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SYNCHRONIZATION, NOISE AND ELECTRORECEPTORS

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Classical notion of synchronization, introduced originally for periodical self-sustained oscillators, can be extended to stochastic systems. This can be done even in the case when the characteristic times of a system are fully controlled by noise. Stochastic synchronization is then defined by imposing certain conditions to various statistical measures of the process. We review various approaches to stochastic synchronization and apply them to study synchronization in the electrosensory system of paddlefish.

1. Introduction

Among other nonlinear effects, the phenomenon of synchronization is probably the most often observed in the great variety of systems of different origins. From a general point of view synchronization represents the relation between two objects that are oscillating in time. The oscillators are said to be synchronized, or in «synchrony», when there exists a fixed phase relation between them.

Besides man-made systems where synchronization is actually used [1], this phenomenon has been observed in biological systems [2] starting from microscopic level of cell populations [3] and single neurons [4 - 6] to large neural networks [7], human cardio-respiratory dynamics [8] as well as external synchronization of human cardio rythm [9], and behavior of large populations of living objects [10]. We refer to a recent book [11] for a comprehensive review on modern theories and applications of synchronization.

Synchronization occurs when a nonlinear oscillator, possessing a stable periodic motion, is subjected to an external time-dependent force or is coupled with another oscillator. Classical theory of synchronization operates with so-called self-sustained periodic oscillators. The characteristics of stable periodic oscillations of such systems, represented by a stable limit cycle in the phase space, are determined by natural properties of the oscillator and do not depend upon initial conditions [12]. When a self-sustained oscillator is driven by an external periodic force of appropriate amplitude and frequency, the oscillations of the system occur in phase with the external signal. Synchronization is thus defined as phase locking and frequency entrainment. The same effect occurs when two (or more than two) self-sustained oscillators are coupled.

Recent studies have shown that the class of systems and driving signals which exhibit synchronization could be significantly extended. Different types of synchronization have been found in chaotic systems, including the classic type of phase synchronization in periodically driven and coupled chaotic systems [13 - 16].

In this paper, we are concerned with noisy synchronization. Though originally studied quite early [17], the theory of stochastic synchronization has only recently been applied to biological or medical systems. As intuitively expected, noise usually acts against synchronization. However, recently it has been shown that for a large class of stochastic systems the phenomenon of noise enhanced phase synchronization can be observed [18].

2. Stochastic synchronization

Synchronization of coupled periodic self-sustained oscillators is understood as adjustment of their phases and frequencies. If $\Phi(t)$ is the phase of one oscillator and $\Psi(t)$ is the phase of another oscillator (or the phase of periodic driving force), then the phase locking condition reads:

$$|\dot{\phi}(t)| < \text{const}, \quad \dot{\phi}(t) = n\dot{\Phi}(t) - m\dot{\Psi}(t), \quad (1)$$

where n and m are integer numbers. The phases $\Phi(t)$, $\Psi(t)$ are defined on a whole real line. In the regime of synchronization, the phase difference, $\phi(t)$, therefore, remains constant forever. In the simplest case of 1:1 synchronization the response of the oscillator is represented by one complete cycle per one period of driving force. More general case is $m:n$ synchronization, which means that during m complete cycles of driving signal there occur n complete cycles of the oscillator. For periodic oscillators the synchronization condition Eq. (1) is equivalent to the notion of frequency locking $n\omega = n\dot{\Phi} = m\Omega = m\dot{\Psi}$.

The concept of synchronization for stochastic systems is not trivial. As is well known [17] noise influence on a self-sustained oscillator results in the diffusion of its phase. That is why the properly defined phase difference ϕ is also diffuses so that the condition Eq. (1) never fulfills in the presence of Gaussian noise. The phase locking may occurs only for random periods of time and is interrupted by so-called phase slips. Thus, the definition of synchronization in the presence of noise appears to be «blurred». That is why the conditions of synchronization should be defined in statistical way and we have to use the notion of «effective» or «stochastic» synchronization [19,20]. It can be defined by imposing restrictions on (i) signal-to-noise ratio, in the case of periodically driven self-sustained oscillator; (ii) frequency fluctuations; and (iii) phase fluctuations.

