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Quantitative morphology and synaptology of cerebellar glomeruli in the rat

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Summary. Computer-assisted stereological and quantitative morphological approaches were used to analyse cerebellar glomeruli of the "simple type" in serial ultrathin sections. It was found that, of the total volume (110–200 μm^3) of the glomeruli studied, 53% was occupied by granule cell dendrites, 34% by mossy terminal and 13% by Golgi axons. None of the four analysed glomeruli contained Golgi cell dendrites. The mossy terminals that were studied received, on the average, 53 granule cell dendrites. All of the dendrites originated from different granule cells and all made synaptic contacts with mossy terminal. However only about 60% of granule cell dendrites made synapses with Golgi axons. The surface of the mossy terminals occupied by synaptic junctions, was found to be 5.4–5.5%. Each granule cell dendrite emitted 3–5 terminal protrusions ("dendritic digits"). Each digit receives one or more synaptic contact from either the mossy terminal (67% of all digits), or from Golgi axon varicosities (25%). Only about 8% of all digits were contacted synaptically by both types of axonal terminals. All of the dendritic digits that were observed made synaptic connections. Each digit was, on the average, connected by symmetric attachment plaques to 4 neighbouring digits. Three-dimensional reconstructions of mossy terminal and some of contacting granule cell dendrites demonstrated that the dendrites curved around the central mossy terminal and were much longer than expected from earlier Golgi-impregnation studies. In addition to mossy terminals and Golgi axons, an axon terminal of small calibre that contained large, empty, spheroid vesicles were occasionally observed. These terminals, which are most likely the axonal varicosities of ascending parallel fibers, made synaptic contacts exclusively with granule cell dendrites at the periphery of the glomeruli.

The results demonstrate that, in the rat cerebellum, there is a high degree of convergence of granule cells at a glomerulus (53 to 1); and that there is a rich inhibitory input to about 60% of all granule cell dendrites. It is also shown that the main postsynaptic targets, for both mossy and Golgi axons, are the dendritic digits. The presence of synaptic contacts between parallel-fiber-like varicosities and granule cell dendrites may be an additional source of excitation within the glomerulus.

Key words: Cerebellar cortex – Synaptic glomerulus – Mossy terminal – Quantitative morphology – Three-dimensional reconstruction

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Introduction

The cerebellar glomerulus is one of the most complex arrangements of synapses found in the central nervous system. The structural organization has been described in detail in different species (Gray 1961; Palay 1961; Hámori 1964; Hámori and Szentágothai 1966; Fox et al. 1967; Larramendi 1969a, b; Llinas and Hillman 1969; Mugnaini 1972; Palay and Chan-Palay 1974). In most cerebellar glomeruli, two presynaptic elements, the excitatory mossy terminals and the inhibitory Golgi axon varicosities, establish multiple synaptic contacts with the numerous dendritic processes of the granule cell dendrites. This arrangement represents a favourable structural basis for divergence of mossy fiber impulses to the postsynaptic granule cells.

A quantitative determination of the transfer of information from mossy terminals to granule cells requires reliable quantitative estimates of the numbers of pre- and postsynaptic elements and the number of synaptic contacts within one synaptic glomerulus. The number of granule cell dendrites entering a glomerulus was estimated by Fox et al. (1967) and by Eccles et al. (1967) to be 15 and 20 in the cerebellum of monkey and cat, respectively. In a subsequent quantitative study (Palkovits et al. 1972), utilizing light- and electron microscopic preparations, the number of granule cell dendrites in the glomeruli of the cat was calculated to be much higher (112 dendrites per glomerulus). However, none of these studies dealt with numerical estimations of synaptic junctions within the glomeruli, an important structural parameter when evaluating impulse transfer in this complex synapse. The determination of quantitative relations within the glomerulus requires quantitative investigation of the components of individual glomeruli. This paper describes a quantitative analysis of the components of four simple cerebellar glomeruli in the rat cerebellum that utilizes 3-D reconstructions from serial sections and stereological methods.

