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GABAergic Cells in the Dentate Gyrus Appear to be Local Circuit and Projection Neurons*

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Summary. Immunocytochemical results indicate that GAD-positive neurons are found in the molecular and granule cell layers of the dentate gyrus as well as in the hilar region. GAD-positive cells in the molecular and granule cell layers are identified as various types of local circuit neurons. Most of the GAD-positive puncta found throughout the molecular layer and within the granule cell layer are interpreted as axon terminals of these neurons, including five types of basket cells. This interpretation is based on data that indicate the axons of basket cells form synapses with the somata and proximal dendrites of granule cells. The results in the hilus show that 60% of the hilar neurons are GAD-positive. Since previous studies have indicated that 80% of hilar neurons give rise to both associational and commissural pathways, many GABAergic neurons in the hilus are probably projection neurons. This finding is consistent with recent physiological data which suggest that commissural pathway stimulation directly inhibits granule cells. Therefore, GABAergic cells in the dentate gyrus appear to be both projection and local circuit neurons.

Key words: Dentate gyrus – Hilus – Commissural pathway – GABAergic inhibition – Basket cells

Introduction

The hippocampus of the rat has become an important brain region to neuroscientists for identifying the

location of neurotransmitters and for analyzing the electrophysiological properties of neuronal circuits because it is a well organized and laminated structure. The cell types and the neuronal circuits within the hippocampus were first described in Golgi studies by Ramón y Cajal (1968) and Lorente de Nó (1934). Their results indicated that: (1) the granule cells were the only source of projections from the dentate gyrus to the other parts of the hippocampus, and (2) many different types of local circuit neurons existed in the dentate gyrus including the hilus. More recent Golgi studies by Amaral (1978) and Seress and Pokorny (1981) have provided additional details about these local circuit neurons and have classified them into numerous types. Four basic types of basket cells exist either subjacent to or within the granule cell layer (Seress and Pokorny 1981). Furthermore, an additional basket cell type was observed in the molecular layer. Neurons in the hilus were extensively described by Amaral (1978) who showed 20 cell types, including local circuit neurons, such as stellate and fusiform cells. These polymorph neurons of the hilus are recognized as a part of the dentate gyrus rather than of the Ammon's horn (Blackstad 1956; Amaral 1978). More recent data have confirmed this notion because most hilar cells have associational and commissural projections to the dentate gyrus (Swanson et al. 1978, 1981; Laurberg 1979; West et al. 1979; Berger et al. 1981; Voneida et al. 1981). These results indicate that both long projecting and local circuit neurons exist in the hilus.

The results of a previous study that localized glutamate decarboxylase (GAD) to cells in the dentate gyrus (Ribak et al. 1978) showed GAD-positive reaction product in "pyramidal basket cells" and "other short-axon neurons, especially the horizontal neurons". Since local circuit neurons were not thoroughly described at the time of this initial study of the GABAergic cells in the dentate gyrus, we have

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undertaken a re-examination of these preparations to better identify the GAD-containing neurons in this part of the hippocampal formation. A localization of GAD within these recently described cell types (Amaral 1978; Seress and Pokorny 1981) could provide important data about GABA-mediated inhibition in the dentate gyrus. A preliminary report of these results was recently presented (Seress and Ribak 1982).

Methods

Adult Sprague-Dawley albino rats were used in this study. All rats were perfused transcardially with solutions containing 4% paraformaldehyde, 0.1–0.5% glutaraldehyde and 0.002% CaCl_2 in 0.12 M phosphate buffer at pH 7.2. Six rats that received 2 μl colchicine (10 $\mu\text{g}/\mu\text{l}$ Saline, Sigma Chemical Co.) injections into the hippocampus had a 24 h survival time.

Immunocytochemistry

Brains were dissected from the crania the day following the perfusion, and specimens of hippocampus were obtained and immersed overnight in a cryoprotectant 30% sucrose solution. Blocks of tissue were rapidly frozen in an embedding medium with dry ice and sectioned on a cryostat in the coronal plane at a thickness of 40 μm . After rinsing in buffer overnight, selected sections in close proximity to the injection site of colchicine were processed for GAD immunocytochemistry as described previously (Ribak et al. 1978, 1979, 1981; Vaughn et al. 1981). Briefly, sections were incubated in normal rat serum for 1 h and then rinsed in phosphate buffer before being incubated for 1 h in either rabbit anti-GAD serum or control rabbit serum. Following a 2.5 h buffer wash, the sections were incubated for 1 h in goat anti-rabbit serum (Antibodies, Inc.). Sections were then washed in buffer for 2.5 h, incubated in a peroxidase-antiperoxidase Fab complex for 1 h and washed again for 2.5 h in buffer before being reacted with 3',3'-diaminobenzidine - 4 HCl (Sigma Chemical Co.) and H_2O_2 for 30 min. Following the immunocytochemical reactions, the sections were washed for 30 min in buffer and osmicated for 30 s in a solution containing 0.1% OsO_4 in 0.12 M phosphate buffer to stabilize the brown reaction product. Sections were then rinsed, floated onto glass slides, dehydrated and coverslipped. The sections were the same ones used in a previous study (Ribak et al. 1978).

