

Mini Review

Olfactory Bulbs of the Rat - Cyto- and Chemoarchitectonics

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Abstract

The olfactory bulbs form the anterior part of the telencephalon and are the central part of the olfactory analyzer. They have a cortical structure with a characteristic layered organization. The olfactory cortex is phylogenetically the oldest part of the cerebral cortex.

The data presented in the article can serve as a fundamental basis for further study of the parts of the rat brain in normal and pathological conditions with further extrapolation of the obtained data to humans.

Keywords: Olfactory bulbs; Rat; Cytoarchitectonics; Chemoarchitectonics

Introduction

The olfactory bulbs form the anterior part of the telencephalon and are the central part of the olfactory analyzer. They have a cortical structure with a characteristic layered organization [3]. The olfactory cortex is phylogenetically the oldest part of the cerebral cortex.

In many mammals, they occupy a significant volume in the rostral part of the skull. In humans, the olfactory bulbs are relatively small and are displaced by the basilar brain into the area below the ventral surface of the frontal lobes. The accessory olfactory bulb - *bulbus olfactorius accessorius* - is located dorsally and somewhat medially, between the main olfactory bulb and the rostral olfactory nucleus - *nucleus olfactorius rostralis* - in the form of a lenticular inclusion in the olfactory bulb. The accessory olfactory bulb in rats, as in other rodents, lagomorphs and insectivores, has a thick inner reticular layer. In fact, this layer consists of a wide band of white matter - the dorsal lateral olfactory tract - *tractus olfactorius lateralis dorsalis*.

In the olfactory bulb, there are: a layer of olfactory neurons, a glomerular (glomerular) layer, an olfactory glomerulus, an outer reticular layer, a layer of mitral cells, an inner reticular and a layer of granular cells.

There are several main types of olfactory bulb neurons: mitral, fascicular, amacrine, periglomerular and short-axon. Beam neurons, in turn, are divided into external, middle and internal,

short-axon - into superficial and deep. Beam and mitral cells play the role of relay neurons, while the value of periglomerular, amacrine and short-axon neurons (interneurons) is reduced to the modulation of their neuronal activity.

On the frontal section in the direction from the surface inward, six layers of the olfactory cortex are distinguished - concentric zones:

Layer of Olfactory Neurons

Unmyelinated axons of sensory neurons approach the olfactory bulb in the form of separate bundles and intertwine on its surface, forming a layer of nerve fibers.

Glomerular Layer

Glomeruli are branching axons of receptor cells of the olfactory organ surrounded by dendrites of periglomerular neurons and illustrate the principle of grouping neuronal elements and synapses into anatomically distinguished modules [9,12]. Each axon innervates only one glomerulus. After entering the glomerulus, the olfactory axon branches, breaking up into processes with varicose veins and terminal thickenings. Each glomerulus is surrounded by numerous small periglomerular cells (6-8 μm along the long axis). The dendrites of periglomerular cells branch and terminate within one or more glomeruli. Glomeruli, a distinctive feature of the olfactory bulb, illustrate the "principle of grouping neuronal elements and synapses into anatomi-

cally distinguishable modules" [7]. The most likely mediators of periglomerular neurons are GABA and dopamine.

Outer Mesh Layer

The layer is formed by dendrites of mitral neurons and contains a relatively small number of perikarya of bundle neurons. Dopamine is the putative mediator of bundle neurons.

Mitral Layer

This layer contains the perikarya of mitral neurons. Their axons, together with the axons of the fascicular cells, form the lateral olfactory tract. The transmitter in dendrodendritic synapses between mitral/fascicular cells and interneurons is also glutamate, which acts predominantly through NMDA receptors [20]. Postsynaptic responses of mitral cells against the background of stimulation of olfactory axons are mediated by the work of two types of ionotropic glutamate receptors [5]. Early rapid response is mediated by activation of AMPA glutamate receptors, while NMDA receptors mediate prolonged excitation [16]. The action of the latter promotes synaptic integration and plasticity, and thus can play an important role in the processing of olfactory information and memory [10,19]. GABA [13] and dopamine [18] can act as glutamate release modulators.

