# MORPHOLOGY AND PATHOMORPHOLOGY

## COMPARATIVE MORPHOLOGY OF THE INTERNEURONAL SYNAPSES IN THE OLFACTORY ANALYZER

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UDC 611.86-018.81-019

The author has previously shown [9,10] that the neurons concerned in the formation of feedbacks in the system of the olfactory analyzer differentiate and form synapses with other neurons later than the other neurons. Comparison of the results of neuromorphological and physiological investigations [3,4,6,7,11,13] has shown that the ability to perceive and react to olfactory stimuli appears in animals and man before synapses have formed between the centrifugal nerve fibers and the nerve structures of the olfactory bulbs. A conclusion of fundamental importance follows from these comparisons, namely that the formation of the feedback system directly concerned with the mechanisms of central regulation of the inflow of sensory impulses [8] can be directly associated with the development of the ability to form and consolidate conditioned reflexes, and to develop differentiation, i.e., with the capacity for more complex mechanisms of high nervous activity with which the olfactory analyzer is related.

For this reason the investigation of the comparative morphology of the interneuronal synapses in the system of the olfactory analyzer is important. Such information is valuable primarily for determining the principles governing the increasing complexity of the structure and the functional perfection of the olfactory analyzer during evolution. It is also important for the study of the structural bases of conditioned-reflex activity perfected in the process of evolution.

### EXPERIMENTAL METHOD

The morphology of the olfactory bulbs of the following members of a phylogenetic series was studied. Fishes (the mirror carp, the pike, the Black Sea horse mackerel), amphibians (the green frog), reptiles (turtle, the sheltopusik-Ophisaurus apus), birds (cock, pigeon, brown owl — Buteo buteo), and mammals (hedgehog, albino rat, guinea pig, rabbit, cat, dog).

Sagittal tangential sections of the olfactory bulbs were stained by Nissl's method and impregnated with silver by Kampos's method.

To study the interneuronal synapses in the olfactory analyzer, besides experiments on mammals [8,9], experiments were also carried out on lower vertebrates (carp, frog, turtle), in which the olfactory tract was divided.

The experimental material was treated by methods enabling degenerating and intact nerve structures to be detected (by the methods of Kampos, Cajal, and Glees); the material was taken from the animals on the 5th-8th day after the operation, because obvious signs of degeneration of nerve structures in cold-blooded animals are found much later than in mammals.

### EXPERIMENTAL RESULTS

Comparison of the cytoarchitectonic pictures of the olfactory bulb of the members of the phylogenetic series showed first, that the olfactory bulbs of mammals are laminated structures so far as the character of distribution of the nerve cells, especially the mitral cells, is concerned. In the lower vertebrates (fishes, amphibians), and also in birds, the laminated structure of the nerve cells in the olfactory bulbs is much less obvious (Fig. 1, a-c). In this respect the olfactory bulbs of the pike are noteworthy, for their mitral cells show a tendency towards distribution not in a single layer, but in separate groups (Fig. 1a). In other words, in this case we have an intermediate stage between a nuclear and a screened type of structure.

The observations on the nerve elements forming the structural basis of the mechanism of regulation of the inflow of sensory impulses are much more important. This applies above all to the neurons with short axons situated

