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CURRENT VIEWS ON THE STRUCTURAL ORGANIZATION OF THE RAT CEREBRAL CORTEX

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In recent years, the structural organization and neurotransmitter nature of neurons in different parts of the rat cerebral cortex have provided the basis for further study and allowed the resulting experimental data to be extrapolated to humans in those aspects that are not related to the second signal system that is unique to humans. Advanced research methods have expanded the possibilities for research, so interest in studying the structural organization of the cerebral cortex has not abated to date. The cerebral cortex is the highest portion of the central nervous system. It is the youngest phylogenetically and the most complex part of the brain in terms of morphological and functional organization. It is the place of the highest analysis and synthesis of all the information entering the brain. It is the place where complex forms of behavior are integrated. The cerebral cortex is responsible for consciousness, thinking, memory, and "heuristic activity" (the ability to generalize and discover). A structural model based on systematic cortical variation captures the overall laminar structure of brain regions by dividing the cortical architectonic continuum into discrete categories (cortical types) that can be used to test hypotheses about cortical organization and function in different species, including humans. The architectonics data obtained from animal models provide an invaluable opportunity to reveal the complex interplay between structure and function in the mammalian brain. Extrapolation of these data from rodents to humans requires knowledge of the similarities and differences between species in anatomical features, and the factors that contribute to functional connectivity. Homologous functional networks are compared between species, and aspects such as global signal topography and the relationship between structural and functional connectivity are considered.

Key words: cerebral cortex, rats, allocortex, olfactory sensory neurons, cortical amygdaloid nuclei, hippocampus, postrhinal cortex, isocortex.

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СУЧАСНІ УЯВЛЕННЯ ПРО СТРУКТУРНУ ОРГАНІЗАЦІЮ КОРИ ГОЛОВНОГО МОЗКУ ЩУРІВ

Упродовж останніх років структурна організація та нейромедіаторна природа нейронів, різних відділів кори головного мозку щурів, дають основу для подальшого вивчення і дозволяють екстраполювати на людину отримані експериментальні дані в тих аспектах, які не пов'язані з другою сигнальною системою, унікальною для людини. Сучасні методи дослідження розширили можливості для дослідів, тому інтерес до вивчення структурної організації кори головного мозку не вщухає і сьогодні. Кора великих півкуль головного мозку – вищий відділ центральної нервової системи. Вона являє собою найбільш молодий філогенетично і найбільш складний по морфофункціональної організації відділ головного мозку. Це місце вищого аналізу та синтезу всієї інформації, що надходить у мозок. Тут відбувається інтеграція складних форм поведінки. Кора мозку відповідає за свідомість, мислення, пам'ять, «евристичну діяльність» (здатність до узагальнення, відкриття). Структурна модель, заснована на систематичній варіації кори головного мозку, захоплює загальну ламінарну структуру областей мозку, шляхом поділу коркового архітектонічного континіуму на дискретні категорії (коркові типи), які можуть бути використані для перевірки гіпотез, про коркову організацію та функції, у різних видів, в тому числі і у людини. Дані архітектоніки, отримані на моделях тварин, дають безцінну можливість виявити складну взаємодію між структурою та функціями в мозку ссавців. Екстраполяція цих даних, від гризунів до людини, вимагає знань про подібності та відмінності між видами в анатомічних особливостях, та факторів, що сприяють функціональній зв'язаності. Гомологічні функціональні мережі порівнюються між видами, та розглядаються аспекти, такі як топографія глобального сигналу та взаємозв'язок між структурною та функціональною зв'язаністю.

Ключові слова: кора головного мозку, щури, аллокортекс, нюхові сенсорні нейрони, кортикальні ядра мигдалика, гіпокамп, постринальна кора, ізокортекс.