Materials and methods

Two adult female albino rats were anesthetized with chloral-hydrate (350 mg/kg i.p.) and perfused with a fixative solution consisting of 1% paraformaldehyde and 1% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4. After removing the brain from the skull, small tissue blocks were cut from the hemispheres of the cerebellum and immersed in the same fixative overnight at 4° C. The specimens were

then postfixed in 2% OsO_4 solution diluted in phosphate buffer, dehydrated in graded ethanol series, and embedded in Durcupan.

Serial ultrathin (ca. 80 nm) sections were cut by an LKB V. ultrotome. Ribbons of 120–200 consecutive sections were mounted on formvar coated single-slot grids, and stained with uranyl acetate and lead citrate. Serial sections were examined by a JEOL 100B electron microscope.

Serial sections of four complete cerebellar glomeruli were photographed at 12000×, and analysed at 27000×. The following numbers of successive sections covered the glomeruli that were studied:

glom. I. —131 sections
glom. II. —123 sections
glom. III. —159 sections
glom. IV. —170 sections

The area of all axonal and dendritic profiles belonging to the glomeruli, the perimeter and area of mossy terminals, as well as the length of postsynaptic membrane specializations facing the mossy swellings, were measured with an electronic graphic calculator (Numonics corp., North Wales, Pa). Three-dimensional structural models of the cerebellar glomeruli were constructed with the aid of a computer reconstruction system consisting of: a PDP 11/34 minicomputer, Quantimet 720 image analyser, Macroviewer table and Canon camera for image-input, and Hewlett-Packard 7221B 4-colour plotter as graphical output device. The system was controlled by computer programs AP1 and AP3 (Zsuppán 1985). The contours of profiles selected for reconstruction were digitized and input to the computer. Three-dimensional reconstruction was restricted to a relatively small number of representative glomerular elements, using every third or fourth section in the series. The models were constructed from series of contours with the aid of a hidden-line routine. Different sides of the glomeruli could be visualised by rotating the structure around X, Y and Z axes. The volume and surface of the reconstructed structures were computed by the computer-program AP3 and checked by planimetric measurements.

Results

For methodological reasons only glomeruli of the "simple" type were investigated in this study since the maximum 200 serial sections were not sufficient to include the entire extent of large "complex" glomeruli, (i.e. glomeruli with more than one mossy terminal). The consequences of this selection will be discussed later.

The four glomeruli, which were partially enveloped by thin glial sheath, were composed of the following elements (Fig. 1):

1) One mossy fiber terminal, which contained large, spheroid synaptic vesicles, and occupied the centre of the glomerulus. Although not all mossy fiber swellings were of the terminating type, and 2 of the 4 swellings that were studied were "en passant" boutons (Table 1), all four of these will be called mossy terminals (MT in abbreviations) in this study in accord with the accepted terminology.

2) Dendrites of granule cells, which surrounded the mossy terminal and made axo-dendritic synaptic connections.

3) Varicosities of Golgi axons (Ga), which contained ovoid synaptic vesicles and established synaptic junctions with granule cell dendrites at the periphery of the glomeruli.

None of the four glomeruli studied, contained Golgi cell dendrites, which normally are present in low numbers in the cerebellar glomeruli (Hámori and Somogyi 1983b).

On the basis of the position of the mossy swelling, the four glomeruli studied could be classified as either the "terminal" type or the "en-passant" type (Fig. 2). The latter is a varicosity of a fiber that continues to another glomerulus. The granule cell dendrites, which curve around the mossy terminal (3D reconstruction, Fig. 2), are longer than expected from Golgi studies. When observing the entire extent of granule cell dendrites from their perikaryal origin, none of the dendrites were found to bifurcate or to give rise to side-branches before entering the glomerulus. Those seen to bifurcate or to branch, did so within the glomerulus. All of the dendrites were also seen to terminate in the glomerulus that they entered. No granule cell sent more than one dendrite to the same glomerulus. That is, each granule cell dendrite entered only one glomerulus, and each dendrite belonging in a glomerulus originated from a different granule cell. All granule cell dendrites were characterized by terminal end bulges, the so called "dendritic digits", which were seen to establish synaptic contacts with the mossy fiber. All dendritic digits synapsed with at least one mossy, or one Golgi axon terminal.