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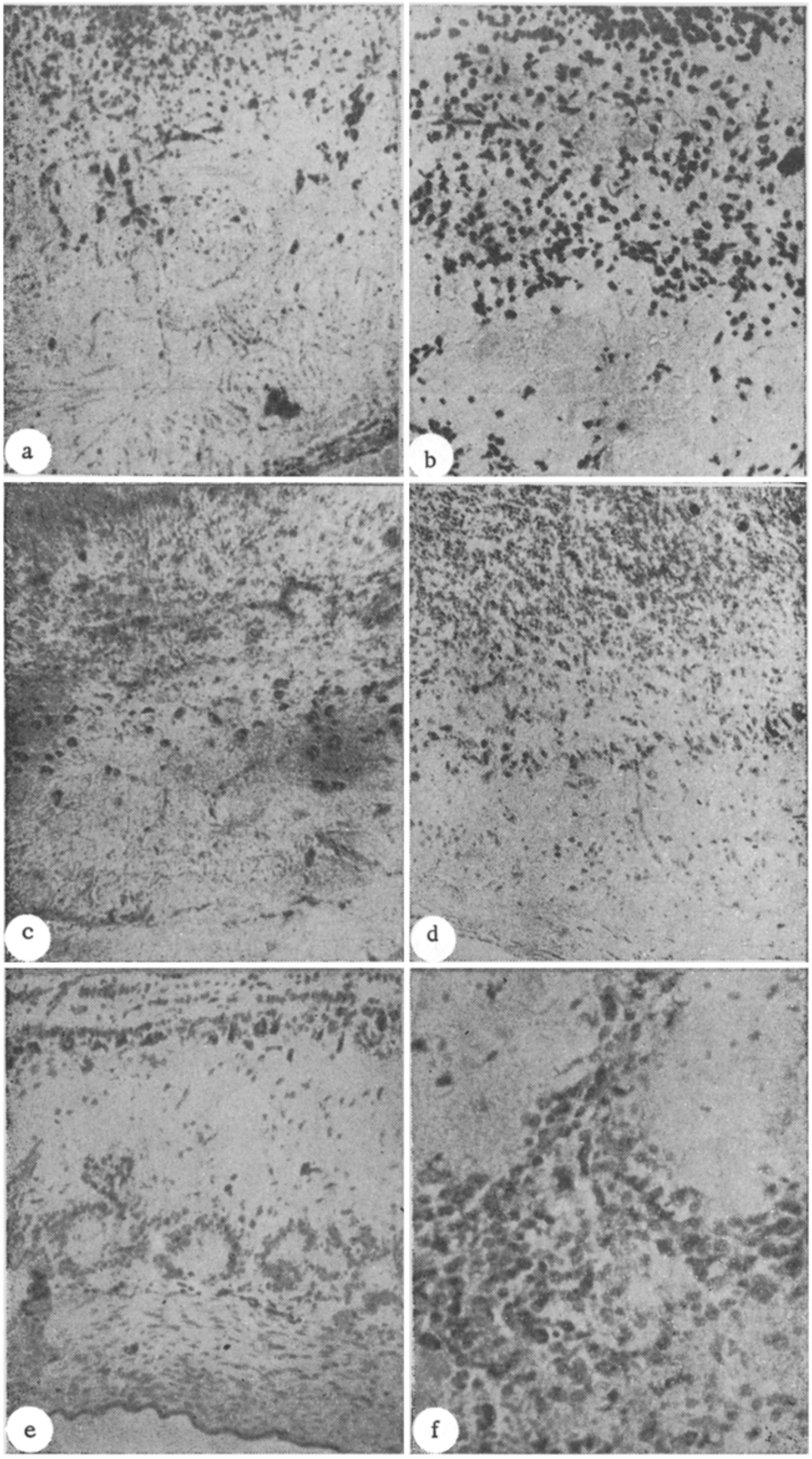



Fig. 1. Olfactory bulbs of the pike (a), frog (b), cock (c), turtle (d), guinea pig (e), and dog (f). Tangential section. Stained by Nissl's method.

in the layer of the olfactory glomeruli in the olfactory bulbs. In their morphological significance, the latter correspond to the connector neurons of the retina (the horizontal and amacrine cells), of the cerebellum (the basket cells), and the spinal cord (Renshaw cells), and to some short-axon neurons in the cerebral cortex [9]. In this case these nerve elements attract attention because it is with these cells that the centrifugal nerve fibers form synapses [8,9]. Consequently, the presence or absence of short-axon neurons of this type may to some extent be used as evidence of the presence and degree of development of the feedback system in a given analyzer.

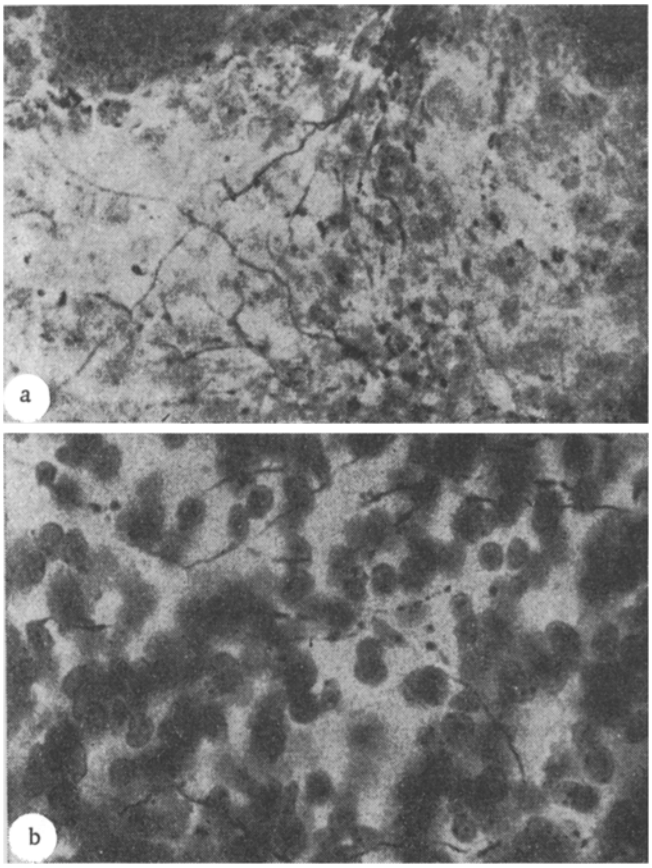

Fig. 2. Degeneration of nerve structures of the system of centrifugal fibers after division of the olfactory tract in the olfactory bulb of the turtle (a) and albino rat (b).

