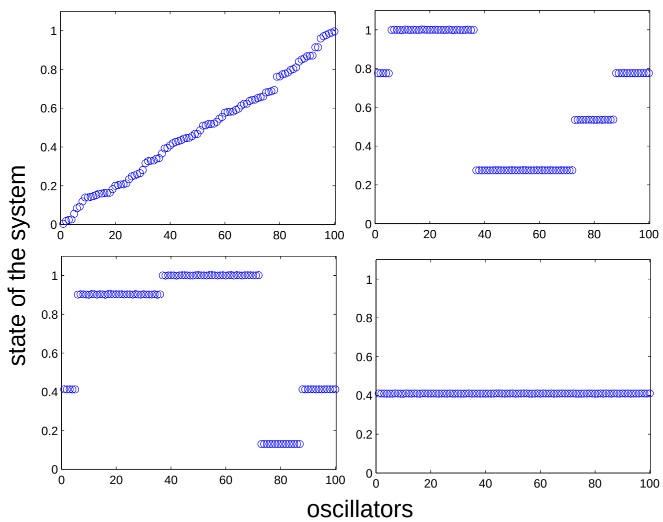

Fig. 9 The figure in the upper left corner depicts the initial positions, the one in the upper right corner depicts the situation just before the thirtieth jump, the one in the lower left corner - just before the sixtieth jump, and the final figure - before the ninetieth jump of the system. The flat sections of the graph are groups of synchronized oscillators.

In Figure 9 one can see the result of the simulation, where the upper left figure corresponds to the initial states, the upper right one shows the situations just before the thirtieth jump, the lower left one - just before the sixtieth jump, and the final one - before the ninetieth jump of the system.

4 Integrate-and-fire oscillators with retarded couplings

4.1 The couple of identical oscillators

Let us start with the analysis of two identical oscillators, which satisfy, if they do not fire, the following differential equations

$$x_i' = S - \gamma x_i, \tag{1}$$

where $0 \le x_i \le 1, i = 1,2$. It is assumed that S,γ are positive numbers and $\kappa = \frac{S}{\gamma} > 1$. In (1) each $x_i, i = 1,2$, is a voltage-like state variable, S is an external stimulus, and γ is the leakage coefficient.

When $x_j(t) = 1$, then the oscillator fires, $x_j(t+) = 0$. The firing changes the value of the another oscillator, x_i, such that

$$x_i(t+) = 0, \tag{2}$$

if $x_i(t) \ge 1-\varepsilon$, and

$$x_i(t+\tau+) = \begin{cases} x_i(t+\tau)+\varepsilon, \text{if} x_i(t+\tau) < 1-\varepsilon, \\ 0, \text{ otherwise}, \end{cases} \tag{3}$$

otherwise.

Thus, from (3) it implies that $t+\tau$ is a firing moment for x_i, if the jump makes the value of the oscillator not smaller than 1.

In paper [50], the following coupling mechanism was introduced. If oscillator x_j fires at the moment t, then the firing changes the value of the another oscillator, x_i, such that

$$x_i(t+) = \begin{cases} x_i(t)+\varepsilon, \text{if} x_i(t) < 1-\varepsilon, \\ 0, \text{ otherwise}. \end{cases} \tag{4}$$

That is no delay was assumed for the pulse-coupling.

In what follows, assume that

$$\frac{\kappa-1}{\kappa-1+\varepsilon} < \mathrm{e}^{-\gamma\tau}. \tag{5}$$

We have that

$$x_i(s) = x_i(t)\mathrm{e}^{-\gamma(s-t)} + \int_t^s \mathrm{e}^{-\gamma(s-u)} S du$$

near t, where t is assumed again the firing moment for x_j, and

$$x_i(s) \le (1-\varepsilon)\mathrm{e}^{-\gamma\tau} + \kappa(1-\mathrm{e}^{-\gamma\tau}).$$

From (5) it implies that if $x_i(t) < 1-\varepsilon$, then $x_i(s) < 1$, for all $s \in [t, t+\tau]$. In other words, the oscillator x_i does not achieve the threshold within interval $[t, t+\tau]$, if the distance of $x_i(t)$ to threshold is more than ε. This is important for the construction of the prototype map, and makes a sense of condition (3).

One must emphasize that couplings of units are not only delayed in our model. By (2) oscillators interact instantaneously, if they are near the threshold. This assumption is natural as firing provokes another oscillator, which is being close to the threshold "is ready" to react instantaneously. Otherwise, the interaction is retarded.

Next, we shall construct the prototype map. Fix a moment $t = \zeta$, when x_1 fires, and suppose that oscillators are not synchronized. In interval $[\zeta, \zeta+\tau]$ the oscillator x_2 moves according to the law $x_2(t) = x_2(\zeta)\mathrm{e}^{-\gamma(t-\zeta)} + \int_\zeta^t \mathrm{e}^{-\gamma(t-u)} S du$, and

$$x_2(\zeta+\tau) = [x_2(\zeta) - \kappa]\mathrm{e}^{-\gamma\tau} + \kappa. \tag{6}$$

Let us, firstly, handle the problem in the case that $x_2(\zeta+\tau)+\varepsilon < 1$. One can verify that this is true if $x_2(\zeta) < \overline{v}$, where $\overline{v} = \mathrm{e}^{\gamma\tau}(1-\varepsilon-\kappa)+\kappa$. It is important that $\overline{v} < 1-\varepsilon_1$, where $\varepsilon_1 = \varepsilon \mathrm{e}^{\gamma\tau}$. Take $\tau > 0$ so small such that the inequality

$$\mathrm{e}^{-\gamma\tau} > \varepsilon \tag{7}$$

holds. From (7) it implies that $\varepsilon_1 < 1$. If we denote by $t = \eta$ the firing moment of x_2, then one can reveal that

$$x_2(\eta) = [x_2(\zeta+\tau)+\varepsilon]\mathrm{e}^{-\gamma(\eta-\zeta-\tau)} + \kappa[1-\mathrm{e}^{-\gamma(\eta-\zeta-\tau)}].$$

