Anat. Embryol. 149, 251—258 (1976)
© by Springer-Verlag 1976

Course and Distribution of Apical Dendrites of Layer V Pyramids in the Barrel Field and Area Parietalis of the Mouse*

Klaus Detzer

Anatomisches Institut der Universität Bonn

Received December 23, 1975

Summary. In the mouse cerebral cortex the course and distribution of apical dendrites of layer V pyramids are investigated. Striking differences are found between the area parietalis and the neighbouring regio temporalis I and II, i.e. the barrel field region of Woolsey and van der Loos (1970). Whereas in area parietalis dendrites and dendritic bundles run straight through layer IV, in the barrel field their course is deflected by the barrels. It is shown that the dendrites bend beneath the bottom of the barrels so as to enter the spaces between the sides. These findings in the mouse are at variance with the results obtained by Feldman and Peters (1974) in the rat.

Key words: Mouse — Cerebral cortex — Dendritic bundles-Barrel field.

Introduction

In many areas of the cerebral cortex of rat, mouse, rabbit and other species, apical dendrites of layer V pyramids approach each other so as to form vertical bundles in layer IV. There are regional differences in the compositon of these bundles and they can be regarded as an architectonic characteristic for certain regions of the cortex (cf. Fleischhauer and Detzer, 1974). In some species another characteristical architectonic pattern has been found in the form of the so-called barrel field which in rodents is restricted to that region of the somatosensory cortex in which the vibrissae are represented (cf. Woolsey, Welker and Schwartz, 1975).

Recently, Feldman and Peters (1974) have studied the course and distribution of dendritic bundles in the barrel field of the rat. The authors came to the conclusion that in the rat there is no topographical relationship between barrels and dendritic bundles. With respect to some important points our own findings in the mouse differ from the results obtained by Feldman and Peters (1974). Therefore, the findings obtained in the barrel field and in the neighbouring area parietalis of the mouse will be presented in detail.

Material and Methods

Male and female white mice of the strain NM/Han were subjected to thoracotomy in pentobarbitone sodium anaesthesia, and after access had been gained to the right ventricle were exsanguinated with Periston (Bayer) and subsequently perfusion fixed either with a

* Supported by a grant of the Deutsche Forschungsgemeinschaft (F1 26/13)

10% formalin solution or with Bouin's fluid. To avoid postmortem cellular changes the brains were not removed until 4–5 h after fixation (cf. Cammermeyer, 1962; Peters, 1972).

For animals earmarked for preparation of *thick celloidin* sections, formalin was used as the fixative. After dissection, the brains were postfixed for 12 hrs, dehydrated through an alcohol series and embedded in Ceducol (Merck, Darmstadt). The specimes were stained by joggling in an alcohol solution of toluidin blue at a temperature of 70° C.

The animals assigned for preparation of *paraffin sections* were fixed with Bouin's fluid. After dissection, the brains were postfixed in the same solution for 12 h, dehydrated and embedded in paraffin. In most brains, the region of the barrel field was sectioned either frontally or tangentially in the plane recommended by Woolsey and van der Loos (1970). Series of 8, 10, 15 and 20 μm were cut. In two brains, frontal and tangential sections of 8, 16 and 24 μm in alteration were made, the sections being throught singly onto slides.

The sections were stained with haematoxylin-eosin or with Luxol fast blue and counterstained with PAS, the latter method being particularly well suited for studying dendritic bundles (Fleischhauer, Petsche and Wittkowski, 1972); a further series was silver impregnated according to Bodian in a modification of Luna (1964).

Semi-diagrammatic figures were produced as follows: From enlargements of the original photographs, all distinguishable dendrites were traced onto tracing paper. The resulting diagrams were photographed and reduced to the size of the originals.

The terminology used is that of Rose (1929) and Woolsey and van der Loos (1970).

Results

Area Parietalis

In 8 μm thick Klüver-PAS stained frontal sections through the area parietalis of the mouse, dendritic bundles can be identified. They course through the cortical layer IV in a direction perpendicular to the surface of the pia. As shown in Figures 1a and b the pattern resembles that observed in other species by Peters and Walsh (1972, rat), Fleischhauer, Petsche and Wittkowski (1972, rabbit) and Fleischhauer (1974, cat). From Figure 1a is further discernible that most of the dendrites arborize at the border between layer IV and III. In layer III or II the branches may converge to again form bundles. In Figure 1b it is seen that the distances between the bundles are fairly regular. Each bundle is formed by several apical dendrites originating from pyramidal cells in layer V and is accompanied by dendrites of layer IV cells. The dendrites arising from layer IV cells have a distinctly smaller diameter than the dendrites coming from layer V and arise from cells that in many cases are situated immediately next to the bundle. The cells in question are best seen in tangential sections through layer IV such as visualized in Figure 1b. They are surrounded by the dendrites of a bundle.

