TYPES OF SYNAPSES IN THE CEREBRAL AND CEREBELLAR CORTEX OF THE ALBINO RAT

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Due to their higher ranks in the order of reflex hierachy, the cerebral and cerebellar *cortex* exhibit those basic properties of nervous tissue as divergence and convergence of impulses in a much higher degree than the peripheral and the autonomic nervous systems do. The ultrastructural mechanisms, underlying these functional characteristics are, however, only partly understood. We decided to study the electron microscopic synaptology of the *cortex* in the albino rat since this animal is commonly used in biological and medical experimentation on the central nervous system. The areas examined were the parietal *cortex* and the cerebellar *cortex;* in this respect, recent studies performed on the cat cerebellar *cortex* [7] were of major help in orientation and identification of cellular, axonal and dendritic elements.

Material and Methods

14 albino rats (150–180 g body weight) were used in these experiments. Samples from the parietal and the cerebellar *cortex* (Lob. VI) were excised under hexobarbital *anesthesia,* fixed in the Millonig osmic acid solution [9] and embedded, after alcohol dehyration, in Araldite (Fluka). Ultrathin sections were obtained on an LKB Ultrotome, using glass knifes. Sections were collected on 150–300 mesh grids and stained with lead citrate [10]. Inspection and photography of the preparations has been performed on a Tesla 242 D Type table electron microscope.*

Results

The *stratum zonale* of the parietal *cortex* consists of an elaborate network of ascending apical dendrites of pyramidal cells, axons and dendrites of the Cajal-type horizontal cells and the axons of the Martinotti cells. The most common type of synaptic junction is the axo-dendritic synapse, characterized by an accumulation of synaptic vesicles in the pre-synaptic axoplasm and a thickening of the post-synaptic (dendritic) membrane. Divergence of neural impulses is established by bifurcating axonal branches, synaptizing with two or more dendrites. On the other hand, quite often could be found an arrangement, obviously furnishing the structural basis for convergence, consisting of more than one praesynaptic endings

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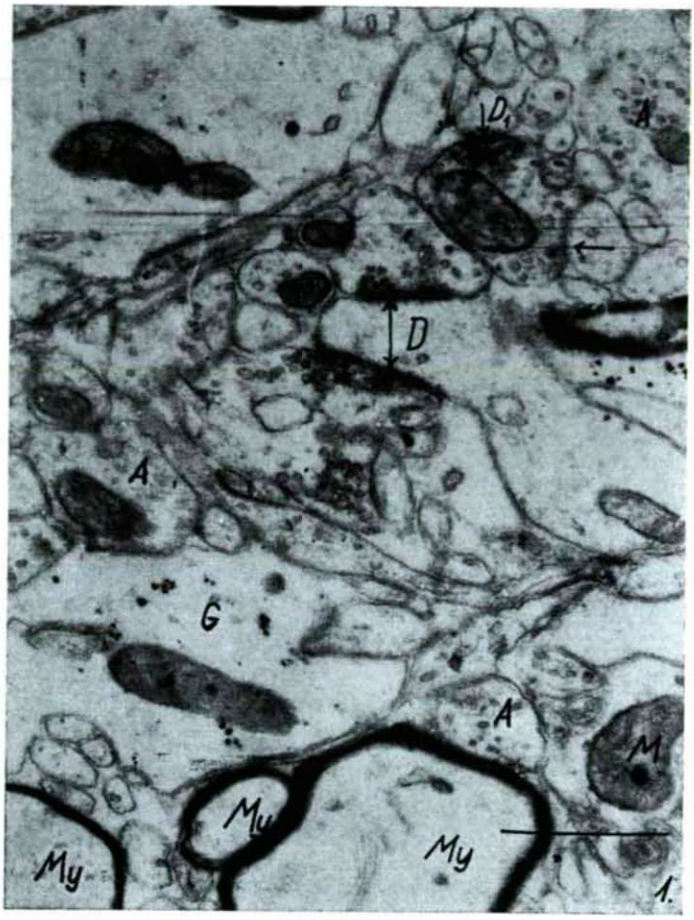

Fig. 1. Parietal *cortex* of the rat. Convergence of axonal impulses. Synapses belong to the GRAY I type: aggregation of synaptic vesicles in the pre-synaptic axoplasm, thickening of the postsynaptic membrane. Two axons sandwich the large dendrite (D); other dendrite (D_1) receives a single axonal junction (arrow). Numerous axonal profiles, filler with vesicles, without establishing synaptic contacts (A). *Mitochondria* (M) have a characteristic appearance of *cristae*. MY: myelinated nerve fibers (probably MARTINOTTI axons). G: glial cell process.

upon one and the same dendritic branch. Less often could dendritic spines be observed; lacking, however, the so- called *„spine apparatus"* deseribed by GRAY and GUILLERY in the visual *cortex* (3). Axo-axonal junctions could sometimes be observed at the axonal „neck", right before the axon itself gave off synaptic terminations to dendrites.

