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SYNCHRONIZATION IN NETWORKS OF PULSE OSCILLATORS WITH TIME-DELAY COUPLING

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Abstract

The paper is devoted to study of synchronization in small neural networks with coupling delays. We concentrate on two problems: i) long-range synchronization of cortical areas and ii) control of patterns of rhythmic activity of central pattern generators. We show that precise zero lag synchronization is possible even for distant areas, which interact with large coupling delays. In context of CPGs dynamics coupling delays may provide a mechanism for control of rhythmic patterns.

Key words

Synchronization, phase locking, coupled oscillators, time delay.

1 Introduction

Mutual synchronization of interacting oscillators is a fundamental effect observed in all fields of physics. Particularly, there is lot of evidence that this effect plays crucial role in many aspects of brain functioning. For example, there is an important link between synchronization of distributed neural activity and complex informational processing in cortical networks. A number of experiments in visual cortex and other cortical areas of animals show that discharges of different areas often demonstrate precise and context dependent temporal relations [Engel *et al.*, 1991; Frien *et al.*, 1994; Steriade *et al.*, 1996; Courtemanche and Lamarre, 2005]. This synchronization is shown to be provided by reciprocal cortical-cortical connections. A fact of great interest is that systematic phase lags may be established even between the discharges of neurons from distant areas. In many cases precise zero-lag synchronization between distant areas is observed. This effect may be very important because it is hypothesized to provide a mechanism for the large-scale integration of distributed brain activity. Different aspects of the integral cognitive process occur in different areas, and the temporal synchronization between these areas ensures binding of all these subprocesses [Gray *et al.*, 1989; Ulhaas *et al.*, 2009].

Another instance of importance of synchronization in neural networks concerns control of motions. Rhythmic motions of animals, such as walking, scratching or breathing, are shown to be controlled by rhythmic activity of the so-called central pattern generators. CPGs are neural networks that produce rhythmic outputs autonomously, i.e. without sensory or central input. For example, locomotion of mammals were proved to be concerned with activity of such networks located in spinal cord [Ijspeert, 2008; Guertin, 2009; Duysens and Can de Crommert, 1998]. From dynamical point of view CPGs are systems of coupled oscillators which undergo mutual synchronization. Phase relations between the neural oscillators determine output rhythmic patterns of neural activity which underlie motor patterns. Different kinds of rhythmic motions correspond to different phase relations between neurons discharges [Collins and Stewart, 1993; Collins and Richmond, 1994; Abarbanel *et al.*, 1996], that is why variability of phase patterns of CPG is of great importance.

Theoretical study of synchronization in neural networks faces one with many specific features of neuronal coupling. Let us dwell on two of them. Firstly, dynamics of neural networks is often concerned with temporal delays in communication between the neurons. These delays arise from two reasons: i) chemical synapses inertness and ii) finite velocity of spikes propagation along axons. Synaptic delays are usually about 1 ms, but axonal delays depend on distance between communicating neurons and may reach values of several tens on milliseconds. Large coupling delays may strongly change synchronization, that is why it is important to study how they influence dynamics of neural networks [Ermentrout and Koppel, 1998; Earl and Strogatz, 2003; Bazhenov *et al.*, 2008; Jahnke *et al.*, 2008; Schöll *et al.*, 2009; Panchuk *et al.*, 2012]. Secondly, coupling in neural networks has strongly discontinuous character. Typical signals between the neurons represents series of pulses, or spikes, which are often short in relation to intervals between them.

These two features of neural coupling define the motivation of the present paper. We consider synchronization in networks of pulse oscillators with time-delayed couplings developing the approach introduced in our previous works [Klinshov and Nekorkin, 2011]. We are mainly concentrated on two things. Firstly, we are interested how oscillators may synchronize with zero lag in the presence of large delays which are of order and even larger than the period of the oscillations. This question concerns the problem of long-range synchronization of distant brain areas and binding of their activity. Secondly, we are interested in synchronization and phase patterns in CPGs. We examine how introduction of delays influences the dynamics of CPGs and show that it may cause sufficient variability of demonstrated output patterns. This may provide a mechanism for rhythmic patterns control and switching which concerns the problem of motion control.

