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SYNCHRONIZATION OF ELECTRIC OSCILLATIONS IN THE ORGANIZATION OF SOCIAL LIFE OF MICROORGANISMS

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Many microorganisms form communities whose members coordinate their actions in solving common problems. One form of such communities is a biofilm. In the experiments on recovering the integrity by a damaged biofilm, data were obtained on oscillators in relatively quiet and active loci of the film formed by cyanobacteria Oscillatoria terebriformis. To study the interaction between different parts of the biofilm, field potentials were recorded simultaneously from two loci. The presence of a functional connection between different zones of the biofilm was revealed by calculation of the cross-correlation coefficients. The level of synchronization of field potentials between areas was determined using the coefficients of frequency and frequency-time coherence. In the loci of increased and decreased activity, different values of the frequency and amplitude of electrical oscillations were revealed. A high level of synchronization was registered between the active zones, which persisted for several seconds. The registered synchronization of oscillations between the active and quiet loci was considerably lower. The results that characterize the organization of the process of problem solving by a cyanobacterial film as an integral unit can serve as a model of the processes of organization of other biosocial structures for solving problems.

Keywords: cyanobacteria, social organization, electrical oscillations, biofilms, synchronization, coherence, coordination, integration.

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СИНХРОНИЗАЦИЯ ЭЛЕКТРИЧЕСКИХ ОСЦИЛЛЯЦИЙ В ОРГАНИЗАЦИИ СОЦИАЛЬНОЙ ЖИЗНИ МИКРООРГАНИЗМОВ

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Многие микроорганизмы образуют сообщества, члены которых координируют свои действия при решении общих задач. Одной из форм таких сообществ являются биопленки. В опытах по восстановлению целостности биопленки получены данные о состоянии осцилляторов в относительно спокойных и в активных локусах пленки, формируемой цианобактериями Oscillatoria terebriformis. Для изучения взаимодействия между различными частями биопленки регистрировались полевые потенциалы одновременно из двух локусов. Наличие функциональной связи между разными зонами биопленки выявлялось при помощи коэффициентов кросскорреляции. Уровень синхронизации полевых потенциалов между областями определялся при помощи коэффициентов частотной и частотно-временной когерентности. Локусы повышенной и пониженной активности характеризуются разными значениями частоты и амплитуды электрических осцилляций. Между активными зонами характерен высокий уровень синхронизации, который сохраняется в течение довольно длительного времени. Синхронизация осцилляций между активным и спокойным локусами существенно ниже. Полученные результаты, характеризующие организацию процесса решения задачи цианобактериальной пленкой как целостной единицы, могут служить моделью процессов организации других биосоциальных структур для решения задач.

Ключевые слова: цианобактерии, социальная организация, электрические осцилляции, биопленки, синхронизация, когерентность, координация, интеграция.

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Introduction of new objects into the field of psychological research is of great importance for gaining knowledge about the evolutionary genesis and the variety of mental phenomena. Such new objects can be microorganisms, starting with prokaryotes. Microorganisms, depending on the levels of consideration, represent a convenient model that allows experimentation with the use of invasive and destructive techniques, in particular, the registration of such objective indicators as field potentials [1, 8, 9, 23, 29].

Microorganisms form communities, a biofilm being one of them. The biofilm formation occurs under the influence of signals coming from the environment and from the intercellular interactions [28, 29]. The complexity of the structure of biofilms and the variety of relationships between their constituent units turn them into an analogue of a multicellular organism [14]. This concept is also supported by the phenomenon of apoptosis discovered in bacteria, previously known only in multicellular organisms, which is involved in the processes of differentiation and morphogenesis and controls the arrangement of cells and the creation of organs of complex shape [7, 31].

Social life of the constituent units of biological communities, regardless their evolutionary stage, involves interactions in such forms as cooperation, competition, division of labor [9, 13, 14, 17, 33]. Cooperative ties provide advantages in reproduction, feeding, and so on, and therefore are widely represented in the biological world at all levels of organization of living beings, from genes to society [21, 23, 28, 35]. Cooperation increases the gross benefit of the population due to such processes as the division of labor and the production of the common good [17, 31], but individuals may also compete with each other for limited resources, for a place in the biofilm structure, etc. [20, 22]. The observed phenomena are associated with the formation of social priorities, which are often in conflict with the need for individual survival. Microorganisms that build biofilms, which in their organization are prototypes of multicellular eukaryotic organisms, are also capable of cooperative “altruistic” behavior. We assume that different stages of the social life of cyanobacteria are characterized by a “special” type of electrical oscillations, expressed by a certain frequency and space-time structure [9]. Apparently, these parameters of field potentials determine the level of activity of community members involved in the process of biofilm formation [3].

