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### Permalink

<https://escholarship.org/uc/item/5jb1664b>

### Journal

Experimental Brain Research, 81(3)

### ISSN

0014-4819

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### Publication Date

1990-08-01

### DOI

10.1007/bf02423498

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## The synaptic connections of basket cell axons in the developing rat hippocampal formation

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Received January 2, 1990 / Accepted April 17, 1990

**Summary.** Recent studies have indicated that hippocampal basket cells in both the dentate gyrus and Ammon's horn develop their somal and dendritic features during the first two postnatal weeks in rats. Their axon terminals form exclusively symmetric synapses that are found as early as 5 postnatal days in both regions. The present study used Golgi-electron microscopic material from 10 and 16 day old rats to demonstrate that the axon terminals of basket cells form synapses not only with somata, dendrites, and dendritic spines as reported for adult material but also with axon initial segments. However, the terminals forming synapses with axon initial segments and dendritic spines represent only a minor portion of the total number of basket cell terminals. Quantitative results indicate that 36–62% of the total number of these terminals form axosomatic synapses and 32–50% form axodendritic synapses depending on the analyzed cell. These data indicate that hippocampal basket cells have an axonal distribution similar to that found for cortical basket cells.

**Key words:** Dentate gyrus – Ammon's horn – Synapses – Golgi-gold labeled terminals – Light and electron microscopy – Rat

### Introduction

The light microscopic features of the basket cells have been described for both the neocortex and hippocampal formation by the pioneering investigators who used the Golgi impregnation method (Lorente de Nó 1934; Ramón y Cajal 1911). The main characteristic of the axonal plexus of basket cells is that it gives rise to axon collaterals in the immediate vicinity of the parent cell body and richly arborizes among the cell bodies of prin-

incipal neurons. In the hippocampus, the basket cells have traditionally been associated with inhibition (Andersen et al. 1964a, b; Blackstad and Flood 1963). They were thought to form inhibitory synapses with the cell bodies of neurons, where they would be strategically located to prevent the excitatory impulses received by the dendrites from reaching the trigger zone of the axon hillock (Andersen et al. 1964a, b).

Immunocytochemical studies have shown that basket cells of the hippocampal formation contain glutamate decarboxylase (GAD), the synthesizing enzyme for the inhibitory neurotransmitter GABA (Ribak et al. 1978; Seress and Ribak 1983). However, GAD-positive terminals form synapses not only with cell bodies, but also with dendrites, dendritic spines and axon initial segments of the principal neurons (Ribak et al. 1981). Subsequent studies have confirmed this synaptic relationship in adult and developing hippocampal formations (Kosaka et al. 1984; Kunkel et al. 1986; Lübbers and Frotscher 1987; Seress et al. 1989; Somogyi et al. 1983). This finding raises the question whether basket cells of the hippocampal formation form synapses with all parts of the target neurons or only with the cell bodies, while other specialized local circuit neurons form synapses with these other postsynaptic sites. Such a specialization of local circuit neurons has been suggested for GABAergic neurons of the neocortex where basket cells, chandelier cells and double bouquet cells are different with respect to the cellular distribution of their terminal fields (De Felipe et al. 1989; Hendry et al. 1989). However, some overlap in termination can be expected because large basket cells of the visual cortex were reported to form synapses with all parts of the target pyramidal cells with a preference for the cell bodies and dendrites (Somogyi et al. 1983). They also showed that the same axon branch can contact the cell body of one neuron and a dendrite of another. Such results accordingly contradict the concept of selectivity for the postsynaptic site of basket cell axons.

In the monkey Ammon's horn and the rat dentate gyrus, specific axoaxonic cells have been described (Somogyi et al. 1983; Soriano and Frotscher 1989). How-

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ever, a Golgi-electron microscopic analysis of the axonal plexus of basket cells did reveal axosomatic, axodendritic and axospinous synapses both in the Ammon's horn and dentate gyrus (Ribak and Seress 1983; Seress and Ribak 1985). In those studies, the basket cell terminals did not form synapses with axon initial segments of principal neurons, but the studies were made in adult rats where the axonal plexus is not optimally impregnated. Thus, the preparations did not allow for a quantitative evaluation about the terminal field of the basket cell axonal plexus because it only labeled a small number of terminals.

Golgi studies of young rats have demonstrated an extensive axonal arborization of basket cells of the dentate gyrus as early as the second postnatal week (Seress and Pokorny 1981). Basket cell axons form synapses with granule and pyramidal cells in the hippocampal formation from 5 day old rats (Seress et al. 1989), but not all of the terminals display specific synaptic specializations at this age (Kunkel et al. 1986; Seress et al. 1989). Ever since the rapid Golgi method was invented, it has been known that the impregnation of axons is most complete in young animals (Ramón y Cajal 1911). Therefore, an investigation of the axon terminal field of basket cells in the hippocampus of juvenile rats may allow for a more accurate determination of the frequency of the different postsynaptic sites.

