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Short Communication

Role of Basal Ganglia in Integrative Brain Activity and Behavioral Organization

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ABSTRACT

The functional manifestations of the basal ganglia are determined not so much by the connections of its individual nuclei among themselves as by the connections of each of them with other brain structures, of which the neocortex, the nonspecific nuclei of the thalamus, the subthalamic nucleus, the substantia nigra, and the hypothalamus are the most important. Further progress in the study of the morphofunctional basis of the brain as a whole will allow us to further reveal the role of the basal ganglia in the analysis and integration of neural processes.

KEYWORDS

Basal Ganglia, Integrative Brain Activity, Behavioral Organization

INTRODUCTION

Information about the role of the basal ganglia in the integrative activity of the brain and the organization of complex behavior is based on data obtained by direct stimulation of these structures, their destruction, or by recording electrical activity in them.

The responses of animals to direct stimulation of the neostriatum through chronically implanted electrodes are relatively poor. They are reduced to turning the head and trunk to the side opposite to the stimulation and, in some cases, to contraction of the contralateral limb. If a number of unfavorable factors contributing to the physical spread of the current to the structures adjacent to the neostriatum are eliminated beforehand, the

possibility of inducing motor reactions decreases even more. Thus, Laursen has shown in chronic experiments on cats that after degeneration of cortico-fugal fibers bordering the caudate nucleus and transiting through it, electrical stimulation ofthis nucleus did not entail flexor reactions of the limbs [4-7].

At the same time, there are zones in the neostriatum, stimulation of which not only does not cause activity in animals, but, on the contrary, leads to a delay in any behavioral reaction that has already begun - orienting, emotional, and food-producing. Animals, according to a figurative comparison, "freeze, as if the moving picture film was stopped". Delayed behavioral reactions are accompanied by the development of slow high-voltage activity in the cortex of the large hemispheres. Among the "inhibitory" points of the neostriatum there are such points, stimulation of which, causing delay of purposeful reaction, simultaneously suppresses or prevents pain sensations - a fact first described at the end of the last century on dogs under weak morphine anesthesia, later - on narcotized cats [1-5]. In experiments on non-narcotized dogs it was also demonstrated that it was possible to completely prevent the violent reaction from strong nociceptive electrocutaneous irritation on the background of stimulation of the ventral anterior zone of the caudate nucleus through chronically implanted electrodes. When the stereotactic method began to be used in neurological clinics for the treatment of patients, cases of relief of severe pain sensations in the facial nerve area during stimulation with a weak pulsed current of the caudate nucleus were described. Special cases of striatal inhibition of interest include the property of the caudate nucleus to suppress fluctuations in muscle tone caused by stimulation of one of the supraspinal nuclei in patients with hyperkinesis [2-5].

Another peculiarity of the neostriatum - its influence not only on motor but also on autonomic components of complex behavior - was revealed by the method of electrical stimulation. Morphofunctional heterogeneity of the caudate nucleus has been established. Electrical stimulation of the dorsomedial zone of the nucleus in dogs increased the secretion of the salivary gland on presentation of a conditioned stimulus, whereas stimulation of the ventrolateral zone of the same nucleus decreased the value of conditioned secretion [4].

In contrast to the neostriatum, direct stimulation of another nucleus of the basal ganglia, the pallidum, does not cause pronounced inhibition. The responses of animals are dominated by motor reactions of elementary type in the form of contractions of limbs, jaw, neck or facial muscles. In patients during stereotactic surgeries during stimulation of the pale globe, depending on the frequency of the pulse current, the amplitude of tremor increased or decreased [3-5].

By the method of direct stimulation of limited areas of the pallidum it was possible to find out its functional connection with those areas of the hypothalamus which are considered as motivational. It is known, for example, that by electrical stimulation of the "food centers" of the lateral hypothalamus it is possible to reproduce all

components of the conditioned food-digestive reaction, and from the first application, without giving a conditioned stimulus and without reinforcement by an unconditioned stimulus. It turned out that the same phenomenon could be obtained by irritation of the pale globe. Although this required 2-2.5 times greater stimulus strength than for the hypothalamus, the effect was weaker and less regular; the number of such active points in the pale globe is limited, which is consistent with the diffuse system of pallidohypothalamic fibers. The results of these experiments suggest the possibility of a modulating influence of the pale globe on the lateral hypothalamus relevant to the organization and triggering of food motivation. Such an assumption finds support in the changes in the neural activity of the posterior hypothalamic region during pale ball stimulation. The neurons of this hypothalamic region that responded to remote sensory signals were identified in cats; the rate and frequency of discharges of these cells changed significantly under the influence of stimulation of the pale globe [2-8].