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The knowledge about the structure and development of various parts of the rat brain provides a fundamental basis for various research projects. However, clear understanding of the structural organization and neurotransmitter nature of different parts of the rat cerebral cortex is crusial for extrapolation the data obtained in animal experiments to humans. Furthermore, experimental methods that can only be used in mammals have revealed the pattern of neuronal generation and demonstrated different ways of neuronal migration and neural pathway formation.

Similar to all mammals, the rat cortex is divided into allocortex and isocortex. The allocortex is a heterogeneous cortex, a phylogenetically earlier part of the cerebral cortex consisting of paleocortex and

archicortex. The archicortex contains the olfactory cortex, amygdala, hippocampus, dentate gyrus, and piriform cortex. Although, according to another classification, the archicortex is the cortex of the olfactory bulbs, and paleocortex is represented by the cortical part of the amygdala, hippocampus, and dentate gyrus with the piriform cortex. The transitional zones between the paleocortex and the neocortex (periallocortex) are the retrosplenial, entorhinal, and cingulate cortices [14].

The neocortex, as defined by Zymatkin S.M. and Bon E.I., also called the isocortex (neopallium or homogenous cortex), covers most of the dorsal, a significant part of the lateral, and small areas of the medial and basal sides of the brain. In the rat, it occupies 30–60 % of the total cortical surface. The isocortex includes the frontal, parietal, occipital, and temporal cortices [13].

Adult cortical regions are composed of specific cell types that support unique higher-order cognitive functions. How regional diversity originates from the primordium of the single-layer neuroepithelium has been the subject of decades of fruitful research, and advanced technologies, including single-cell transcriptomics, are providing a new perspective on area-specific molecular diversity.

The rat orbital cortex (ORB) comprises five divisions: the medial (MO), ventral (VO), ventrolateral (VLO), lateral (LO) and dorsolateral (DLO) orbital cortices. Using the *Phaseolus vulgaris leucoagglutinin* that is an anterograde anatomical tracer, the efferent projections from the five divisions of the orbital cortex to the thalamus in the rat were described. It has been demonstrated that with some overlap, each ORB division was distributed in a specific (and unique) way to the thalamic nuclei. Overall, the ORB projected to a relatively limited number of sites in the thalamus and strikingly extended entirely to medial/midline thalamic structures, completely avoiding lateral regions or principal nuclei of the thalamus. The major terminal sites in the thalamus were the paratenial nucleus (PT) and nucleus reuniens (RE) of the midline thalamus, the medial (MDm) and central (MDc) divisions of the mediodorsal nucleus, the intermediodorsal nucleus, and the central lateral, paracentral, and central medial nuclei of the rostral nucleus (SM). With a few exceptions, the medial ORB divisions (MO, VO) mainly targeted “limbic-associated” nuclei such as PT, RE, and MDm, while the lateral division (VLO, LO, DLO) predominantly extended to “sensorimotor-associated” nuclei, including MDc, SM, and the rostral intralaminar complex.

The medial midline thalamus may represent an important link (or bridge) between the orbital cortex and the hippocampus, and between the ORB and the medial prefrontal cortex. Thus, the findings show that each division of the orbital cortex projects in a specific way to the thalamic nuclei, which implies unique functions for each division of the orbital cortex [11].

At the cellular level, the cerebral cortex is composed of approximately 16 billion neurons, which makes up more than 80 % of the total brain mass. The amazing diversity of neuronal types has been studied, but there is still a lack of a comprehensive overview of neuronal diversity in the cerebral cortex, including how morphological, molecular, and physiological diversity is related to functional cortical areas. Even less is known about the developmental processes that give rise to these diverse cell types.

Recent advances in molecular profiling, including at single-cell resolution, have made it possible to revisit these developmental processes at the level of genes and regulatory pathways [4].

