ONTOGENETIC DEVELOPMENT OF STRUCTURAL ORGANIZATION OF THE OLFACTORY ANALYZER

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Synapses of the olfactory system of the rabbit develop from thin terminal filaments of the axon and range from terminal thickenings of various types of typical endings. Connections between neurons of the olfactory bulbs are established successively with neurons of the prepyriform cortex, nuclei of the amygdala, and the periamygdalar cortex. Connections of centrifugal nerve fibers of the olfactory analyzer are formed from the 2nd week of postnatal development. Data are given showing the order of differentiation of neurons of the olfactory analyzer.

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In this investigation the order of morphological differentiation of neurons and formation of the neuronal organization of the olfactory analyzer during ontogenesis were studied.

EXPERIMENTAL METHOD AND RESULTS

Experiments were performed on rabbits and albino rats of different ages. The degree of morphological differentiation of the neurons was determined from the accumulation of tigroid substance (Nissl's method). Establishment of synaptic connections between neurons was studied in experiments in which the filla olfactoria and olfactory tract were divided. Material was impregnated by the method of Campos and Gliss, revealing degenerating and intact nerve structures.

Experiments in which the filla olfactoria were divided showed that the synaptic connections between processes of the olfactory cells and dendrites of the mitral cells of the olfactory bulbs in rabbits and rats appear on the first days after birth. The synaptic endings consist of thin terminal filaments with no special structure of their nerve endings. They remain the same in adult animals.

Experiments with division of the olfactory tract (16 experiments on rabbits and 48 experiments on rats) showed that synapses of the axons of the mitral cells of the olfactory bulbs with neurons of the prepyriform cortex are established also on the first days after birth. The number of degenerating nerve structures under these conditions increases regularly with age.

Comparison of forms of synaptic endings in experimental and control animals of different ages shows how the synaptic structures acquire their form during individual development. In the early stages of ontogenesis synaptic connections between neurons take place through thin terminal filaments of the axon without any specially constructed endings or with very small terminal thickenings (Fig. 1a). At the first week of development ramifications of the terminal filaments are more frequently seen (Fig. 1b), and terminal thickenings of the axons of different sizes. Toward the end of the first week synaptic endings are found in small numbers, consisting of loops and rings, their number increasing with age (Fig. 1c and d).

Synaptic connections of axons of the mitral cells appear and develop at different times. At various stages of development, synaptic structures of different types can be seen in the same field of vision of the microscope: terminal filaments, terminal thickenings, and definitive loops and rings (Fig. 1e and f). The latter, it is important to note, are endings of thicker nerve fibers.

These results also shed light on the principles of formation of the olfactory analyzer as a single system. Connections between the olfactory bulbs and the various parts of the central representation of the analyzer are not all formed at the same time. Whereas connections of axons of mitral cells with regions of

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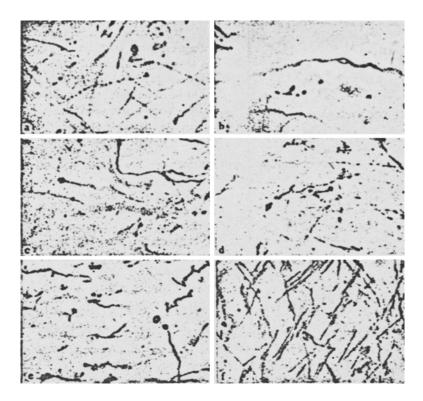


Fig. 1. Establishment of structure of synaptic endings of axons of mitral cells. a) Terminal structures of axons of mitral cells of olfactory bulbs in a rabbit aged 1 day; b) the same in a rabbit aged 3 days; c, d) synaptic endings of different types in the prepyriform cortex of a rabbit aged 7 days; e) the same of a rabbit aged 2 weeks; f) synaptic structures consisting of terminal filaments and a terminal loop in the prepyriform cortex of a rabbit aged 18 days.

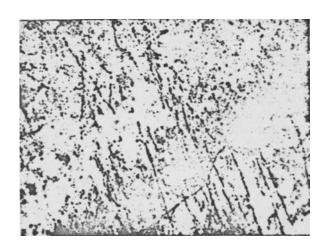


Fig. 2. Degeneration of centrifugal fibers in olfactory bulb of rabbit aged 14 days, after division of olfactory tract.

the prepyriform cortex lying next to the olfactory tracts can be found in animals aged only 1 day, connections with nuclei of the amygdala appear distinctly at the second week, and with the periamygdalar cortex by the 3rd week of postnatal ontogenesis.

The second factor of fundamental importance in the development of the olfactory system is the formation of connections of the centrifugal nerve fibers. As our previous investigation showed [2], these fibers constitute the structural basis of the nervous mechanism defined as the mechanism of central regulation of the inflow of sensory impulses. This investigation showed, in particular, that after division of the olfactory tract in adult animals, mass degeneration of centrifugal fibers and their synaptic endings takes place in the molecular and glomerular layers of the olfactory bulbs.

In the present investigation the experiments with division of the olfactory tract in rabbits and rats at different periods of postnatal ontogenesis showed

that connections between the centrifugal fibers and olfactory bulbs are not observed until the 2nd week of postnatal development. Mass degeneration of the centrifugal fibers is found later still (in rabbits from the end of the 2nd week, in rats at the beginning of the 3rd week of development).

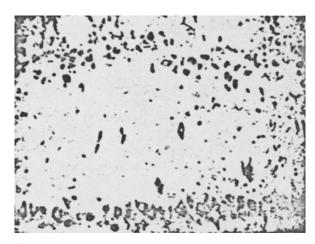


Fig. 3. Differentiation of neurons of olfactory bulb of a rabbit aged 10 days. a) Layer of olfactory glomeruli; b) layer of mitral cells.

It must be particularly emphasized that the centrifugal fibers grow into the olfactory bulbs at different times, and this undoubtedly indicates that they originate from different sources. In some cases it could be seen that fibers entering the olfactory bulbs were grouped into separate bundles (Fig. 2). Some of them terminated in the molecular layer while others reached the glomerular layer.

These results demonstrating differences in the time of formation of connections between neurons in the olfactory analyzer system are in good agreement with data for the order of differentiation of the neurons. Our observations show that the main types of neurons constituting the structure of the olfactory analyzer mature at different times. This principle is well illustrated by the example of the neurons of the olfactory bulb, where the mitral cells differentiate first, and contain tigroid substance in the neonatal period. The last to mature are the periglomerular

cells of the olfactory bulbs, which form connections with the centrifugal nerve fibers. As Fig. 3 shows, these cells in the olfactory bulb of a rabbit aged 10 days are significantly behind the mitral cells in their development. This figure also shows that the nerve cells of the mitral layer (b), like the analogous cells of the glomerular layer (a), differ significantly not only in their staining properties, the number and character of their tigroid granules, but also in their size. Reports that neurons of the olfactory bulbs of puppies mature at different times are given by E. M. Kalinina [1].

The results indicating the order of differentiation of neurons suggest that not only different types of neurons, but neurons possessing similar function, may also differentiate at different times.

Comparison of the results described above with those of comparative morphological investigations [3] shows that the development of structural organization of the olfactory analyzer in phylogenesis and ontogenesis shares certain common features.

The second conclusion of fundamental importance is derived from comparison of our results with those of the physiological investigations mentioned above. It can be concluded from this comparison that ability to form stable conditioned reflexes to odiferous stimuli is directly related to the degree of formation of the system of centrifugal nerve fibers of the olfactory analyzer, constituting a special type of feedback in the structural organization of the nervous system.

LITERATURE CITED

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