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Review Article

Morphofunctional Connections of the Basal Ganglia

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Abstract

The nuclei of the basal ganglia are interconnected and connected to other structures of the brain by conducting pathways. The most accurate information about their course is provided mainly by the results obtained by morphological methods. Here we will consider only those for which certain functional relationships have already been established or the ground has been prepared for physiological interpretations.

Keywords: basal ganglia; brain; functional relationships

Connections of the Neostriatum with the Pallidum. Inhibitory and Excitatory Effects

A significant part of the fibers originating in the coniferous nucleus and shell, crossing the inner capsule, go to the pallidum, where they end at the neurons of both its segments [1]. After focal lesions in the caudate nucleus, the disintegration of the terminals of these fibers, ending mainly in the dendrites of pallidar neurons, is detected. This fact has been established by electron microscopy in monkeys; it has also been shown that the area of all dendrites of a single neuron is approximately 100 times larger than the area of the soma of a cell; the axons of neostriatum neurons are very thin, up to 1 μm. Two conclusions follow from the described ultrastructural properties: striopallidal synaptic connections, mainly axodendritic; excitation from the neostriatum to the pallidum is slow.

Electrophysiological studies have clarified the relationship of nervous processes in the neurons of the pallidum with direct irritation of the neostriatum. The main fact obtained in acute experiments on cats under conditions of extracellular abduction by means of microelectrodes was that the background activity of part of the neurons of the pale globe was suppressed in response to a single stimulus applied to the head of the caudal nucleus; some of the neurons, although the smaller one was stimulated under the same conditions of nuclear stimulation, and a number of “silent” neurons were discharged [2]. The results of later studies conducted on monkeys with microelectrodes chronically implanted in the pallidum region confirmed the main pattern: of the 43 extracellularly studied pale globus neurons, 35 showed a complex reaction in response to irritation of the caudate nucleus, when a pronounced suppression of neuron activity was preceded by arousal. Experiments with intracellular registration have clarified the ratio of excitatory and inhibitory responses of cells of the pallid globe and the entopeduncular nucleus [3].

When the head of the caudate nucleus of cats was irritated, more than half of the pale globe cells studied gave a mixed response in the form of VPSP-TPSP; pure TPSP and least of all pure VPSP were recorded in some cells [4]. Thus, the results of microphysiological studies on various animals have shown that the neostriatum has a dual effect on the neurons of the pallidum - excitatory and inhibitory. This fact indicates the manifestation of a certain universal property that takes place on all floors of the central nervous system. And this circumstance removes the exclusivity that was the basis for understanding the effect of neostriatum on pallidum and dominated physiology for quite a long time [5].

The successes of modern stereotactic neurosurgery also do not agree with the idea of only the inhibitory effect of the neostriatum on the pallidum [6]. In addition to the striatum and pallidum, many brain structures are involved in the genesis of motor pathology, from the tremorogenic zones of the brainstem to the cerebral cortex with the inclusion of the subthalamic nucleus, substantia nigra, thalamus, deep nuclei of the cerebellum, and the midbrain covering in their infinitely complex relationships. The neostriatum sends direct efferents not only to the pallidum, but also to the substantia nigra. Strionigral connections are monosynaptic and two-way in nature. Of great interest is the recently physiologically investigated feedback from the substantia nigra to the neostriatum, which requires a special discussion [7].

The connection of the Black Substance with Neostriatum. The Role of Dopamine

The neurochemical nature of the strionigral mine synaptic connection has been widely discussed over the past 10 years. Histochemical fluorescence has shown that the destruction of substantia nigra in various animal species leads to a sharp decrease in the concentration of dopamine (1-3,4-dihydroxyphenylethyl-amine) in the neostriatum. Consequently, axons of neurons of the substantia nigra converging to the shell and caudate nucleus provide transport of this amine [8]. After the electrolytic destruction of the substantia nigra in the ipsilateral caudate nucleus of cats, the dopamine content drops by 49%. It has been established that dopamine is synthesized in the compact zone of the substantia nigra, in the pericaryon of its cells. In the neostriatum, it is concentrated in the extensions of the axon terminals. The rate of dopamine transport along the axons from the substantia nigra to the caudate nucleus is approximately 0.8 mm per 1 hour [9].

The role of dopamine as a mediator is also studied by physiological methods [10].

