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Short Communication

Dynamics of Electrical Activity of Limbic Structures During Various Motivational-Emotional Reactions and The Wakefulness-Sleep Cycle

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Abstract

Soon after the classic work describing the activating influence of the reticular formation of the midbrain on neocortical structures, an equally significant work appeared, which showed that in response to stimulation of the mesencephalic reticular formation and the posterior hypothalamus, as well as to peripheral sensory stimuli, in parallel with desynchronization of the electroneocorticogram, the opposite picture is observed in the hippocampus - hypersynchronization of slow electrical activity in the theta rhythm range. Further experiments showed that the hippocampal theta rhythm does not always develop against the background of desynchronization of the electroneocorticogram, i.e. it is not characteristic of all types of stimulation reactions. In response to electrical stimulation of the reticular formation during the slow-wave sleep phase, it is possible to cause an isolated electroencephalographic "awakening" without a behavioral reaction, during which the hippocampal electrical activity also desynchronizes almost in the same way as the neocortical one. However, if stimulation of the same point of the reticular formation causes behavioral awakening with emotional coloring (alertness), then against the background of desynchronization of the electroneocorticogram in the hippocampus, the development of a pronounced theta rhythm is observed.

Keywords: electrical activity; limbic structures; motivational-emotional reactions; wakefulness-sleep cycle

