Comparison of the localization of monoamines and monoamine oxidase in the rabbit hippocampus shows that most pyramidal and all granular neurons contain no monoamines. Up to 1% of pyramidal and about 3% of polymorphic neurons are noradrenergic, and some of the latter are basket cells. Their terminals, containing both noradrenalin and monoamine oxidase, are in contact with the bodies and processes of the pyramidal and granular neurons. Single serotoninergic polymorphic neurons are found in sectors H1 and H2 of the cornu ammonis and in sector H4 of the fascia dentata of the hippocampus; they have few terminals. Noradrenergic afferents enter the cornu ammonis in the external bundle of the alveus and in the septal tract, which runs along the inner surface of the fimbria. Noradrenergic terminal plexuses surround the bodies of the pyramidal cells and are concentrated at the level of the apical dendrites of the pyramids and at the base of the granular neurons of the fascia dentata. Convergence of noradrenergic and serotoninergic terminals is found on some pyramidal, granular, and polymorphic neurons. The high concentration of serotonin in the hippocampus despite the minimal number of serotoninergic neurons can be explained by the large number of serotonin-containing stellate cells of nonneural nature. They are localized on groups of pyramidal neurons in sectors H1 and H2 and also on blood vessels. Individual variations are found in the number of serotonin-containing neurons in the hippocampus and in the number and distribution of serotonin-containing stellate cells.

INTRODUCTION

Information on the monoamine content in the hippocampus is contradictory. Enzymes connected with metabolism of the biogenic amines — catechol-O-methyltransferase [6], monoamine oxidase, 5-GTP-decarboxylase [12] — have been detected by biochemical methods. So far as the biogenic amines themselves are concerned, small quantities of noradrenalin [8, 9, 23, 24] and dopamine [9, 8] and a high concentration of serotonin [28, 12] have been found in the hippocampus. A study of the localization of monoamines by Falck's histochemical method has yielded contradictory results even in the hands of the same workers studying the same object.

Considerable species differences also have been found [11]. Whereas serotonin is found in axo-somatic terminals on pyramidal neurons in the cat hippocampus [18], in the rat hippocampus specific luminescence of serotonin [27] was observed in the pyramidal neurons themselves. Some workers [27] claim that pyramidal neurons contain serotonin or serotonin and dopamine at the same time. Other investigators [11, 17, 22] disagree for they indentified noradrenalin-containing fibers and terminals in the plexuses of the radiatum layer and at the base of the granular neurons as well as serotonin-containing terminals in the rat hippocampus. A similar localization of noradrenalin has also been demonstrated by autoradiography [23]: radioactive noradrenalin and dopamine, injected into rats, accumulated at the level of the radiatum layer, i.e., in the region containing structures synthesizing noradrenalin. The publications listed above contain all that is known about the content of monoamines in the hippocampus.

Fig. 1. Distribution of NE-afferent fibers and monoamine-containing neurons: A) afferents entering in the alveus (groups 1, 2, 3), B) entering in the septal tract. Black ovals and lozenges denote monoamine-containing neurons in rabbit hippocampus, dots indicate zones of concentration of serotonin-containing stellate cells, wavy line shows NA-containing plexuses.

EXPERIMENTAL METHOD

The concentration of monoamines in the hippocampus of adult intact rabbits was determined by Falck's histochemical luminescence method [20, 21]. To correct the possible errors of the method monoamine oxidase was detected in a parallel series of sections. The control of the specificity of the reaction suggested by Falck was used: preliminary injection of reserpine or the monoamine oxidase inhibitor, iproniazid. The specimens were examined with the ML-2 luminescence microscope using filters FS-1, SS-15, ZhS-18, and ZhS-19.

RESULTS

As a result of the specific green luminescence of noradrenalin (NA) and the intensive reaction for monoamine oxidase (MAO) in the transverse sections through the hippocampus, the conducting tracts and nerve plexuses containing noradrenalin were revealed. A bundle of noradrenergic (NE) fibers running to the cornu ammonis from the subiculum was traced throughout the extent of the lower third of the alveus layer (Fig. 1A). This bundle gradually splits into three groups of fibers: the first group of NE-fibers at the level of sector H1 turns toward the pyramidal cells, cuts across the alveus and the stratum oriens, runs as bundles of 3-15 fibers between the pyramidal neurons and penetrates into the stratum radiatum and stratum lacunosum, after which they rejoin and then branch again in the plexuses of the neuropil of the molecular layer in sector H1 of the cornu ammonis. The second group of NE-fibers of this bundle reaches the entrance to the fascia dentata where it radiates fanwise and ramifies in the nucleus proprius of the fascia dentata. The third group of NE-fibers from the subiculum traverses the cornu ammonis en passant, enters the outer of the fimbria, and leaves the hippocampus.

A bundle of NE-fibers from the fimbria also enters the hippocampus (Fig. 1B) and it runs in the composition of the septal tract along the inner surface of the cornu ammonis, entering the fascia dentata and becoming lost in the neuropil of sectors H4 and H5. Some of these fibers enter the molecular layer. This topography of distribution of NA-containing afferents is found in all parts of the rabbit hippocampus. The reaction for MAO showed that all the NE-pathways described above entering the hippocampus consist of myelinated fibers of medium and thin caliber.

Localization of Monoamines in Neurons. Most of the pyramidal, granular, and polymorphic hippocampal neurons are luminescent. Correspondingly, the reaction for MAO is minimal or completely absent in all neuron populations, so that the "empty" cell bodies stand out clearly through their bright luminescence (Fig. 2A-C) and the reaction for the enzyme in the surrounding NE-terminal plexuses (Fig. 3A, B). Only solitary neurons - about 1% of pyramidal and not more than 3% of polymorphic - give bright green luminescence (Figs. 1 and 2D) and a strong reaction for MAO (Fig. 3C). Luminescence of NA in the perikaryon and processes of these neurons is uneven. It is particularly bright around the nuclei, gradually