Quantitative data

The estimates of glomerular volume, and volumes and surfaces of the mossy fiber swellings are given in Table 1. The volume of the four glomeruli ranged from 110 and 200 μm^3. The shape of the terminal-type mossy swelling (Fig. 2) was more irregular than that of the en-passant-type. This was reflected by the "shape-factor", which was defined as the ratio of surface to volume (area of MT: volume of MT). Thus a high value for the shape-factor indicates a more irregular shape (see Table 1).

The areas of the profiles of mossy terminals (MT), Golgi axon branches (Ga) and granule cell dendrites (Grd) were also computed. The area fraction of a particular element, (according to the rule of Delesse, 1847), is an expression of its volume fraction. The volume fractions of the glomerular components are shown in Table 2. In addition, the volumes of 20 dendritic digits were measured in each glomerulus, and an average digit-volume of 0.20 μm^3 ($\pm$0.08 S.E.M.) was found. It was found that 50–70% of the Grd-volume consisted of the distal portions of the dendrites including the dendritic digits, while the remaining 30–50% was composed of the proximal parts, i.e. the "necks", of the granule cell dendrites. The range of the lengths of the long axes of the simple glomeruli was 8–12 μm, while that of the short axes 6–9 μm. The fraction of the surface occupied by synaptic junctional complex was 5.4 to 5.5%. The synapse-number per unit surface of mossy terminal (MT-synapses/μm^2) ranged from 0.669 to 0.726.

The number of granule cell dendrites that were identified and followed along the entire extent of their branches and protrusions (digits), and the number of digits, which were counted are shown in Table 3. An MT was found to receive an average of 53 granule cell dendrites, and all Grd-s were found to originate from separate granule cells. A granule cell dendrite emitted an average of 3–5 digits. While all Grd-s formed one or more synaptic contacts with the mossy

