SENSORY STRUCTURES OF THE PARS INTERMEDIA OF THE PITUITARY

A. A. Voitkevich* and É. L. Soboleva

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Cells of different types were found in the pars intermedia of the pituitary in rats irradiated once, the cytoplasm of which contained specialized microciliary organoids and also structures corresponding to the various stages of their formation (centrioles and their precursors). Irradiation stimulates differentiation of cells possessing sensory microcilia.

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Neurosecretory hypothalamic fibers, detectable in the parenchyma of the pituitary by Gomori's method, are known to run from the posterior lobe into the pars intermedia. Fibers of this type are now generally called peptidergic, in contrast to cholinergic and adrenergic fibers, which are more numerous in the pars intermedia than the former [3]. Information on the composite innervation of the pituitary gland and data on synchronization of its morphological changes with reactions of the neurosecretory cells and neurohypophysis in animals during stress [1, 2] have stimulated investigation of its fine structure.

In the present investigation the electron microscope was used to study sensory structures in the pars intermedia of the pituitary in irradiated rats.

EXPERIMENTAL METHOD AND RESULTS

The pars intermedia of the pituitary of August rats irradiated in a single dose of 600 R from a cobalt source and decapitated 3 h later was studied in the electron microscope. Fixation with OsO_4 and embedding of the fragments of pituitary were carried out by Palade's method, followed by embedding in methacrylate. Ultrathin sections were studied in the JEM-5y electron microscope.

During the first few hours after single irradiation, differentiation of the cells of the pars intermedia took place much more intensively, some of them forming a structure sui generis. These were intermediate cells containing special organoids or microcilia (Fig. 1a). As well as these cells with characteristic features of sensory function there were less highly differentiated cells, the cytoplasm of which exhibited intermediate stages of formation of the special microcilia. Microcilia in the cells of the pars intermedia as in many other typical sensory cells, possess the characteristic formula $9 \times 2 + 2$, i.e., they consisted of 9 pairs of peripheral and 2 unpaired central fibrils.

Organoids of this type were localized in the cytoplasm of light and dark intermediate cells. The cytoplasm of the latter was filled with electron-dense dust-like granules, an area of which is illustrated in Fig. 1a. The so-called dark cells were subdivided into two categories. The first included cells with a long, dense nucleus, an extremely drawn out cytoplasm, and polymorphic processes, in contact with similar structures. The second category included dark cells of irregular, polygonal shape, with a well developed cytoplasm. Their matrix was filled with numerous free-lying microgranules, a partially reduced Golgi complex, endoplasmic membranes, and fully formed cilia. Cells of this type lay next to the residual cavity of the pituitary and were the principal components of its lining. The microcilia faced the pituitary cavity, into which solid processes of cytoplasm frequently projected deeply along with them. These microcilia had atypical definitive architectonics, and no structures characteristic of the intermediate stages of their formation were observed in the cytoplasm. However, intermediate structures could be observed in the cytoplasm of extremely hypertrophied, pale cells. These consisted of vesicles and of separate fragments of granular

*Corresponding Member, Academy of Medical Sciences of the USSR.

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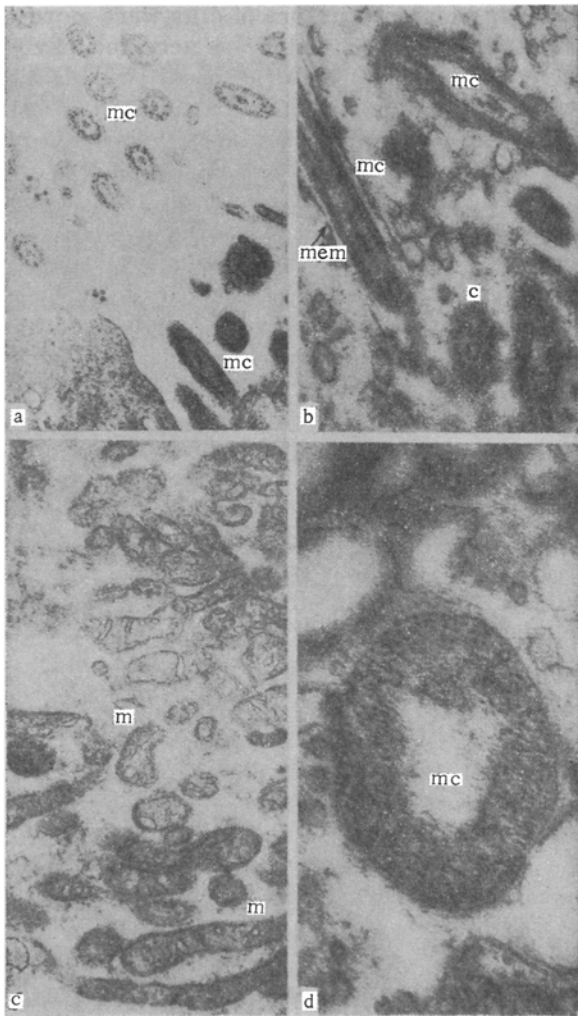

Fig. 1. Pars intermedia of the pituitary of an irradiated rat. a) Microcilia (mc) of intermediate cells with microgranular cytoplasm, bounding residual cavity of pituitary (18,000 ×); b) centrioles (c) and microcilia (mc) at different stages of formation; mem) membrane of microcilia (18,000 ×); c) numerous long and round mitochondria in an intermediate cell (18,000 ×); d) transverse section through developing microcilium (mc) with well marked fibrillary structure and electron-transparent center (65,000 ×).

and agranular endoplasmic reticulum, lying in different directions and forming a few tubules and cysterns. The cytoplasm of some of these cells contained numerous mitrochondria and also structures which were precursors of the developing cilia (Fig. 2).