The equation $x_2(\eta) = 1$ implies the following

$$\mathrm{e}^{-\gamma(\eta-\zeta)} = \frac{1-\kappa}{x_2(\zeta)-\kappa+\varepsilon_1}. \tag{8}$$

It follows from $x_1(\eta) = \kappa[1-\mathrm{e}^{-\gamma(\eta-\zeta)}]$ that

$$x_1(\eta) = \kappa\frac{1-(x_2(\zeta)+\varepsilon_1)}{\kappa-(x_2(\zeta)+\varepsilon_1)}. \tag{9}$$

Introduce the following map

$$L_D(v,\varepsilon) = \kappa\frac{1-(v+\varepsilon_1)}{\kappa-(v+\varepsilon_1)}, \text{ for } 0 < v < \overline{v}, \tag{10}$$

such that $x_1(\eta) = L_D(x_2(\zeta)), \varepsilon)$.

Next, let us consider the case that $1 \leq x_2(\zeta+\tau)+\varepsilon$. By (3) we have that $\eta = \zeta+\tau$, and $x_1(\eta) = \kappa[1-\mathrm{e}^{-\gamma\tau}]$. Set $\tilde{v} = \kappa[1-\mathrm{e}^{-\gamma\tau}]$, and introduce

$$L_D(v,\varepsilon) = \tilde{v}, \ \text{ for } \bar{v} \leq v < 1-\varepsilon. \tag{11}$$

In what follows we assume that

$$\mathrm{e}^{\gamma\tau} < \sqrt{\frac{\kappa}{\kappa-1+\varepsilon_1}}. \tag{12}$$

Now, we will define an extension of L_D on $[0,1]$ in the following way. Let

$$\omega = \kappa\frac{1-\varepsilon_1}{\kappa-\varepsilon_1}. \tag{13}$$

One can see that $1-\varepsilon < \omega < 1$, provided that

$$\mathrm{e}^{\gamma\tau} < \frac{\kappa}{\kappa-1+\varepsilon_1}. \tag{14}$$

In the sequel, we assume that the number ε is sufficiently small such that (5) implies (14). We set $L_D(0,\varepsilon) = \omega$, and define $L_D(v,\varepsilon) = 0$, if $1-\varepsilon \leq v \leq 1$.

The derivatives of the map in $(0,\bar{v})$ satisfy

$$L_D'(v,\varepsilon) = \kappa\frac{1-\kappa}{(\kappa-(v+\varepsilon_1))^2} < 0, \tag{15}$$

and

$$L_D''(v,\varepsilon) = 2\kappa\frac{1-\kappa}{(\kappa-(v+\varepsilon))^3} < 0. \tag{16}$$

It is possible to verify that there is a fixed point of the map,

$$v^* = (\kappa-\frac{\varepsilon_1}{2}) - \sqrt{\kappa^2-\kappa+\frac{\varepsilon_1^2}{4}}, \tag{17}$$

and that

$$L_D'(v^*,\varepsilon) < -1. \tag{18}$$

Stated in other words, the fixed point v^* is a repellor. The inequality $v^* < \bar{v}$ holds, if the condition (12) is valid, and consequently, all our previous evaluations are justified.

Suppose, additionally, that

$$\kappa(1-\mathrm{e}^{-\gamma\tau}) < \frac{\varepsilon\kappa}{\kappa-1+\varepsilon} - \varepsilon\mathrm{e}^{\gamma\tau}. \tag{19}$$

Denote by $v = a_2$ the solution of the equation $L_D(v,\varepsilon) = 1-\varepsilon$. We find that $a_2 = \frac{\varepsilon\kappa}{\kappa-1+\varepsilon} - \varepsilon e^{\gamma\tau}$. By means of the last inequality we have $\tilde{v} < a_2$.

We call τ the *small delay* since (5), (7), (12), (14) and (19) are assumed to be true. The graph of L_D (in red) under above mentioned conditions is illustrated in Figure 10. One can see that L_D is a piecewise map. This is a curios fact, since in previous our papers for non-delayed pulse couplings or continuous couplings, the prototype map was continuous. Obviously, the discontinuity of the map gives more possibilities for various dynamical collective effects of integrate-and-fire oscillators.

To emphasize a significance of this map for the present analysis, let us see how iterations of it can help to observe the synchronization. Fix $t_0 \geq 0$, a firing moment, such that $x_1(t_0) = 1$ and $x_1(t_0+) = 0$. When the couple x_1 and x_2 are not in syn-