Regio Temporalis

In thick celloidin sections through layer IV of the regio temporalis I and II, Woolsey and van der Loos (1970) detected the typical cell aggregates called barrels. In Figure 2 the structure of the barrels is shown in a 100 μm thick tangential section. However, while such celloidin sections are good for demonstrating barrels, they are not suitable for visualizing dendrites and dendritic bundles. Fleischhauer, Petsche and Wittkowski (1972) showed that for this purpose Klüver-PAS stained paraffin sections of only 8 μm thickness are particularly suitable. But in histological sections of this thickness barrels are no longer recognizable.

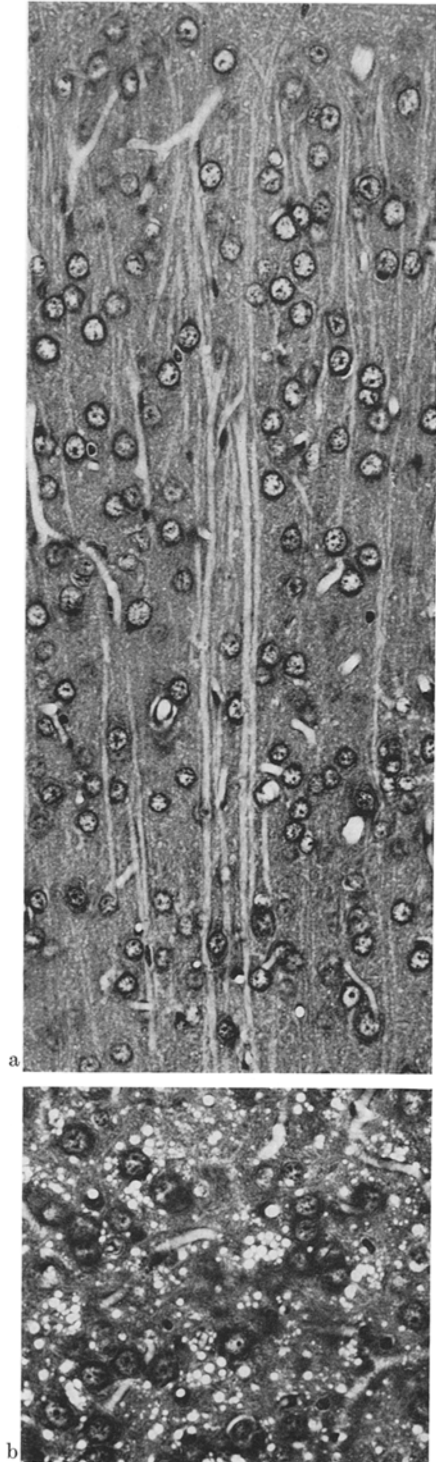

Fig. 1a and b. Frontal (a) and tangential (b) sections through area parietalis of the mouse. In (a) a bundle of apical dendrites is seen to run straight through layer IV and to branch beneath the border with layer III. In (b) the cross sectioned bundles are seen to consist of cell processes with different diameters. 12 μm paraffin section. Klüver-PAS, × 250