We use here the strongest definition of stochastic synchronization based on statistics of phase fluctuations. Statistical measures of synchronization can be based on the stationary probability density of the phase difference wrapped into $[0, 2\pi]$. A well-expressed maximum will correspond to a strong synchronization in statistical sense. This can be further quantified by the synchronization index [7] as the first Fourier mode of the stationary probability density of the phase difference: $\gamma^2 = \langle \sin \phi \rangle^2 + \langle \cos \phi \rangle^2$. The synchronization index changes from 0 (no synchronization, uniform distribution of the phase difference) to 1 (perfect synchronization, δ -type distribution of the phase difference).

Another way to characterize stochastic synchronization is to calculate the effective diffusion coefficient for the phase difference. The system is effectively synchronized by external periodic force if the mean time in course of which the instantaneous phase of the system is locked, is larger than some given value. The quantity related to this definition which can be used as a measure of phase coherence is the effective diffusion constant D_{eff} , defined as $D_{\text{eff}} = 1/2 d/dt [\langle \phi^2(t) \rangle - \langle \phi(t) \rangle^2]$. The effective diffusion constant describes spreading of an initial distribution of the phase difference due to noise-induced diffusion. It can be shown that the effective diffusion constant D_{eff} is inverse proportional to the mean time interval of phase locking.

Phase synchronization in conventional oscillatory systems, for instance, the van der Pol oscillator, is usually destroyed by noise [17]. However, in systems exhibiting the

phenomenon of stochastic resonance noise can enhance synchronization [23,18]. Periodically driven bistable or excitable stochastic systems can be considered from the synchronization point of view. However, in order to study phase synchronization we need to introduce instantaneous phase of the system. The problem is that for aperiodic signals the definition of the phase becomes ambiguous.

Several approaches can be used. The formal but general definition of instantaneous phase is based on the concept of analytic signal [21], whereby the instantaneous phase is defined as the argument of the analytic signal. The analytic signal is a complex function of time with the real part being the original signal and the imaginary part being the Hilbert transform of the original signal. This approach was used to study phase synchronization of chaotic systems [16] and stochastic resonance systems [18].

In the case of bistable or excitable systems the phase can be associated with the moments of time t_n when a particle crosses a barrier [18] or with occurrences of spikes in the case of excitable systems. For such stochastic point processes the phase increases by 2π every time t_n and linearly interpolated between t_{n+1} and t_n [18,20]. Another approach was recently proposed in [22] where time t_n were associated with a level crossings. This approach allowed to calculate analytically so-called Rice frequency and to compare it with other approaches, for example with analytic signal approach [22].

As soon as the phase is defined we can pose synchronization problem: whether the instantaneous phase of the switching and the corresponding mean switching frequency can be locked by external periodic force. In [23,18] it was shown that the mean switching frequency in periodically driven bistable systems can be locked in a finite range of noise intensities, while the effective diffusion coefficient exhibits a minimum being plotted versus the noise intensity. In [24] mutual synchronization of two coupled stochastic bistable systems was studied. An analytical approach for calculations of the effective diffusion constant was developed in [25]. In this way the notion of synchronization can be extended to a wide class of systems whose characteristic time scales are completely controlled by noise.

3. Electoreceptors in paddlefish

The paddlefish *Polyodon spathula*, named for its long flattened spatula-like appendage extending in front of the head, the «rostrum» (see Fig. 1). The rostrum is covered with tens of thousands of sensory receptors, morphologically similar to the ampullae of Lorenzini of sharks and rays, well-known to be passive electoreceptors. These ampullary-type electoreceptors respond to the microvolt-scale electrical signals emitted by planktonic prey such as *Daphnia*, and are used by paddlefish to locate plankton during feeding behavior [26]. The location of the rostrum, out in front of the mouth, allows it to function as an «early warning system» for approaching prey, as the fish swims forward continuously. Hence the rostrum functions as an antenna, carrying arrays of electrosensors.