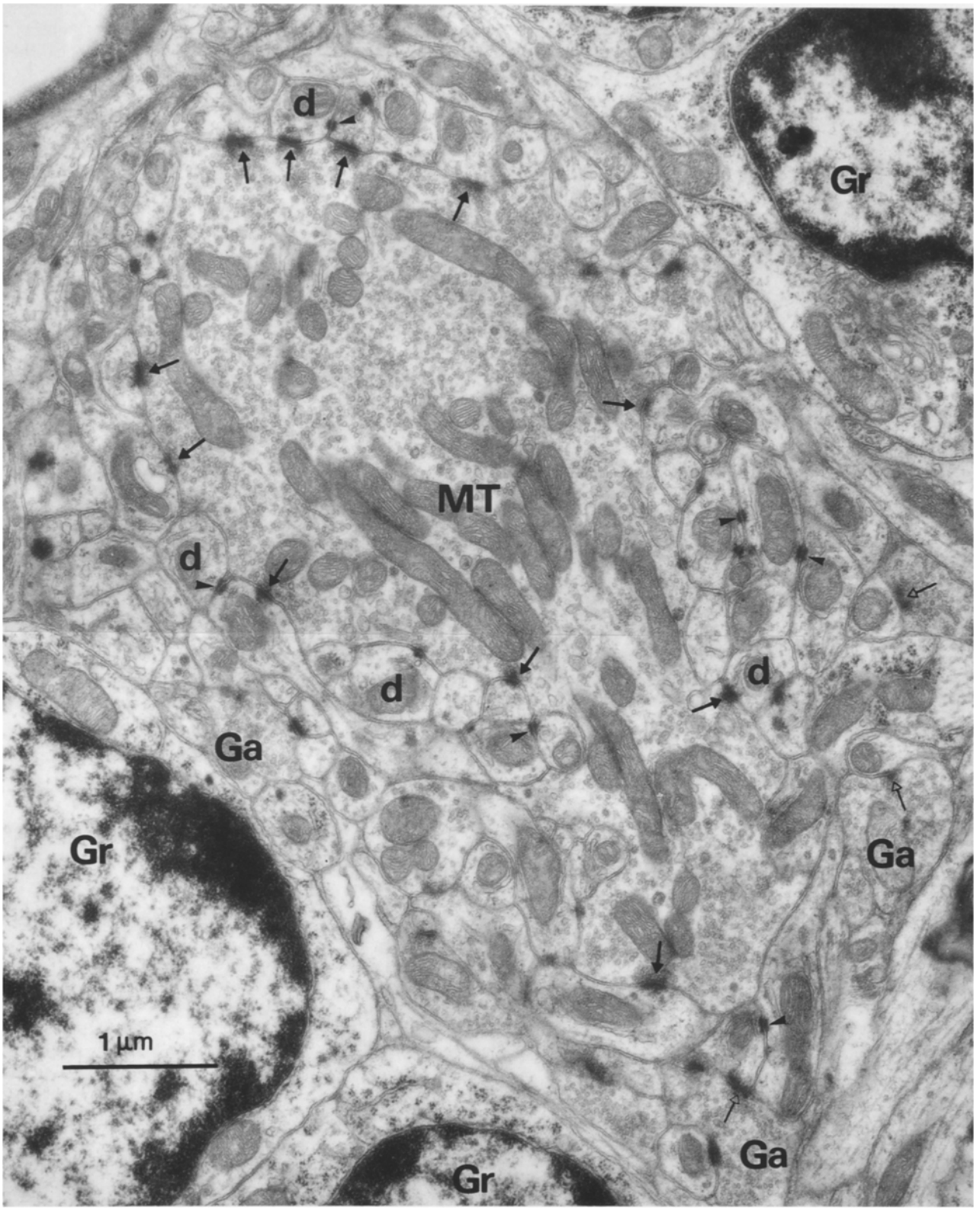

Fig. 1. Cross-section of a "simple" cerebellar glomerulus. The mossy terminal (*MT*), the core of the glomerulus, is surrounded by granule cells (*Gr*) and their dendrites and by dendritic digits (*d*). Varicosities of Golgi axons (*Ga*) are located at the periphery of the glomerulus. The digits of granule cell dendrites form numerous synapses with the mossy terminal (*arrows*) and with Golgi axons (*open arrows*). *Arrowheads* indicate attachment plaques between dendritic digits. × 27000

Table 1. Volume of cerebellar glomeruli and mossy terminals (MT)

	Type of MT	Glom. volume (μm^3)	MT-volume (μm^3)	MT-surface (μm^2)	Shape factor
Glom. 1 (131 serial sections)	Terminal	114.53	39.40	194.38	4.934
Glom. 2 (123 serial sections)	En passant	142.44	45.58	168.66	3.70
Glom. 3 (159 serial sections)	Terminal	193.0	57.90	266.39	4.601
Glom. 4 (170 serial sections)	En passant	155.52	60.84	220.38	3.622