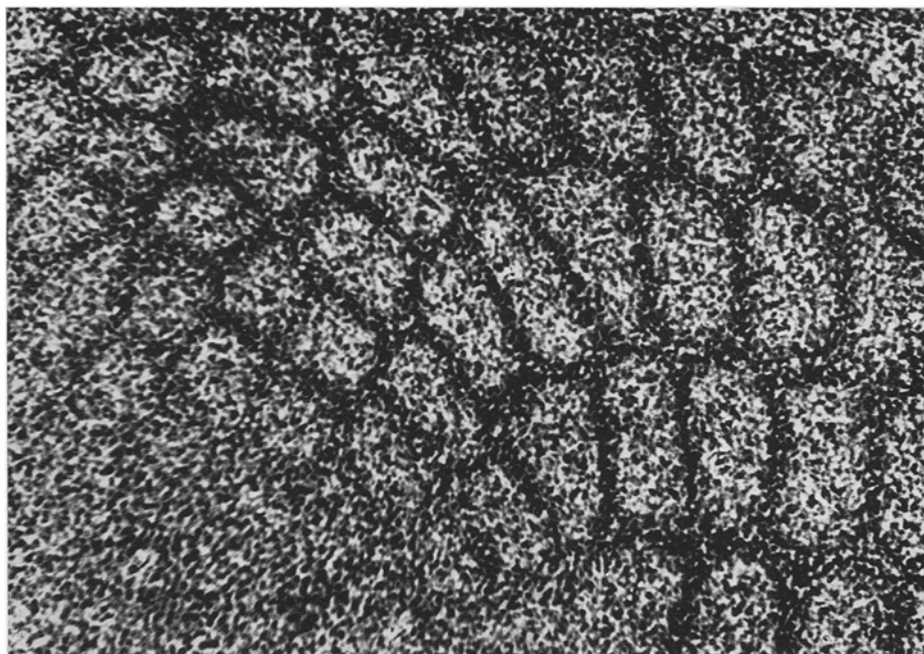

Fig. 2. Tangential section through layer IV in regio temporalis I and II of the mouse to show the honeycomb arrangement of the nerve cells forming the barrels. 100 μm celloidin section, toluidin blue, × 250

To investigate the relationship between barrels and, if present, dendritic bundles, it was therefore necessary to compare paraffin sections of different thickness and to find out whether there is a thickness of sectioning which permits studying barrels as well as dendrites in one section.

When comparing thick celloidin sections with paraffin sections of different thickness such as shown in Figures 3a–c, the following is noted: The outer boundaries of the barrels, which in thick celloidin sections (Fig. 2) appear as a closely contiguous row of cells, are less and less well discernible the thinner the sections become until in the 8 μm section the pattern can no longer be seen with any degree of certainty. On the other hand, the subdivisions of the barrel walls into side and space as described by Woolsey and van der Loos (1970) can only rarely and in favourable places be detected in the 100 μm sections, whereas in 24 μm sections these components of a wall are readily distinguishable. They are most easily discernible in regions that were termed space connections by Woolsey and van der Loos (1970). These structures can still be detected in sections of a thickness between 12 and 15 μm, cut in a plane which is at right angles to the longitudinal axis of the barrel. In such sections it is also possible to detect the apical dendrites of layer V pyramids. Figures 4a and b show a 12 μm thick section in which two barrels are transversally cut. The dendritic bundles and most cross-sectioned cell processes are found to be restricted to the spaces. This is obvious if Figure 4a is investigated at higher magnification or if the dendrites and cell processes are traced as shown in Figure 4b. The few cross-sectioned cell