The slides were examined in the light microscope, and neurons containing GAD-positive reaction product within their somata and dendrites were drawn at $\times 1,000$ magnification using a

light microscope fitted with a drawing tube. In addition, the GAD-positive neurons in the hilus were counted in three representative sections, and they were identified by reaction product within the perikaryal cytoplasm and by an unstained nucleus. The four types of basket cells subjacent to, or within, the granule cell layer were omitted from this quantitative study, because they were considered a part of the granule cell layer.

Golgi Staining

Both Golgi-Cox and rapid Golgi methods were used in this study (Ramón-Moliner 1970; Valverde 1965). For this series of preparations, 40 well-impregnated brains were cut in serial frontal sections at 100–150 μm . Specimens containing the hippocampus were analyzed in these sections using a light microscope. Drawings of stained basket cells that were isolated from other impregnated neurons were made with the use of a drawing tube attachment.

Nissl Staining

Five adult rats were perfused with 10% formalin at pH 7.4. The brains were embedded in paraffin and sections were cut at both 40 and 10 μm in the frontal plane and stained with cresyl violet. All counts were made from these sections as described previously (Seress and Pokorny 1981). Counts were made at a total magnification of $\times 1,000$, and only hilar neurons with nuclei and a stained perikaryal cytoplasm were included.

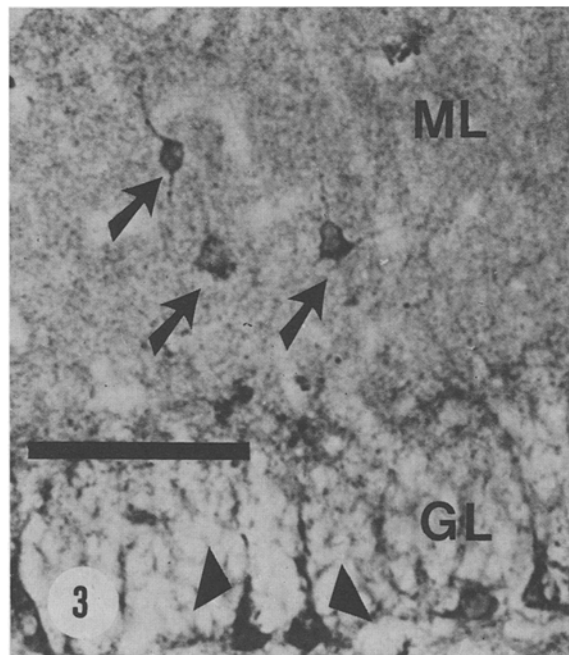
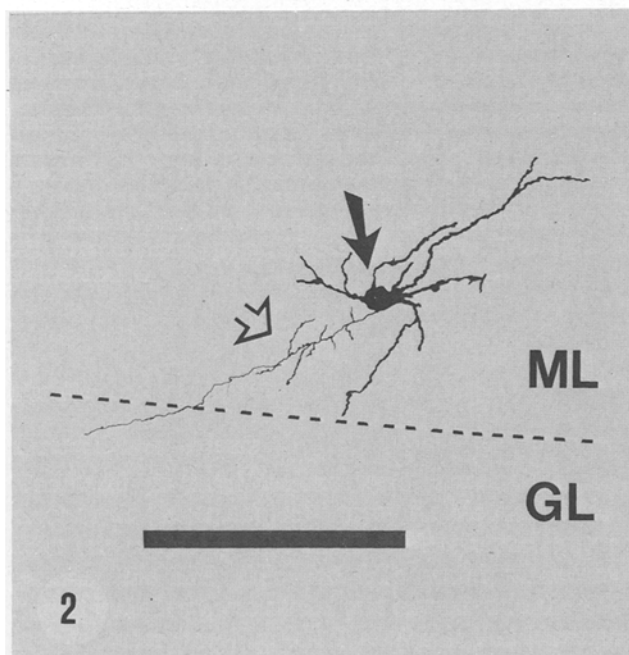
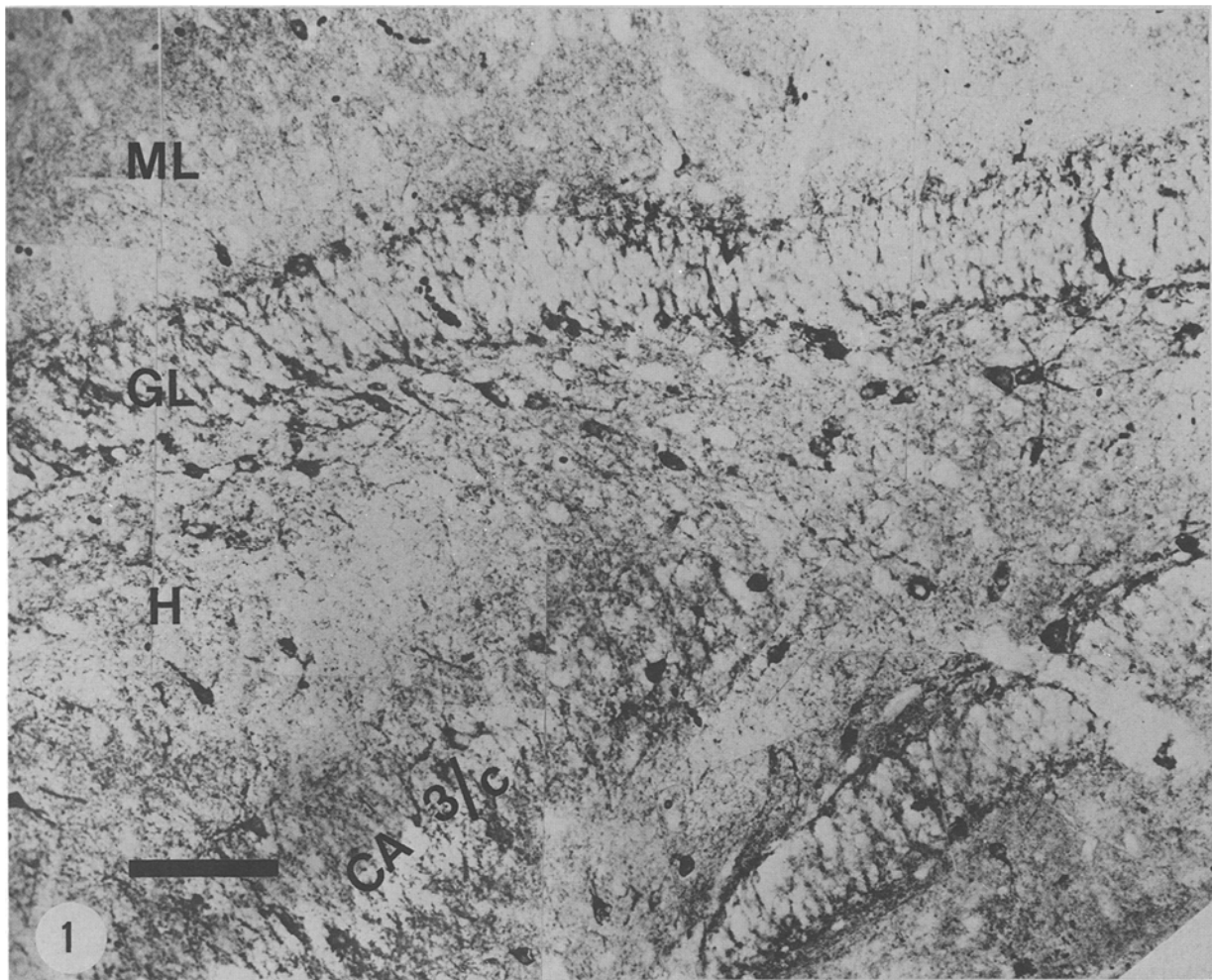
Results