The results of experiments with electrical stimulation of the claustrum have revealed a wide range of influences of this nucleus on behavioral reactions and its individual components. If we compare the data of different authors obtained on different animals, it turns out that it participates in the regulation and organization of various functions - motor and vegetative: from pylorospasm to cardiac contractions and external respiration, participates in the organization of emotions, regulation of sleep, is recognized as an important integrative olfactory-associative center, is related to the orienting reflex, to food and sexual behavior, is part of the general inhibitory system of the brain. Such "kaleidoscopic", as Gabor puts it, activity of this limited area of the brain may seem implausible. It may be explained in part by the richness of the efferent pathways of the claustrum, innervating almost all fields of the neocortex and subcortical formations. More recently, experiments on dogs with electrodes chronically implanted in different parts of the claustrum have brought some order to this question. Stimulation of the rostral and caudal parts of it causes mainly elements of the food response, and the ventral and dorsal parts - an orienting reaction and isolated contractions of the trunk and head muscles; irritation of the lateral part caused an emotional reaction resembling fear [4].

A significant addition to the physiological characterization of the basal ganglia is made by the results of studies with switching off each of the nuclei of this complex [8].

At the end of the last and beginning of this century, clinical literature began to report cases of hyperkinesis accompanied by necrotic foci in the area of the shell and/or caudate nucleus; the idea arose to obtain experimental models of motor pathology in animals by destroying these nuclei. The results of nearly 80 years of research have shown the following. Damage in the area of neostriatum in subprimates gave a negative result: in rats, rabbits, cats, dogs it was not possible to obtain any pronounced symptoms of hyperkines is such as chorea or athetosis. In inferior monkeys there were involuntary mimic reactions and tremor of the fingers, but

these symptoms subsided over a period of several days to several weeks after the operation. In anthropoids, focal lesions in the region of the caudate nuclei entailed choreoathedoid movements of the limbs that lasted much longer than in inferior apes. The reason for these phylogenetic differences remains not quite clear. Also surprising is the fact that the content of dopamine, the deficiency of which is one of the causes of movement disorders, is equally high in the neostriatum of all representatives of mammals, from rodents to humans. Apparently, the lack of this amine in the central nervous system affects higher mammals much more [1-8].

Another circumstance important for understanding the role of the neostriatum in behavior should be noted. Symptoms of hyperkinesis in humans seem to last for years, but it is impossible to consider them as a "disease of the neostriatum". It is a pathology of the whole system - from the brain stem to the new cortex with a violation of neurogenic and neurochemical mechanisms. In favor of this position we can cite a very interesting, although unique case of lesion of both caudate nuclei by astrocytoma, as a result of which the nuclei were temporarily switched off from function. The patient did not show any pronounced motor disorders, except for a slight decrease in the tone of the limb muscles; at the same time, some disturbances were found in mental activity. After the operation, which freed the caudate nuclei from the benign tumor, all symptoms disappeared. Consequently, when the caudate nuclei were shut off from function more or less in isolation (tumor compression) and there were no accompanying factors of motor pathology with inevitable involvement of other brain structures, the symptoms were of a different character, more closely resembling those that occur in a number of experimental cases after caudatotomy [9-11].

Indeed, in caudatotomized animals, as will be seen from further description, changes in another sphere of nervous activity rather than in motor activity often come to the fore. Interesting in this respect is the experience made on monkeys. After the destruction of even one caudate nucleus, the animals developed a peculiar symptom of hyperactivity: the number of aimless movements in space increased 5-7 times and more per day compared to the norm. The hyperactivity symptom persisted for the whole period of observations - up to 1.5 years. This circumstance excludes to a great extent the consequences of trauma from damage of such a large brain structure as the caudate nucleus. Hyperactivity of caudatotomized monkeys is explained by the disruption of the balance of nervous processes between the cortical fields perceiving tactile and visual stimuli and the centers of the extrapyramidal system [6-8].