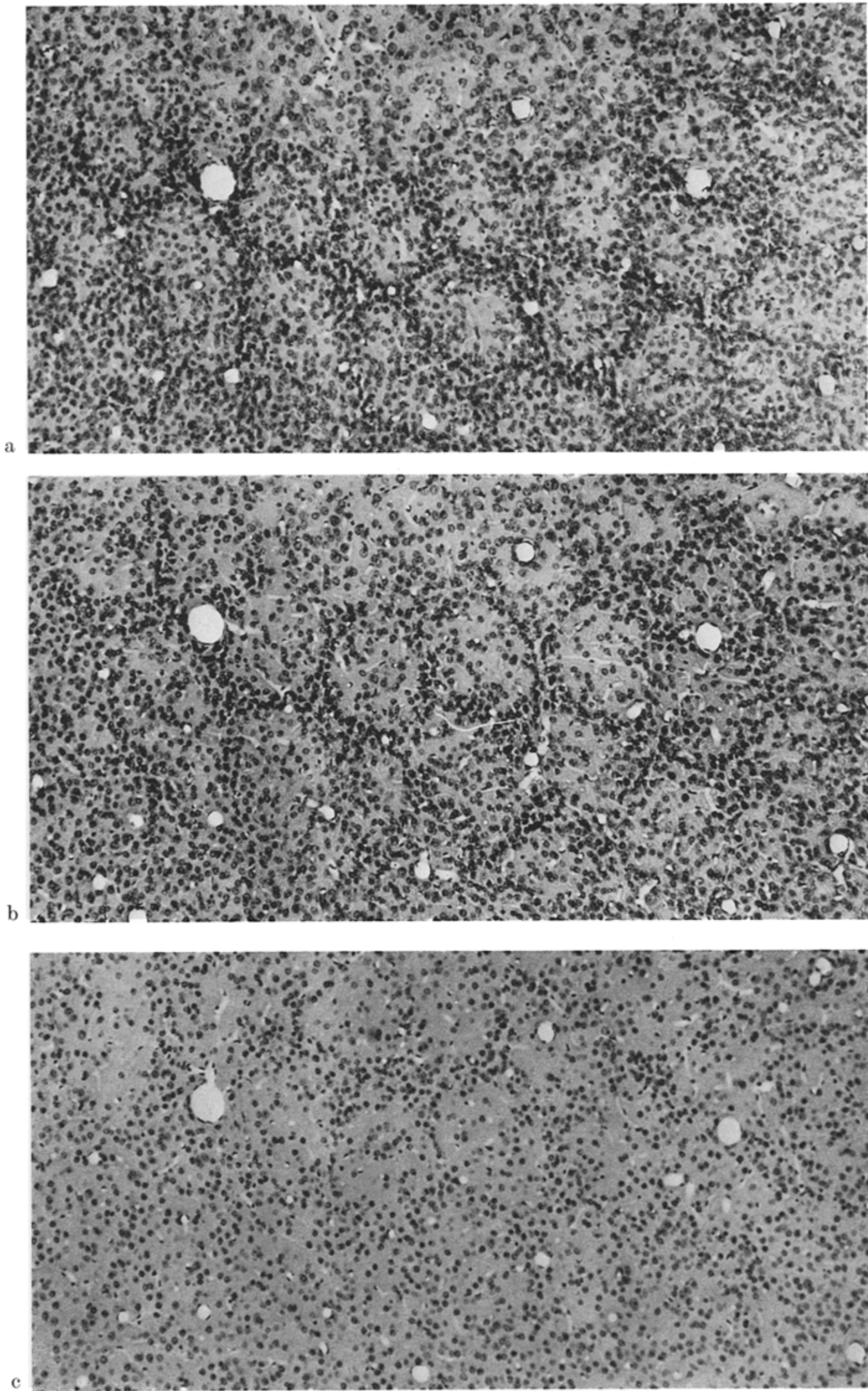

Fig. 3a—c. Three consecutive tangential sections with decreasing thickness (a = 24μm, b = 16 μm, c = 8 μm) through the barrel field of the mouse cortex. The barrels are less and less well discernible the thinner the section becomes. Paraffin sections, Klüver-PAS, × 240