The present analysis was limited to the molecular layer and granule cell layer (GL) of the dentate gyrus and to the hilus (Fig. 1). It is mainly the somata of granule cells that form the prominent GL of the dentate gyrus, while the dendrites of these same cells arborize extensively in the molecular layer that contains axons of many hippocampal afferents. The hilus is not as well defined because its polymorph cells form a loose aggregate of neuronal somata between the GL and CA 3/c of the hippocampus. Although Ramón y Cajal (1968) included pyramidal basket cells in the category of polymorph cells, his limiting subzone that contains the basket cells will be classified as the hilar border of the GL for this study. The remaining types of polymorph cells will be considered as hilar neurons according to the defini-

Fig. 1. Montage of a 40 μm coronal section of the dentate gyrus incubated with anti-GAD serum. Several cells in the molecular layer (*ML*), granule cell layer (*GL*) and hilus (*H*) contain GAD-positive reaction product, while the granule and pyramidal cells (*CA 3/c*) lack immunoreactivity for GAD. Compare distribution of cells in this montage with the drawing in Fig. 15 of Ribak et al. (1978). The abbreviations for the regions of the dentate gyrus (*ML*, *GL* and *H*) will be used in all subsequent figures. Bar represents 100 μm

Fig. 2. Camera lucida drawing of a Golgi-stained, local circuit neuron in the molecular layer of the dentate gyrus. The soma (*arrow*) is slightly larger in size than that of the granule cells, and it has a multipolar dendritic arborization. The axon (*arrowhead*) arborizes in the molecular layer before entering the GL. Bar represents 100 μm

Fig. 3. Photomicrograph of a section of the dentate gyrus incubated with anti-GAD serum. Three GAD-positive cells (*arrows*) are shown in the molecular layer. GAD-positive pyramidal basket cells (*arrowheads*) are present in the GL. Bar represents 100 μm



Figs. 1-3

tion of Blackstad (1956) and Amaral (1978). Pyramidal neurons in CA 3/c and remaining parts of the hippocampus will not be included in this analysis.

Cells in the Molecular Layer

Golgi preparations revealed large and medium-size local circuit neurons in the molecular layer (Ramón y Cajal 1968; Lorente de Nó 1934). Generally, the larger neurons were found in the part of the molecular layer adjacent to GL and they had multipolar shapes and axons directed toward the GL (Fig. 2) or terminating in the GL (Seress and Pokorny 1981). The smaller neurons were located in the outer part of the molecular layer and their axons also remained in close proximity to the dendritic field.

In sections incubated with anti-GAD serum, GAD-positive somata were distributed in the molecular layer and had similar shapes and sizes as the medium-size and large local circuit neurons observed in Golgi specimens (Fig. 3). When dendritic staining was present, it appeared that these cells were multipolar with dendrites originating from different parts of the somata (Fig. 3). GAD-positive reaction product was also observed in small punctate structures throughout the molecular layer. A significant increase in the density of these puncta occurred at the transition between this layer and the GL.