Electoreceptors in paddlefish form a passive sensory system, meaning that

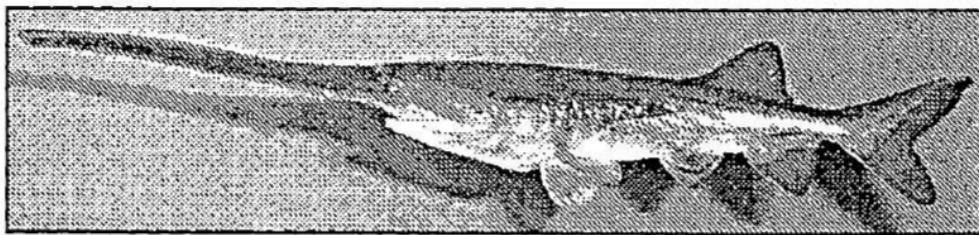


Fig. 1. Photo of a juvenile paddlefish

paddlefish only receive signals from external sources. An external opening (pore) in the skin, $80-210 \mu$ diameter, leads into a short canal $\approx 200 \mu$ long. The pores are organized into clusters of 5-20 on the rostrum, but there are much larger clusters on the head, gill covers, and near the mouth. The internal end of each canal is covered with a sensory epithelium. An epithelium is a layer of cells, one cell thick, typically lining a hollow organ. The epithelium contains two types of cells. It is the «hair cells» which are considered electrosensitive. The number of receptor cells per epithelium is ≤ 400 . The hair cells are interspersed among «support cells». The support and hair cells form «tight» intercellular junctions, or high-resistance seals, which block extracellular paths from the canal to the interior of the body, reducing the flow of electrical current. The term «electroreceptor» is thus refers to the entire structure of pore + canal + epithelium + primary afferent axon. Although the hair cells are the actual sensors, the spike-train coded output of the primary afferent is what is most often recorded, using a microelectrode placed in the sensory ganglion (collection of nerve cell bodies), located near but outside the brain. A key feature of the spike trains from the primary afferents of ampullary electroreceptor is their spontaneous quasi-periodic noisy firing patterns. It was recently discovered that the electroreceptors in paddlefish possess a novel type of organization of being composed from two distinct types of oscillators [27]. One oscillator resides in a population of epithelial cells and is synaptically and unidirectionally coupled with second oscillator, located in the afferent terminal. The fundamental frequency of epithelial oscillator is 25-27 Hz at 22°C for different electroreceptors, while the mean firing rate for different afferents varies in a wide range of 35-65 Hz. The unidirectional coupling of these oscillators results in a specific biperiodic firing patterns. However, only afferent oscillator is affected by external electrical stimuli [27].

Thus, the electroreceptor can be represented by a dynamical system of two unidirectionally coupled oscillators. Therefore, it is natural to expect that electroreceptor cells can be synchronized by a weak external periodic field.

In vivo electrophysiological experiments has been performed with juvenile paddlefish. A detailed description of the experimental setup can be found in [26,27].

4. Synchronization of electroreceptors by periodic electric field

We stimulated electroreceptors by a weak electric field generated by a dipole located near the rostrum of the fish. The electric field strengths were comparable in magnitude to those generated by zooplankton (a few tens of $\mu\text{V}/\text{cm}$). We recorded the spike train generated by a primary afferent and the periodic electric signal from the dipole simultaneously.