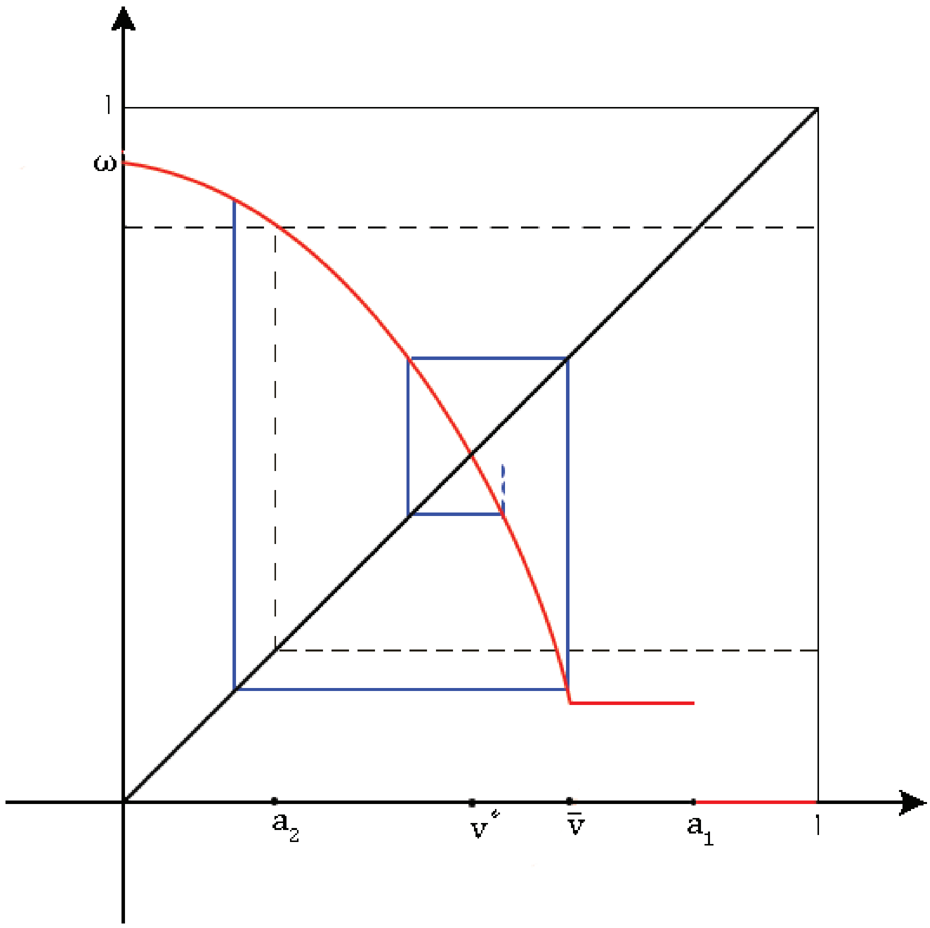

Fig. 10 The graph of map L_D in red, fixed point v^*, and stabilized trajectory are seen.

chrony, there exists a sequence of moments $t_0 < t_1 < \ldots$ such that x_1 fires at t_i with even i and x_2 with odd indices. Denote $u_i = x_1(t_i)$, if i is odd, and $u_i = x_2(t_i)$, if i is even. One can easily see that $u_{i+1} = L_D(u_i,\varepsilon), i \geq 0$. The pair synchronizes if and only if there exists $j \geq 1$ such that $x_1(t) \neq x_2(t)$, if $t \leq t_j$, and $x_1(t) = x_2(t)$, for $t > t_j$. In particular, both oscillators have to fire at t_j. In other words, the inequalities $1-\varepsilon \leq u_{j-1} < 1$ are valid. In particular, we have that $L_D(0) = \omega$ satisfies this condition. In the same time, if $1-\varepsilon_1 \leq u_{j-3} \leq 1$, then $u_{j-2} = 0 = L_D(u_{j-3})$ and $1-\varepsilon < u_{j-1} = \omega < 1$ again. That is, we have found that if there exists an integer $k \geq 0$ such that $1-\varepsilon \leq L_D^k(v) \leq 1$, then the motion $(x_1(t), x_2(t))$ with $x_1(t_0+) = v, x_2(t_0+) = 0$, synchronizes at the $k-$th firing moment. Conversely, if a motion $(x_1(t), x_2(t))$ synchronizes, then one can find a firing moment, t_0, such that $x_1(t_0+) = 0, x_2(t_0+) = v, v \in [0,1]$, and a number k with the property that $1-\varepsilon \leq L_D^k(v) \leq 1$.

Thus, the last discussion confirms that the analysis of synchronization is consistent fully with the dynamics of the introduced map $L_D(v,\varepsilon)$ on $[0,1]$, and the map L_D can be applied as the main instrument of the paper. That is why, we use this function as a prototype map in our investigations.

Now, by the help of the properties of the map L_D, and analyzing self-compositions of the map, one can easily attain that for all $k \geq 0$ functions L_D^k have only one fixed point, v^*, and $|[L_D^k(v^*,\varepsilon)]'| > 1$. We skip the discussion as it is respectively simple, and requests a large place. Since all the maps L_D^k have one and the same fixed point, v^*, there is not a $k-$periodic motion, $k > 1$, of the map. Consequently, for arbitrary point $v \neq v^*$ one has a stabilized trajectory as presented in Figure 10. The couple synchronizes when $L_D^k(v,\varepsilon) \geq 1-\varepsilon$.

Next, we investigate the rate of synchronization. Set $a_0 = 0, a_1 = 1-\varepsilon$ and $a_{k+1} = L_D^{-1}(a_k), k = 2,3,\ldots$ (See Figure 11).

Denote by S_k the subset of the interval $[0,1]$, consisting of the points v which are synchronized after exactly k iterations of the map L_D. It is easy to verify that $S_0 = [a_1,1], S_1 = [a_0,a_2]$ and $S_k = (a_{k-1},a_{k+1}]$, if $k \geq 3$, is an odd positive integer, and $S_k = [a_{k+1},a_{k-1})$, if $k \geq 2$, is an even positive integer. One can observe that $a_k \to v^*$ as $k \to \infty$. We shall call $S_k, k \geq 0$, the rate intervals.

From the discussion mentioned above it follows that no finite time is available such that *all* points of the unit square synchronize at that moment. The closer v is to the equilibrium v^*, the later is the moment of synchronization.