2 Model

In our model we represent an individual neuron as an oscillator with phase $\varphi \in [0;1]$ growing uniformly with the velocity $d\varphi/dt = \omega$. For $\varphi = 1$, the oscillator reaches threshold, emits a pulse, and resets its phase to zero. We consider an ensemble of N non-identical neurons with frequencies ω_j interacting with a time lags. It is described by the following system:

$$\frac{d\varphi_j(t)}{dt} = \omega_j + \sum_{k=1}^{N} G_{jk}(\varphi_j(t), \varphi_k(t-\tau_{jk})). \quad (1)$$

We use technique of phase response curves (PRCs) to describe interaction between the neurons. In this technique, coupling function is chosen in the form $G_{jk}(\varphi_j(t), \varphi_k(t-\tau_{jk})) = \mu_{jk}F(\varphi_j(t))\delta(\varphi_k(t-\tau_{jk}))$. This means that when k-th neuron emits a pulse, it is received by j-th neuron with delay τ_{jk}. When j-th neuron receives a pulse its phase instantly changes on value $\Delta\varphi = \mu_{jk}F(\varphi_j)$. This value is the so-called phase response curve. Further we use function $F(\varphi) = -\sin 2\pi\varphi$. Such form of PRC belongs to the so-called second class [Hansel *et al.*, 1995], which means that incoming pulses may either delay or advance neuron excitation.

Strictly speaking, (1) is the system with time lagging, so it has infinite dimension and is very difficult for studying. But because of using of PRC approach this system can be reduced to the map of finite dimension, which simplifies its investigation. The technique of such reduction was introduced in [Klinshov and Nekorkin, 2011] for the case of two units and may be generalized for the case of arbitrary N. The main idea of this reduction is that system dynamics consists of discrete events which occur when the neurons emit or receive pulses. During these events (the so-called G-events) the neurons phases are perturbed, and between these events they grow uniformly. We construct the map that describes how the system state changes between sequential G-events (the so-called G-map, see Methods). The further study of the system dynamics is based on this map.

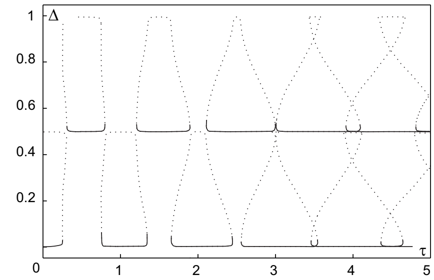


Figure 1. Synchronous regimes in a pair of oscillators with simmering coupling: phase lag versus coupling delay. Solid lines correspond to stable solutions, dotted lines correspond to unstable ones. Parameters: $\mu = 0.1, \omega_1 = 1, \omega_2 = 1.01$.

3 Long-Range Synchronization

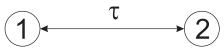
Let us begin from studying of the effect of long-range zero-lag synchronization. We call the synchronization "zero-lag" if it occurs with the zero phase shift, i.e. the units undergoing zero-lag synchronization fire strictly simultaneously. And we call it "long-range" meaning that the coupling delay is large enough in respect to the period of intrinsic spiking. In our previous works we have proved, that synchronization of pulse oscillators is possible for arbitrary large coupling delays. For a pair of neurons with symmetric delayed coupling ($N = 2$, $\mu_{12} = \mu_{21} = \mu$, $\tau_{12} = \tau_{21} = \tau$) we have proved that synchronization occurs for the frequency mismatches limited by

$$\omega_2 - \omega_1 \le \zeta_0 = \frac{2\mu\omega_1}{1-\mu}. \quad (2)$$

Synchronous regimes are observed in the so-called "synchronization intervals" of coupling delay τ (Fig. 2). For the case of close frequencies $\omega_1 \approx \omega_2$ these intervals cover almost all values of τ. This may explain long-range synchronization, but not zero-lag one. The point is that the phase lag Δ between instants of neurons firing depends on τ and strongly changes from interval to interval. The intervals with in-phase and antiphase synchronization alternate while τ grows. This feature does not allow to obtain perceive zero-lag synchronization with arbitrary coupling delay.