The Non-Granule Neurons in the GL

Examination of GAD-positive somata in the GL revealed four neuron types. The somata of these neurons were all substantially larger than the GAD-negative somata of granule cells. The first of these GAD-positive cell types was previously classified by Ribak et al. (1978) as the pyramidal basket cell. This

cell had a triangular shaped soma located on the hilar border of the GL and an apical dendrite which could be followed deep inside the GL (Figs. 3 and 4). In addition, thick basal dendrites arose from each of the lower corners of the soma (Fig. 4). These features were consistent with data for the pyramidal basket cells described in Golgi preparations (Fig. 9). These cells were also recognized in Nissl-stained sections based on the location, shape and size of the somata (Fig. 8) (Seress 1978; Ribak and Anderson 1980). The flat basal portion of the somata of these cells was usually located slightly below the margin of the GL.

A second type of GAD-positive cell that was found in the GL was a large fusiform cell (Fig. 5). Its soma was located in the lower half of the GL and its apical dendrite ascended through this layer to reach the molecular layer. Unlike the pyramidal basket cell, the fusiform cell was found to have only one main basal dendrite and this dendrite was usually oriented directly opposite its apical dendrite. Thus, the cell shape appeared fusiform because both the apical and basal proximal dendrites had similar diameters. In Golgi preparations, fusiform cells with similar features often displayed axons which arose from an apical dendrite and formed a basket plexus in the GL (Fig. 10).

A third type of GAD-positive cell observed in the GL was an intermediate form between the pyramidal basket cell and the fusiform cell. This third cell type was identified as a horizontal basket cell (Fig. 4). The main basal dendrite and its branches were oriented parallel to the GL and were located entirely within the hilus. The somata of horizontal basket cells usually were located subjacent to the GL, and a prominent apical dendrite was directed toward the molecular layer (Fig. 4). In Golgi preparations, similar cells had two equally large dendrites and an axon with a typical basket plexus (Fig. 11). Their apical dendrites were shown to divide in the molecu-

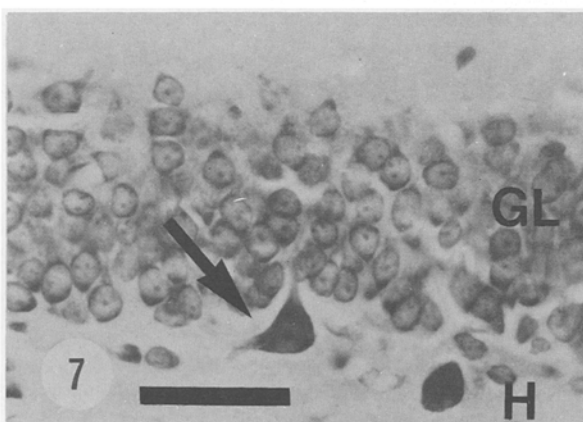
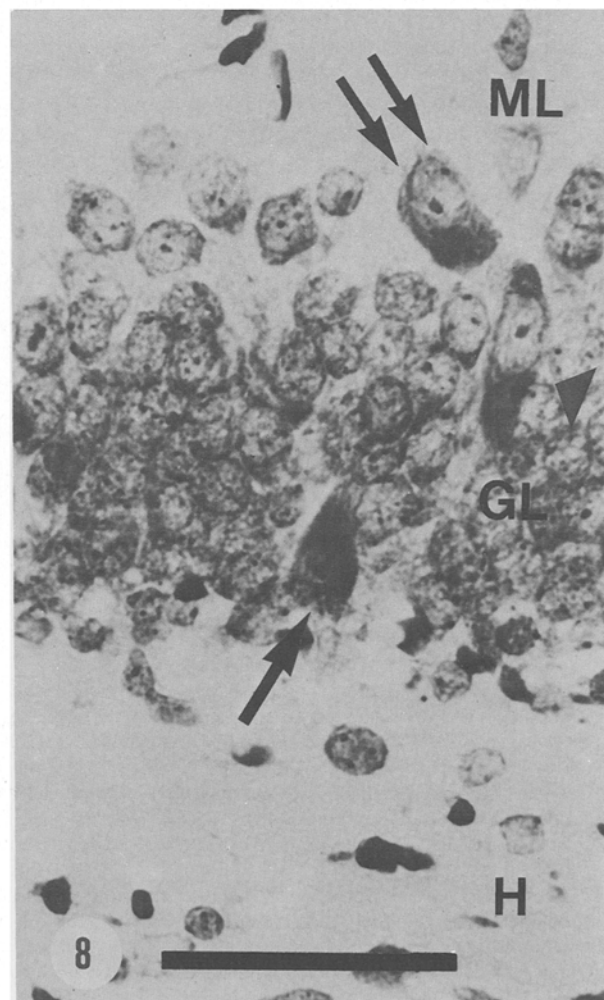
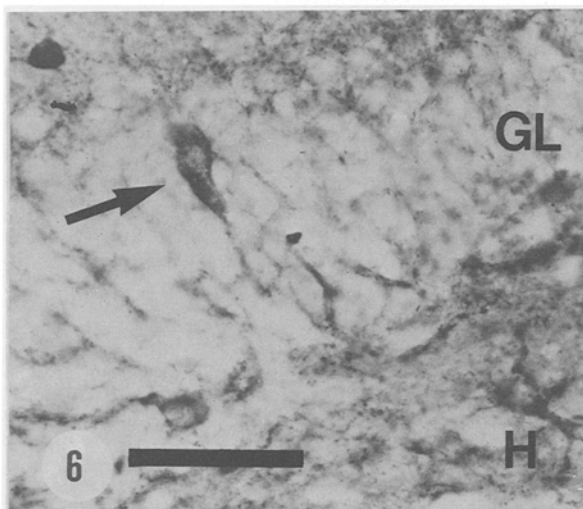
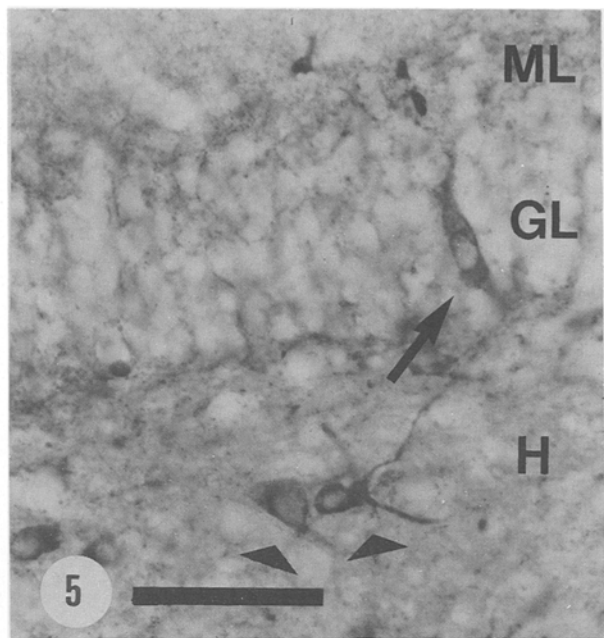
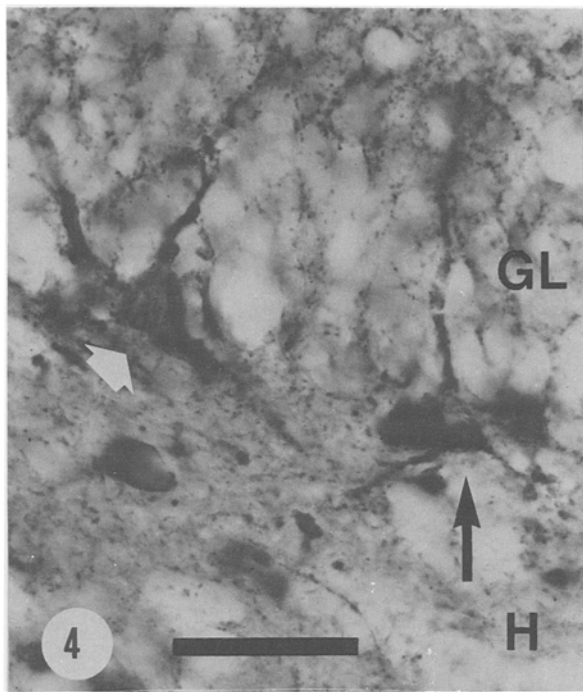
Fig. 4. Photomicrograph of GAD-positive basket cells located on the border of the GL and the hilus. One of these cells, a pyramidal basket cell (*arrow*), has two basal dendrites while the other, a horizontal basket cell (*arrowhead*) has only one basal process. Bar represents 50 μ m