## Material and methods

Twenty Sprague-Dawley rats, 10 and 16 days of age, were fixed by intracardiac perfusion with a solution of 4.0% paraformaldehyde, 1.25% glutaraldehyde, and 0.002% calcium chloride in 0.12 M phosphate buffer, pH 7.2. The perfused animals were stored overnight at 4° C, before the hippocampus was dissected out and processed for the Golgi-electron microscopic method according to Fairén et al. (1977). Briefly, the hippocampus was rinsed and placed into a solution containing 0.2% OsO<sub>4</sub> and 2.4% K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>. Each specimen was immersed in 50 ml of this solution and kept in the dark for four days. The tissue was then washed briefly in 0.75% AgNO<sub>3</sub> and stored in this solution for three days. Following impregnation, the blocks were passed through 20, 40, 60, 80 and 100% solutions of glycerol, embedded in agar and sectioned with a Sorvall tissue chopper. Sections were cut at 100 µm, collected on slides, coverslipped with 100% glycerol and examined with the light microscope. Identified basket cells with an extensive axonal plexus were selected from the CA 1 and CA 3 areas of Ammon's horn and from the granule cell and inner molecular layers of the dentate gyrus. The axonal plexus of these neurons could be followed and drawn with a Zeiss microscope equipped with a drawing tube.

To process the cells selected for electron microscopic examination, the sections with basket cells were hydrated through a series of glycerol solutions and placed into a chilled (4° C) 0.05% gold chloride solution for about 60 minutes with agitation. After three rinses in cold distilled water, they were placed into cold 0.05% oxalic acid for two minutes, brought to room temperature and placed into a 1% solution of sodium thiosulphate for 1–1.5 h. The sections were then rinsed and examined with the light microscope to confirm the presence of the de-impregnated, gold-toned neurons. In some cases, parts of the axonal plexus were lost through the gold-toning procedure as it has been recently described for dendrites by Lang and Frotscher (1990) in young animals. The basket cells with axonal plexuses were prepared for electron microscopy by using a routine schedule that included postfixation with OsO<sub>4</sub>, rapid dehydration

with acetone, and embedding in Epon. The use of sections 100 µm in thickness allowed us to visualize the de-impregnated cells in the polymerized resin blocks. Serial thin sections were made of the selected neurons. All sections were stained with uranyl acetate and lead citrate before examination with the electron microscope.

## Results

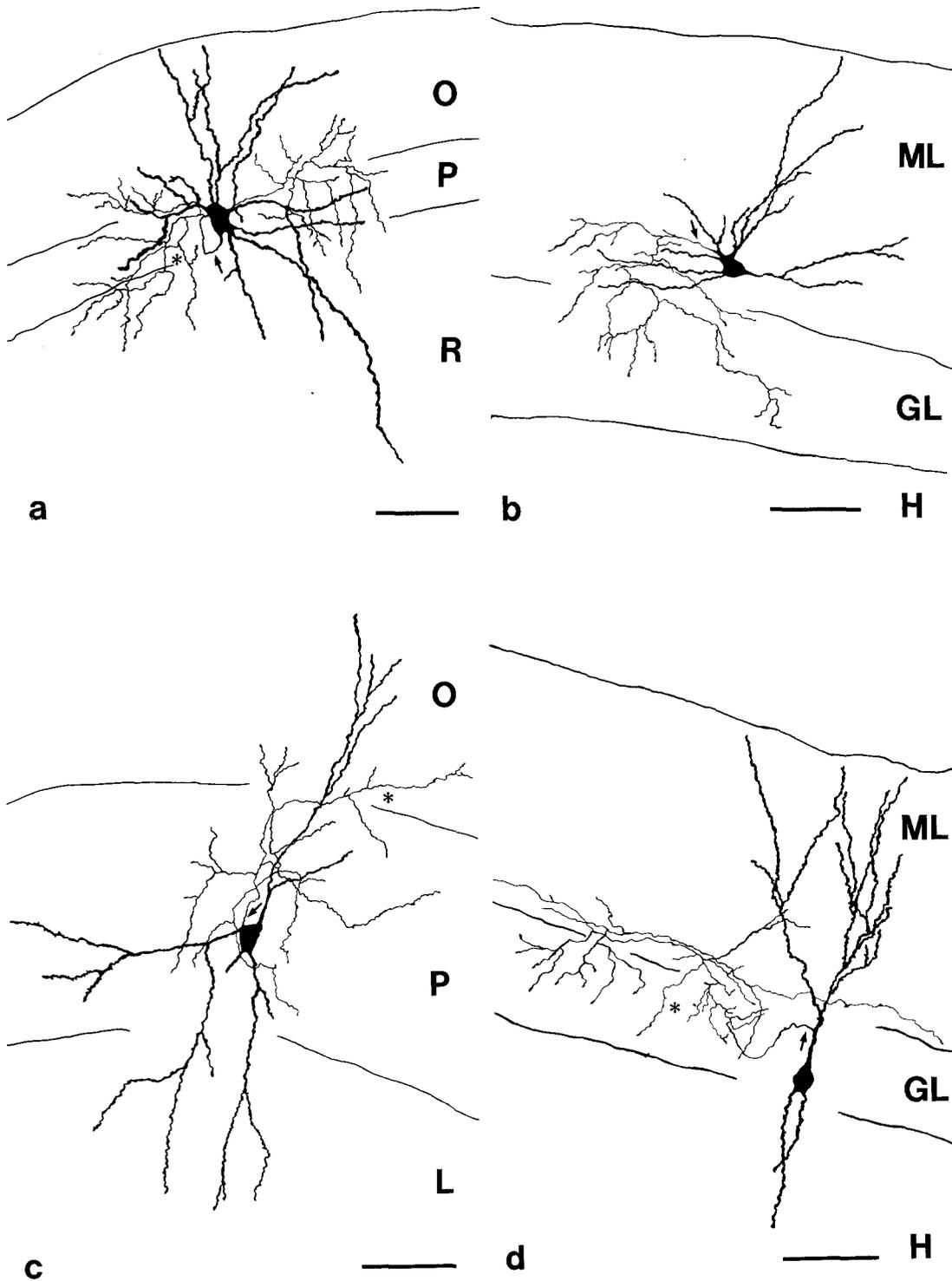
Eight cells were analyzed in this study; two from CA 1, two from CA 3 and 4 from the dentate gyrus (Figs. 1 and 2). The terminal fields of the axon plexus of the observed neurons were similar in that they formed a basket plexus with the principal neurons, either pyramidal or granule cells. Four cells that displayed the most elaborate axonal plexus were selected for the quantitative analysis and are documented in Table 1.