The frequency of stimulation was always significantly lower than the mean firing rate (mean frequency) of the electroreceptors, since electroreceptors respond best at low frequencies 4-10 Hz [26]. Thus we can expect higher order synchronization where there are several spikes per one stimulation period. A generic model for a periodically driven self-sustained oscillator is the circle map [2]. The circle map represents a stroboscopic Poincaré map of a quasi-periodic motion. It has a general form of

$$\phi_{n+1} = \phi_n + \rho + f(\phi_n) \bmod 2\pi, \quad (2)$$

where the parameter ρ has the meaning of the ratio of fundamental frequencies of the oscillator and the driving force without coupling between them and $f(\phi)$ is a 2π periodic function. In our particular case we can strobe the phase of the periodic stimulus $2\pi f_s t$ at the moments of time t_n when the afferent spikes occur. In other words, we calculate the phase of a spike ϕ_n relative to the stimulus phase: $2\pi f_s t_n$ and then define ϕ_n on a unit circle:

$$\phi_n = f_s t_n \bmod 1, \quad (3)$$

where f_s is the stimulus frequency. In the case of perfect synchronization the circle map (2) possesses a periodic cycle, such that the dependence of ϕ_n versus n (time) will be represented by several horizontal lines. The number of lines is determined by a particular phase locking regime. For example, in the case 1:5 synchronization we will observe 5 horizontal lines. The results of calculations using Eq. (3) are presented in Fig. 2. Three different regimes can be clearly distinguished. At a low stimulus frequency (5 Hz) the high-order mode-locking of 1:17 is realized during some time segments. The pronounced 1:5 phase locking occurs at $f=17$ Hz. The five horizontal stripes correspond to phase locking segments, while the inclined lines correspond to phase slips. The phase locking occurs during a few hundreds of stimulus periods. Finally, at higher frequency $f=21$ Hz we observe quasi-periodic behavior with no synchronization. The synchrograms (see also [8]) shown in Fig. 2 has qualitatively the same structure as iteration sequences of stochastic circle map.

The statistical evidence of synchronization behavior is also presented in Fig. 2 as the probability density of the cyclic phase difference. In the case of strong 1:5 mode synchronization, the probability density consists of well expressed peaks corresponding to the phase-locking patterns.

In the examples shown above synchronization occurs without significant modulation of the firing rate of the afferent neurons, that is, spikes are uniformly distributed over the periods of external stimuli. We observed, however, different type of