Set $T = \frac{1}{\gamma}\ln\frac{\kappa}{\kappa-1}$ and denote by $\tilde{T}$ the time needed for solution $u(t,0,v^*)$ of the equation $u' = S-\gamma u$, to achieve threshold. Since all oscillators fire within an interval of length T and the distance between two firing moments of an oscillator are not less than $\tilde{T}$, we can conclude the validity of the following theorem.

Theorem 7. *Assume that the conditions (5), (7), (12), (14) and (19) are valid. If $t_0 \geq 0$ is a firing moment, $x_1(t_0) = 1, x_1(t_0+) = 0$, and $x_2(t_0+) \in S_m$ for some natural number m, then the couple x_1, x_2 of continuously coupled identical biological oscillators synchronizes within the time interval $[t_0 + \frac{m}{2}\tilde{T}, t_0 + Tm]$.*

4.2 Non-identical oscillators: the general case

To make our investigation closer to the real world problems, one has to consider an ensemble of non-identical oscillators. We will discuss the following system of equations

$$x_i' = (S+\mu_i) - (\gamma+\zeta_i)x_i, \tag{20}$$

where $0 \le x_i \le 1+\xi_i, i = 1,2,\dots,n$. The constants S and γ are the same as in the last section such that $\kappa = \frac{S}{\gamma} > 1$. Moreover, constants μ_i and ζ_i are sufficiently small satisfying $\kappa_i = \frac{S+\mu_i}{\gamma+\zeta_i} > 1$. When $x_j(t) = 1+\xi_j$, the oscillator fires and $x_j(t+) = 0$. The firing changes values of other oscillators $x_i, i \ne j$, such that

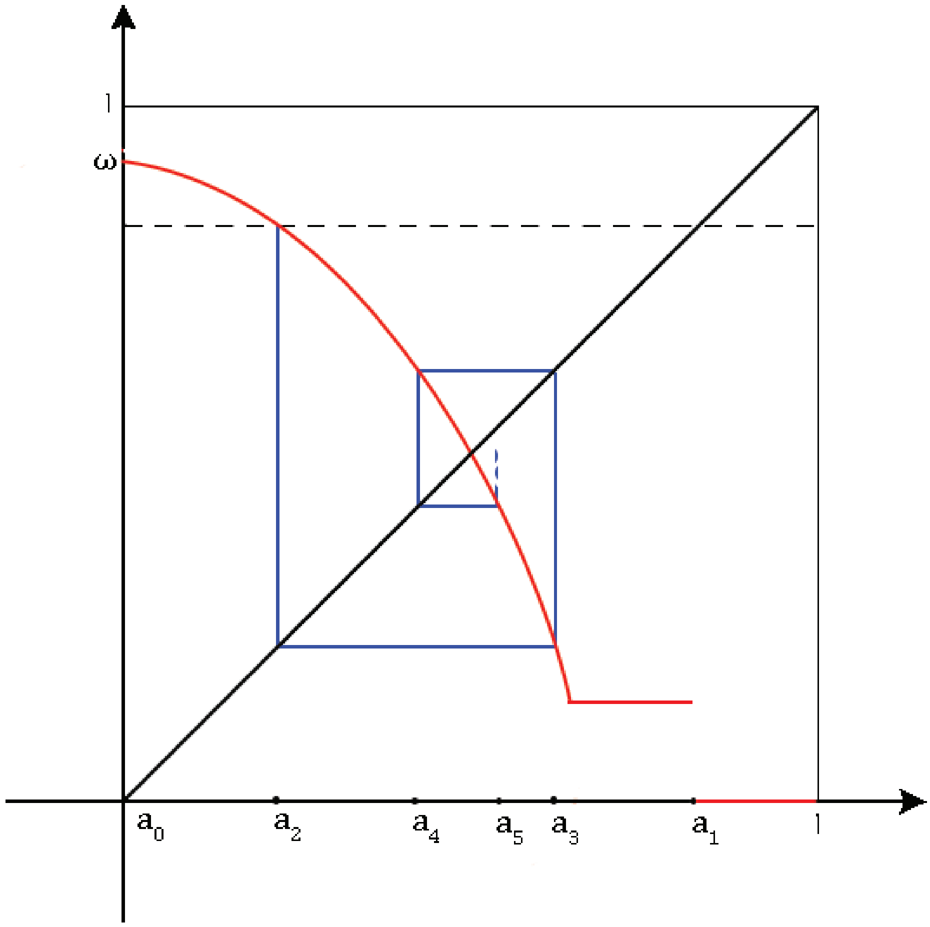

Fig. 11 Boundaries, a_i, of rate intervals are seen.

$$x_i(t+) = 0, \text{ if} x_i(t) \geq 1 - \varepsilon \tag{21}$$

and

$$x_i(t+\tau+) = \begin{cases} x_i(t+\tau)+\varepsilon, \text{ if} x_i(t+\tau) < 1-\varepsilon, \\ 0, \text{ otherwise}, \end{cases} \tag{22}$$

otherwise.

In what follows, we call real numbers $\varepsilon, \mu_i, \zeta_i, \xi_i, \varepsilon_i$, *parameters*, assuming the first one is positive. Moreover, constants $\mu_i, \zeta_i, \xi_i, \varepsilon_i$ will be called *parameters of perturbation*. To achieve the model of *identical oscillators*, assume that the parameters are all zero. In our case, an exhibitory model is under discussion, that is $\varepsilon+\varepsilon_i > 0$ for all i. Coupling is all-to-all such that each firing elicits jumps in all non-firing oscillators. If several oscillators fire simultaneously, then other oscillators react as just one oscillator fires. In other words, any firing acts only as a signal which abruptly provokes a state change, the intensity of the signal is not important, and pulse strengths are not additive. Moreover, we have that

$$x_i(s) = x_i(t)\mathrm{e}^{-(\gamma+\zeta_i)(s-t)} + \int_t^s \mathrm{e}^{-(\gamma+\zeta_i)(s-u)}(S+\mu_i)du,$$

near t.