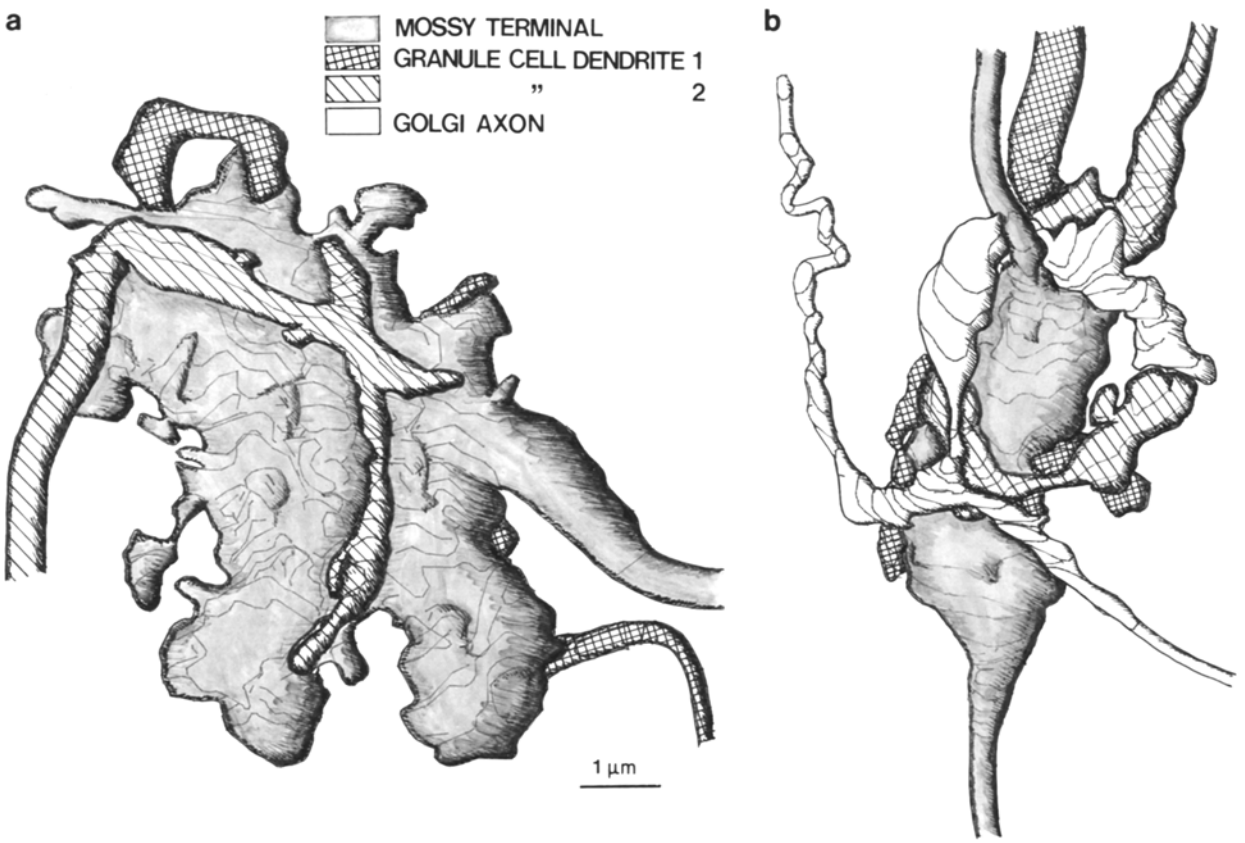

Fig. 2a, b. Spatial reconstruction of a few representative glomerular elements, using every third or fourth section in the series. **a** Mossy terminal of terminal type. **b** Mossy terminal of en passant type

Table 2. Volume distribution of mossy terminals (MT), Golgi axons (Ga) and granule cell dendrites (Grd)

	MT (%)	Grd (%)	Ga (%)
Glom. 1	34.4	58.2	7.4
Glom. 2	32.0	53.1	14.9
Glom. 3	30.0	53.9	16.1
Glom. 4	39.1	45.9	15.0
Average (±S.E.M.):	33.9% (±1.96)	52.8% (±2.55)	13.3% (±2.0)

ending, only about 60% of Grd-s received synaptic contacts from Golgi axon varicosities.

The number and incidence of granule cell dendrites synapsing with Golgi axons; digits synapsing only with MT, Ga or both type of axon terminals; are presented in Table 3. It should be noted, that all dendritic digits had synaptic connections. Seventyfive % (67%+8%) of the digits formed synapses with mossy terminal, while 33% (25%+8%) made contact with a Golgi axon. A digit formed, in most cases, only one synaptic contact. In some cases digits synapsed with both MT and Ga axons (8% of all digits), with more than one Golgi varicosities, or with mossy terminals through two separate synaptic junctions. Consequently the total number of synapses (MT-syn+Ga-syn) in glomerulus was slightly higher than the number of digits.

Table 4 shows the total number of synaptic contacts, established between mossy terminals and granule cell dendrites (MT-synapses) and between Golgi axon and granule cell dendrites (Ga-synapses), as well as the number of Golgi axon varicosities per glomerulus. The number of synapses per granule cell dendrite and the number of Ga-synapses belonging to one Golgi axon varicosity were also determined and are shown in Table 4. All MT-synapses were

Table 3. Number of granule cell dendrites (Grd) and digits within the glomeruli

	N° of Grd	N° of digits	N° of digits/Grd	N° of Grd-s synapsing with Ga	MT (%)	Ga (%)	MT and Ga (%)
Glom. 1	54	167	3.1	29 (53.7%)	73.0	21.5	5.5
Glom. 2	47	150	3.2	28 (59.6%)	64.9	26.3	8.8
Glom. 3	57	285	5.0	42 (73.7%)	63.6	26.6	9.8
Glom. 4	53	228	4.3	29 (54.7%)	66.5	25.6	7.9
Average (±S.E.M.):	53	208	3.9	60.4% (±4.6)	67.0% (±2.08)	25.0% (±1.18)	8.0% (±0.92)