In the molecular layer of the cerebellar *cortex,* the most conspicuous type of junctions is the *„crossing over"* synapse between parallel axons (originating from the bifurcated branches of granule cell neurites) and the tertiary dendrites (*„spiny*

branchlets") of PURKINJE cells. Dendritic spines often invaginate into parallel axons, right the same way as described by HÁMORI and SZENTÁGOTHAI (7) in the cat. Climbing fibers could not be identified with certainty; however, vesicular type axonal profiles not unfrequently synaptize with large primary PURKINJE dendrites. These vesicular profiles probably correspond to axonal recurrents from PURKINJE neurites. In the granular layer of the cerebellar *cortex*, the well – known structure of the cerebellar *glomeruli* could be identified. The expanded mossy fiber endings synaptize with granule cell dendrites, intermingled with GOLGI axon terminals.

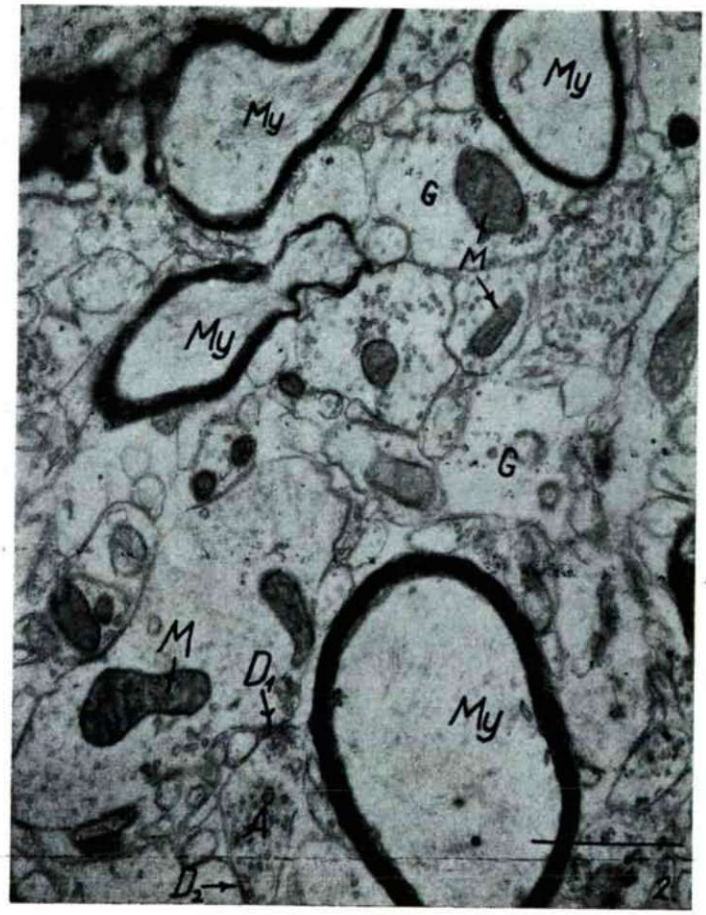

Fig. **2.** Parietal *cortex* of the rat. Divergence of axonal impulses. A: small axon, giving off two synapses to dendrites (D_1 and D_2). Synapses designated by arrows. M: *Mitochondria*. MY: myelinated nerve fibers. G: glial cell.