Under the circumstances that condition (5) is valid, and constants μ_i and ζ_i are sufficiently small such that

$$\frac{\kappa_i - 1}{\kappa_i - 1 + \varepsilon} < \mathrm{e}^{-(\gamma+\zeta_i)\tau}, \tag{23}$$

we have $x_i(s) < 1$ for all $s \in [t, t+\tau]$, provided that $x(t) < 1-\varepsilon$.

We begin the present section by analyzing a couple of oscillators of the ensemble of n oscillators, and find that the couple synchronizes if parameters close to zero. After this, synchronization of the ensemble will be proved.

Consider the model of n non-identical oscillators given by relations (1) and (3). Fix two of them, let us say, x_l and x_r.

Lemma 3. *Assume that the inequalities (5), (7), (12), (14) and (19) are valid and $t_0 \geq 0$ is a firing moment such that $x_l(t_0) = 1+\xi_i, x_l(t_0+) = 0$. If parameters are sufficiently close to zero and absolute values of parameters of perturbation are sufficiently small with respect to ε, then the couple x_l, x_r synchronizes within the time interval $[t_0, t_0+T]$ if $x_r(t_0+) \notin [a_0, a_1)$ and within the time interval $[t_0 + \frac{m-1}{2}\tilde{T}, t_0 + (m+1)T]$, if $x_r(t_0+) \in S_m, m \geq 1$.*

Proof. If $1+\xi_r - \varepsilon - \varepsilon_r \leq x_r(t_0) \leq 1+\xi_r$, then two oscillators fire simultaneously, and we have only to prove the persistence of the synchrony, that will be discussed later. So, fix another oscillator $x_r(t)$ such that $0 \leq x_r(t_0) < 1+\xi_r-\varepsilon-\varepsilon_r$. If the couple is not synchronized, then there is a sequence $\{t_i\}$ of firing moments such that $0 \leq t_0 < t_2 < \ldots$, and the oscillator x_l fires at t_i, with i even, and x_r fires at t_i with odd i. For the sake of brevity let us notate $u_i = x_l(t_i), i = 2j+1$ and $u_i = x_r(t_i), i =$

$2j, j \geq 0$. In what follows we shall show that how one can evaluate u_{i+1} through $L(u_i)$. Consider the case i is even. There are $k \leq n-2$ distinct firing moments of the motion $x(t)$ in the interval (t_i, t_{i+1}). Denote by $t_i < \theta_1 < \theta_2 < \ldots < \theta_k < t_{i+1}$, the moments of firing, when at least one of the coordinates of $x(t)$ fires. We have that

$$
\begin{aligned}
&x_r(\theta_1+\tau) = (x_r(t_i+\tau)+\varepsilon+\varepsilon_r)\mathrm{e}^{-(\gamma+\zeta_r)(\theta_1+\tau-t_i)} + \\
&\kappa_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(\theta_1+\tau-t_i)}),\\
&x_r(\theta_2+\tau) = (x_r(\theta_1+\tau)+\varepsilon+\varepsilon_r)\mathrm{e}^{-(\gamma+\zeta_r)(\theta_2-\theta_1)} + \\
&\kappa_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(\theta_2-\theta_1)}),\\
&\ldots\ldots\\
&x_r(\theta_j+\tau) = (x_r(\theta_{j-1}+\tau)+\varepsilon+\varepsilon_r)\mathrm{e}^{-(\gamma+\zeta_r)(\theta_j-\theta_{j-1})} + \\
&\kappa_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(\theta_j-\theta_{j-1})}),\\
&\ldots\ldots\\
&x_r(t_{i+1}) = (x_r(\theta_k+\tau)+\varepsilon+\varepsilon_r)\mathrm{e}^{-(\gamma+\zeta_r)(t_{i+1}-\theta_k-\tau)} + \\
&\kappa_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(t_{i+1}-\theta_k-\tau)}).
\end{aligned} \tag{24}
$$

The moment t_{i+1} satisfies the following

$$1+\xi_r-\varepsilon-\varepsilon_r \leq x_r(t_{i+1}) \leq 1+\xi_r, \tag{25}$$

and continuously depends on parameters and $x_r(t_i)$.

We have also that

$$
\begin{aligned}
&x_l(\theta_1+\tau) = \kappa_l(1-\mathrm{e}^{-(\gamma+\zeta_l)(\theta_1+\tau-t_i)}),\\
&x_l(\theta_2+\tau) = (x_l(\theta_1+\tau)+\varepsilon+\varepsilon_l)\mathrm{e}^{-\gamma(\gamma+\zeta_l)(\theta_2-\theta_1)} + \\
&\kappa_l(1-\mathrm{e}^{-(\gamma+\zeta_l)(\theta_2-\theta_1)}),\\
&\ldots\ldots\\
&x_l(\theta_j+\tau) = (x_l(\theta_{j-1}+\tau)+\varepsilon+\varepsilon_l)\mathrm{e}^{-(\gamma+\zeta_l)(\theta_j-\theta_{j-1})} + \\
&\kappa_l(1-\mathrm{e}^{-(\gamma+\zeta_l)(\theta_j-\theta_{j-1})}),\\
&\ldots\ldots\\
&x_l(t_{i+1}) = (x_l(\theta_k+\tau)+\varepsilon+\varepsilon_l)\mathrm{e}^{-(\gamma+\zeta_l)(t_{i+1}-\theta_k-\tau)} + \\
&\kappa_l(1-\mathrm{e}^{-(\gamma+\zeta_l)(t_{i+1}-\theta_k-\tau)}).
\end{aligned} \tag{26}
$$

The last two formulas describe the dependence of u_{i+1} on u_i. One can easily find a similar relation for the case i is odd.