To explain zero-lag long-range synchronization the so-called "dynamical relaying" concept was suggested in [Vincente *et al*, 2008; Vincente *et al.*, 2009]. In this

(a) Direct communication:



(b) Dynamical relaying:

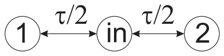


Figure 2. Direct communication (a) and dynamical relaying (b) of two cortical areas. In the last case the cortical areas “1” and “2” communicate through the third intermediate area.

concept it is assumed that synchronizing cortical areas communicate not directly but through some other intermediate area. This scheme is illustrated in Fig. 3. The authors report that dynamical relaying allows to achieve precise zero-lag synchronization with high probability for all values of coupling delay.

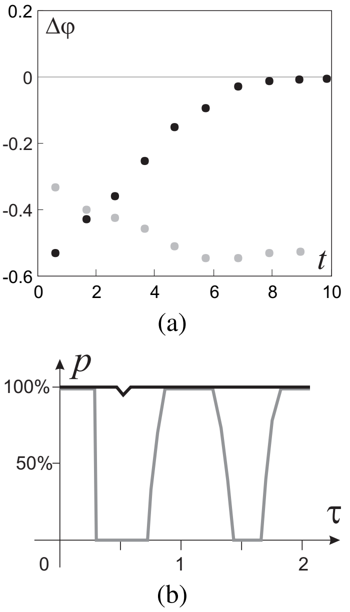
To test this hypothesis and explain the mechanism of dynamical relaying we considered the system (1) for the case of $N = 3$ identical neurons ($\omega_j = 1$) which are connected as it is shown in Fig. 3. In this scheme the nonzero parameters are as follows:

$$\begin{aligned}
\tau_{1i} &= \tau_{i1} = \frac{\tau}{2},\\
\tau_{2i} &= \tau_{i2} = \frac{\tau}{2},\\
\mu_{1i} &= \mu_{2i} = \frac{\mu}{2},\\
\mu_{i1} &= \mu_{i2} = \mu.
\end{aligned}$$

We studied the dynamics of this system and found that the oscillators 1 and 2 really undergo strict zero-lag synchronization for all values of τ and almost all initial conditions. The typical evolution of the system is depicted in Fig. 3(a). One can see that the phase lag between the units 1 and 2 quickly tends to zero, while the intermediate unit stays in antiphase with them.

We studied the probability P_z of the zero-lag synchronization in the cases of direct coupling and dynamical relaying, which are depicted in Fig. 3(b) versus delay τ. In the first case, this probability equals 100% inside the in-phase intervals and 0% inside the antiphase ones. Near the borders of the intervals they overlap and the system is multistable, which results in medium values of the probability P_z. For the case of dynamical relaying the probability P_z almost always equals 100%. Only small dip for $\tau = 0.5$ is observed. This is because synchronization for such delays occurs slowly, and it was not established yet during the finite time of simulation.

To explain the dynamical mechanism of precise zero-lag synchronization via dynamical relaying we used our earlier results on synchronization of directly coupled oscillators. As it was stated above, two directly coupled identical oscillators synchronize in phase or in antiphase depending on the value of the coupling delay.



(b)

Figure 3. (a) Synchronization of two oscillators interacting via dynamical relaying. Phase lag between units “1” and “2” is plotted with black dots, and phase lag between the intermediate unit and the first unit is plotted with gray dots. Coupling delay $\tau = 1.3$. (b) Probability of zero-lag synchronization for direct coupling (gray) and dynamical relaying (black).

In the case of dynamical relaying scheme the situation is similar. When the value $\tau/2$ belongs to the inphase synchronization interval, the intermediate unit synchronizes in phase with the first one and with the second one, so they are in phase with each other as well. When the value $\tau/2$ falls into the antiphase synchronization interval, the intermediate unit is in antiphase with units 1 and 2, and they turn out in-phase synchronized again.