Not all cells of the pars intermedia reacted to irradiation by characteristic swelling of the mitochondria and partial reduction of their cristae. The mitochondria illustrated in Fig. 1c show signs of defragmentation of cristae with transformation into long vesicles. The extremely great increase in number of mitochondria in some epithelial cells of the pars intermedia may perhaps be the result of division of these structures. The mitochondria increased considerably in length and gave off smaller, round structures by a process of budding (Fig. 1c). Besides mitochondria, the pale hypertrophied cells frequently contained round structures possessing a microgranular matrix, the tiny granules being located more frequently around the periphery of the circular structure in one or several rows. The central part could be denser, but not granular or electron-transparent (Fig. 1d; Fig. 2). Finally, pale cells with cytoplasm filled with typical centrioles and cilia of different shapes as well as the structures described previously, were found in the parenchyma of the gland. The centrioles on longitudinal section consisted of a system of densely arranged fibrils. In transverse section the centriole or centrosome was formed of 9 groups of tubules, each 150-200 Å in diameter, arranged around the circumference. Ciliary vesicles were also present, and as the cilium grew they surrounded it with a characteristic membrane (Fig. 1b).

Serial comparisons of the structures observed revealed a definite rule in the sequence of stages of formation of microcilia in the epithelial cells of the pars intermedia of the rat pituitary. Closely connected with the centricles were round structures, whose matrix was filled with electron-dense microgranular substance. In some cases, these structures contained on electron-transparent center, while the dense granules or fibrils were displaced toward the periphery, thus giving this structure some resemblance to the centricle. Such structures were regarded as precursors of cilia, i.e., as a definite stage in their formation, when the microgranular substance on transverse section or the system of fibrils on longitudinal section had not yet the characteristic tubules of the centricles. The basal part of the cilium, and hence the cilium as a whole, grew from the latter. A row of vesicles, known as ciliary vesicles, lie above the growing cilium, creating a distinctive channel along which the cilium can grow from the region of the perikaryon toward the cell surface. These confluent vesicles lined the path of the growing microcilium and were gradually converted into its membrane. The data showing the formation of cilia in cells of the pars intermedia are in agreement with corresponding observations of the formation of microcilia in fibroblasts in vitro [4]. The gradual conversion of the centriole into a cilium with its characteristic structure was observed under these conditions. In the cells of the pars intermedia, on the other hand, a very intensive formation of cilia were observed in the presence of large collections of centrioles and their precursors and derivatives in the cytoplasm. Whether these were formed in the cells de novo or whether they were the result of autoreproduction is not known.

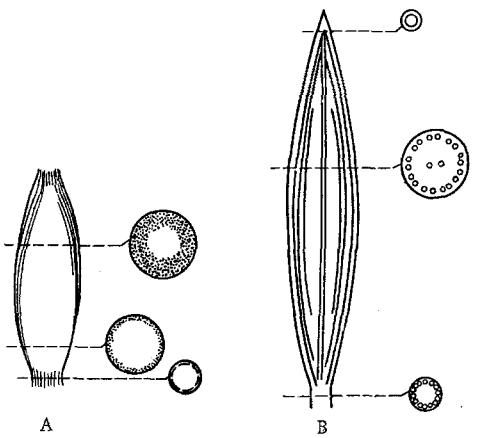

Fig. 2. Diagram showing a microcilium and its transverse sections at different stages of formation. a) Initial stage of cilium formation; b) fully formed cilium.

When comparing serial sections through the intermeidate cells and picking out those in which precursors of cilia were more numerous, the possibility of their division was accepted. Evidence of this is given by the close contact of these structures with each other, signs of development of a central constriction, and the appearance of pinhead forms. Another directly connected factor could be the sharp increase in the number of mitochondria in the cells, and fragmentation of the mitochondria, preceded by a considerable increase in their length. These phenomena in other cells were synchronized with an increase in the number of precursors of cilia and an accompanying decrease in the number of mitochondria. Possibly in the course of division the mitochondria gave off round bud-like structures which, in turn, divided, passed through the centriole stage, and were transformed into a microcilium. However, we have no solid evidence to compel acceptance of this explanation of the sharp increase in number of centrioles and of their precursors in the cells. The abundance of mitochondria may perhaps ensure a definite level of energy supplied to the cell when forming this large number of additional specialized organoids in its cytoplasm. However, centrioles and their precursors are unquestionably an original structure in the process of formation of microcilia in cells of the pars intermedia.

We consider that irradiation stimulates the formation of specialized organoids or metaplasmatic structures, taking the form of microcilia in the cells of the pars intermedia. This does not mean that such structures are absent in the pituitary of intact animals. We have observed cilia in the intercellular spaces of the parenchyma of the pituitary in intact animals. The presence of cilia with the formula $9 \times 2+2$ among cells of the pars intermedia has been observed in the rat and cat by Bargmann [3] and Ziegler [6]. Wheatley [5] described two cilia, but with the formula $9+0$, in cells of the rat adenohypophysis. Stimulation of morphological and functional activity of the gland, in the direction of the formation of sensory elements and their discharge into the residual cavity of the pituitary, has not yet been described.

Specialized organs such as microcilia are also characteristic of typical receptor cells. The fact that large numbers of microcilia are present in cells of the pars intermedia of the pituitary enables their physiological role to be reassessed. Microcilia localized between the cells of the pars intermedia, and especially those facing the residual cavity of the pituitary, may be chemoreceptors, receiving information from the reservoir of hormone products of the adenohypophysis. The presence of terminals of various nerve fibers in the parenchyma of the pars intermedia [3] does not rule out the possibility of transmission of nervous impulses in a centripetal direction.

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