Fig. 5. Photomicrograph of a GAD-positive, fusiform basket cell (*arrow*) located with its nucleus in the lower half of the GL. The cell has two main dendritic shafts which arise at opposite ends of the soma. Two GAD-positive cells (*arrowheads*) are shown in the hilus. Bar represents 50 μ m

Fig. 6. Photomicrograph of a GAD-positive inverted fusiform basket cell soma (*arrow*) located within the outer half of the GL. A dendrite from this cell is directed toward the hilus. Bar represents 50 μ m

Fig. 7. Photomicrograph of the GL of the dentate gyrus from a cresyl violet preparation. A soma of a probable horizontal basket cell (*arrow*) is shown at the border with the hilus. Bar represents 50 μ m

Fig. 8. Photomicrograph of the dentate gyrus stained with cresyl violet shows three types of probable basket cells. The soma of a pyramidal basket cell (*arrow*) appears on the border between the GL and hilus. An inverted fusiform basket cell soma (*arrowhead*) is shown with its nucleus in the outer half of the GL. In the molecular layer a round soma of a probable basket cell (*double arrows*) is shown. Note that the granule cells have smaller somal diameters than these three cells. Bar represents 50 μ m



Figs. 4-8

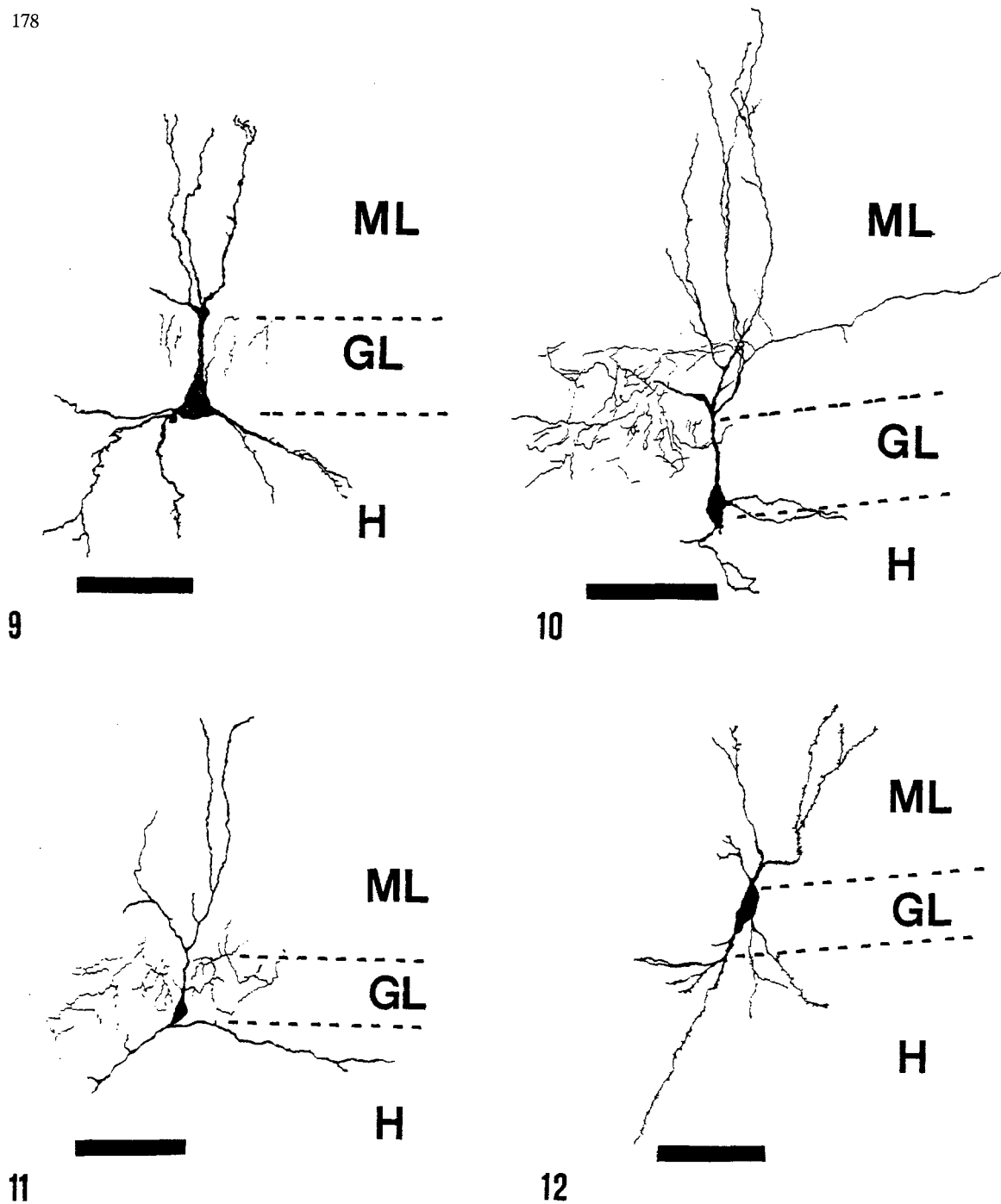
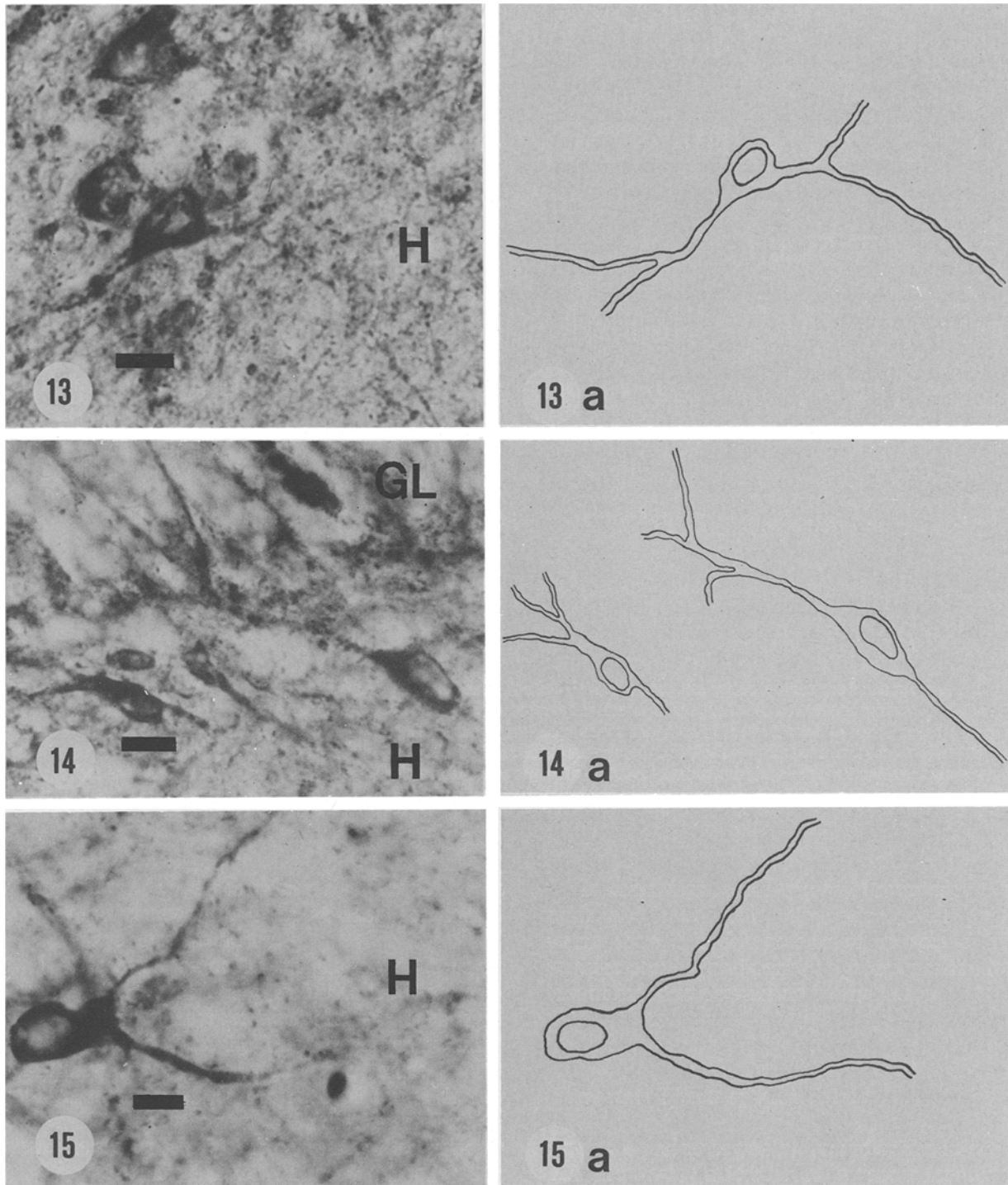