The processes of information processing in different areas of the rat cerebral cortex are based on some universal mechanisms for all parts of the nervous system, which are based on the processes that change the excitability of nerve cells. A nerve impulse is transmitted from one neuron to another via a neurotransmitter, a chemical messenger. The neurotransmitter interacts with specific receptors of another neuron, or cells of the active organ, changing its functional activity through secondary intracellular messengers. In general, about a hundred different neurotransmitters and, accordingly, neurons of different neurotransmitter nature have been identified in the nervous system. Moreover, each neuron can terminate in axons of neurons of different neurotransmitter nature. Generating neuronal diversity is a biological strategy that is widely used in the brain to process complex information.

The olfactory bulb is the first relay station for olfactory information in the vertebrate central nervous system. In the olfactory bulb, the axons of olfactory sensory neurons form synapses with the dendrites of projection neurons that transmit olfactory information to the olfactory cortex [8]. The olfactory bulbs form the anterior part of the medulla. 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 brain to the area under the ventral surface of the frontal lobes. The accessory olfactory bulb is located dorsally and somewhat medially, between the main olfactory bulb and the rostral olfactory nucleus as a lenticular inclusion to the olfactory bulb.

Like other rodents, hares, and insectivores, the rat accessory olfactory bulb has an internal reticular layer of great thickness. In fact, this layer consists of a wide band of white matter – the dorsal lateral olfactory tract.

Olfactory sensory neurons extend their axons exclusively to the olfactory bulb, which is designed to process information about odors. The olfactory bulb is divided into several layers, and different types of neurons are located in each layer. Therefore, the neurons in the olfactory bulb have been conventionally classified based on the layers in which their cell bodies are located; namely, juxtaglomerular cells in the glomerular layer, tufted cells in the external plexiform layer, mitral cells in the mitral cell layer, and granular cells in the granular cell layer [6].

Historically, the projection neurons of the olfactory bulbs have been classified into two populations, mitral cells and tufted cells. The bodies of these cells are clearly separated in the layers of the olfactory bulb; mitral cells are located in the mitral cell layer, while tufted cells are located in the external plexiform layer. Although mitral and tufted cells share many morphological, biophysical, and molecular characteristics, they differ in body size, projection patterns of their dendrites and axons, and odor responses.

Furthermore, tufted cells are further subdivided based on the relative depth of their bodies in the external plexiform layer. It has been reported that different types of tufted cells have distinct cellular properties and play different roles in the processing of olfactory information. Therefore, mitral and different types of tufted cells are considered as starting points for parallel pathways for processing olfactory information in the brain. Moreover, recent studies show that mitral cells also consist of heterogeneous subpopulations with different cellular properties, despite the fact that the mitral cell layer is a single-cell layer.

The following layers of olfactory neurons are distinguished in the olfactory bulb: the glomerular layer, the olfactory glomerulus, the external reticular layer, the mitral cell layer, the inner reticular layer, and the granular cell layer.

There are several main types of neurons in the olfactory bulb: mitral, tufted, amacrine, periglomerular, and short-axon. Tufted neurons, in turn, are divided into external, middle, and internal, and short-axon neurons are divided into superficial and deep. Tufted and mitral cells act as relay neurons, whereas the role of periglomerular, amacrine, and short-axon neurons (interneurons) is to modulate their neuronal activity [10].

More recently, numerous studies have revealed the heterogeneous nature of each of these cell types, allowing them to be further divided into subclasses based on differences in morphological, molecular, and electrophysiological properties. Moreover, advanced technologies and achievements have led to an increase in the number of studies on cell types other than the conventionally classified ones described above, including short-axon cells and interneurons. Thus, the expanding diversity of cells in the olfactory bulb is now recognized [16].

On the frontal section, in the direction from the surface inward, six layers of the olfactory cortex – concentric zones – are distinguished [1]. First, there is the 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. Then the glomerular layer is isolated. The glomeruli are branches of the axons of the olfactory receptor cells, which are surrounded by dendrites of the periglomerular neurons and illustrate the principle of grouping neuronal elements and synapses into anatomically distinguishable modules. The most probable neurotransmitters of the periglomerular neurons are GABA and dopamine.