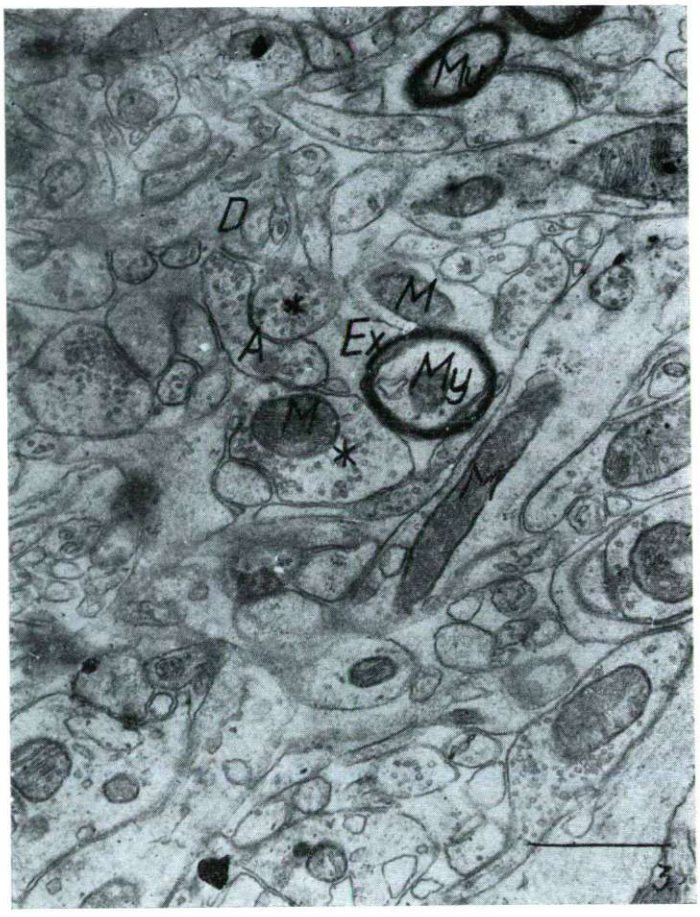

Fig. 3. Presynaptic inhibition in the parietal *cortex*. The small axon (A) synaptizing with a dendrite (D) is cuffed by two other axons at the neck before establishing synaptic contact with the dendrite. The inhibitory axons are designated by asterisks. M: *mitochondria;* My: myelinated fibers. Note the extracellular space, expanded around the inhibitory synapse (Ex).

Discussion

The arrangement of synaptic apparatuses in the rat *cortex* is essentially the same as that observed in other mammals. It should be emphasized, however, that even though the majority of the synapses corresponded to the GRAY I type (assymmetric thickening at the post-synaptic side) the intersynaptic perforated membrane, described by GRAY in his publications, (11) could only very unfrequenty be observed. Special attention should be paid to the axo-axonal junctions at the synaptic *„neck"*, which, in all probability, is designed for presynaptic inhibition (5). The lack of spine apparatuses in the parietal *cortex* renders GRAY's idea on the possible role

of the spine apparatus in the function of cellular memory (6) quite improbable. The fact that not only parieto-cortical synapses, but also the junctions between parallel exons and PURKINJE dendritic spines are of the vesicular (and not of the filamentar)type makes GRAY's suggestion on the liht microscopic visibility of filamentous axons versus non-filamentous ones (3) extremely hard to understand, since the latter junctions are well-known ever since the beginning of the era of light microscopic silver impregnation methods.

Finally, the presence of synaptic vesicles in synapses of the parietal *cortex* as well as in those in the molecular layer of the *cerebellum* should be discussed. It is one of the histologists' common places that presence of synaptic vesicles equals

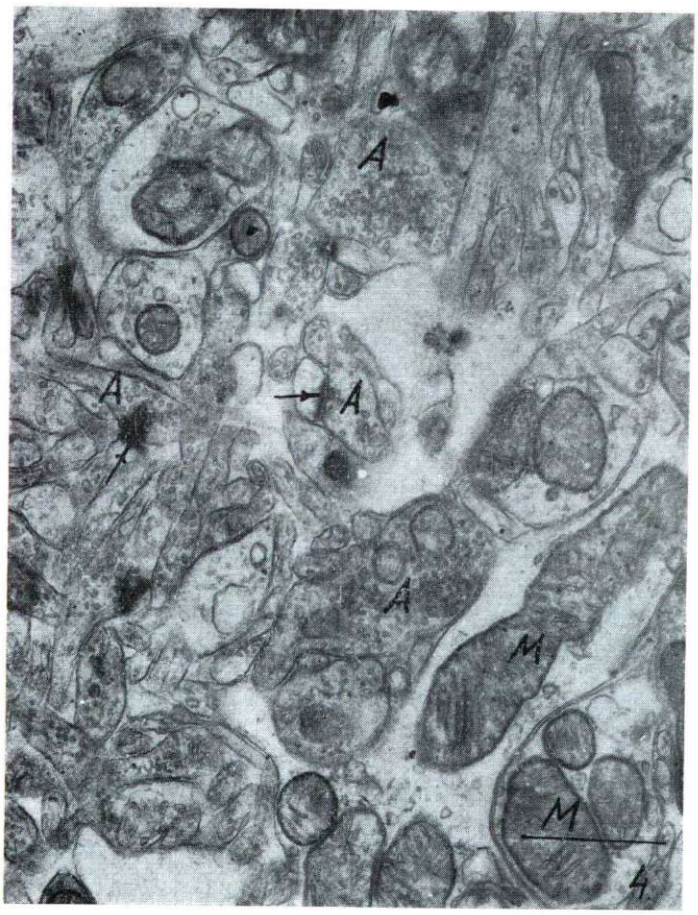

Fig. 4. Axodendritic synapses in the caudate *nucleus*. Axons, filled with vesicles (A) synapse with dendritic branches (arrows). Note the huge *mitochondria* (M) characterizing this area. Mitochondrial *cristae* are clearly visible.

