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Short Communication

Integrative Mechanisms of the Cerebral Cortex and its Functional and Structural Features

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Abstract

The cerebral cortex is the highest section of the central nervous system. It is the material basis with which complex forms of behavior of higher animals and humans are associated.

In recent years, microelectrode technology has been widely used to study the physiology of the cerebral cortex, along with traditional approaches (extirpation, stimulation, conditioned reflex method), the capabilities of which allow us to study processes occurring directly in nerve cells. This has made it possible to obtain fundamentally new data on the mechanisms of analysis of specific afferent signals at the level of individual neurons, the study of processes underlying the integration of different-modal specific and non-specific afferent impulses, and the nature of cortical inhibition.

Key Words: integrative mechanisms; cerebral cortex; brain

Introduction

The cerebral cortex is the highest section of the central nervous system. It is the material basis with which complex forms of behavior of higher animals and humans are associated [7].

In recent years, microelectrode technology has been widely used to study the physiology of the cerebral cortex, along with traditional approaches (extirpation, stimulation, conditioned reflex method), the capabilities of which allow us to study processes occurring directly in nerve cells [4]. This has made it possible to obtain fundamentally new data on the mechanisms of analysis of specific afferent signals at the level of individual neurons, the study of processes underlying the integration of different-modal specific and non-specific afferent impulses, and the nature of cortical inhibition [8].

The first studies conducted using the method of extirpation and stimulation of the area of neocortex sections provided convincing evidence that the various zones of the cortex are not equipotential [22]. These ideas were confirmed by a detailed study of the localization of functions in the cerebral cortex, carried out by the method of studying evoked potentials arising in response to sensory stimuli of different modalities [3]. It was shown that along with the areas of the cortex to which afferents of one modality are projected, multimodal afferent influences converge to vast zones of the neocortex, which creates conditions for complex integrative activity [4].

The processes of information processing in various areas of the neocortex are based, as has now been precisely established, on certain mechanisms that are universal for all parts of the nervous system, based on processes that change the excitability of nerve cells [1]. At the same time, each area of the cortex (somatosensory, visual, auditory, associative) has its own morphological and functional features. Therefore, this chapter, devoted to the physiology of the cerebral cortex, consists of several sections, each of which contains detailed information about certain projection or associative areas of the neocortex [5].

The integrative function of the somatic cortex is of decisive importance in animal behavior, and therefore the neural mechanisms that underlie it have been studied especially intensively in recent decades [4]. The meaning of integrating the numerous and varied signals coming to a neuron or a certain neural structure comes down to evaluating and selecting the most important of them, and to developing on this basis, in the form of a corresponding flow of impulses, the only correct response in specific conditions that provides a separate structure, systems of structures, and ultimately the organism as a whole with favorable conditions for existence. According to generally accepted ideas, this process is carried out at the synaptic inputs of neural elements and finds its final reflection in the impulse activity of neurons. The true meaning of this impulse activity is revealed only through the functional-structural organization of the somatic cortex [11].

Using the method of evoked potentials and mapping their distribution over the surface of the cortex, first on cats and then on other animal species, including humans, projection zones of somatic sensitivity were established [6].

In marsupials, the sensory and motor representation of various parts of the body in the cortex completely coincide. In low-organized placental mammals, it can overlap to a significant extent and only in primates does it achieve pronounced isolation. Nevertheless, a month after removal of the motor cortex, stimulation of the sensory zone in monkeys was accompanied by a contraction of the skeletal muscles of the contralateral side [19]. Chronic experiments on cats with electrodes implanted in the anterior and posterior sigmoid gyri showed that both gyri play a similar role in the control of motor activity. At the same time, it is well known that somatic sensitivity projects to the motor cortex of the brain [2]. Thus, somatic afferent impulses arrive not only to the somatosensory, but also to the motor cortex, and the somatosensory cortex takes part in the formation of motor pathways. Therefore, it is logical to consider the projection zones of somatic sensitivity and the zones giving rise to motor pathways as a single somatic cortex [10].

The somatic cortex is divided into: 1) somatosensory area I (C1) — for the postcentral gyrus and its homologues, in cats the posterior sigmoid gyrus is posterior to its fossa; 2) somatosensory area II (SN) — in cats it occupies the anterior ectosylvian gyrus; 3) motor sensory area I (M1) — the precentral gyrus in primates, the anterior sigmoid and rostral part of the posterior sigmoid gyrus in cats; 4) motor sensory area II (MN), located on the inner surface of the hemisphere [3].

Some researchers also distinguish somatosensory zone III (SS), which in cats occupies the dorsal part of the anterior suprasylvian gyrus. These projection zones in cats are occupied by cytoarchitectonic motor fields 4 and 6 (M1 and MN) and somatosensory fields 1, 2, 3, 53 (C1); 2, 3, 5 (SI and SS) [3].