4 Rhythmic Patterns of CPGs

Let us pass from zero-lag synchronization to more complex synchronous regimes, namely rhythmic patterns of central pattern generators. We say that the CPG demonstrates a patterned rhythmic activity if all the neurons discharge periodically with the same period and constant phase relations between them. These phase relations are used to characterize the rhythmic pattern.

Let us study rhythmic activity of CPGs in presence of coupling delays. Rhythmic patterns can be found even in the ensemble of two unit. In this simplest CPG only two stable “patterns” are possible. They correspond to in-phase and antiphase synchronization of the units. The main properties of the coupling delay in this case are the following (see Fig. 4, modified from [Klinshov and Nekorkin, 2011]). First of all, introducing of the delay increases the patterns variability: without delay the only in-phase pattern is possible, while in the presence of delay the antiphase one appears. Secondly, varying of the delay results in controllable switching of

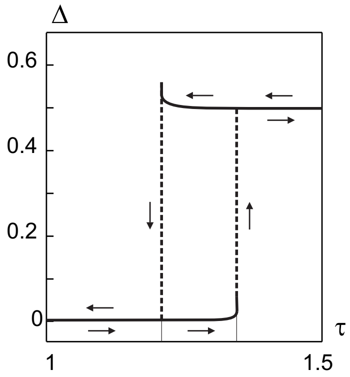


Figure 4. Switching between in-phase and antiphase "patterns" in the system of two symmetrically coupled oscillators.

the patterns. And finally, this switching is connected with hysteresis.

These key features of rhythmic patterns turn out to be typical for CPGs with greater number of units with time-delayed coupling. As an example of such CPG we consider a network of four globally coupled neurons which is depicted in Fig. 5(a). Four neurons are located in corners of a square, delays between neighboring neurons equal $\tau/2$, delays between diagonal neurons equal τ. Coupling strength between each pair of neurons equals $\mu = 0.1$. Frequencies ω_j have Gaussian distribution with median value $\omega = 1$ and dispersion $\sigma = 0.01$. We set them not identical to study the influence of possible parameters varying and make sure that the regimes we obtain are not sensible to them.

Studying of the network showed that depending on the delay parameter τ it may produce a number of various rhythmic patterns. We mark these patterns with sets of four numbers $(\varphi_1, \varphi_2, \varphi_3, \varphi_4)$, where φ_j means the phase lag between the first and the j-th neurons firing. The most typical are the following patterns: i) The pattern (0,0,0,0) of global synchronization, when all the units fire simultaneously in the same phase. ii) The pattern (0,0.5,0,0.5) or partial pairwise synchronization, when the first unit fires in phase with the third one, and the second unit fires sin phase with the fourth one, while these pairs fire in antiphase. iii) The pattern (0,0.25,0.5,0.75) of sequential firing, when all the units fire one after another with the quarter-period lag.

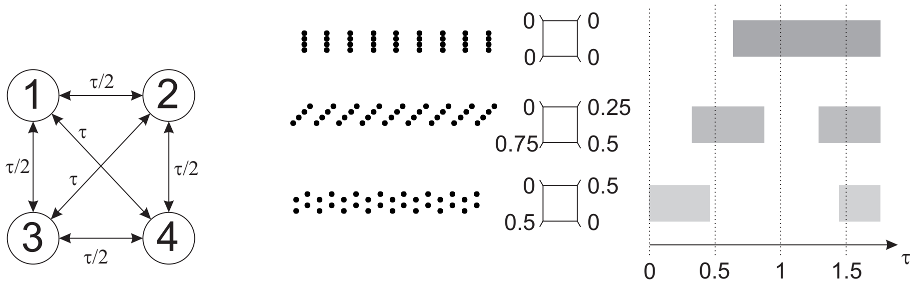
Each of these three patterns exists in definite interval of delay coefficient τ. These intervals are depicted in Fig. 5(b). One can see that the key features of the system dynamics are similar as in the case of two units. Slow increasing of the parameter τ results in sequential switching between the patterns. For $\tau = 0$ the only pattern (0,0.5,0,0.5) exists. When $\tau = \tau_1 \approx 0.37$ the second pattern (0,0.25,0.5,0.75) appears. And for $\tau = \tau_2 \approx 0.61$ the third pattern (0,0,0,0) appears. The switching between the patterns is concerned with hysteresis which comes from the system instability near the points in which new patterns are born. For example, the pattern (0,0.25,0.5,0.75) appears for $\tau = \tau_1$, but the pattern (0,0.5,0,0.5) disappears only for $\tau = \tau_1' \approx 0.48$. This means that when τ increases the switching (0,0.5,0,0.5)→(0,0.25,0.5,0.75) takes place for $\tau = \tau_1'$. But when the τ decreases the opposite switching takes place only for $\tau = \tau_1$.