All of the axonal plexuses analyzed in this study belonged to Golgi-impregnated basket cells with light microscopic features similar to those described for basket cells in adult animals (Amaral 1978; Lübbers and Frotscher 1987; Ribak and Seress 1983; Seress and Ribak 1985). Briefly, the basket cell bodies were multipolar (Figs. 1 and 2). Their dendrites were varicose and smooth and had some side-branches. The axon originated from either the cell body (Fig. 1a, c) or a proximal dendrite (Fig. 1b, d). In the electron microscope, the basket cell bodies had the typical features of basket cells. These neurons showed a rich perikaryal cytoplasm with Nissl bodies, Golgi complex and large numbers of mitochondria. The nucleus was infolded and contained intranuclear rods in the 16 day old animals. Since this study is concerned with the axon terminal field of basket cells and since the features of developing somata and dendrites of basket cells in Ammon's horn and the dentate gyrus have been elaborately described recently (Lang and Frotscher 1990; Seress and Ribak 1990), the details of the electron microscopic features of basket cell somata and dendrites are not documented here.

The axonal plexus of each analyzed basket cell arborized extensively near the parent cell body within the principal cell layer among the somata and dendrites of

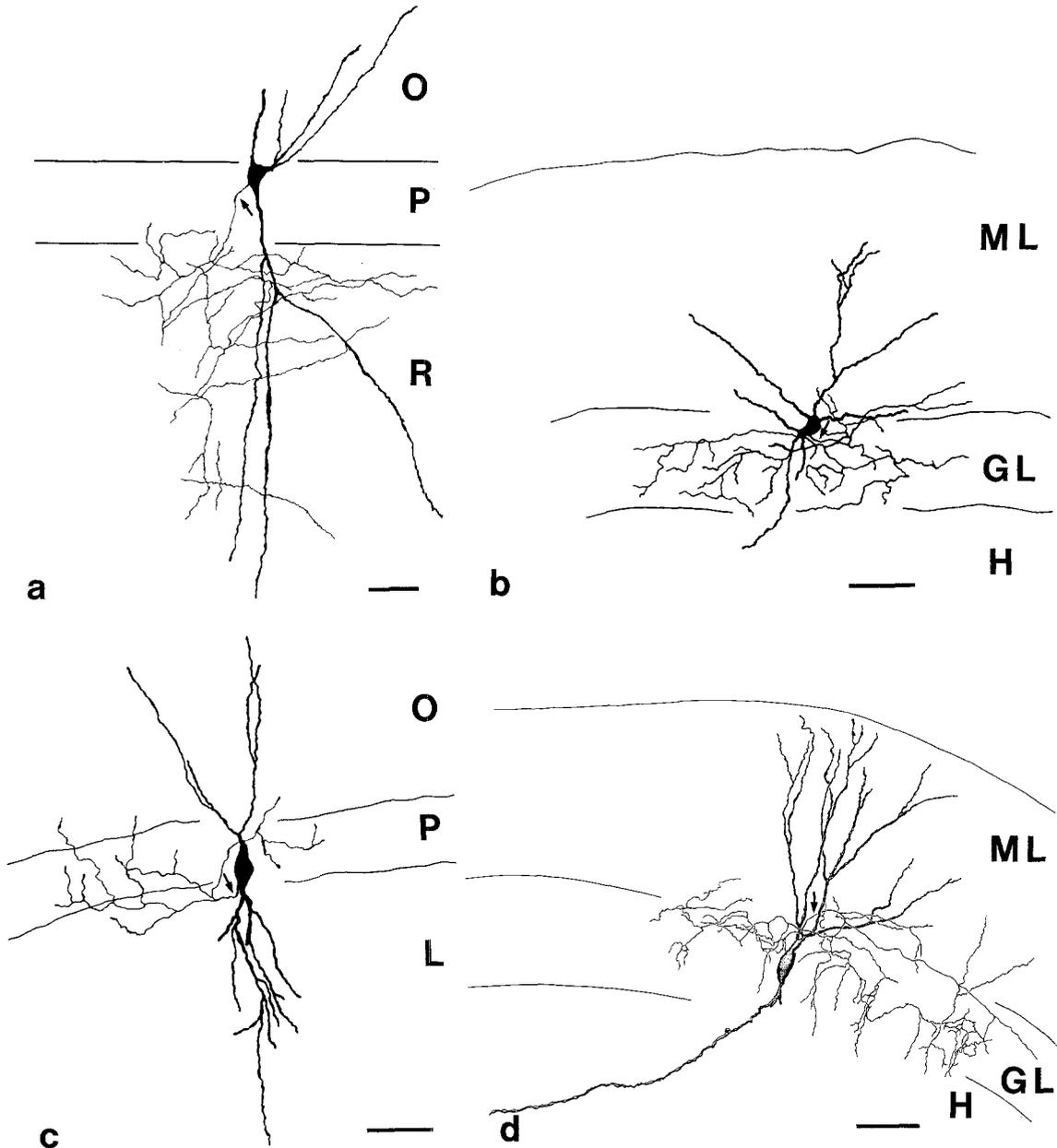
**Table 1.** Quantitative data for the axon distribution of the four basket cells shown in Fig. 1

Basket cell location	Number of synapses made with specific postsynaptic structures				
	Cell body	Dendrite	Spine	Axon initial segment	Total
Molecular layer of dentate gyrus	27 (60%)	18 (40%)	0	0	45
Hilar border of the granule cell layer	22 (36%)	31 (50%)	7 (11%)	2 (3%)	62
CA 3/c of Ammon's horn	24 (51%)	21 (45%)	1 (2%)	1 (2%)	47
CA 1 of Ammon's horn	37 (62%)	19 (32%)	1 (2%)	3 (5%)	60



**Fig. 1a-d.** Drawings of four of the analyzed basket cells from the rat hippocampal formation at 10 and 16 days of age. Arrows point to the axon that originates either from the cell body or a proximal dendrite. All axons displayed a rich collateral network. The asterisks indicate the location of synapses made with axon initial segments. **a** Basket cell from the CA 1 area of Ammon's horn from a 10 day old rat. The cell body is multipolar and located within stratum pyramidale (P), whereas the dendrites penetrate into strata radiatum (R) and oriens (O). Bar represents 65  $\mu$ m. **b** Basket cell in the inner molecular layer (ML) of the dentate gyrus of a 16 day old rat. The dendrites remain in this layer whereas the axon (arrow)

arborizes in both the molecular and granule cell (GL) layers, but not in the hilus (H). Bar represents 80  $\mu$ m. **c** Basket cell in stratum pyramidale (P) of the CA 3c area of Ammon's horn from a 16 day old animal. The dendrites penetrate into both strata oriens (O) and lucidum (L) whereas the axon arborizes only within strata pyramidale (P) and oriens (O). Bar represents 85  $\mu$ m. **d** Basket cell at the hilar border of the granule cell layer (GL) in the dentate gyrus from a 16 day old animal. Apical dendrites arborize in the molecular layer (ML) and basal dendrites extend into the hilus (H). The axon has branches both in the molecular and granule cell layers. Bar represents 80  $\mu$ m