We experimented on cyanobacteria, one of the oldest forms of life on Earth, the evolutionary age of which, according to some data, is approaching 3.7 billion years [30]. Cyanobacteria *Oscillatoria terebriformis* build a biofilm that meets external circumstances and the intrasocial needs of the community, transforming the spatial form of its organization and differentiating organ-like formations [12, 13]. It is very likely that the most ancient associations of cyanobacteria formed complex systems that controlled their own morphogenesis, which allowed them to synchronously carry out purposeful collective behavior, in which the spatial movements of individual filaments were determined by the goals of the community as a whole.

The objective of the experiments was to elucidate the role of the level of synchronization of the electrical activity of the cyanobacteria *Oscillatoria terebriformis* at different stages of the biofilm reconstruction.

Method

Procedure of the electrical activity measurement. In the experiments, we used the method of recording electrical activity using glass electrodes filled with 1 M KCl. We used from one to three electrodes placed in different loci of the biofilm, which was determined by the objectives of the experiments. Cyanobacteria *Oscillatoria terebriformis* were kept in an aquatic medium of the following composition (grams per liter): $NaHCO_3$ — 3, Na_2CO_3 — 17, K_2HPO_4 — 0.5, NaCl — 30, KNO_3—2.5, $MgSO_4$ — 0.2, $CaCl_2$ — 0.04, $FeSO_4$ — 0.01, which is the closest to the natural source where the sample was taken for research.

Data processing. Fragments of the recording of electrical activity were digitized and subjected to spectral analysis in the R 3.0 statistical processing environment [2, 3]. The spectral analysis was performed for the original recording by constructing a periodogram using the fast Fourier transform [32]. To analyze the interactions of units, the coefficients of cross-correlation and coherence were determined. The duration of the digitized sections was 3 s. A total of 120 fragments of records of *Oscillatoria terebriformis* biofilm were processed, of which 53 were obtained by recording the electrical activity with one electrode, 67 — with a pair of electrodes localized in active and quiet areas of the biofilm. We further present individual spectrograms of the digitized fragments.

Results

The biofilm formed by cyanobacteria does not have a uniform color: its color varies from light green to almost brown and depends on the state and activity of its constituent cyanobacterial filaments. Experiments were carried out in which field potentials were recorded using glass electrodes from different areas of the biofilm of *Oscillatoria terebriformis* intact (relatively calm) and those formed in the damaged area (increased activity). Data were obtained on the state of oscillators in biofilm loci that differ in color: calm (yellowish-green); active, having an intense green color; light green, in which the formation of structures has just begun.

The measurements showed that the frequency and amplitude of the electrical oscillations depend on the location of the recording electrodes, namely, in the loci that differ in color, that is, in the loci of low or increased activity (Figure 1, 2A). Electrical activity is represented by oscillations, the frequency of which is from 0.5 to 45 Hz. For quiet zones, field potentials with a frequency of 2—7 Hz are typical, and for active ones, 20—30 Hz. However, both expansion and narrowing of the frequency range of oscillations of electrical potentials may occur. Oscillations can form patterns (mostly, "spindles") of different lengths and have a different temporal structure (Figure 1A, 1B). Autocorrelation analysis was used to identify the temporal structure of the spindles.

To study the interaction between different parts of the biofilm, experiments were performed to register the potentials simultaneously from two loci. The presence of a functional connection between different zones of the biofilm was revealed using the cross-correlation coefficients; these connections were also subjected to coherence analysis.