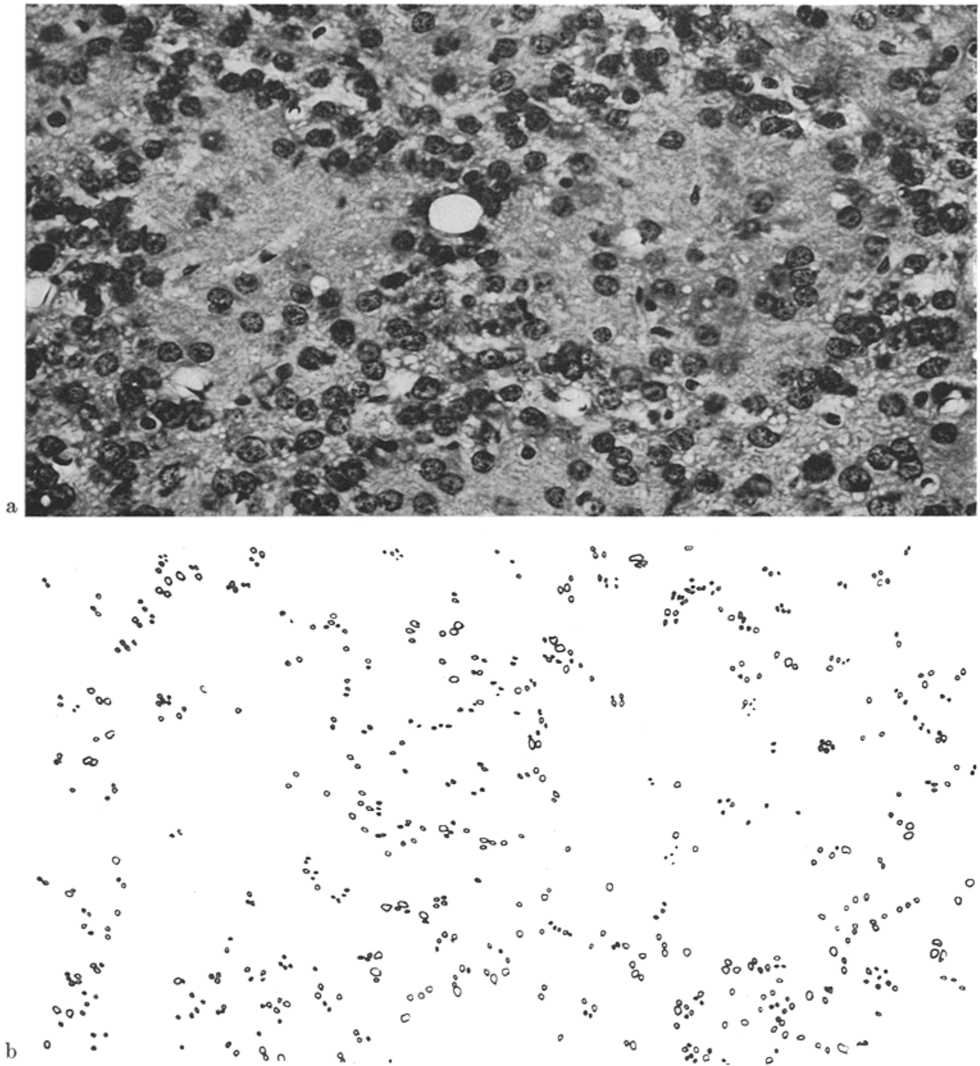

Fig. 4. (a) Tangential section through the barrel field of the mouse. 12 μm paraffin section, Klüver-PAS, ×400. (b) Semi-diagrammatic tracing of all cell processes cross sectioned in (a). The cell processes are seen to be mainly restricted to the spaces between the barrels. The few cell processes in the interior of the barrels are smaller than those in the spaces

processes in the interior of the barrel have a diameter distincly smaller than that of those in the spaces.

In Figure 5a a 15 μm frontal section through a barrel is seen in the original photograph (left) and in a diagrammatic tracing (right). The apical dendrites of the large pyramidal cells of layer V are seen initially to run straight towards layer IV. At the border of this layer they become deflected from their straight course so as to circumvent the interior of the barrel and run into the space. Other dendrites appear near the bottom of the barrel but they actually bend