Set $\delta_i(\mu_i,\zeta_i) = \kappa_i - \kappa$. It is clear that $\delta_i(0,0) = 0$. By means of (24) and (26), it is possible to achieve that

$$x_r(t_{i+1}) = (x_r(t_i+\tau)+\varepsilon)\mathrm{e}^{-\gamma(t_{i+1}-t_i)}\mathrm{e}^{-\zeta_r(t_{i+1}-t_i)} +$$
$$\kappa(1-\mathrm{e}^{-(\gamma+\zeta_r)(t_{i+1}-t_i)}) + \varepsilon_r \mathrm{e}^{-\gamma(t_{i+1}-t_i)}\mathrm{e}^{-\zeta_r(t_{i+1}-t_i)} +$$
$$(\varepsilon+\varepsilon_r)\sum_{j=1}^{k}\mathrm{e}^{-(\gamma+\zeta_r)(t_{i+1}-\theta_j-\tau)} + \tag{27}$$
$$\delta_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(t_{i+1}-t_i)}), \tag{28}$$

and

$$x_l(t_{i+1}) = (\kappa+\delta_l)(1-\mathrm{e}^{-(\gamma+\zeta_l)(t_{i+1}-t_i)}) +$$
$$(\varepsilon+\varepsilon_l)\sum_{j=1}^{k}\mathrm{e}^{-(\gamma+\zeta_l)(t_{i+1}-\theta_j-\tau)}. \tag{29}$$

Now, recall the map L_D defined in the last section. One can find out that

$$\phi(\overline{t}_{i+1}) = (x_r(t_i+\tau)+\varepsilon)\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i-\tau)} +$$
$$\kappa(1-\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i)}), \tag{30}$$

where $\overline{t}_{i+1}$ satisfies

$$\phi(\overline{t}_{i+1}) = 1, \tag{31}$$

and

$$\psi(\overline{t}_{i+1}) = \kappa(1-\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i)}). \tag{32}$$

By the help of the definition of L_D, we attain that $L_D(u_i) = \psi(\overline{t}_{i+1})$.
Without loss of generality assume that $\overline{t}_{i+1} \le t_{i+1}$. In this case, one has

$$\phi(\overline{t}_{i+1}) - x_r(\overline{t}_{i+1}) = 1 - x_r(\overline{t}_{i+1}) =$$
$$\Phi_1(\varepsilon,\varepsilon_r,\zeta_r,\delta_r,\tau), \tag{33}$$

where

$$\Phi_1(\varepsilon,\varepsilon_r,\zeta_r,\delta_r,\tau) =$$
$$\kappa(1-\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i)})(\mathrm{e}^{-\zeta_r(\overline{t}_{i+1}-t_i)}-1) -$$
$$(x_r(t_i+\tau)+\varepsilon)\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i)}(\mathrm{e}^{-\zeta_r(\overline{t}_{i+1}-t_i)}-1) -$$
$$\varepsilon_r\mathrm{e}^{-\gamma(\overline{t}_{i+1}-t_i)}\mathrm{e}^{-\zeta_r(\overline{t}_{i+1}-t_i)} - (\varepsilon+\varepsilon_r)\sum_{j=1}^{k}\mathrm{e}^{-(\gamma+\zeta_r)(\overline{t}_{i+1}-\theta_j-\tau)} -$$
$$\delta_r(1-\mathrm{e}^{-(\gamma+\zeta_r)(\overline{t}_{i+1}-t_i)}),$$

and the last expression tends to zero as all of its arguments tend to zero. Next, by utilizing (25) and (33) we achieve that $t_{i+1}-\overline{t}_{i+1} \le \Phi_2(\varepsilon,\varepsilon_r,\zeta_r,\delta_r)$, where

$$\Phi_2(\varepsilon,\varepsilon_r,\zeta_r,\delta_r,\tau) \equiv \frac{|\xi_r|+\varepsilon+|\varepsilon_r|+\Phi_1(\varepsilon,\varepsilon_r,\zeta_r,\delta_r,\tau)}{S-|\mu_r|-\gamma-|\zeta_r|}.$$

Now, by means of the last equation, (29) and (32), one can see that

$$|L_D(u_i)-K_i(u_i)| = |x_l(t_{i+1})-\psi(\bar{t}_{i+1})| \le |x_l(t_{i+1})-x_l(\bar{t}_{i+1})|+$$

$$|x_l(\bar{t}_{i+1})-\psi(\bar{t}_{i+1})| \le \Phi_2(S+|\mu_l|+\gamma+|\zeta_l|)+\Phi_1.$$

That is, difference $L_D(u_i,\varepsilon)-u_{i+1}$ can be made arbitrarily small if the parameters are sufficiently close to zero. Moreover, we should assume smallness of absolute values of the parameters of perturbation with respect to ε, to satisfy (25). This convergence is uniform with respect to u_0. We can also vary the number of points θ_i and their location in the intervals (t_j,t_{j+1}) between 0 and $n-1$. The convergence is indifferent with respect to these variations, too.

Consider $L_D^i(u_0,\varepsilon)$. It is true that $L_D^m(u_0,\varepsilon)\in[1-\varepsilon,1]$. Assume, without lost of generality, that m is an even number. Since L_D is a continuous function, we can find recurrently, by applying the following sequence of inequalities $|u_i-L_D^i(u_0,\varepsilon)| \le |u_i-L_D(u_{i-1},\varepsilon)|+|L_D(u_{i-1},\varepsilon)-L_D(L_D^{i-1}(u_0,\varepsilon))|, i=1,2,\ldots,$ that either $1+\xi_r-\varepsilon-\varepsilon_r<u_m<1+\xi_r$ or $1+\xi_l-\varepsilon-\varepsilon_l<u_{m+1}<1+\xi_l$, if the parameters are sufficiently small. From the notation it implies that each of the last two inequalities bring the couple to synchronization. Similarly, one can discuss relations connected to inequality (19).