The level of synchronization of field potentials between the zones was determined using the coefficients of frequency and frequency-time coherence (Figure 2B, 2C). A high level of synchronization, at which the frequency coherence coefficient reaches its maximum value, is characteristic between the active zones (Figure 2B). The graph of time-frequency coherence shows that the high level of synchronization persists for a rather long time: in the given case, 6 s (possibly longer so far as the analyzed interval was limited by the observation time). The indicators show-

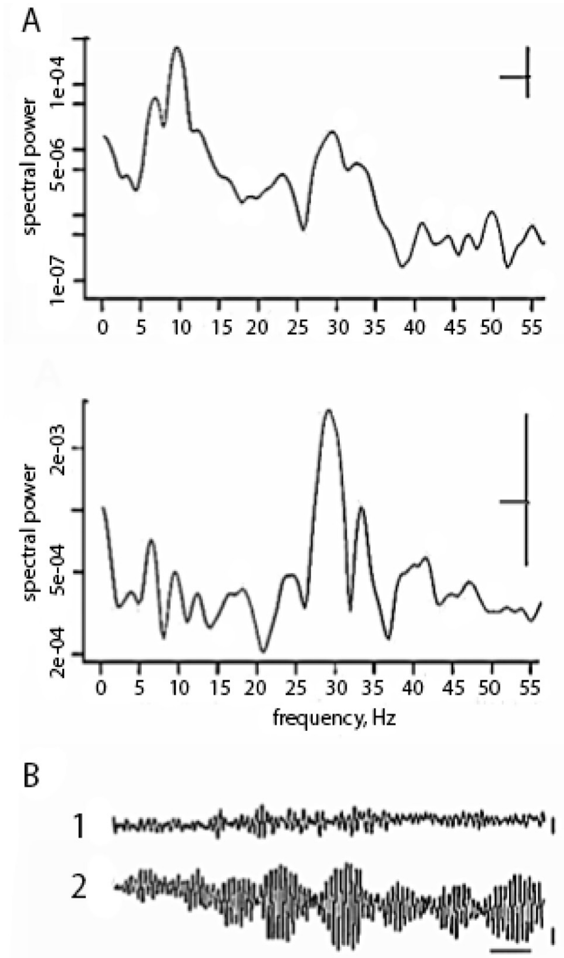

Fig. 1. Frequency characteristics of the electrical oscillations in two loci of the cyanobacterial film (calm and increased activity). A – the periodograms of the activities as shown in B. The abscissa: the frequency (Hz); the ordinate: the spectral power (arbitrary units). The horizontal bar is the bandwidth, the vertical bar is the confidence interval (95%). B – field potentials recorded simultaneously in the calm and active loci of the Oscillatoria terebriformis biofilm: B1 — oscillations of the quiet zone; B2 — oscillations in the active zone. Calibration: 20 μV, 300 ms.

ing the synchronism of oscillations between the active and quiet loci look different (Figure 2B): the achievement of the maximum value of the coherence coefficient in this case is short-lived, it can be located both at low and high frequencies, which is reflected in the graph of time-frequency coherence.

Discussion

The experiments performed on cyanobacteria have shown that synchronized electrical oscillations can be objective indicators characterizing the activity of the microbial social structure. The main result of the experiments showed that to perform a socially significant task, a high level of synchronization of electrical activity initiated by community members is required.

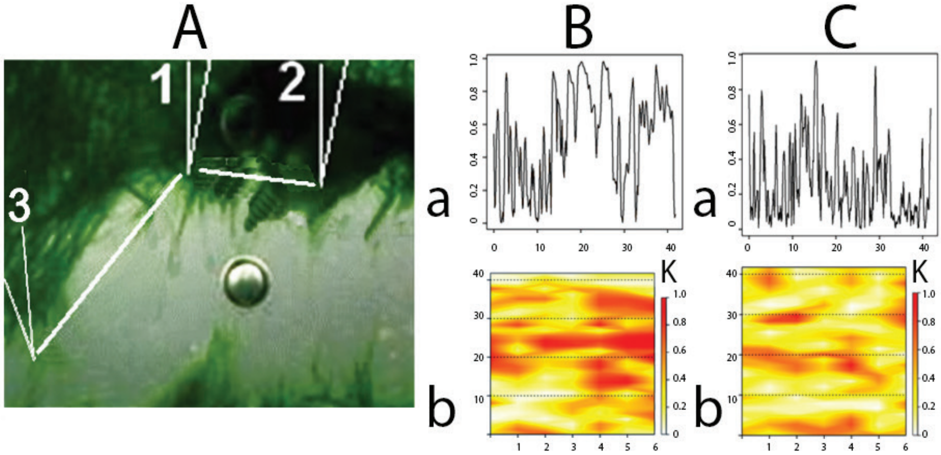

Fig. 2. Interaction between the loci of the cyanobacterial film, the units of which are to varying degrees involved in active building behavior. A — the location of the electrodes; B — phase-frequency (a) and frequency-time (b) coherence of the electrical activity of units located in the center of the activity zone (electrodes 1 and 2); C — same, in the registration zone of the electrodes 3 and 1. Designations: for (a): abscissa — frequency (Hz), ordinate — coherence coefficient; for (b): abscissa — time in seconds, ordinate — frequency in Hz; K is the coherence coefficient.