Based on morphological data, the functional diagram of the neocortex was one of the first to be presented. According to it, the signal along the afferent fibers approaches the pyramidal neurons of the lower layers of the cortex and the Martinotti cells [9]. Through the axons of the latter, it approaches the apical dendrites of neurons, including neurons of layer II, which do not have a direct connection with the afferent fibers, and to the neurons of Cajal of layer I. The tangential fibers of the Cajal cells, together with the horizontal segments of the axons of the Martinotti cells, participate in the additional activation of the dendrites of the superficial layers of the cortex [9].

There have been attempts to isolate an elementary structural cortical unit that is supposedly capable of performing the entire process of signal transmission from its entry along the afferent fiber to its exit to the efferent neuron [14]. According to these ideas, all layers, with the exception of I and II, contain cells that contact specific afferent fibers. At the same time, each layer, except I, has neurons whose axons reach the white matter. From this point of view, no layer can be called "receptor" or "effector", although in the somatic cortex a powerful efferent tract begins from layer V [9].

Functionally, the cortex consists of vertical neural circuits. The most important place is occupied by input neurons, to which specific afferent fibers and axons of neurons of the outer layers of the cortex approach. Neurons of the outer layers send impulses through descending axons to neurons located in layers V and VI, and they in turn send impulses not only to the underlying structures, but also back to layers II and III. The circulation of impulses in such a circuit can be modified in layers II, III, VI due to the activity of associative fibers approaching here [9]. Cortical circuits are fundamentally similar to neuronal circuits in any other parts of the nervous system. Their important features are, firstly, that they are all a superstructure on the simplest circuit, consisting only of a connection of an afferent fiber and an efferent cell, and secondly, they include closed circuits that ensure the circulation of excitation [16]. Closed circuits may include only short connections (between cells of one layer) or consist of long connections, in the formation of which neurons of different layers participate. Long connections in the cerebral cortex of different animals vary slightly, the number of short connections increases progressively from mice to humans. Since the signal received via afferent fibers leaves the cortex through pyramidal cells, the role of cortical neurons cannot be other than regulating the discharge of efferent neurons [12].

The afferent fiber gives off branches that occupy a space that ultimately has the shape of a cylinder; the efferent cell and the intermediate neurons located in such a cylinder that regulate the discharges of the efferent neuron constitute a structural and functional unit [17]. All analogous functional units are composed of several types of neurons that are repeated in each unit. Therefore, the layers can be considered as cortical areas containing the bodies of a few types of neurons that have analogous connections in the neural circuits that make up the functional units [15].

Apparently, the most vulnerable point of the functional organization scheme proposed above is that it does not take into account the presence of inhibitory neurons in the cortex, since at that time nothing was known about their function [18].

A logical continuation of this scheme can be considered the works in which, tracing the development of the human motor cortex, the concept of a basket-pyramidal system of neurons was developed [13].

According to these data, the axonal ramifications of the cortical basket cells are localized within the flat vertical plates of the gray matter located perpendicular to the length of the convolutions. They encompass all the pyramidal cells of a given plate [23]. Each such plate is 200 μm thick and 1-2 mm long and occupies the vertical space from layer II to layer VI. Between the ramifications of the basket cells of different layers and the pyramidal cells of the same layers, rows of horizontal neural chains are formed [24]. During ontogenesis, both neuronal systems (basket and pyramidal) develop and mature in parallel after the sprouting of afferent fibers to the corresponding level of the cortex. First, the pyramidal neurons of layer V, partially the lower third of layer III, and the large basket neurons of layer IV mature. Later, such a system of neurons matures in layers II and III. It is assumed that basket neurons inhibit the activity of pyramidal neurons in the lamellar areas of the cortex [28].

Thus, the developed ideas differ from the above-mentioned hypothesis not only by the introduction of inhibitory neurons, but also by the fact that now the large pyramidal neuron and the auxiliary neurons associated with it, which together form a functional unit, are united with a number of other functional units into a special basket-pyramidal system of neurons with the help of a basket cell [21].

Certain confirmation of the special structural organization of the cortex was demonstrated in the somatosensory cortex of the rat [27]. Tangential sections and corresponding histological processing made it possible to reveal in layer IV peculiar barrel-shaped clusters of neurons surrounded by fibrous structures. The diameter of these column-barrels fluctuates from 100 to 400 μm, and their number reaches 200 [25]. It was suggested that each such structural unit is associated with certain large hairs of the rat - vibrissae. Later, similar barrel-shaped figures were shown in the somatic cortex of the cat, monkey, and man [20].

Experiments with destruction of one row of whiskers or of all whiskers except one row at birth of the animal have shown the disappearance of the corresponding barrels in the projection cortex as a result of transneuronal degeneration [29]. This example clearly demonstrates that individual units of a complex sensory organ (a single whisker is supplied with several hundred primary afferent fibers) have a clearly isolated and structurally recognizable receptive organ in the sensory cortex, which is the main site of arrival of specific sensory afferents [26].

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