Since each of the iterations of L_D is done within interval with length not more than T, we obtain now that the couple x_l,x_r is synchronized not later than $t=t_0+(m+1)T$.

We have found that oscillators x_l and x_r fire in unison at some moment $t=\theta$. Next, we show that they will save the state, being different. To find conditions for this, let us denote by $\tau>\theta$ the next moment of firing of the couple. Let say, x_r fires at this moment. Thus, we have that $x_l(\theta+)=x_r(\theta+)=0$. Then $x_l(t)=x_r(t), \theta\le t\le\tau$. It is clear that to satisfy $x_l(\tau+)=x_r(\tau+)=0$, we need $1+\xi_r-\varepsilon-\varepsilon_r\le x_l(\tau)$. By applying formula (25) again, this time with $t_i=\theta, t_{i+1}=\tau$, one can easily obtain that the inequality is correct if parameters are close to zero and absolute values of the parameters of perturbation are small with respect to ε. Thus, one can conclude that if a couple of oscillators is synchronized at some moment of time than it continues to fire in unison for ever. The lemma is proved.

Let us extend the result of the last Lemma for the whole ensemble.

Theorem 8. *Assume that the conditions (5), (7), (12), (14) and (19) are valid, and* $t_0\ge 0$ *is a firing moment such that* $x_j(t_0)=1+\xi_j, x_j(t_0+)=0$. *If the parameters are sufficiently close to zero, and absolute values of parameters of the perturbation are sufficiently small with respect to* ε, *then the motion* $x(t)$ *of the system synchronizes within the time interval* $[t_0,t_0+T]$, *if* $x_i(t_0+)\notin[a_0,a_1), i\ne j$, *and within the time interval* $[t_0+\frac{\max_{i\ne j}k_i-1}{2}\tilde{T}, t_0+(\max_{i\ne j}k_i+1)T]$, *if there exist* $x_s(t_0+)\in[a_0,a_1)$, *for some* $s\ne j$ *and* $x_i(t_0+)\in S_{k_i}, i\ne j$.

Proof. Consider the collection of couples $(x_i, x_j), i \neq j$. Each of these pairs synchronizes by the last Lemma within interval $[t_0 + \frac{\max_{i\neq j} k_i - 1}{2}\tilde{T}, t_0 + (\max_{i\neq j} k_i + 1)T]$. The theorem is proved.

Let us introduce a more general system of oscillators such that Theorem 8 is still true.

Consider a system of n oscillators given such that if $i-$th oscillator does not fire or jump up, it satisfies $i-$th equation of system (1). If several oscillators $x_{i_s}, s = 1,2,\ldots,k$, fire such that $x_{i_s}(t) = 1 + \phi(t, x(t), x(t-\tau_{i_s})$, where $|\phi(t, x(t), x(t-\tau_i)| < \xi_i, i = 1,2,\ldots,n$, and $x_{i_s}(t+) = 0$, then all other oscillators $x_{i_p}, p = k+1, k+1, \ldots, n$, change their coordinates by law

$$x_i(t+) = 0, \text{if} x_i(t) \geq 1 - \varepsilon \tag{34}$$

and, if $x_i(t) < 1 - \varepsilon$, then

$$x_i(t+\tau+) = x_i(t+\tau) + \varepsilon + \sum_{s=1}^{k} \varepsilon_{i_p i_s}. \tag{35}$$

One can easily see that the last theorem is correct for the model just have been described, if $\varepsilon + \sum_{s=1}^{k} \varepsilon_{i_p i_s} > 0$, for all possible k, i_p and i_s, and we assume that ε_{ij} are also parameters of perturbation. Moreover, one can easily see that initial functions for thresholds conditions can be chosen arbitrarily with values in the domain of the system.

Remark 6. Our preliminary analysis shows that the dynamics in a neighborhood of v^* can be very complex. We do not exclude that a chaos appearance can be observed, and trajectories may belong to a fractal, if parameters are not small. It does not contradict to the zero Lebesgue measure of non-synchronized points. Possibly, analysis of non-identical oscillators with not small parameters is of significant interests to explore arrhythmias, earthquakes, chaotic flashing of fireflies, etc.

Remark 7. The time of synchronization for a given initial point does not increase if the number of oscillators increases (but the parameters needed to be closer to zero). This property, possibly, can be accepted as a small-world phenomenon.

4.3 The simulation result

To demonstrate our main result numerically, let us consider a model of 100 oscillators, which initial values are randomly uniform distributed in $[0,1]$. Their differential equations are of form

$$x_i' = (4.1 + 0.01 * sort(rand(1,n)) - (3.2 + 0.01 * sort(rand(1,n))x_i,$$

and thresholds

$$1+0.005*sort(rand(1,n)), i = 1,2,\ldots,100,$$

where deviations of coefficients the threshold are also uniformly random in $[0,1]$. We place the result of simulation with $\varepsilon = 0.06$ and $\tau = 0.002$ in Figure 12, where the state of the system is shown at the initial moment, before the $183-$th jump, before the $366-$th jump and the last is before the $549-$th jump. That is, it is obvious that eventually all oscillators fire in unison.

We verified that all conditions (5),(7),(12),(14) and (19) are valid.