**Fig. 2a–d.** Drawings of four other basket cells that were not used for the quantitative analysis because they displayed low numbers of identifiable axon terminals in thin sections. Arrows indicate the origin of axons. Each bar represent 60  $\mu\text{m}$ . **a** Basket cell from the CA 1 area of Ammon's horn from a 16 day old rat. Its multipolar cell body is located in stratum pyramidale (P) whereas its dendrites penetrate into strata radiatum (R) and oriens (O). The axonal plexus richly arborizes in the stratum radiatum (R). **b** Basket cell in the inner molecular layer (ML) of the dentate gyrus of a 16 day old rat. Some of the dendrites penetrate into the granule cell layer (GL) and one enters the hilus (H) but the majority remain in the

inner molecular layer. The axonal plexus is located within the granule cell layer (GL). **c** Basket cell in stratum pyramidale (P) of the CA 3 area of Ammon's horn from a 10 day old animal. The dendrites penetrate into strata oriens (O) and lucidum (L) whereas the axon has branches mainly inside stratum pyramidale. **d** Basket cell in the granule cell layer (GL) of the dentate gyrus from a 16 day old animal. Apical dendrites arborize in the molecular layer (ML) and basal dendrites extend into the hilus (H). The axon has branches both in the molecular and granule cell layers. A detailed description of the ultrastructure of this neuron's cell body, dendrites and axon terminals is given elsewhere (Seress and Ribak 1990)

**Fig. 3a–e.** Electron micrographs of Golgi-impregnated, gold-labeled axon terminals from the basket cells in the Ammon's horn shown in Figs. 1a, c. **a** An axon terminal (T) from the basket cell in the CA 3 area forms a symmetric synapse (arrows) with an axon initial segment (i.s.) of a pyramidal cell. Open arrows mark the characteristic undercoating of an initial segment. X65 000. **b** An axon terminal (T) from the basket cell in the CA 1 area forms a synapse (arrow) with a small spine-like profile in stratum oriens. X46 000. **c** An axon terminal from the analyzed basket cell in the CA 3 area.

The terminal (T) forms a symmetric synapse (arrows) with the cell body of a pyramidal neuron (P). Note the vesicle accumulations near the mitochondrion and the synaptic cleft. X70 000. **d** An axon terminal from the basket cell in the CA 3 area. The terminal (T) forms two synapses (arrows) with two adjacent pyramidal cells (P). Note vesicle accumulations at the synaptic junctions. X46 000. **e** An axon terminal from the analyzed basket cell in the CA 1 area. The terminal (T) forms a symmetric synapse (arrows) with a large proximal dendrite (D) of a pyramidal cell. X38 000