Fig. 9. Camera lucida drawing of a pyramidal basket cell obtained from a rapid Golgi preparation. A number of dendrites arise from this soma's basal portion and branch in the hilus. The apical dendrite passes through the GL before branching in the molecular layer. Part of this neuron's axon is shown to form descending processes in the GL. Bar represents 100 μm

Fig. 10. Camera lucida drawing of a fusiform basket cell located with its soma in the lower half of the GL. Only one basal process arises from the soma while another dendrite arises from the side of the soma. The axon arises from the apical dendrite in the molecular layer and then forms a veil-like plexus around granule cell somata. Bar represents 100 μm

Fig. 11. Camera lucida drawing of a horizontal basket cell from a Golgi-Cox preparation. The axon of this cell arborizes in the GL, and its only basal dendrite branches immediately upon entering the hilus. Bar represents 100 μm

Fig. 12. Camera lucida drawing from a Golgi-Cox preparation of an inverted fusiform basket cell. This cell has one thick dendrite inside the hilus and other thinner dendrites in the molecular layer. The dendrites are either aspiny or sparsely-spiny, but one dendritic branch in the molecular layer has several spines. The axon of similar cells ramify in the GL as do the axons of the other types of basket cells. Bar represents 100 μm



Figs. 13–15. Photomicrographs and line drawings of GAD-positive somata in the hilus of the dentate gyrus. **Figures 13 and 13a** show a GAD-positive cell with a bipolar shape. **Figures 14 and 14a** show two other fusiform or bipolar GAD-positive cells in the hilus beneath the GL. **Figures 15 and 15a** show an example of a GAD-positive stellate cell in the hilus. Bar represents 10 μ m

lar layer about 100–150 μ m from the somata, while the basal dendrites divided much closer (Fig. 11). This bipolarity was also observed in Nissl preparations (Fig. 7).

The fourth type of GAD-positive cell found in the GL was classified as an inverted fusiform cell (Fig. 6). The large somata of these cells were located in the outer half of the GL, the part adjacent to the

molecular layer. A thick dendrite arose from each end of the ovoid soma of these inverted fusiform cells. Neurons with similar sizes and locations were found in Golgi preparations where they displayed dendrites which branched in the hilus and molecular layer (Fig. 12). Such neurons had axons that formed a basket plexus in the GL (Seress and Pokorny 1981). Somata of inverted fusiform cells were also observed in Nissl preparations (Fig. 8). It is worth noting that the only types of non-granule neurons identified in Nissl specimens of the GL were the same cell types that have been described above to contain GAD-positive reaction product.

The only other GAD-positive structures in the GL were the 1–2 μm diameter puncta which apposed the somata and proximal dendrites of granule cells. As reported previously (Ribak et al. 1978) the granule cells did not contain GAD-positive reaction product (Figs. 3–6).

Neurons in the Hilus

Sections incubated in anti-GAD serum displayed numerous GAD-positive neurons within the hilus (Fig. 1). These neurons were located throughout the hilus but were most numerous beneath the suprapyramidal blade of the GL (Figs. 1, 5, and 14). The GAD-positive hilar cells displayed a wide variety of shapes and sizes and the majority of these neurons had round somata of medium size (20 μm somal diameter) and two or three main dendrites (Figs. 13–15). They were either multipolar, bipolar or fusiform. Because of the wide range of shapes and sizes of their somata and dendrites, it was difficult to determine if they corresponded to all 20 types of hilar neurons described by Amaral (1978). Nonetheless, the GAD-positive hilar cells that displayed fusiform and bipolar shapes (Figs. 13–15) closely resembled the fusiform and stellate cells which were described as local circuit neurons of the hilar region (compare with Figs. 19 and 20 of Amaral 1978). Also, GAD-positive puncta were observed in the hilus with an even distribution.

In Nissl preparations, the largest number of neurons in the hilus were found in the suprapyramidal portion, and this concentration of neurons is similar to that for the GAD-positive cells. Counts were made of the actual number of GAD-positive cells in the hilus from a number of sections to determine their relative numbers. For each 40 μm section, 40–50 GAD-positive cells were found in the hilus (Fig. 1). The number of neurons in 40 μm Nissl-stained sections of the hilus was compared to the number in these immunocytochemical preparations,

and the counts indicated that at least 60% of hilar neurons were GAD-positive.