5 Conclusion

There are two main approaches to analyze the conjectures, which were first applied in [47] and [50]. The phase description method has dominated the field in last decade, has been utilized in deterministic and indeterministic analysis, and used in addressing various real world problems. One can say that our results give a new impact to C. Peskin's proposal. There is a rich collection of results on synchronization, obtained through experiments and simulations. The results of the present paper can give theoretical background for them and form a basis for new ones. They can be applied, by using the theory of maps and their perturbations, not only to the problems of synchronization, but also to periodic, almost periodic motions, and complex behavior of biological models. New small-world phenomena can be discovered.

The famous two conjectures of C. Peskin [50] were developed for further applications. One of important additional questions is: Do continuous or piece-wise continuous couplings synchronize the model? In the present paper, sufficient conditions for a positive answer are found. The method of investigation is based on a specially constructed map. One can remark that the systems investigated in this chapter are, in fact, cooperative discontinuous systems [28]-[33] with monotone dynamics [56]. Consequently, by applying the methods of dynamical systems with discontinuities

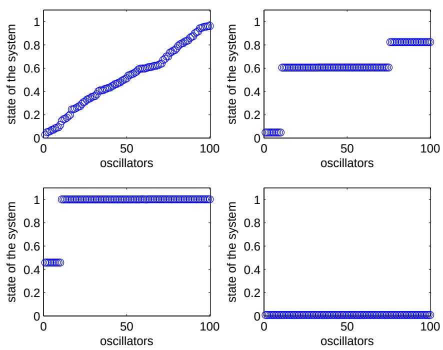

Fig. 12 The state of the model before the first, the $183-$th, $366-$th, and $549-$th jump is seen. The flat fragments of the graph are groups of oscillators firing in unison.

at variable moments [2] one can obtain more results concerning biological processes in the future.

The cardiac pacemaker model of identical and non-identical oscillators with delayed pulse-couplings is considered in the chapter. We apply the method developed in [5]-[3], which is based on a specially defined map. Sufficient conditions are found such that involvement of delay in the Peskin's model does not change the synchronization result for identical and non-identical oscillators [50, 47, 5]. What we have done admits a biological sense, since retardation is often presents in biological processes and if one proves that a phenomenon preserves even with delays, that makes us more confident that the model is adequate to the reality. Moreover, the method of treatment of models with delay can be useful for neural networks and earthquake faults [17, 20, 27, 30, 49] analysis. All the proved assertions are true with $\tau = 0$. Indeed, it is easy to see that conditions (5), (7), (12), (14) and (19) are valid with $\tau = 0$. Thus, the synchronization results for the Peskin's model in [5, 3] are confirmed one more time. In next our papers we suppose to give analysis for models with non-small delays. There are several interesting problems, which can develop results of the present paper further. Let us name some of them. Suppose that condition (19) is violated. That is, $\tilde{v} > a_2$. Consider two identical oscillators. The corresponding graph of the map looks as in Figure 13.

One can see from the picture that the couple synchronizes after not more than three iterations, if $v \notin [b, a_1]$. Otherwise the pair moves periodically with period 2 ultimately. Considering this simple case of two identical oscillators, one can predict that for an ensemble of oscillators (identical or not quite identical) there should be two or more clusters of synchronized oscillators, and the clusters may move periodically, if $\tilde{v}$ is near a_2. In our simulations, we observe clustering as well as periodicity in the motion of the clusters. Since the number of clusters changes with the variation of the parameters, one can investigate bifurcation of periodic solutions as well as the number of clusters.

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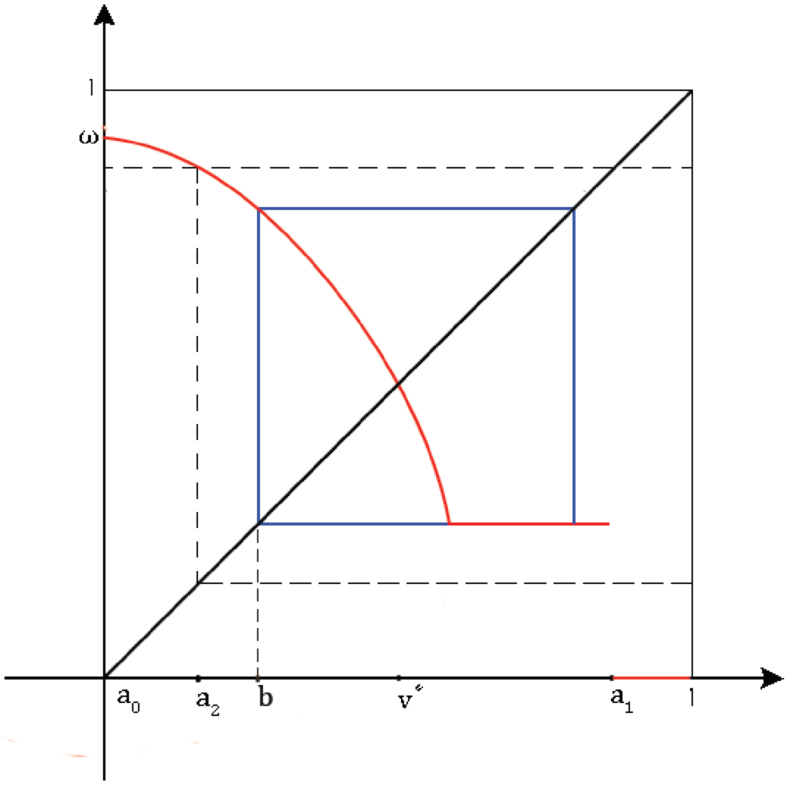

Fig. 13 The state of the model before the first, the 183−th, 366−th, and 549−th jump is seen. The flat fragments of the graph are groups of oscillators firing in unison.

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