The external reticular layer is formed by mitral neuronal dendrites and contains a relatively small number of perikarya of tufted neurons. The presumed neurotransmitter of tufted neurons is dopamine [17].

Then comes the mitral layer, which contains perikarya of mitral neurons. Their axons, together with those of the tufted cells, form the lateral olfactory tract. The transmitter in dendrodendritic synapses, between mitral/tufted cells and interneurons is also glutamate, which acts mainly through NMDA-receptors. The postsynaptic responses of mitral cells, on the background of olfactory axon stimulation, are mediated by two types of ionotropic glutamate receptors. The early rapid response is mediated by activation of AMPA glutamate receptors, whereas NMDA-receptors mediate prolonged excitation. The action of the latter promotes synaptic integration and plasticity, and thus may play an important role in the processing of olfactory information and memory. GABA and dopamine can act as modulators of glutamate release.

The narrow inner reticular layer, practically devoid of cellular elements, is formed by collaterals of processes of tufted, mitral, amacrine, and periglomerular neurons. Short- axon neurons are also present in this layer.

Granular neurons, which form the granular cell layer, are most numerous in the olfactory bulb. The presence of gap junctions between adjacent cells contributes to the synchronization of neuronal activity. It is believed that granular cells perform a lateral inhibition function in the processing of olfactory information; GABA acts as the main neurotransmitter.

The amygdala, one of the best-studied brain structures, integrates heterogeneous inputs from the entire brain and manages multidimensional outputs to control a variety of behaviors central to survival.

The nucleus accumbens (NAc) has been shown to be crucial in mediating pleasure seeking and is also involved in the processing of negative emotions [5], and the molecularly integrated amygdalo-fronto-striatal network coordinates flexible learning and memory [3]. But how amygdalar neural input-output circuits are organized remains unclear [2].

A comparative analysis of the cytarchitectonics of the portions, as well as a comparative study of the neural organization of the cortical amygdaloid nucleus, showed that it was a heterogeneous entity. Anterior cortical nucleus, medial part of posterior cortical nucleus, lateral part of posterior cortical nucleus, posterior cortical nucleus of the hippocampus transitional area are the zones of diffusely located neurons, and periamygdaloid cortex of the rostral level of the central portion and periamygdaloid cortex of the caudal level of the central portion and posterior region of amygdaloid complex are paleocortex.

Superficially, the cortical nuclei contain a molecular layer of small, non-pyramidal neurons, then a dense-cell layer with the bodies of pyramidal neurons, and a multiform layer.

The neurotransmitters of pyramidal neurons of the amygdaloid cortex are serotonin, acetylcholine, aspartate, while GABA is the neurotransmitter of non-pyramidal neurons of the multiform and molecular layers.

The hippocampus is the “flash drive” of the human brain and is often associated with memory consolidation and decision-making, but it is much more complex in structure and function. The hippocampus is a convex elevation of gray matter tissue within the parahippocampal gyrus, inside the inferior temporal horn of the lateral ventricle. It can be described more holistically as a curved sheet of cortex that folds into the medial surface of the temporal lobe [7].

The hippocampus consists of cells densely packed in a band structure that stretch along the medial walls of the lower horns of the lateral ventricles of the brain in an anteroposterior direction. Both parts of the hippocampus are connected by commissural nerve fibers.

The hippocampus is a structure of the limbic system, which is characterized by a complex macro- and microscopic structure [12]. According to the current histological nomenclature, the hippocampus proper has three layers: molecular (stratum moleculare), including supramolecular (substratum eumoleculare), lacunar (substratum lacunosum), and radial (substratum radiatum) sublayers; pyramidal (stratum pyramidale) and marginal (stratum oriens) layers [9].

The organization of the layers is usually the same for all hippocampal fields [15]. The molecular layer contains the bodies of three types of non-pyramidal GABAergic neurons. The supramolecular sublayer contains a bundle of afferent fibers from the entorhinal cortex and nuclei of the medial thalamus, and the lacunar sublayer contains axons coming from the hippocampus.