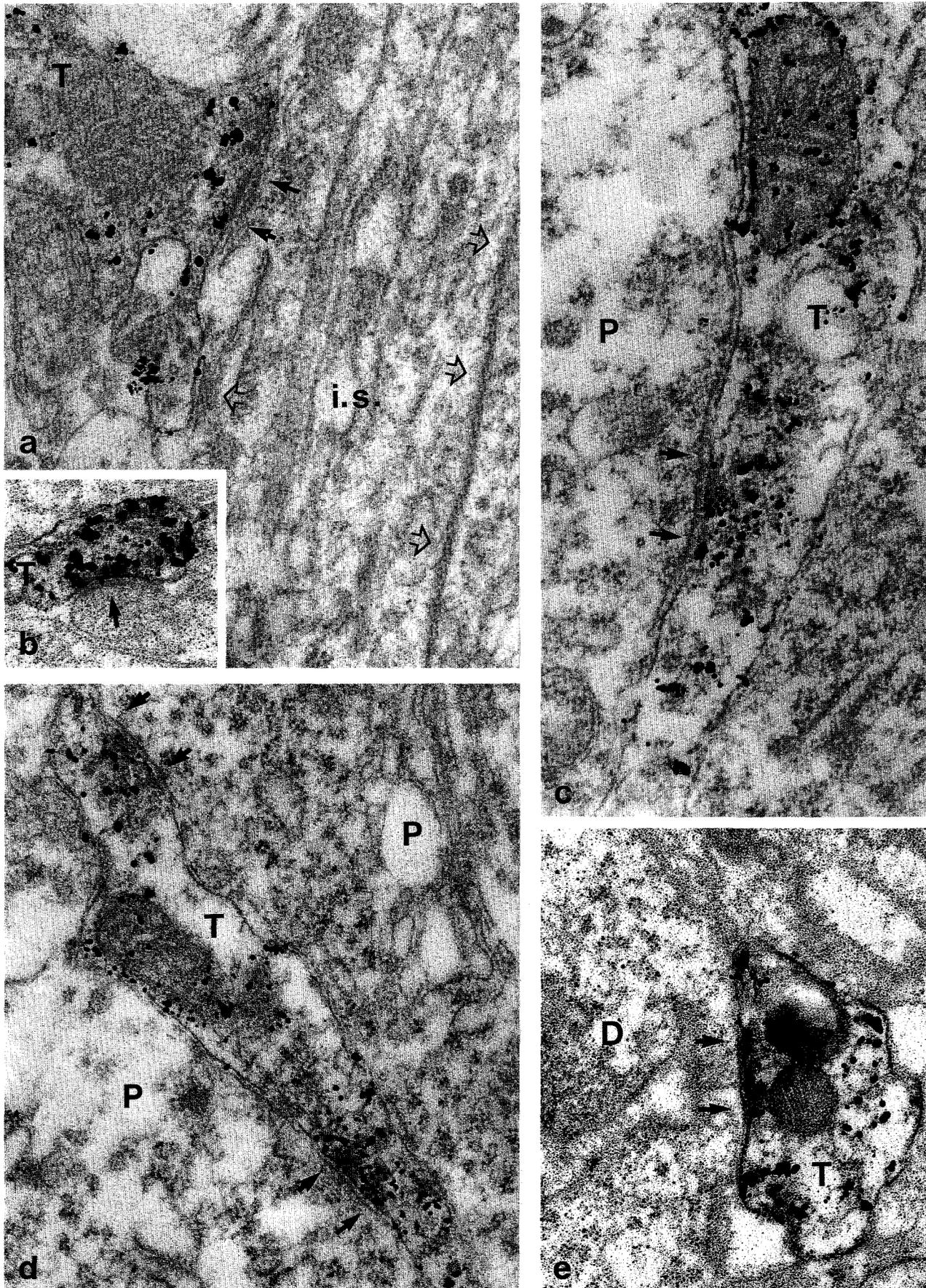