The phenomenon of hyperactivity was later reproduced in cats with electrolytic destruction of both caudate nuclei. At the same time, it was shown that daily hyperactivity in cats is accompanied by prolongation of the waking phase over the sleeping phase, which is reflected not only in behavior but also in the electroencephalogram: in the anterior cortical sections of one hemisphere, ipsilateral to the switched-off caudate nucleus, the "awake", desynchronized rhythm prevailed; at the same time, from symmetric points of the cortex

of the opposite hemisphere, the synchronized rhythm was registered more often [1-5].

Partial bilateral destruction of the neostriatum also affects conditioned reflex activity. The result depends on the localization of the destruction. After damage to the body of the caudate nucleus, the previously developed conditioned reflexes in dogs suffered to a greater extent than after damage to the head of this nucleus, which manifested itself in a sharper disturbance of differentiation of visual signals, inability to reproduce delayed reactions and delayed choice reactions. Such shifts of higher nervous activity lasted the whole period of observations - half a year and more [12].

The role of the neostriatum in the organization of complex behavior, at least in subprimates, is shown in another very demonstrative form of experience. As long as the caudate nuclei are preserved in cats with removed neocortex, the animals are able, albeit simplified, to perform three forms of behavior: movement in space, search and simple previously developed conditioned reflexes. But if in decorticated cats the caudate nuclei are also damaged, such "thalamic animals" cannot realize any of the three forms of behavior even in a primitive form. The result of this experiment testifies to the compensatory role of the neostriatum in relation to the neocortex. Such a capacity is called "vicarious." Of course, the substitutive, or vicarious, function of this subcortical nucleus is not full-fledged and is weaker the higher the phylogenetic stage of the animal [7-14].

Switching off the pallidum led to different results. If in caudatotomized animals the tendency to hyperactivity prevailed (sharp increase in spontaneous movements in space, prolongation of the phase of wakefulness over the phase of sleep), in pallidotomized animals the tendency to decrease activity prevails: general adynamia, drowsiness, "as if aversion to any movement".

Bilateral complete electrolytic destruction of the pallidum entails a very severe condition in animals such as rats, cats, dogs with damage to almost all systems, including metabolism and food reflexes. Those animals that survive pallidotomy remain for long periods of time, lasting months, profoundly defective, adynamic, emotionally obtuse. The small volume of the pallid ball excludes the determining role of the traumatic factor. One morphological peculiarity of the pallidum area, which distinguishes it from most other subcortical formations, acquires a well-known significance: in both of its segments there is a dense concentration of fibers, a significant part of which are transient, i.e. passing through the pallidum and not terminating in it. Using the method of destruction, the researcher inevitably damages and crosses a large mass of fibers that do not belong to this nucleus. Morphofunctional differentiation of the cell-neuropil mass of the pale globe from the passing bundles of fibers in the future may make it easier to understand the reason for such a severe condition of pallidotomized animals [1-8].

Unilateral damage to the pallidum is much easier for animals due to compensation by the preserved part of the pallidum. In such animals it has been shown experimentally that the pallidum takes part in the coordination of movements. To illustrate this, the following experience is usually cited. After unilateral switching off of the pallid ball, the monkeys preferred to use the opposite, in relation to the removed nucleus, forelimb when grasping food. One of the causes of coordination disorders lies in the development of reflex hypertonus of contralateral extensors; a certain role is played by the change in excitability of gamma-motoneurons of the spinal cord. After incomplete bilateral damage to the pale ball, defects in purposeful behavior are also observed: it is expressed, for example, in difficulty or inability to implement a conditioned reflex or develop a new one. A number of researchers agree that the motivational, i.e. motor, component is affected, as a result of which the initiation or motor support of a purposeful reaction is impeded [13].

Bilateral destruction of the claustrum in cats and dogs does not cause clear changes in behavior; they are reduced to weakly expressed disorders of positional reflexes and vegetative reactions, to temporary disturbance of conditioned reflex activity. And after removal of the auditory zone of the cortex, dogs continued to differentiate sound stimuli of different tonality, but after the claustrum was destroyed in these dogs, the ability to differentiate tones disappeared [10-15].