Discussion

The combined use of immunocytochemical, Golgi and Nissl-stained preparations has facilitated the identification of many GABAergic cell types in the dentate gyrus of the rat. The data from each of these techniques were consistent with data obtained from the other methods. For example, the four types of GAD-positive non-granule neurons found in the GL had similar: (1) somal features to those for non-granule neurons in Nissl-stained preparations, and (2) proximal dendritic branching angles and patterns to those basket cells in Golgi preparations. Thus, the use of these methods in separate specimens provides valuable data about the GABAergic cells of the dentate gyrus.

GABAergic Cell Types in the Molecular Layer and GL

The results of our previous study of GAD-positive cells in the dentate gyrus (Ribak et al. 1978) indicated that at least two cell types were GABAergic, i.e., the pyramidal basket cell and other short axon cells. The present analysis is consistent with these findings but extends the identification of the other short axon neurons in the GL and molecular layer to a number of specific cell types, all of which appear to be local circuit neurons. These include three other types of GAD-positive basket cells in the GL: fusiform, horizontal and inverted basket cells. Together, the four basket cell types are the only non-granule neurons in the GL. They have axons that form most of the pericellular plexus with somata of granule cells. Recently, we have demonstrated that these axons form symmetric synapses with the somata and proximal dendrites of granule cells (Ribak 1982). The localization of GAD within somata of all four types of basket cells and within axon terminals that form such a pericellular plexus around somata of granule cells indicates an abundance of GABAergic synapses at this site. The reported high concentration of GABA receptors in the neuropil between granule cells is consistent with this idea (Chan-Palay 1978). Since GABA is an inhibitory neurotransmitter in the hippocampus (Curtis et al. 1970), the finding that basket cells are GABAergic is consistent with physiological data that indicate axons of basket cells are inhibitory in nature (Andersen et al. 1966).

GAD-positive cells were less frequent in the molecular layer than in the GL of the dentate gyrus. This finding is consistent with quantitative data that show a similar relationship based on observations made in Nissl-stained preparations (Seress and Pokorny 1981). When the GAD immunocytochemical preparations were compared to the Golgi preparations, it appeared that some of the GAD-positive cells in the part of the molecular layer which is nearest to the GL were basket cells. Based on the large number of GAD-positive terminals in the molecular layer and previous electron microscopic observations, the more superficial GAD-positive cells in the molecular layer probably give rise to the terminals that form axodendritic symmetric synapses with granule cells (Ribak et al. 1978). The wide variety of shapes and sizes of most of these molecular layer cells precludes the type of rigorous classification that was used for the basket cells in the GL. Nonetheless, it is likely that most of the non-granule neurons in the molecular layer are GABAergic local circuit neurons.

GABAergic Cell Types in the Hilus

Many varieties of GAD-positive cells are found in the hilus. Some of them have been identified as fusiform and stellate cells (Amaral 1978) based on their somal size and dendritic branching pattern. Such hilar cells have aspiny dendrites and locally arborizing axons which are characteristics common to basket cells in the GL (Ribak and Anderson 1980; Seress and Pokorny 1981). These findings indicate that GABAergic hilar neurons have similar morphological features to the local circuit GABAergic neurons in other parts of the dentate gyrus.

The most impressive finding about these hilar GAD-positive cells is their large number. Results of retrograde transport studies have indicated that 80% of hilar neurons give rise to both associational and commissural projections, i.e. their axons project to both the ipsilateral and contralateral dentate gyrus, respectively (Swanson et al. 1978, 1981; Laurberg 1979; West et al. 1979; Berger et al. 1981; Voneida et al. 1981). The sizes, shapes and locations of such retrogradely labeled, associational and commissural neurons are similar to those features of GAD-positive hilar cells. Since 60% of hilar neurons are GAD-positive, these data indicate that many GABAergic hilar cells give rise to associational and commissural projections. This interpretation is consistent with recent physiological data which show that stimulation of the contralateral CA3-4 areas causes inhibition of spontaneous cell firing in 25% of the

granule cells (Buzsáki and Czéh 1981). Since GABA has an inhibitory effect on hippocampal neurons (Curtis et al. 1970) many of the GABAergic cells of the hilus are probably inhibitory projection neurons. These findings are consistent with the existence of GABAergic projection cells in other brain regions such as the neostriatum and cerebellar cortex (Ribak et al. 1978, 1979, 1981).

Conclusions

The GABAergic cells in the dentate gyrus appear to be both projection and local circuit neurons. The idea that inhibitory GABAergic neurons have hilar association and commissural projections changes the traditional view of these pathways as being exclusively excitatory (Deadwyler et al. 1975). Thus, the recent electrophysiological results which suggest feed-forward inhibition of granule cells by commissural excitation (Buzsáki and Czéh 1981) may be explained in either of two ways: (1) excitatory axons of the commissural pathway may synapse with inhibitory basket cells which inhibit the granule cells, or (2) inhibitory axons of the commissural pathway may synapse directly on granule cells to inhibit them. Our recent observations that degenerated commissural terminals synapse with basket cell bodies and dendrites as well as that degenerated terminals in the molecular layer form both symmetric and asymmetric synapses provide morphological evidence to support both feed-forward and direct inhibition through the commissural pathway (Ribak and Seress 1982).

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