The pyramidal layer is the main layer of the hippocampus proper. It contains pyramidal, basket, trilaminar neurons and candelabra cells [15].

The narrow, relatively cell-free marginal layer contains basal dendritic branches of pyramidal neurons, as well as bodies and dendritic branches of polymorphic (non-pyramidal) interneurons. Eight types of neurons are distinguished in the hippocampus proper. The main ones, pyramidal, are cholinergic, and the rest are GABAergic.

In addition to pyramidal neurons, the pyramidal layer of the hippocampus contains a heterogeneous population of basket cells of various sizes and shapes. The axons of basket neurons extend transversely from the cell body and form plexuses in the form of baskets that form synapses with the bodies of pyramidal neurons of the hippocampus. The basket neurons receive excitatory impulses from the pyramidal neurons, and they themselves have an inhibitory effect. Pyramidal cells generate recurrent excitation, which is an important mechanism of memory formation.

The hippocampus has three distinct areas: the dentate gyrus, the hippocampus proper, and the subiculum. The dentate gyrus and the hippocampus proper form two C-shaped interconnected rings. Thus, the subiculum is a transitional zone, connecting the hippocampus proper with the dentate gyrus. The parahippocampal gyrus and cingulate sulci are located on the medial surface of the hemispheres, forming a C-shaped ring.

The medial cortex of the temporal lobe includes major subdivisions, such as the hippocampus and entorhinal cortex. The hippocampus (from the anterior end in the amygdala to the posterior end near the corpus callosum) is divided into the head, body, and tail. The head of the hippocampus is separated from the parahippocampal gyrus by the necal sulcus. The surface of the hippocampus is covered with ependymal epithelium inside the ventricular cavity.

There are four subfields of the hippocampus: CA1, CA2, CA3, and CA4. CA3 and CA2 border the hilus of dentate gyrus on both sides. CA3 is the largest in the hippocampus and receives fibers from dentate granular cells on their proximal dendrites. There are about ten layers of cells in the pyramidal cell layer.

The postrhinal cortex (POR) is located near the caudal pole of the rat brain, adjacent to the perirhinal cortex (PER). Originally, the POR was the caudal part of the PER. This area was identified and defined as the POR based on cytoarchitectonic, topographic and functional criteria.

The POR is bordered dorsally by the visual association cortex, ventrally by the medial entorhinal cortex, and medially by the agranular cortex of the retrosplenial cortex (RSP).

Below the hippocampus, in the anterior part of the brain and medial to it, is the dentate gyrus (parahippocampus). It consists of three layers. On the frontal sections, the deepest is the molecular layer (stratum moleculare), then the granular layer (stratum granulare), and the highest is the multimorphic layer (stratum multiforme). These layers contain 9 types of neurons.

The molecular layer contains the bodies of fine basket neurons, whose axons end on the basket cells of the granular layer, and whose dendrites do not leave the molecular layer. The second type of neurons in the molecular layer are candelabra cells. These types of neurons receive impulses via the excitatory perforant pathway, are GABAergic, and have an inhibitory effect on granular neurons. In addition, this layer contains dendrites of the granular, basket, and polymorphic neurons.

There are two types of neurons in the granular layer. Granular neurons have elliptical perikaryons. Between granular and polymorphic neurons are basket cells. Granular neurons use glutamate and dynorphin as neurotransmitters, while basket cells use GABA and parvalbumin. Noteworthy, granular layer neurons continue to differentiate in adult rats [2].

Five types of neurons are identified in the polymorphic layer. The most common of these are mossy neurons. In addition to mossy cells, there are fusiform cells, small polymorphic cells, stellate neurons, and candelabra cells. They receive afferent innervation from mossy fibers, and their axons either form synapses within the polymorphic layer or extend into the hippocampal fields, to its pyramidal neurons. All neurons of the polymorphic layer contain the GABA neurotransmitter and have an inhibitory effect on the pyramidal cells of the hippocampal fields and adjacent neurons of their own layer.