5 Discussion

We have studied influence of coupling delay on dynamics of small neural networks. We have shown that even large coupling delay does not prevent mutual synchronization of coupled neurons or neuronal areas. This may explain long-range synchronization observed in numerous experiments. More complex schemes of coupling, such as dynamical relaying, may explain precise zero-lag long-range synchronization or cortical areas.

Another result is that the coupling delay may be an instrument for control of rhythmic patterns of central pattern generators. We show that varying delays in a small network of coupled oscillatory neurons allows to change phase relationships between the units. In previous works [Masoller and Marti, 2005; Motter *et al.*, 2005; Kanter *et al.*, 2011] the authors reported that the structure of the connections in the network defines the properties of its synchronization. Particularly, in [Kanter *et al.*, 2011] it was shown that the distribution of the delays determines the number of clusters which appear in the network. To find this number the authors calculate the greatest common divisor (GCD) of the summary delays of the loops composing the connections graph. In our small network the GCD equals 2 which means that the expected regime is coexistence of two clusters with zero-lag synchronization inside them. However, we observe the regimes with 1, 2 or 4 clusters, and each of them is stable in different interval of τ. Observing of the regimes with quantity of clusters exceeding the GCD can is because in contrast with [Kanter *et al.*, 2011] we considered not chaotical oscillators, but periodical ones with a very simple (pulsative) coupling, and there is no need for all the inputs to be strictly identical. And the influence of the value of τ is alteration of the stability of different regimes.

Changing of the synchronization regimes by the delay may be also related to the problem of control of rhythmic patterns which attracts a lot of attention in connection with motion control studying. Particularly, a number of papers was devoted to locomotion of tetrapod animals or robots [Collins and Stewart, 1993; Collins and Richmond, 1994; Abarbanel *et al.*, 1996; Kimura *et al.*, 1999; Shinkichi *et al.*, 2006]. The authors considered networks of four coupled oscillators each of which controls the motion of one limb. In this case different patterns of the rhythmic activity of the network correspond to different gait types – walk, trot, gallop and so on. For example, the pattern (0,0.5,0,0.5) corresponds to trot, (0,0.25,0.5,0.75) is walk, and (0,0,0,0) is "pronk" [Collins and Stewart, 1993]. In the previous works the authors specially tuned the parameters



(a) (b)

Figure 5. (a) CPG consisting of four neurons with delayed coupling. (b) Possible output rhythmic patterns and τ intervals inside which they exist. Sequences of black dots determine series of pulses emitted by the oscillators.

of the networks for each gait: to establish the certain phase relations they changed the intrinsic parameters of thew oscillators and coupling parameters. In our model switching of the patterns occurs when we change only one parameter, namely delay parameter τ.

One may object that in real CPGs it is difficult to vary all the coupling delays simultaneously. But the point is that absolute values of delays do not play any crucial role, and the only thing which is important is relation between them and oscillations frequency. From this point of view varying of delays is equal to changing of network oscillations frequency ω. This frequency defines the rate of limbs motion, i.e. the speed of the animal movement. Thereby, in our model switching of gaits takes place when the speed of the animal changes. No any other parameters tuning is necessary.