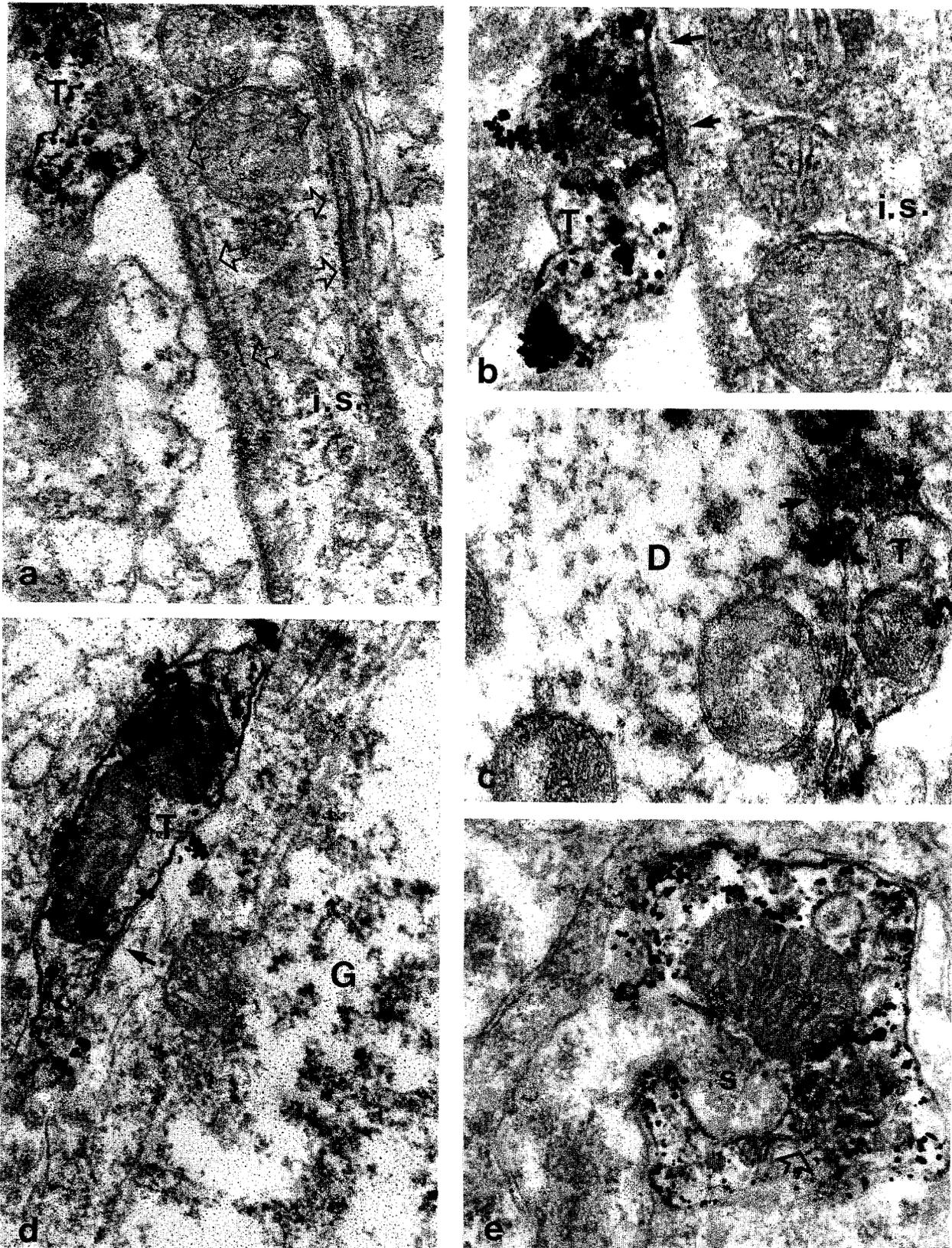