Fig. 5. Molecular layer of the cerebellar *cortex*. Cross section of a tertialy PURKINJE dendrite („*spiny branchlet*", spb), embedded into glial envelope. Arrows point at the tips of the spines, that, however, are devoid of synaptic contacts. p: parallel fibers, cut tangentially. A: axonal profiles, probably corresponding to transversely cut parallel fibers.

the presence of acetylcholine. However, when using histochemical techniques, no acetylcholinesterase activity can be found either in the parietal *cortex* or in the molecular layer of the *cerebellum* (acetylcholinesterase activity is limited to the granular layer of the *cerebellum* amongst the areas discussed here (1, 8). Thus, if one assumes that synaptic vesicles actually correspond to storage sites of acetylcholine, one has to suppose that the enzymic breakdown of the transmitter is exerted in the parietal *cortex* and in the molecular layer by an enzyme differing from acetylcholinesesterase. In view of our present finding (2) of a copper-sensitive arylesterase, capable of hydrolyzing acetylcholine, in the parietal *cortex* and in the molecular layer suggests that the hydrolysis of acetylcholine is actually exerted here by an enzyme not identical with acetylcholinesterase.

Fig. 6. Molecular layer of the cerebellar *cortex*. A large axonal profile (A), probably a recurrent collateral of the PURKINJE neurite, in synaptic conttact with a primary PURKINJE dendrite (PD). p: parallel fibers. M. *mitochondria*. G: glial cell. Inv: invaginated spine of a tertiary PURKINJE dendrite, PD_2, PD_3: Secondary and tertiary PURKINJE dendritis.

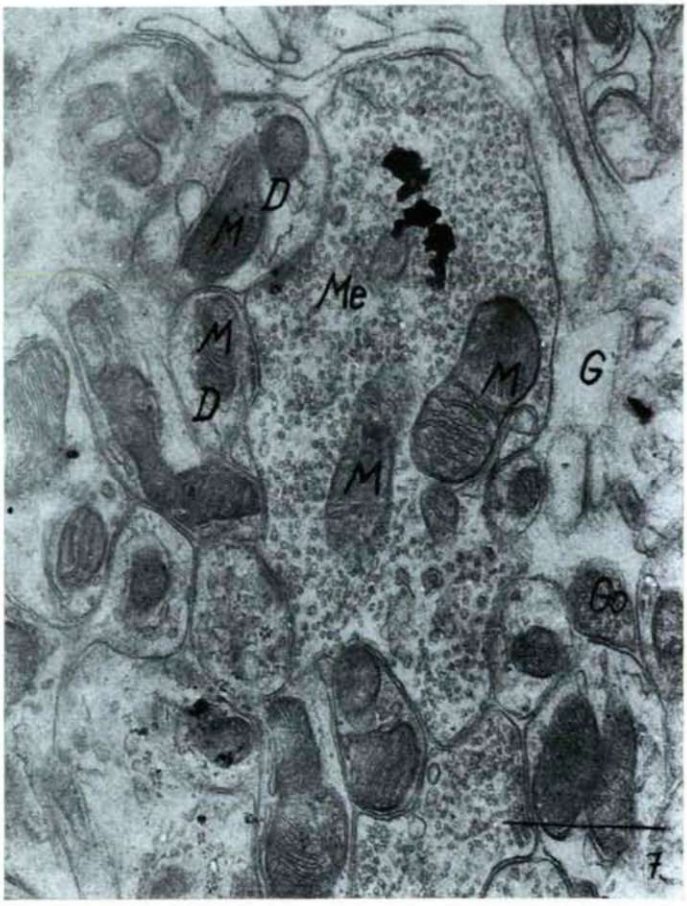

Fig. 7. Granular layer of the cerebellar *cortex*. A large single mossy fiber ending (Me) in the middle of the picture, synaptizing with dendritic protrusions of granule cells. (D). Large *mitochondria*, equipped with conspicuous *cristae*, are present (M). Note the glial envelope (G) around the mossy ending, and the small profile of a GOLGI axon (Go).

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