In acute experiments on cats, microionophoretic dopamine application immediately suppressed the background activity of most caudate nucleus neurons; fewer neurons showed relief. It was shown in acute experiments on cats that the background activity of a certain part of the caudate nucleus neurons was suppressed by electrical stimulation of the substantia nigra; the activity of these neurons was also suppressed under the influence of iontophoretic microinjection of dopamine into the substantia nigra; The discharges of other caudate nucleus neurons (not identified by stimulation of the substantia nigra) did not change or increased in frequency [11]. Based on these data, it was suggested that dopamine is a specific transmitter that activates inhibitory interneurons of the neostriatum and thus suppresses the activity of its cells. But there may also be a direct inhibitory effect of dopaminergic neurons of the substantia nigra on the neurons of the caudate nucleus and shell. This view is not shared by everyone. Some studies suggest that after the destruction of the substantia nigra in cats and monkeys, no clear relationship was found between the change in the neural activity of the ipsilateral caudate nucleus and the dopamine content in it after the destruction of the substantia nigra. This amine was considered as a “metabolic regulator” [12].

In addition to the theoretical aspect, its involvement in pathology is of particular importance in the study of the mediator and metabolic function of dopamine. It was found that in patients with motor disorders, the concentration of dopamine in both nuclei of the neostriatum, the caudate and the shell, sharply decreases [13]. The depletion of the dopamine reserve in such patients occurs to approximately the same level as after the experimental destruction of the substantia nigra. It should be noted that in the beginning, dopamine deficiency was given too much importance to explain motor pathology. Now it is becoming obvious that his role is more limited. A lack of dopamine leads to the development of a mainly rigid kinetic form, which is less common by the way. Replenishing the lack of dopamine by injecting its procursor (L-DOPA) into the blood has a beneficial effect precisely in akinetic forms.

Striothalamic Connections. On the Participation of the Neostriatum in the Synchronization of Bioelectric Activities

It can be considered established that slow-wave electrical activity is determined by the activity of the talamic nuclei, which send impulses to the cortex along the ascending paths of the radiant crown [14]. If these paths are cut, the slow-wave potentials disappear [15]. The thalamus, therefore, acts as a pacemaker of high-amplitude rhythmic potentials. Microelectrode studies have shown that both nonspecific and specific thalamic nuclei can participate in the genesis of this activity, and that recurrent inhibition, highly characteristic of thalamic neurons, plays an essential role in their generation [16].

Studies were conducted on anesthetized cats, which for the first time showed that rhythmic high-amplitude activity in the cortex can be caused not only by irritation of the thalamus, but also of the neostriatum. It is now known that direct stimulation of the head of the caudate nucleus or the shell can cause any type of high-amplitude rhythmic activity, just as with stimulation of the thalamic nuclei. Based on this fact, two assumptions are possible:

a) there is a duplicate (relative to the thalamus) in the neostriatum the mechanism of generation of high-amplitude rhythmic activity;

b) the neostriatum, at the moment of its direct irritation, triggers the pacemaker of this activity embedded in the thalamus [17].

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In order to accept, at least theoretically, the existence in the neostriatum of a duplicative mechanism for generating high-amplitude rhythmic activity, it is necessary that this subcortical structure possess an independent system of mono-pathways to the cerebral cortex. But even if we admit the existence of a very small number of fiber bundles from the caudate nucleus to the new cortex, it is doubtful that they generate high-amplitude slow rhythmic activity in the cortex. This is evidenced by a demonstrative experiment conducted on cats. After surgical separation of the caudate nucleus from the thalamus, a single irritation of the caudate nucleus resulted in the appearance of only a negative peak potential; slow-wave rhythmic activity was no longer recorded [18]. Therefore, there is not yet sufficient reason to look for a duplicate mechanism for generating high-amplitude rhythmic activity in the striatum. However, it would be simplistic to reduce the role of this subcortical structure to just a "relay" that triggers the thalamic pacemaker. In a naturally functioning brain, the caudate nucleus and the shell exert more complex and subtle physiological influences on the activity of the thalamic nuclei.