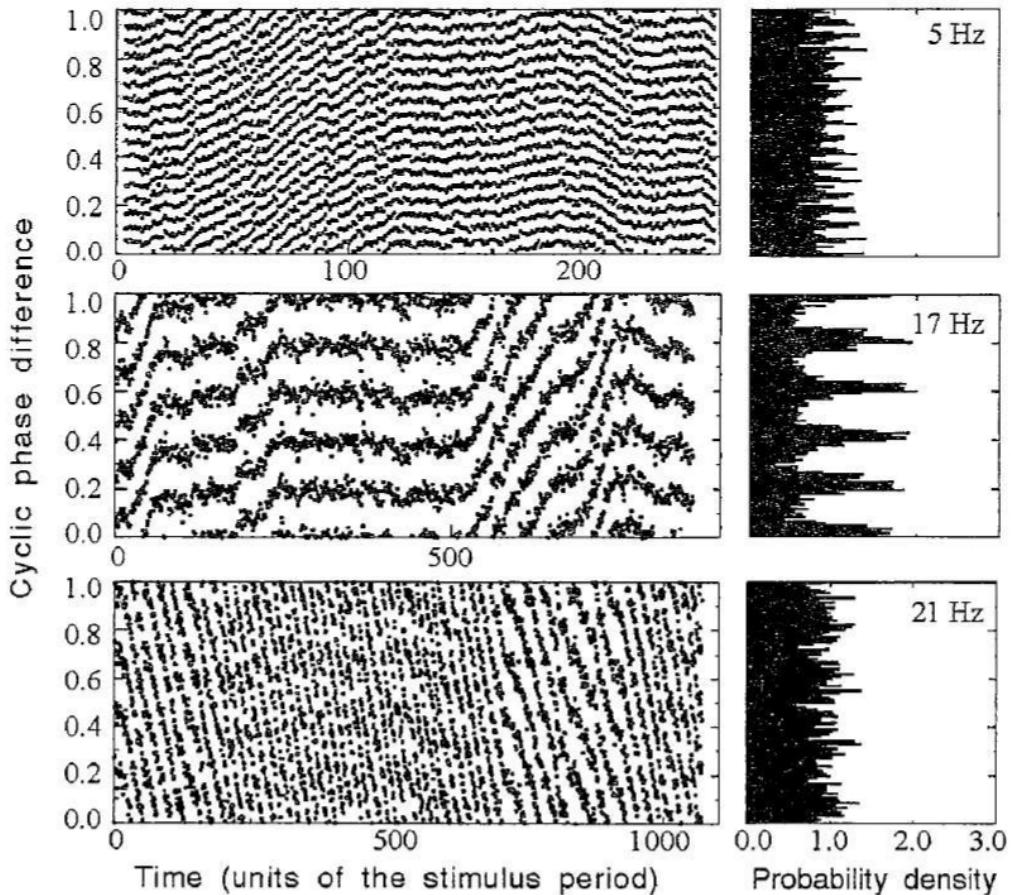


Fig. 2. The cyclic phase difference of spike trains, calculated using Eq. (3), for the indicated values of dipole electric field frequency. The corresponding probability densities of the cyclic phase difference are shown at the right sides

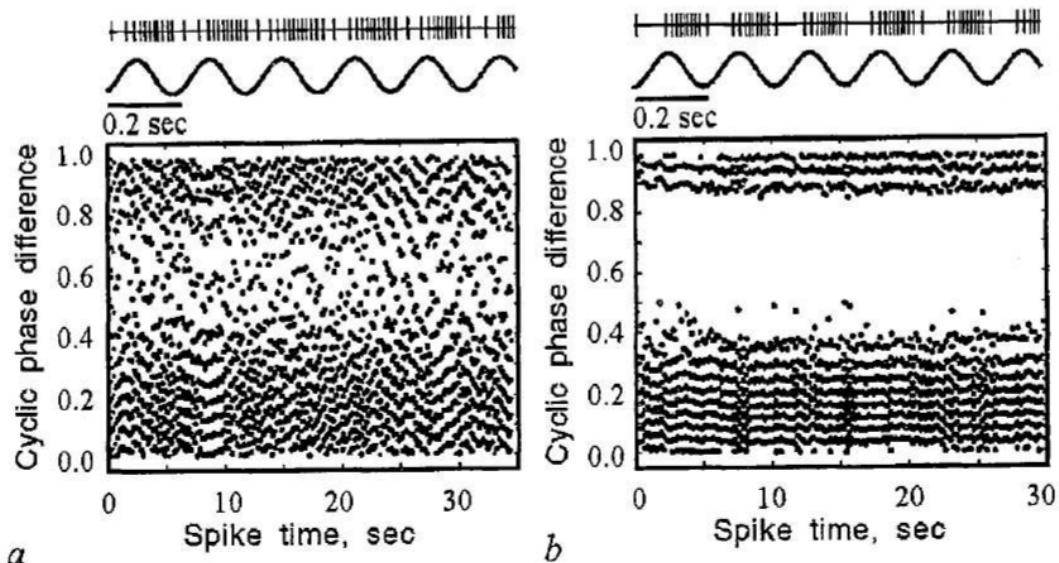


Fig. 3. Examples of recordings of spike train from an electroreceptor cell stimulated by a dipole electric field at 5 Hz with two different amplitudes. Corresponding calculation of the cyclic phase difference are shown below

primary afferents responses to external stimuli in terms of bursts [28]. In such a case external stimulus induces qualitative change in the firing patterns of afferent neurons: transition to bursting mode, when spikes concentrated in groups of bursts. With periodic stimuli we again observed synchronization, but now the firing rate is modulated significantly by the stimulus. An example of such synchronization is shown in Fig. 3, where an electroreceptor was stimulated by 5 Hz electric field. For a small amplitude (Fig. 3, a) the afferent already exhibits bursts, but synchronization is very poor: there is only one short phase locking segment. For a larger amplitude of periodic stimulus synchronization is clearly observed (Fig. 3, b): spike train is organized in bursts of 10-11 spikes. Moreover, individual spikes inside bursts are locked to specific positions on the stimulus period, which reflects phase synchronization.