Introduction

Soon after the classic work describing the activating influence of the reticular formation of the midbrain on neocortical structures, an equally significant work appeared, which showed that in response to stimulation of the mesencephalic reticular formation and the posterior hypothalamus, as well as to peripheral sensory stimuli, in parallel with desynchronization of the electroneocorticogram, the opposite picture is observed in the hippocampus - hypersynchronization of slow electrical activity in the theta rhythm range [2]. Further experiments showed that the hippocampal theta rhythm does not always develop against the background of desynchronization of the electroneocorticogram, i.e. it is not characteristic of all types of stimulation reactions. In response to electrical stimulation of the reticular formation during the slow-wave sleep phase, it is possible to cause an isolated electroencephalographic "awakening" without a behavioral reaction, during which the hippocampal electrical activity also desynchronizes almost in the same way as the neocortical one [5]. However, if stimulation of the same point of the reticular formation causes behavioral awakening with emotional coloring (alertness), then against the background of desynchronization of the electroneocorticogram in the hippocampus, the development of a pronounced theta rhythm is observed [3]. A detailed analysis of the background total electrical activity of the hippocampus and its comparison with neocortical electrical activity can be made in the wakefulness-sleep cycle [9]. Simple unemotional wakefulness in a cat is characterized by desynchronization of the electroneocorticogram and the absence of pronounced regular synchronized slow electrical activity of the hippocampus in the theta rhythm range, although, as shown by the integrated values of individual rhythms, delta and theta rhythms are expressed more in the hippocampus than in the neocortex [11]. With the transition to a drowsy state and against the background of superficial slow sleep in the neocortex, slow electrical activity breaks down in the range of predominantly alpha rhythm, and no special changes are observed in the electrohippocampogram and delta and theta rhythms again prevail. During the deep slow-wave sleep phase, both the neocortex and the hippocampus emit slow and high-amplitude waves characteristic of this state, with subdelta, delta, and theta rhythms predominating [13]. Sharp changes in the electrical activity of the hippocampus develop during the paradoxical sleep phase. At this time, in parallel with the desynchronization of the electrical activity of the neocortex, the most rapid development of the hippocampal theta rhythm is observed [14]. The brain (systemic) organization of the hippocampal theta rhythm is now well understood. It was shown long ago that the development of the hippocampal theta rhythm in response to electrical stimulation of the reticular formation requires intact hypothalamus and septum [17]. After damage to these structures, the theta rhythm does not develop. From this we can conclude that the pacemaker of the hippocampal theta rhythm is the septum. They also showed the importance of the medial nucleus of the septum in triggering the theta rhythm. This was subsequently confirmed by many researchers even at the neuronal level. It is believed that the septum plays the same role in the formation of the hippocampal theta rhythm as the thalamus does in the organization of the neocortical alpha rhythm [18].The debate about the cellular electrical correlates of the theta rhythm in the hippocampus itself is not over at the present time. There were suggestions that the theta rhythm of the hippocampus reflects the development of postsynaptic inhibitory potentials arising as a result of activation of the mechanism of recurrent inhibition [15]. But there is also an opposite position: in their opinion, the theta rhythm mainly reflects the development of postsynaptic excitatory potentials in hippocampal neurons. The theta rhythm reflects both inhibitory and excitatory postsynaptic potentials of hippocampal neurons [12]. Discussing the extensive literature on this issue, it is considered more likely that inhibitory postsynaptic potentials participate in the formation of the theta rhythm. At the same time, it indicates that the mechanism of recurrent inhibition should not be necessary for the generation of the theta rhythm, since the hippocampus receives already quantized impulses in the theta rhythm range from the septum [19].No less controversial and still unresolved is the issue of behavioral correlates of the hippocampal theta rhythm [10]. According to some data, it was believed that the development of the hippocampal theta rhythm is associated with the awakening reaction. It is also believed that the theta activity of the hippocampus can be a good indicator of the activation of the reticular formation and especially the posterior hypothalamus [19]. Considering the data that the mechanisms that trigger behavioral awakening are localized in the posterior hypothalamus, the development of the hippocampal theta rhythm could be associated with behavioral awakening, and not with the awakening reaction in general. Studying the dynamics of the hippocampal theta rhythm during conditioned reflex activity, they came to the conclusion that its development is associated with the orienting reaction. Later, the hippocampal theta rhythm was associated with the development of motivational processes underlying both the development of the orienting reaction and other behavioral acts [22].This interpretation is supported by other authors. Some find a clear correlation between the hippocampal theta rhythm and voluntary movements. However, this does not deny the importance of motivational processes in the formation of the theta rhythm [8]. Voluntary movements in animals are triggered by motivational processes, and it is not surprising if they have a common electroencephalographic correlate. It turned out that the expression of the hippocampal theta rhythm during the same voluntary movements depends on the degree of the motivation that triggers the motor acts [6].The most popular position is that the development of the hippocampal theta rhythm is associated with the brain's processing of information and with the organization of various stages of memory. A large number of studies have been conducted in this direction, especially after the appearance of works describing regular frequency shifts of the hippocampal theta rhythm depending on the degree of information processing and memory organization during the development of discrimination of conditional sounds and delayed reactions [16]. However, there is no consensus on this issue even among scientists who consider the hippocampus to be the most important link in the memory organization system. Different authors associate the development of the hippocampal theta rhythm with different stages of memory organization, such as information registration, consolidation of memory traces, and the process of reading out memory traces [20].However, the dynamics of the total electrical activity of both the neocortex and the archipaleocortex structures is of little information (or not informative at all) in terms of understanding the function of the structure from which the activity is diverted [7]. After all, it is well known that desynchronization of the electroneocorticogram, which, by the way, mainly occurs in parallel with the development of the hippocampal theta rhythm, gives us information about the functions of the activating reticular formation, and not the neocortex itself. In the same way, the development of spindle-shaped activity at the cortex level indicates the pacemaker functions of the thalamus, and not the neocortex itself [7]. There is good reason to assert that the dynamics of hippocampal electrical activity also reflect the functions of the mesodiencephalon structures, and not the hippocampus itself. The method of evoked potentials has shown that the structures of the limbic system are characterized by polysensory. They integrate information from both external and internal receptors [17]. One of the most important formations of the limbic system, the hypothalamus, contains neurons with various specialized receptors in various nuclei that respond to diverse shifts in the internal environment. As a result of the excitation of these neurons in the presence of biological needs, corresponding motivations are formed, integrated by the entire limbic system [14]. All this is reflected in the dynamics of the electrical activity of these formations, in particular, in the