There are a number of established facts in Favor of this assumption. One of them is that among the subcortical structures that send direct routes to the thalamus (pallidum, amygdala, substantia nigra), high-amplitude periodic oscillations can be caused only in response to irritation of the neostriatum [19]. The second fact was obtained in cats with irritating and diverting electrodes chronically implanted in the cortex and deep structures of the brain. After switching off the caudate nucleus, direct stimulation of the nuclei of the ipsilateral thalamus continued to cause slow-wave activity in the sensorimotor cortex in the form of an engagement and spindle reaction, but the duration of these reactions and the amplitude of their potentials decreased over a long period of observations. Thus, the neostriatum is in close relationship with the thalamus and cortex in performing complex operations of the higher brain regions. Studies of high-amplitude slow rhythmic oscillations partly reflect these relationships.

In conclusion, we should focus on one more significant detail in the striocortical relationship. The neostriatum, as mentioned above, has no clearly expressed monosynaptic connections with the cerebral cortex; the same can be said about direct striothalamic pathways: their reliable presence has not been established. Consequently, the physiological connection of the neostriatum with the cortex, as well as with the thalamus, is mediated; such an anatomical link is the pallidum. After it was shown that the neurons of the pale globe respond to stimulation of the caudate nucleus with two different states of post-synaptic potential (TPSP, VPSP, or TPSP+ VPSP can be assumed that the pallidum is a kind of nonspecific "relay" core, an intermediary in the efferent impulses of the coniferous core and shell. A vicious circle of impulses is postulated: neostriatum-pallidum-thalamus-frontal lobes-neostriatum. This circle of neural network, called the Caudate loop [20], is given great importance in the integration of nervous processes at higher levels of the brain - in the genesis of synchroactivity, in the regulation of sleep.

Corticostriatal Connections. Functional Equipotence

Corticostrial projections in all mammalian species differ in spatial organization. Topographically, this is expressed in the fact that the anterior regions of the cerebral cortex are represented in the head of the caudate nucleus, and the posterior regions are represented in the caudal part of this nucleus. The largest number of fibers to the shell and caudate nucleus comes from the anterior sections of the bark. It has been shown that evoked potentials in the caudate nucleus in cats in the form of a positive-negative complex are most clearly expressed when the posterior sigmoid gyrus is irritated [21] in monkeys - in response to irritation of the precentral gyrus [22]. More limited zones of the crust also have a certain representation in the corresponding areas of the neostriatum; however, it is still difficult to make an accurate topographic map. Recent studies conducted on monkeys by autoradiography have established a special "belt" of cortical projection on the neostriatum. It covers the associative fields in the inferior parietal, temporal, and inferior prefrontal regions [22].

The spatial organization of cortical-striatal connections led to the construction of broad physiological generalizations, in particular, to the idea of functional equipotentiality, the essence of which is that certain areas of the cerebral cortex are similar and even physiologically equivalent to those areas of the neostriatum where these cortical areas give a direct projection. The following facts are given in favor of this view: Monkeys developed a skill based on the type of visual discrimination that disappeared after extirpation of the inferior temporal cortex. It turned out that visual discrimination deficiency also occurs after removal of the posterior part of the caudate nucleus, i.e. that part of it where the inferior temporal region sends direct paths [23]. No less demonstratively, the proof of functional equipotence is based on another form of experiment. Limb irritation in monkeys causes the appearance of potentials in the somatosensory cortex and in a certain area of the neostriatum. After switching off the studied area of the cortex by freezing, it was no longer possible to register the evoked potential in the neostriatum in response to the same irritation of the limb.

The notion of functional equipotence can be accepted, but with some reservations. It is hardly possible to assert the complete identity of the cortical zones to the corresponding areas of the neostriatum. The ability of this subcortical nucleus to compensate for the activity of the new cortex, especially in higher mammals, cannot be fully developed. In addition, cortical-striatal physiological connections cannot be considered in isolation from other higher levels of the brain. In natural conditions, impulses from the cerebral cortex reach the neostriatum not only via direct descending paths, but also indirectly, in particular through the thalamus, especially since morphological methods have recently revealed direct projections to the neostriatum in cats not only from the central medial nucleus of the thalamus, but also from other thalamic nuclei, while A certain topical distribution of thalamic striatal efferents was noted [24].

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Thus, quite complex functional relationships are established between the cerebral cortex and the neostriatum. The cortex regulates the response of neostriatum neurons to sensory flow [25]. This representation later becomes more complicated and detailed: the cortex, especially its anterior sections, extracts a specialized signal from a non-specific sensory stream ascending to the terminal brain through the reticular formation-medial thalamus-neostriatum system.

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Conflicts of Interest

The authors have no conflicts of interest to declare.

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