5. Synchronization due to common noise

In paddlefish electroreceptors, the individual afferents usually possess different mean frequencies (mean firing rates) and different degrees of frequency variability [27]. Moreover, they are noncoupled. It appears, however, that all the electroreceptors have similar slow dynamics, which was revealed by synchronization of noise-induced bursts [28] in different receptors.

We simultaneously recorded the single-unit spikes from pairs of electroreceptor afferents *in vivo*, using metal microelectrodes. One receptive field was on the left side of the rostrum, the other on the right side. Their locations on opposite sides of the rostrum, which are innervated by different nerves, guaranteed that the pairs of afferent neurons were not coupled. We used uniform-field stimulation of all the electroreceptors: stimulus currents were passed between 15×5 cm chlorided silver plate electrodes at the ends of the experimental chamber (see [28] for experimental details). A computer-generated zero-mean Ornstein-Uhlenbeck (OU) noise process was used. The correlation time was set to be 0.002 sec, corresponding to a 500 Hz bandwidth. We generated a sequence of 30 segments of OU noise with incrementing intensities. Each noise segment was 180 sec long, and segments were separated by 5 sec of no stimulus. For comparison, we also used

computer generated white noise, high-pass filtered OU noise, or noise from a General Radio model 1390 B generator which was lowpass filtered by an 8-pole Bessel filter set to 50 Hz.

Stimulation with weak noise ($<2.5 \mu\text{V}/\text{cm}$ rms) did not change the firing mode of an electroreceptor afferent, but rather led to the well-known effect of widening the peak in the probability density of interspike intervals and, correspondingly, the power spectrum peak at the mean frequency of the afferent [27]. When noise of a certain intensity ($>2.5 \mu\text{V}/\text{cm}$ rms) was applied, the firing patterns of the afferents changed drastically such that afferents produced bursts: spikes were concentrated in clusters of bursts which were separated by quiescent epochs. The interspike intervals within a burst decreased towards the center of the burst [28], indicating a parabolic type of bursting [29].

A new slow time scale is introduced by the noise, and can be expressed as the mean interburst interval $\langle \tau_b \rangle$. The mean interburst interval declined exponentially with increasing noise intensity, which was well fitted by the Arrhenius law, $\langle \tau_b \rangle = \text{vexp}(\Delta^2/\sigma^2)$ [28]. This implies that burst generation is excitable, and has a well-defined threshold, Δ , estimated as $\approx 3 \mu\text{V}/\text{cm}$, which is only 3-fold higher than the limit of electroreceptor sensitivity [28].

One of the functional implications of bursting regimes is synchronization [30]. Indeed, the existence of bursts implies a slow time scale which makes synchronization of burst onsets easier in comparison with synchronization of individual spikes.

A representative example of data from two different afferents, recorded simultaneously, is shown in Fig. 4. In the absence of stimulation, the individual spikes in these neurons were not synchronized or correlated, since their mean firing rates were different: afferent #1 fired faster (45.1 Hz) than afferent #2 (33.4 Hz). With noise stimulation switched on, each burst started almost simultaneously in the two neurons, even though the number of spikes inside a burst was different for the two neurons.