Fig. 3



**Fig. 4a-e.** Electron micrographs of Golgi-impregnated, gold-toned axon terminals from the analyzed basket cells in the dentate gyrus shown in Figs. 1b, d. **a** An axon terminal (T) from the basket cell in Fig. 1d is closely apposed to an axon initial segment (i.s.) of a granule cell. Open arrows indicate microtubules that are associated with the characteristic dense undercoating. X54 000. **b** Serial section of the same terminal shown in Fig. 3a. Here, the terminal (T) shows an obvious accumulation of vesicles adjacent to the straight pre-synaptic membrane that is suggestive for a synapse although the postsynaptic membrane (arrows) is obscured by the dense undercoating of the initial segment (i.s.) and the tangential cutting of its membrane. X70 000. **c** An axon terminal from the molecular layer

basket cell in Fig. 1b. The terminal (T) forms a symmetric synapse with a dendrite (D) of a granule cell. X57 000. **d** An axon terminal (T) from the basket cell in Fig. 1d. This terminal forms a symmetric synapse (arrow) with the soma of a granule cell (G). X64 000. **e** Another axon terminal from the basket cell in Fig. 1d. This terminal surrounds a spine (s) in the molecular layer. The vesicle accumulation (open arrow) suggests a synaptic site, although it is possible that this terminal may form a synapse with either the neck portion of the spine or the dendritic shaft. This arrangement is similar to the one shown in the adult dentate gyrus (see Fig. 24 in Ribak and Seress 1983). X53 000

both granule and pyramidal cells (Figs. 1 and 2). However, there were differences in the branching pattern of the axons of the basket cells. Some of them branched mainly inside the layer of principal cell bodies (Figs. 1c and 2c) whereas others have equally distributed axons branching both among principal cell bodies and among their apical or basal dendrites in Ammon's horn (Fig. 1a) and the dentate gyrus (Figs. 1d and 2d). Another variation occurred with one of the CA 1 basket cells that had axonal branches mainly in stratum radiatum and only a few in stratum pyramidale (Fig. 2a).

The axon terminals contained only a few mitochondria and less synaptic vesicles than in adults (Figs. 3a–e and 4a–c). Often, numerous synaptic vesicles were accumulated next to the presynaptic membrane, similar to that described for mature synapses (Figs. 3c, d and 4b, e). All of the Golgi-impregnated, gold-labeled basket cell terminals formed symmetric synapses. The terminal field of the axons from the analyzed basket cells was similar. The postsynaptic targets included mainly the somata (Figs. 3c, d and 4d) and dendrites (Figs. 3e and 4c) of pyramidal and granule cells. In addition, a few terminals formed synapses with the axon initial segments (Figs. 3a and 4a, b) and dendritic spines (Figs. 3b and 4e) of both pyramidal and granule cells. The size of the individual axon terminals varied and most of them formed a single synapse with the postsynaptic element. In some cases, one labeled axon terminal formed multiple synapses with neighboring pyramidal cells (Fig. 3d).

The relative distribution of terminals at the different postsynaptic locations was similar for the four basket cells used in the quantitative analysis (Table 1). For the other four analyzed neurons, the number of identified axon terminals was small (10–15) and did not allow for a quantitative study. However, it should be noted that most of the terminals for all of the analyzed basket cells formed synapses with cell bodies and dendrites. The variability in the distribution of axon terminals could be large for the basket cells used in the quantitative analysis (Table 1). For example, one of the basket cells in the dentate gyrus (Fig. 1d) had 36% of its terminals form synapses with somata of granule cells, whereas the terminals of the CA 1 basket cell (Fig. 1a) nearly made twice that number (62%) of axosomatic synapses. It is important to note that many synapses made with dendrites occurred on their proximal portions within the principal cells layers of both the dentate gyrus and Ammon's horn. Similarly, the labeled terminals that formed synapses with axon initial segments were found inside the principal cell layers for both the CA 1 (Fig. 1a) and dentate gyrus (Fig. 1d).

## Discussion

The main finding of the present study is that the axons of hippocampal basket cells in young 10 and 16 day old rats not only form synapses with somata and dendrites of principal cells as previously described (Lübbers and Frotscher 1987; Ribak and Seress 1983; Seress and Ri-

bak 1985), but also with axon initial segments and dendritic spines. Such a distribution is similar to that described for the large basket cells of the visual cortex (Somogyi et al. 1983). The axons of these neurons primarily formed synapses with somata and dendrites of the cortical pyramidal cells, but synapses with dendritic spines and axon initial segments were also noted in the same relative percentages as described here for the hippocampal basket cells. This finding suggests that the classic basket cells of the hippocampal formation are equivalent to the large basket cells of the neocortex (Jones and Hendry 1984; Somogyi et al. 1983).