Inner Mesh Layer

A narrow layer, practically devoid of cellular elements, is formed by collaterals of the processes of fascicular, mitral, amacrine, and periglomerular neurons. Short-axon neurons are also present in this layer.

Layer of Granular Cells

Granular neurons are most numerous in the olfactory bulb. The presence of gap junctions between adjacent cells contributes to the synchronization of neuron activity [10]. It is believed that granule cells perform the function of lateral inhibition in the processing of olfactory information; GABA acts as the main mediator (Table 1) [13].

Table 1: Neuronal and transmitter organization of the olfactory bulb.

Name of the neuron	Cortical layers	Mediator
Periglomerular neurons	glomerular	GABA
Bundle neurons	outer reticulate	dopamine
mitral neurons	mitral	glutamate
Short-axon neurons	internal reticulated	GABA
Amacrine neurons	mitral, internal reticular, granular	glutamate
Granular neurons	granular	GABA

The triad of neuronal elements in the olfactory bulb, as in other parts of the brain, is formed by incoming fibers, basal cells, and interneurons [11]. There are two main classes of cells in the olfactory bulb: mitral cells and fascicular cells. The axons of the mitral and fascicular cells form a well-defined lateral olfactory tract leading to the anterior olfactory nucleus, anterior hippocampus, olfactory tubercle, prepiriform cortex, amygdala complex, entorhinal cortex, nucleus of the accessory olfactory tract, nucleus of the lateral olfactory tract, and nucleus of the terminal stria [14,17].

Odor coding in olfactory bulbs

In 1991, a large multigene family of olfactory protein receptors was discovered in olfactory sensory neurons. Later, homol-

ogous families were also found in other vertebrate species [1], including humans. In situ hybridization has shown that:

1) each receptor neuron expresses only one olfactory receptor;

2) olfactory neurons expressing a certain olfactory receptor are randomly distributed within one of the 4 spatial zones of the olfactory epithelium;

3) mRNA for olfactory receptors was found in olfactory axons. The latter circumstance made it possible to study the projection pattern of sensory olfactory neurons [4].

It was found that olfactory sensory neurons expressing this receptor give projections to two individual glomeruli located in the dorsomedial and ventrolateral parts of the bulb. In addition, there is a clear correspondence between the number of genes and the number of glomeruli in a sample. Thus, information from this type of olfactory receptors scattered over the olfactory epithelium is transmitted to individual glomeruli, transforming into a spatial map in the olfactory bulb [2,3,10,15].

Further studies have shown that one odorant can activate several types of receptors [6]. It is assumed that different receptors recognize different structural regions of molecules and project them onto certain groups of glomeruli. Thus, odor coding is carried out by an ensemble of glomeruli [8,9,11]. Confirmation of such a combinatorial coding mechanism was obtained using autoradiographic methods. It has also been shown that an increase in the concentration of an odorant can lead to the stimulation of additional glomeruli located far from the glomeruli activated by low concentrations [8].

Signal analysis in the olfactory bulb is carried out at two anatomical levels with the participation of specific intercalary neurons.

Processing of incoming signals occurs in the glomerular layer based on interactions between olfactory axons and periglomerular neurons [7]. The output signal is controlled through interactions between mitral and granular neurons in the outer reticular layer [11].

Centrifugal projections modulate activity at both anatomical levels.

It is possible that, in a number of mammals, bulbs perform not only sensory functions, but are also involved in nonspecific limbic reactions [14]. In bullboxtomized rats, a number of behavioral abnormalities and disturbances in neurotransmitter systems are observed.

The data presented in the article can serve as a fundamental basis for further study of the parts of the rat brain in normal and pathological conditions with further extrapolation of the obtained data to humans.