The results of experiments with direct irritation and switching off of the basal ganglia clearly demonstrate the participation of this complex of subcortical structures in the integration of complex nervous processes in the brain and in the organization of different forms of behavior. It should be noted that higher integration is manifested not only at the behavioral level. Studies of neural activity of basal ganglia in different animals with chronically implanted diverting microelectrodes have allowed us to obtain a number of new and unexpected facts in this direction, although their number is still very limited [11-15].

It turned out that individual neurons of the caudate nuclei, shell, and pallidum reveal a certain specialization, reacting to a change in the situation or to a certain signal having one or another biological significance. There are isolated data on the activation of cells of the caudate nucleus of monkeys in those cases when the images on the screen acquired a signaling value, for example, a square; the same cells did not react to simple screen illumination. Other researchers have shown, also on monkeys, that those neurons of the caudate nucleus, which responded to visual stimuli and easily quenched at their repetition, began to respond to a stimulus of novelty, entailing an orienting reaction of the animal [15]. The anticipatory response of neostriatum neurons is also of known interest. This fact has been shown in non-narcotized cats and rabbits: neurons were found in the caudate nucleus and the shell, the change of activity of which preceded the purposeful movement of the animal. Observations of the anticipatory response of neurons are of particular value in human studies, due to the possibility of making verbal contact with them. Analysis of neuronal activity recorded on patients during

stereotactic surgeries showed that the background activity of individual neurons of the shell and caudate nucleus clearly begins to change first to the given command "clench the hand into a fist" and later to self-movement. Consequently, the neostriatum is involved in the perception of meaningful text [13-16].

Finally, the participation of individual neurons of the basal ganglia in the production and consolidation of various forms of conditioned reflexes can be considered established. Analysis of the facts shows that the general principles of changes in neuronal reactions in the caudate nucleus, shell, and pale globe are similar to those established earlier in the cortex of the large hemispheres. It has been revealed, in particular, in chronic experiments on cats and rabbits with implanted microelectrodes, that the neurons of the basal ganglia, previously unresponsive to "indifferent" stimuli, as they are combined with unconditional stimuli, begin to respond to them. In a different situation, when neurons respond to indifferent stimuli, as a temporary connection is formed and these stimuli acquire signaling value, plastic rearrangements of neuronal activity occur. Studies also show that both excitatory and inhibitory neurons of subcortical structures take part in the process of organizing the temporal connection [14,15].

Summarizing the current knowledge about the activity of the basal ganglia, we note the main point [17].
The traditional idea that the basal ganglia are responsible for the regulation of motor automatisms cannot be accepted in such a limited formulation at present. This complex of subcortical nuclei is more broadly included in the integrative activity of the central nervous system, playing a role in the orientation of animals in space, in the initiation of motor support for food motivation, and in the regulation of the wake-sleep cycle [15-18]. The neostriatum, pallidum, claustrum are part of the program of implementation of the conditioned reflex. All the above mentioned unites separate structures of basal ganglia in their functional characterization [18-21].

There are also individual features in each of the structures. First of all, their role in the realization of simple motor reactions is clarified. The neostriatum takes part in the regulation of slow movements, in which the tonic component predominates [24]. The pallidum differentiates the character of movements: the activity of its neurons in monkeys changed under the influence of pushing movements of the hand, whereas the same neurons did not react to pronation movements. The organization of other functions also shows individual peculiarities [21]. It was found that the background activity of claustrum cells in cats was sharply increased by painful stimuli, while at the same time the activity of putamen and pale ball cells did not change. Direct irritation of the caudate nucleus entails the appearance of synchronized electrical activity in the cortex and thalamus and causes inhibition of any behavioral response. The pallidum, on the other hand, does not exhibit these qualities when directly irritated. It is not excluded that the neostriatum, distinguished by a rich network of interneurons and many afferent inputs, participates in the analysis of complex signals-images [20-25].

CONCLUSION

In conclusion, one more circumstance should be pointed out. The functional manifestations of the basal ganglia are determined not so much by the connections of its individual nuclei among themselves as by the connections of each of them with other brain structures, of which the neocortex, the nonspecific nuclei of the thalamus, the subthalamic nucleus, the substantia nigra, and the hypothalamus are the most important. Further progress in the study of the morphofunctional basis of the brain as a whole will allow us to further reveal the role of the basal ganglia in the analysis and integration of neural processes.

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