We characterized the coincidence of bursts in pairs of neurons in terms of stochastic synchronization, measuring the phases $\phi_{1,2}(t)$ of burst onsets in each neuron, which increases by 2π every time a burst occurs, and interpolates linearly between two sequential burst onsets:

$$\phi_1(t) = 2\pi(t - \tau_k^{(1)})/(\tau_{k+1}^{(1)} - \tau_k^{(1)}) + 2\pi k,$$

$$\phi_2(t) = 2\pi(t - \tau_m^{(2)})/(\tau_{m+1}^{(2)} - \tau_m^{(2)}) + 2\pi m,$$

where $\tau_k^{(1)}$ and $\tau_m^{(2)}$ are bursts onsets in the first and the second neurons, respectively, and $\tau_k^{(1)} < t < \tau_{k+1}^{(1)}$, $\tau_m^{(2)} < t < \tau_{m+1}^{(2)}$. When stochastic synchronization occurs [17], constant segments of the phase difference $\Delta\phi(t) = \phi_1(t) - \phi_2(t)$ (phase locking) are interrupted by

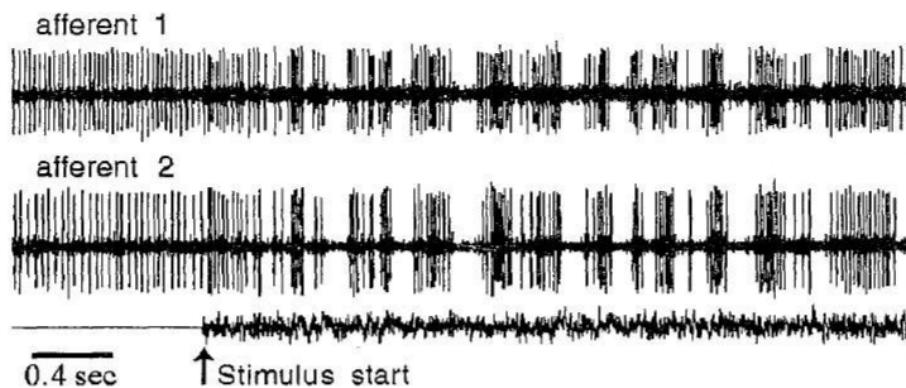


Fig. 4. Example of simultaneous recordings of spike trains from a pair of electroreceptor afferents. The onset of stimulation with computer-generated OU noise of $16.8 \mu\text{V}/\text{cm}$ rms amplitude is marked by the arrow