Given the contradictory data on the structure of the superficial layers of the mammalian neocortex, significant differences in the organization of the superficial glial borderline (SGBL) have been identified. It is believed that neuronal cell parameters, such as body surface area and branching frequency, are determined by biological function and information processing. According to recent research, the morphological features of neurons overlap between neocortical and somatosensory areas.

The rat SGBL is represented by specific astrocytes distributed over the cortical surface. In human, astrocytes have translaminar processes that pass through several cortical layers, while in rats such processes are located within a single layer. The differences identified in the structural organization of astrocytes should be taken into account when interpreting the findings of experimental studies conducted in rats and extrapolating them to humans.

The internal structure of the rat neocortex is generally more homogeneous than believed, and differences in cytoarchitectonics and function reflect differences in relationships.

The isocortex of primates and rodents shows a systematic increase in the number of neurons per unit area of the cortical surface, from its rostrolateral to caudomedial border. The magnitude of the gradient in the number and density of neurons is positively correlated with cortical volume. The relative duration of neurogenesis along the same rostrocaudal gradient accounts for a significant part of this change in neuronal number and laminar position, which consists mainly of neurons of layers II-IV.

The neural organization of the isocortex is characterized by the largest variety of neuronal types among other parts of the central nervous system. According to the histological nomenclature, isocortical neurons are divided into projection, commissural, and association neurons. The first ones include large, giant, and inverted pyramidal neurons, branchial and branchless stellate neurons, fusiform neurons, and ovoid neurons. Association neurons include bipolar, horizontal, basket, candelabra, neurogliomorphic, and bunched bifurcated neurons. The isocortical neurons can be divided into three large groups: pyramidal, non-pyramidal, and transient neurons [16].

The proportion of pyramidal neurons in different cortical layers varies greatly, but in general (depending on the cortical area and field) it ranges from 50 to 90 % of cells. Neurotransmitters in axons are aspartate/glutamate, which excite the target cells. A complex of co-mediators and neuropeptides (enkephalin, acetylcholine, etc.) has also been identified.

Most pyramidal cortical neurons have a complex system of dendritic and axonal branches that form a large network of collaterals within the cortex (an important part of the system of intracortical associative

connections). Inverted pyramidal neurons are present in all layers except the first one and have a polygonal perikaryon and short dendrites.

Non-pyramidal neurons are divided into two large groups: 1) spiny stellate neurons; 2) spineless/sparsely spiny stellate neurons. The first group is heterogeneous. Among them there are long-axon spiny stellate neurons, whose axons reach adjacent hemispheric regions, and spiny short-axon neurons, whose axons spread in a localized area of the cortex within a given layer or adjacent cortical layers. Spineless stellate neurons are represented mainly by short-axon intracortical interneurons, which make up 15 to 30 % of the total number of cortical neurons [12].

Recent studies report that primates and carnivores, including several marine mammals, allocate relatively more neural mass to the isocortex and less to multiple limbic and olfactory structures by delaying and expanding cortical neurogenesis. Additionally, and probably independently, neuronal density in the primate cortex is higher than in rodents and other groups, and the allometry of density change in primates with cortical volume is close to one, while the density in the brains of large rodents is reduced compared to smaller ones.

Conclusion

Rats have always been considered one of the most important objects of experimental research, including the study of the cerebral cortex in normal and pathological conditions. The knowledge on the structure and development of various parts of the rat brain provides a fundamental basis for various research projects. However, in order to extrapolate the data obtained in animal experiments to humans, a clear understanding of the structural organization and neurotransmitter nature of different parts of the rat cerebral cortex is necessary. In addition, experimental methods that can only be applied in nonhuman mammals have revealed the pattern of neuronal generation and demonstrated different ways of neuronal migration and neural pathway formation.

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