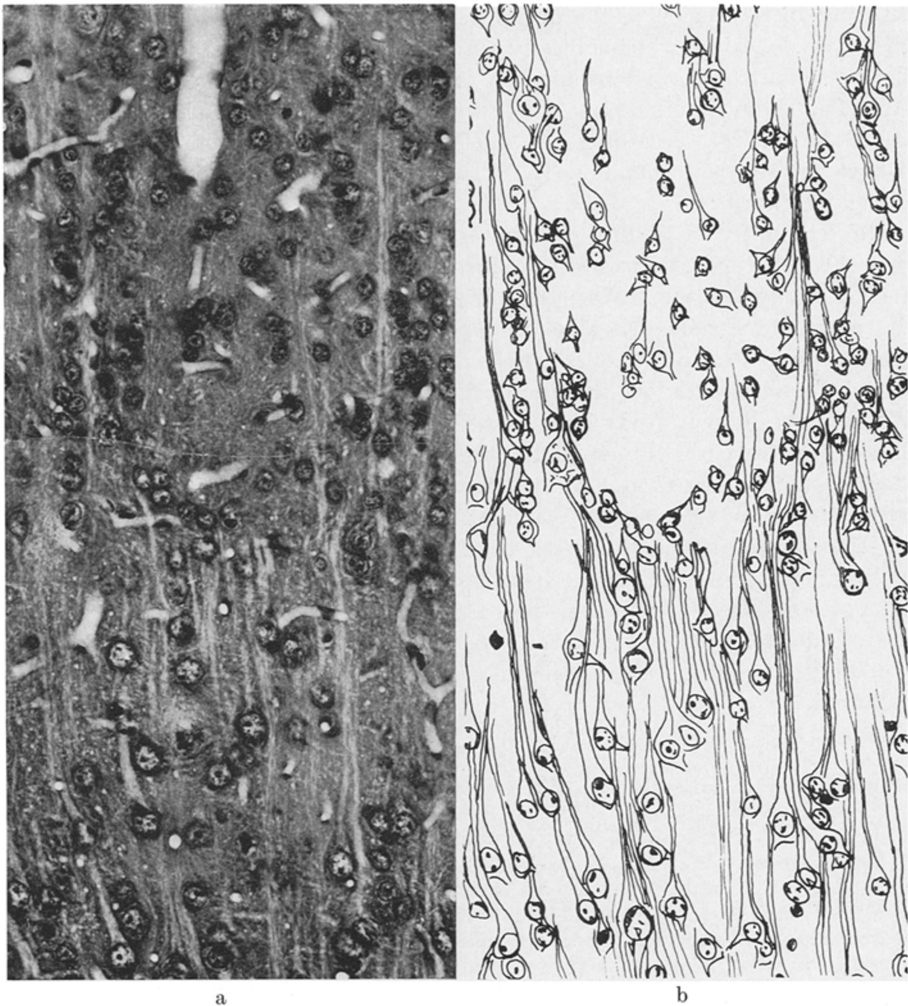

Fig. 5a and b. Frontal section through a barrel in the cerebral cortex of the mouse. The pyramidal cells of layer V and their apical dendrites in (a) have been traced and are shown in (b). The apical dendrites circumvent the interior of the barrel so as to enter the space. 15 μm paraffin section, Klüver-Pas, × 400

out of the plane of the section, as can be inferred from the cross-sectioned dendrites beneath the barrel floor. These findings show that the main stems of the apical dendrites originating from layer V pyramids pass between the barrels and do not reach the hollow which is made up mainly of neuropil.

Discussion

The present findings show that in the cerebral cortex of the mouse the dendritic bundles do not in all areas run straight through layer IV. While the situation in the area parietalis corresponds to that found in other species, it is

different in the region of the barrel field of Woolsey and van der Loos (1970). Here the dendrites which initially run straight towards layer IV depart from their original course and bend so as to enter the space between the barrels in layer IV. These results do not agree with recent findings of Feldman and Peters (1974) in the rat, according to which no spatial relationship exists between barrels and dendritic bundles. To explain this discrepancy, two possibilities are brought forward.:

(a) The different findings are due to species-specific differences. It is known that the structural features of the barrels vary in different species (cf. Woolsey, Welker and Schwartz, 1975); therefore, since the present investigation shows the course of the dendrites to be dependent on the structure of the barrels, species differences in the course of the dendrites would also be plausible.

(b) The contradictions are due to differences in the method of investigation. While in the present study both barrels and dendrites were studied in the same histological section, Feldman and Peters (1974) initially examined thick celloidin sections which were then subjected to renewed fixation and embedment before cutting semithin sections for examination of the dendrites. The authors do not mention any adjustments having been made to counteract possible alterations in form, and there is no photographic evidence to show that the alignment has not been altered during this procedure.

In order to decide which of the two explanations is valid, a renewed examination of the problem in the rat and further studies in additional species are required.

References

Cammermeyer, J.: An evaluation of the significance of the "dark" neuron. Ergebn. Anat. Entwickl.-Gesch. **36**, 1–61 (1962)

Feldman, M. L., Peters, A.: A study of barrels and pyramidal dendritic clusters in the cerebral cortex. Brain Res. **77**, 55–76 (1974)

Fleischhauer, K.: On different patterns of dendritic bundling in the cerebral cortex of the cat. Z. Anat. Entwickl.-Gesch. **143**, 115–126 (1974)

Fleischhauer, K., Detzer, K.: Dendritic bundling in the cerebral cortex. In: G. W. Kreutzberg (ed.), Physiology and pathology of dendrites. Adv. Neurol., vol. 12, p. 71–77. New York: Raven Press 1975

Fleischhauer, K., Petsche, H., Wittkowski, W.: Vertical bundles of dendrites in the neocortex. Z. Anat. Entwickl.-Gesch. **136**, 213–223 (1972)

Luna, L. G.: Further studies of Bodian's technique. Amer. J. med. Technol. **30**, 355–362 (1964)

Peters, A., Walsh, T. M.: A study of the organisation of apical dendrites in the somatic sensory cortex of the rat. J. comp. Neurol. **144**, 253–268 (1972)

Rose, M.: Cytoarchitektonischer Atlas der Grosshirnrinde der Maus. J. Psychol. Neurol. (Lpz.) **40**, 1–51 (1929)

Woolsey, T. A., van der Loos, H.: The structural organisation of layer IV in the somatosensory region of mouse cerebral cortex. Brain Res. **17**, 205–242 (1970)

Woolsey, T. A., Welker, C. and Schwartz, R. H.: Comparative anatomical studies of the Sm I face cortex with special reference of "barrels" in layer IV. J. comp. Neurol. **164**, 79–94 (1975)

Dr. K. Detzer
Anatomisches Institut
Nussallee 10
D-5300 Bonn
Federal Republic of Germany