Comparison of the olfactory bulbs of the objects investigated showed that no nerve cells are present in the region of the olfactory glomeruli in the olfactory bulbs of fishes (carp, pike) (Fig. 1a). Characteristically in these animals in the region where the olfactory filaments unite with the dendrites of the mitral cells, no structurally formed olfactory glomeruli are found such as are typically present in the olfactory bulbs of mammals. The same is true of the olfactory bulbs of the frog and birds (Fig. 1b and c). Cells in the region of the olfactory glomeruli appeared in the reptiles (Fig. 1d) and were especially numerous in mammals (Fig. 1e). The fact was noted that their number (like the number of cells of the granular layer of the olfactory bulbs) was directly associated with the importance of the olfactory analyzer in the life of the particular animal. This was illustrated, in particular, by the tangential section (at the level of the olfactory glomeruli) through the olfactory bulb of the dog (Fig. 1f).

Some very remarkable results in this respect were those indicating that the connector neurons appeared at later stages of evolution in other analyzers. For instance, data from the comparative morphology of the nervous system [3], show that no horizontal cells are present in the retina of lower organisms. Another fact, important on its own account from this point of view, is that the amacrine cells are absent in the region of the macula lutea, in contrast to the peripheral portions of the retina, where they are particularly numerous. This is a fact which must interest the neurophysiologists. Comparison of the functional properties of the macula lutea with the properties of the peripheral portions of the retina must reveal the importance of neurons of this type in the physiology of the optic analyzer.

The same evidently applies also to the connector neurons in other parts of the central nervous system. This is shown, in particular, by observations demonstrating that the bodies of the Purkinje cells of the cerebellum in amphibians are not surrounded by ramifying processes of basket cells, unlike those of the cerebellum of mammals [15].

The results obtained in experimental morphological investigations bore a direct relationship to this question of the establishment and formation of feedbacks during the phylogenesis and ontogenesis of the olfactory analyzer.

In eight experiments in which the olfactory tract was divided in the carp, no degeneration of any of the nerve structures was found in the layer of olfactory glomeruli in the olfactory bulbs. Only isolated fragments of nerve fibers were found, with signs of degenerative changes, in the olfactory bulbs of the frog (16 experiments). Only in the olfactory bulbs of the turtle after division of the olfactory tract (8 experiments) were obvious signs of degeneration of the centrifugal nerve fibers observed, although comparatively few were so affected (Fig. 2a). This was particularly clear when a comparison was made with the nerve structures in the olfactory bulbs of mammals degenerating in these conditions. After division of the olfactory tract in albino rats and rabbits, massive degeneration of the centrifugal nerve fibers and of their synaptic endings in the olfactory bulbs was observed (Fig. 2b).

On the comparative plane, it was also noteworthy that the number of degenerating nerve structures in the olfactory bulbs of the rabbit was much greater than in the olfactory bulbs of the rats.

If follows from the fact described above that one of the more important elements of the neuronal organization of the analyzers, namely the feedback system, arises and matures in the process of evolution of the nervous system. Direct proof of this was obtained by electrophysiological investigations. The study of the mechanisms of regulation of the inflow of sensory impulses in the auditory system of mammals and birds, has shown that blocking auditory impulses by the action of optic and olfactory stimuli in the cat is well defined and takes place at different levels of synaptic transmission in the auditory analyzer. In birds, in the same conditions, the flow of auditory impulses is more constant and the activity of other sensory systems has no appreciable effect on the inflow of sensory impulses into the auditory analyzer [1]. Comparison of the role of the centrifugal systems in the activity of the optic analyzer in mammals and amphibians in turn demonstrates the importance of feedback development in the phylogenesis of analyzer systems [5].

According to the views of some investigators [12,14], the mechanism of the central regulation of the inflow of sensory impulses, the structural basis of which is the system of centrifugal nerve fibers, plays an important role in the mechanisms of formation of temporary connections. Consequently, the results obtained during the study of the development of feedbacks in the process of evolution and in the individual development of the analyzer systems provides a closer understanding of the most general principles governing the structural and functional organization of the central nervous system lying at the basis of the mechanisms of higher nervous activity.

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