The fact that the animal gait change with its speed growth is well known from numerous experiments. The bifurcation diagram in Fig. 9 from [Collins and Stewart, 1993] illustrates this idea for the horse gaits. When the animal moves slowly it walks. Increasing the speed results in transition to trot and then to gallop. Our model describes possible mechanism of these switching, which may be related to coupling delays in CPG. A fact of great interest is that the switching of gaits is experimentally shown to have hysteresis character, which is in good agreement with our results.

6 Conclusions

Coupling delays were shown to exert essential influence on dynamics of small neural networks. In the problem of synchronization of distant cortex areas this influence is negative, but it may be overcome with using indirect coupling schemes such as dynamical relaying. And in context of control of CPG rhythmic activity coupling delays may be even useful. They increase variability of rhythmic patterns and allow their controllable switching.

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Methods

Here we demonstrate the technique of reduction of the system (1) to the map. Let us introduce the state vector

$$\xi(t) = \big(\varphi_1(t), \varphi_2(t), ..., \varphi_N(t), x_1^1, x_1^2, ..., x_1^K,\\ x_2^1, x_2^1, ..., x_2^K, ..., x_N^1, x_N^2, ..., x_N^K\big),$$

where $x_j^k = t - t_j^k$ is the time which passed from the moment when j-th unit emitted k-th pulse. For large enough K the state vector ξ fully describes the state of the system (1) and allows to predict its future dynamics.

Let us study the dynamics of the state vector. Each of its components grows uniformly almost always:

$$\frac{d\varphi_j}{dt} = \omega_j,\\ \frac{dx_j^k}{dt} = 1.$$

However, in certain moments some of the components undergo stepwise changes. These moments are related to events of two types:

i) Pulse emitting by one of the units. This event takes place when the phase of one of the oscillators reaches unity. Then its phase resets to zero, and a new pulse with $t_j^k = t$ appears. Call events of this type E-events. The nearest E-event for the k-th unit takes place at the time $t' = t + \theta_k$, where

$$\theta_k = \frac{1 - \varphi_k}{\omega_k}.$$

Then the state vectors changes as follows:

$$\begin{aligned} &\varphi_k(t') = 0,\\ &\varphi_p(t') = \varphi_p(t) + \omega_p\theta_k,\\ &x_1^k(t') = 0,\\ &x_j^k(t') = x_{j-1}^k(t) + \varphi_k, \quad j > 1,\\ &x_j^p(t') = x_j^p(t) + \varphi_k, \quad j > 1, \end{aligned} \qquad (3)$$

where $p \neq k$. Denote transformation (3) as the map $E_k : \xi(t) \mapsto \xi(t')$.

ii) Pulse receiving by one of the units. This event happens when a pulse produced by one of the units earlier reaches any second unit after some delay. Then the phase of the second unit instantly shifts on some value which depends on the coupling strength and the PRC shape. Call such events F-events. The nearest F-event concerned with action of the pulse produced by m-th unit on k-th unit occurs at the moment $t' = t + \vartheta_{mk}$, where

$$\vartheta_{mk} = \tau_{mk} - x_q^m,$$

where $q = \max\{j|x_j^m < \tau_{mk}\}$. The state vector changes after this event as follows:

$$\begin{aligned} \varphi_k(t') &= \varphi_k(t) + \omega_k\vartheta_{mk} + \mu_{mk} f\left(\varphi_k(t) + \omega_k\vartheta_{mk}\right), \\ \varphi_p(t') &= \varphi_p(t) + \omega_p\vartheta_{mk}, \\ x_j^{k,p}(t') &= x_j^{k,p}(t) + \vartheta_{mk}, \end{aligned} \tag{4}$$

where $p \neq k$. Denote transformation (4) as the map $F_k : \xi(t) \mapsto \xi(t')$.

Name both E- and F-events G-events. Then to determine the nearest G-event one should find the minimum value $\delta_{\min}$ of all values θ_k and ϑ_{mk}. The system state change is defined by the map

$$G : \xi(t) \mapsto \xi(t') = \begin{cases} E_k, & \delta_{\min} = \theta_k, \\ F_{mk}, & \delta_{\min} = \vartheta_{mk}. \end{cases}$$

This map fully describes dynamics of the system (1).

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