References

- Li A, Rao X, Zhou Y, Restrepo D. Complex neural representation of odour information in the olfactory bulb. *Acta Physiol (Oxf)*. 2020; 228: e13333.
- Mori K, Sakano H. Olfactory Circuitry and Behavioral Decisions. *Annu Rev Physiol*. 2021; 83: 231-256.
- Imai T. Construction of functional neuronal circuitry in the olfactory bulb. *Semin Cell Dev Biol*. 2014; 35: 180-8.

4. Iwata R, Kiyonari H, Imai T. Mechanosensory-Based Phase Coding of Odor Identity in the Olfactory. *Neuron*. 2017; 96: 1139-1152.
5. Moran AK, Eiting TP, Matt Wachowiak M. Dynamics of Glutamate Drive Underlie Diverse Responses of Olfactory Bulb Outputs In Vivo. *eNeuro*. 2021; 8: ENEURO.0110-21.2021.
6. Leon M, Johnson BA. Olfactory coding in the mammalian olfactory bulb. *Brain Res Brain Res Rev*. 2003; 42: 23-32.
7. Wachowiak M, Shipley MT. Coding and synaptic processing of sensory information in the glomerular layer of the olfactory bulb. *Semin Cell Dev Biol*. 2006; 17: 411-23.
8. Dibattista M, Reisert J. The Odorant Receptor-Dependent Role of Olfactory Marker Protein in Olfactory Receptor Neurons. *J Neurosci*. 2016; 36: 2995-3006.
9. Mori K, Nagao H, Yoshihara Y. The olfactory bulb: coding and processing of odor molecule information. *Science*. 1999; 286: 711-5.
10. Auffarth B, Kaplan B, Lansner A. Map formation in the olfactory bulb by axon guidance of olfactory neurons. *Front Syst Neurosci*. 2011; 5: 84.
11. Buck LB. Information coding in the vertebrate olfactory system. *Annu Rev Neurosci*. 1996; 19: 517-44.
12. Kosaka K, Kosaka T. Synaptic organization of the glomerulus in the main olfactory bulb: compartments of the glomerulus and heterogeneity of the periglomerular cells. *Anat Sci Int*. 2005; 80: 80-90.
13. Villar PS, Hu R, Araneda RC. Long-Range GABAergic Inhibition Modulates Spatiotemporal Dynamics of the Output Neurons in the Olfactory Bulb. *J Neurosci*. 2021; 41: 3610-3621.
14. Haddad R, Weiss T, Khan R, Nadler B, Mandairon N, et al. Global features of neural activity in the olfactory system form a parallel code that predicts olfactory behavior and perception. *J Neurosci*. 2010; 30: 9017-26.
15. Ghosh S, Larson SD, Hefzi H, Marnoy Z, Cutforth T, et al. Sensory maps in the olfactory cortex defined by long-range viral tracing of single neurons. *Nature*. 2011; 472: 217-20.
16. Zhao F, Wang X, Zariwala HA, Uslaner JM, Houghton AK, et al. fMRI study of the role of glutamate NMDA receptor in the olfactory adaptation in rats: Insights into cellular and molecular mechanisms of olfactory adaptation. *Neuroimage*. 2017; 149: 348-360.
17. Suzuki N, Bekkers JM. Neural coding by two classes of principal cells in the mouse piriform cortex. *J Neurosci*. 2006; 26: 11938-47.
18. Viret PD, Coronas V, Delaleu JC, Moysse E, Duchamp A. Dopaminergic modulation of mitral cell activity in the frog olfactory bulb: a combined radioligand binding-electrophysiological study. *Neuroscience*. 1997; 79: 203-16.
19. Hendin O, Horn D, Tsodyks MV. The role of inhibition in an associative memory model of the olfactory bulb. *J Comput Neurosci*. 1997; 4: 173-82.
20. Bartel DL, Relu L, Hsieh L, Greer CA. Dendrodendritic synapses in the mouse olfactory bulb external plexiform layer. *J Comp Neurol*. 2015; 523: 1145-61.