The idea that the synchronicity of oscillations of biopotentials is one of the electrographically expressed phenomena favorable for the functioning of the elements of a biological system has been known since the 50s of the 20th century [5]. The main method for studying the synchronicity of the electrical activity of different parts of a biological substance is the coherence analysis. For example, in experiments on humans, it was found that when the participants interact while solving a problem to achieve a common goal, the oscillatory activity in certain zones of the brain is synchronized and its peaks are associated with the actions of the partners [24, 25]. The earlier results cover objective indicators in the form of registration of electrically expressed events in human and animal brain, eye movements and verbal reports of the subjects when solving cognitive tasks, listening to music or texts [4, 18, 26, 27]. These activities in achieving the goal develop on the background of synchronized processes in certain zones of the brain in each participant and between participants [34], and depend on their level of readiness for a certain type of activity [19]. The coherence coefficient is the higher, the higher the level of synchronization of electrical potentials.

The results of our measurements allow us to conclude that the synchronization of activities in solving problems requiring joint actions is necessary not only for multicellular creatures, but also for microorganisms that solve problems by combining the efforts of thousands of individuals. The experiments have shown that the level of synchronization, measured by the coefficient of coherence, makes it possible to assess the effectiveness of behavior in living creatures occupying the first lines in the history of life development, in this case, in prokaryotes, namely, cyanobacteria *Oscillatoria terebriformis* (Figure 2B).

Bacteria existing in communities coordinate their behavior to perform specific functions. Genetic and molecular biochemistry techniques combined with microscopic imaging have shown that biofilm development is a well-regulated process in which bacteria integrate into communities through internal and external signaling. The complexity of biofilm creation suggests that this is a mode of development in which changes in form and function play a leading role in the life cycle of bacteria. Community organization requires coordinated actions of the units between which communication takes place [9, 10, 17, 29]. Intercellular contacts, represented by a variety of extracellular structures, such as microfibrils, pineal protrusions, evaginates of cell walls, capsules, reflect a genetically determined pattern of development of microbial populations as self-regulating multicellular systems [8].

Thus, the levels of synchronization of electrical activity in the cyanobacteria *Oscillatoria terebriformis* ensure the efficiency of the behavior of these creatures: the coherence of signals is higher for loci in which the efforts of community elements are purposeful. The cyanobacterial film is not fully covered by the "construction work": the areas are highlighted, where the most active participation is required from the constituent units. This means that there is a differentiation of space, its division into affected zones and zones favorable for the life of the community. Obviously, there is a functional specialization: the cyanobacterial filaments nearest to the site of damage are involved in the work on the restoration of the film. The phenomenon of "division of labor" in microbial society is evidenced by the facts of electrophysiological experiments [2] and data from microbiological studies [11]. The assumption about specialized members of the community is based on the results electron microscopy studies, in particular, a number of works have shown the morphological heterogeneity of microbial populations, and regularities have been established in changing the structure of microbial communities at different stages of development, manifested in a change in the ratio of different types of cells: physiologically active, resting, autolyzed and involutional [11, 36]. The heterogeneity of a population is the result of the realization of the adaptive potential that is originally characteristic of a particular microorganism. In other words, it is a tool for revealing new adaptive capabilities of the same bacterial genome [6].

The results obtained coincide with the results of studies performed on humans and highly organized animals [5, 15, 16, 34]. Experiments on living things of different evolutionary levels show that the origins of selective spatial synchronization, as a result of which functional relationships are established between heterogeneous zones of modern biological systems: brain zones, biofilm areas, etc. — originated in the earliest organisms on our planet. The actualization of these functional relations in the form of certain type of behavior is the result of the integration of the activities of these zones.

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