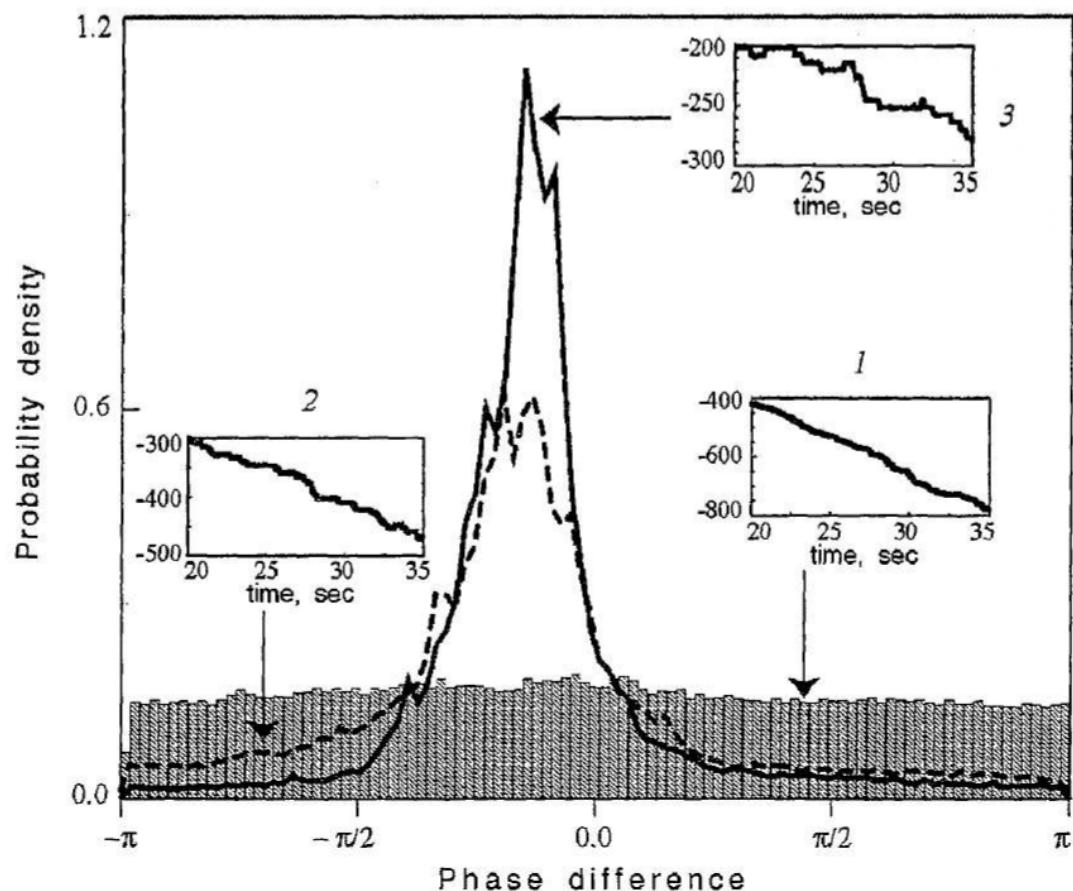


Fig. 5. Probability densities of the phase differences shown in the inset. Insets: Phase differences of burst onsets in a pair of afferents for the following noise rms amplitude: (1) $2 \mu\text{V}/\text{cm}$, (2) $8 \mu\text{V}/\text{cm}$, (3) $20 \mu\text{V}/\text{cm}$

abrupt 2π phase slips. This is illustrated in Fig. 5 for noise-induced bursting, where the phase differences for three different noise intensities are presented. For a large noise intensity (curve 3), the burst onsets are synchronized, which is expressed in the existence of horizontal epochs of phase locking lasting several seconds. The probability density of the phase difference, $P(\Delta\phi)$ (see Fig. 5) characterizes the degree of synchronization: a well-expressed peak in $P(\Delta\phi)$ indicates synchronization, while a uniform distribution indicates its absence. The probability density is nearly uniform for weak noise, when bursts in the two neurons are not synchronized. With increased noise intensity, the probability density of the phase difference developed a well-defined peak, indicating strong synchronization between the bursting neurons.

6. Conclusion

In this paper we demonstrated the phenomenon of stochastic synchronization on a living «model», the electroreceptor system of paddlefish. Two types of synchronization were considered. The first, synchronization of a single electroreceptor by periodic stimuli. And the second, synchronization of two electroreceptors by a common noise field. Young paddlefish use electrosensitivity to feed zooplankton and synchronization mechanism might be responsible for extreme sensitivity of the paddlefish to weak periodic electric field generated by plankton and also for nearly 100 % successful prey capturing. Synchronous burst responses of a population of sensory neurons may be a neural mechanism for coincidence detection, and may substantially simplify the neural operations that a fish's brain must perform to detect prey and to calculate their position and velocity [31]. The impulse-like electrical signal emitted by an individual plankton

prey (e.g. *Daphnia*) moving along the rostrum, or the exponentially correlated Gaussian electrical noise generated by swarms of *Daphnia* [32], may be adequate stimuli for evoking synchronized bursting of different electroreceptors during feeding behavior.

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СИНХРОНИЗАЦИЯ, ШУМ И ЭЛЕКТРОРЕЦЕПТОРЫ

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Классическое понятие синхронизации, первоначально введенное для периодических автоколебаний, может быть расширено на стохастические систе-

мы. Это можно осуществить даже в том случае, когда характерные времена системы полностью управляются шумом. Стохастическая синхронизация при этом определяется как установление некоторых условий для различных статистических мер процесса. Мы проводим обзор разных подходов к стохастической синхронизации и применяем их для изучения синхронизации в электросенсорной системе веслоноса.



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