strengthening of the hippocampal theta rhythm against the background of desynchronization of the electroneocorticogram [3].Interesting data in the study of the organization of neurophysiological mechanisms of motivational-emotional behaviors were obtained by recording limbic structures [20]. For example, we can cite the work on the study of the correlation of the activity of neurons in the lateral and ventromedial nuclei of the hypothalamus with various food motivations, as well as a study to identify detector neurons of aggression. It was shown that with high food motivation, neurons of the lateral hypothalamus are strongly activated, and with satiety - the ventromedial nucleus of the hypothalamus [23]. A little later, specialized neurons were discovered in the central gray matter of the midbrain that participate in triggering the reaction of aggression and are not excited during the development of other reactions. These facts are direct evidence that food motivation at the hypothalamus level is regulated by reciprocal mechanisms between the lateral hypothalamus and the ventromedial nucleus, and in the regulation of aggression, the central gray matter should play a primary role together with the hypothalamus [25].The study of the dynamics of neuronal activity in the preoptic area and posterior hypothalamus reveals the presence of reciprocal mechanisms between them, which should be important in regulating the wakefulness-sleep cycle [27]. It turns out that neurons in the preoptic area are much more excited during the slow-wave phase of sleep compared to wakefulness, while the opposite picture is observed with respect to the activity of neurons in the posterior hypothalamus and reticular formation: they are more excited during wakefulness than during slow-wave sleep [28].The study of the activity of individual neurons also revealed the relationship between the rostral structures of the limbic system and the hypothalamus. In particular, it was shown that when the lateral amygdala is electrically stimulated, the neurons of the ventromedial hypothalamus are activated, while those of the lateral hypothalamus are inhibited. This allows us to describe the pathways of the inhibitory influence of the amygdala on food motivation [7]. Apparently, impulses from the amygdala cause excitation of neurons of the "satiety center" of the ventromedial hypothalamus, and these neurons, for their part, inhibit neurons of the "hunger center" in the lateral region of the hypothalamus [7].Thus, both the results of the study of the dynamics of total electrical activity and the results of the study of neural activity confirm the leading role of the limbic system in the organization of motivational-emotional behaviors [1].The limbic system includes extensive structures of the brain. The limbic system currently includes, along with subcortical structures, not only the structures of the archi- and paleocortex, but also some neocortical formations that participate in the organization of motivational-emotional reactions [3]. When many projections from the frontal lobes of the neocortex to various cortical and subcortical formations of the limbic system were discovered, it was suggested that the anterior frontal region is a neocortical continuation of the limbic system. At the same time, its dorsal part is more closely connected with the hippocampus, and the ventral part with the amygdala. Subsequently, many researchers showed that the limbic frontal cortex takes an active part in the regulation of motivation during learning [12]. Although the morphology of the limbic system has not yet been studied exhaustively, there is already a more or less clear picture of the bilateral neural connections between its various levels and structures. They can be both direct and indirect, as clearly indicated by the data obtained by the method of evoked potentials [24]. These connections, naturally, are of great importance for the functional unification of the cytoarchitectonically extremely differently constructed structures of the limbic system. Particularly important are the connections of the rostral structures of the limbic system with the mesodiencephalic formations, where the triggering mechanisms of motivational-emotional reactions should be localized. It is these mechanisms that can be influenced (inhibitory or excitatory) by structurally and functionally different formations of the higher parts of the limbic system [24]. Due to the bilateral neural connections, various levels and structures of the limbic system act in a coordinated manner in the implementation of any motivational-emotional behavior, both innate and acquired. After classical works, it was believed that the formation of various motivational processes occurs at the level of the hypothalamus [26]. At present, knowledge about the triggering mechanisms of motivational-emotional reactions has been enriched with new facts. It is now known that in these processes, an important role is played by areas of the mesencephalic reticular formation and the anteromedial nuclei of the thalamus, with which the hypothalamus has bilateral connections [29].With their powerful projections, the limbic structures of the mesodiencephalon involve the rostral structures of this system in activity, which integrate the initial processes at a high level, as a result of which goal-directed behaviors can be launched [3].The integrating capacity of the limbic system is expanded by the fact that it receives information about both the external environment and shifts in the internal environment. In one of the nodal formations of the limbic system, the hypothalamus, there are specialized neurons that have receptor properties with respect to various shifts in the internal environment [15]. Thus, they can inform the integrating systems of the brain about the onset of biological needs. After comparing and processing this information, the limbic system, with its efferent connections, can launch vegetative, somatic and behavioral reactions that ensure, on the one hand, the adaptation of the organism to the external environment, and on the other, the maintenance of the internal environment at an optimal level [18]. This is the general function of the limbic system, although when implementing a particular motivational-emotional reaction, certain of its links can be predominantly activated. In this aspect, the limbic system can be divided into subsystems with more or less specific functions [21]. The data obtained by various methodological approaches (damage and stimulation of individual structures, recording of total and neural electrical activity) show the predominant participation of the amygdala-hypothalamic-mesencephalic subsystem in the regulation of motivational-emotional reactions of the aggressive-defensive, food and sexual types, whereas the main limbic circle, described long ago and including the hippocampus, mammillary bodies, anteromedial thalamus and cingulate gyrus, may be more responsible for the regulation of learning and memory [22]. However, this does not mean that these limbic subsystems operate independently of each other. The main limbic circle undoubtedly participates in the organization of motivational-emotional behaviors, just as it is difficult to imagine the organization of learning and memory without the participation of those structures of the limbic system that are more directly related to motivational-emotional reactions [12]. After all, motivation, in the broad sense of this concept, is a necessary factor in learning and the organization of memory traces. Not only individual limbic subsystems (such a division, by the way, is quite conditional), but the entire limbic system cannot function in isolation, without the participation of, for example, such structures as the neocortex and basal ganglia [8]. As was indicated above, a significant part of the neocortex (frontal region) is an organic part of the limbic system. In addition, other areas of the neocortex (including specific analyzer areas) have close connections not only with the structures of the archipaleocortex, but also with such nodal, subcortical formations of the limbic system as the hypothalamus and amygdale [13]. There is no doubt that the intact brain, when performing behavioral acts, as well as during learning, works as an integral, highly coordinated mechanism. However, the limbic system is a critical area for the initiation and further integration of motivational-emotional reactions [17]. Only in this aspect is it expedient and fruitful to combine certain brain structures into the limbic system and study their specific functions.

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