Another interesting conclusion from these results is that already in the early stages of basket cell synaptogenesis, the axons of basket cells form synapses with the same parts of the target cells as they do in the adult animals (Lübbers and Frotscher 1987; Ribak and Seress 1983; Seress and Ribak 1985). Such synapse formation with dendrites and somata was noted for GABAergic basket cells in the hippocampal formation (dentate gyrus and CA 1 area) as early as five days postnatally (Seress et al. 1989). The basket cells analyzed in the quantitative study had an extensive axonal plexus and the axon terminals formed synapses in almost equal numbers with somata and dendrites of principal neurons. It is important to note that the analyzed basket cell in the CA 1 area that showed the greatest percentage of axosomatic synapses was obtained from a younger rat than the other analyzed basket cells. In the younger animals the dendrites of principal neurons are shorter and they have very few side branches. The relatively higher proportion of axosomatic synapses for the basket cell from the 10 day old animal may simply reflect the greater availability of somata relative to dendrites as postsynaptic targets. Since the analyzed sections were only 100  $\mu\text{m}$  thick, only a portion of the complete axonal plexus was present within the section. Therefore, the quantitative data on the distribution of postsynaptic targets of basket cells may be different if the entire plexus were analyzed.

The distribution of the basket cell's axonal plexus shows a significant difference from the axo-axonic or chandelier cell's axonal plexus that has been described for both the neocortex and hippocampal formation (Jones 1975; Somogyi 1977; Somogyi et al. 1983; Soriano et al. 1990; Szentágothai and Arbib 1974). The axo-axonic cells form synapses exclusively with the axon initial segments of the principal neurons. However, some overlap between the axon terminal fields of the large basket cells and axo-axonic cells has been noted in the neocortex (Somogyi et al. 1983). The present results suggest that a similar overlap exists for basket and axo-axonic cells in the hippocampal formation. The size of this overlap has yet to be determined in the hippocampus. It has recently been reported that different subpopulations of GABAergic neurons (either basket or axo-axonic cells) terminate at the same postsynaptic sites (Ribak et al. 1990). These groups of GABAergic neurons contain different peptides and different calcium-binding proteins (Kosaka et al. 1987, 1988; Sloviter 1989; Sloviter and Nilaver 1987). Although the neurons may be chemically different, they look similar in the light microscope, but the terminal field

of their axons cannot be identified unless other methods are used such as Golgi staining or intracellular filling methods. There is a significant overlap between parvalbumin-positive and negative terminals at all post-synaptic sites in the hippocampal formation, including the axon initial segments of the principal neurons of the hippocampus (Ribak et al. 1990). The axo-axonic cells have been shown to be parvalbumin-positive in both neocortex and dentate gyrus (De Felipe et al. 1989; Soriano et al. 1990). Therefore, it is possible that another population of local circuit neurons forms synapses with the axon initial segments or that not all of the axo-axonic cells are parvalbumin-positive in the hippocampus. Additionally, long projection neurons, such as those forming the commissural pathway or the septo-hippocampal projection, may terminate at this site (Freund and Antal 1988; Ribak et al. 1986; Seress and Ribak 1984).

There is no conclusive evidence that the axonal plexuses of basket cells in young and adult animals are identical except for the fact that their target fields are remarkably similar (Ribak and Seress 1983; Seress and Ribak 1985, 1990). It is possible that young basket cells may form exuberant synapses with different postsynaptic targets during development as it was recently described for the neocortex (Zecevic et al. 1989). Exuberant synapses could be the explanation for the finding that basket cell axons form synapses with axon initial segments of principal neurons whereas similar synapses were not reported in adults. However, we do not believe that this is the case because the axons impregnated in adults were not as completely labeled as those found in the young animals in the present study. A study of young and adult basket cell axons using an intracellular filling method could provide a definitive answer to resolve this question.

As previously noted, the basket cell axons of the hippocampal formation form their first synapses with the same postsynaptic targets that are found in adult animals, the somata and dendrites of principal neurons. Many studies have shown that the basket cells receive synapses from the same afferents as the principal neurons do (Frotscher and Zimmer 1983; Léránth and Frotscher 1987; Seress and Ribak 1984, 1985; Zipp et al. 1989). From these anatomical data, it has been shown that the basket cells participate in feed-forward and feed-back inhibition. However, it remains to be determined whether these two types of inhibition begin to function at the same time during development. About half of the axon terminals of basket cells form synapses with dendrites. Therefore, the basket cells have the potential to influence the activity of dendrites locally. That function is different from the complete inhibition of principal neurons hypothesized as a function for the basket cell terminals that form axosomatic synapses (Andersen et al. 1964a, b; Blackstad and Flood 1963). Thus, the basket cells of the hippocampal formation can exert their inhibitory influence both on the proximal dendrites and on the soma.

*Acknowledgements.* The authors gratefully acknowledge the excellent technical assistance of Margot Brundage and Yashoda Jhurani. This work was supported by NSF grant BNS 86-15579.

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