Table 4. Number of synaptic junctions

	N° of MT-synapses	N° of MT-synapses/Grd	N° of Ga-synapses	N° of Ga-synapses/Grd	N° of Ga-varicosities	Ga-synapses/Ga-var
Glom. 1	130	2.41	43	1.48	12	3.58
Glom. 2	113	2.40	54	1.93	13	4.15
Glom. 3	176	3.09	145	3.45	28	5.18
Glom. 4	160	3.02	107	3.69	21	5.09
Average (±S.E.M.):		2.73 (±0.19)		2.64 (±0.55)		4.50 (±0.38)

Table 5. Number of attachment plaques (AP)

	N° of AP/Grd	N° of AP-s belonging to one digit	Number of attachment plaques between		
			Digit and digit	Digit and mossy t.	Digit and Golgi axon
Glom. 1	15.44	4.99	417	13	8
Glom. 2	15.49	4.85	364	5	15
Glom. 3	15.89	3.18	453	19	18
Glom. 4	17.32	4.03	459	18	18
Average (±S.E.M.)	16.03 (±0.44)	4.26 (±0.41)			

established on dendritic digits. A few Ga-synapses, however, were also formed on the "necks" of the dendrites.

The number of symmetric attachment plaques (AP) between two digits, a digit and a mossy terminal, and a digit and a Golgi axon were also counted. These membrane specializations were frequent within the glomeruli. An average of sixteen attachment plaques were found per granule cell dendrite (Table 5). By dividing the total number of attachment plaques with the total number of digits, the AP:digit ratio was between 1.5 and 2.5. Considering that the same attachment plaque connects two digits, the number of AP-s by which one digit is connected to other digits is just the double of the AP:digit ratio. Thus, obviously, one single digit appears to be connected by AP-s to 3–5 neighbouring dendritic digits (see Table 5).

At the periphery of the four glomeruli, a third type of axon terminal, of small calibre and containing large spheroid vesicles, was observed (Fig. 3). The morphological features excluded the possibility, that these were Golgi axons. Tracing these thin axons in the serial sections revealed that they were separate and independent of the mossy terminals. These axon terminals not only contacted the glomerular elements, but also formed synapses (of the asymmetric type) with granule cell dendrites. Morphological characteristics of these axonal profiles, particularly the size and shape of synaptic vesicles, suggested that they were the synaptic varicosities of ascending parallel fibers.

Discussion

1) Shape, size and volume of simple glomeruli

The three-dimensional reconstructions and shape-factors of the glomeruli indicate that mossy fiber swellings of "en passant" type are more regular than those of the "terminal" type.

The computer-reconstruction of cerebellar glomeruli confirmed earlier assumptions with regard to the spatial appearance and extension of these complex synapses, and, as a appearance and extension of these complex synapses, and, as a consequence, the description of the glomerulus-image made by Szentágothai (Eccles et al. 1967, p. 129, Fig. 75) requires no significant revision. This description can be appended with regard to the structure of the granule cell dendrites. These usually do not have short "claws", as seen in the drawing by Szentágothai, but give off long branches that often curve around the whole glomerulus, as seen on the drawing of Chan-Palay (Palay and Chan-Palay 1974, p. 125, Fig. 108). The dendritic digits, described in previous studies (made mostly in cat) as bulbous expansions of the dendritic branches (Eccles et al. 1967; Palkovits et al. 1972), are not bulbous in the rat, but rather digitiform, thin terminals (Palay and Chan-Palay 1974), of a diameter not larger than that of the parent dendrites themselves.

Four glomeruli of the "simple" type were used for quantitative analysis in this study. The sizes of these glomeruli were less than those reported in previous studies. As a consequence, the sample described here is not random, since smaller than average glomeruli were investigated. Eccles et al. (1967) estimated the average long axis of cerebellar glomeruli about 20 μm in the rat. In cat the average long axis of glomeruli was 17 μm, while that of the short

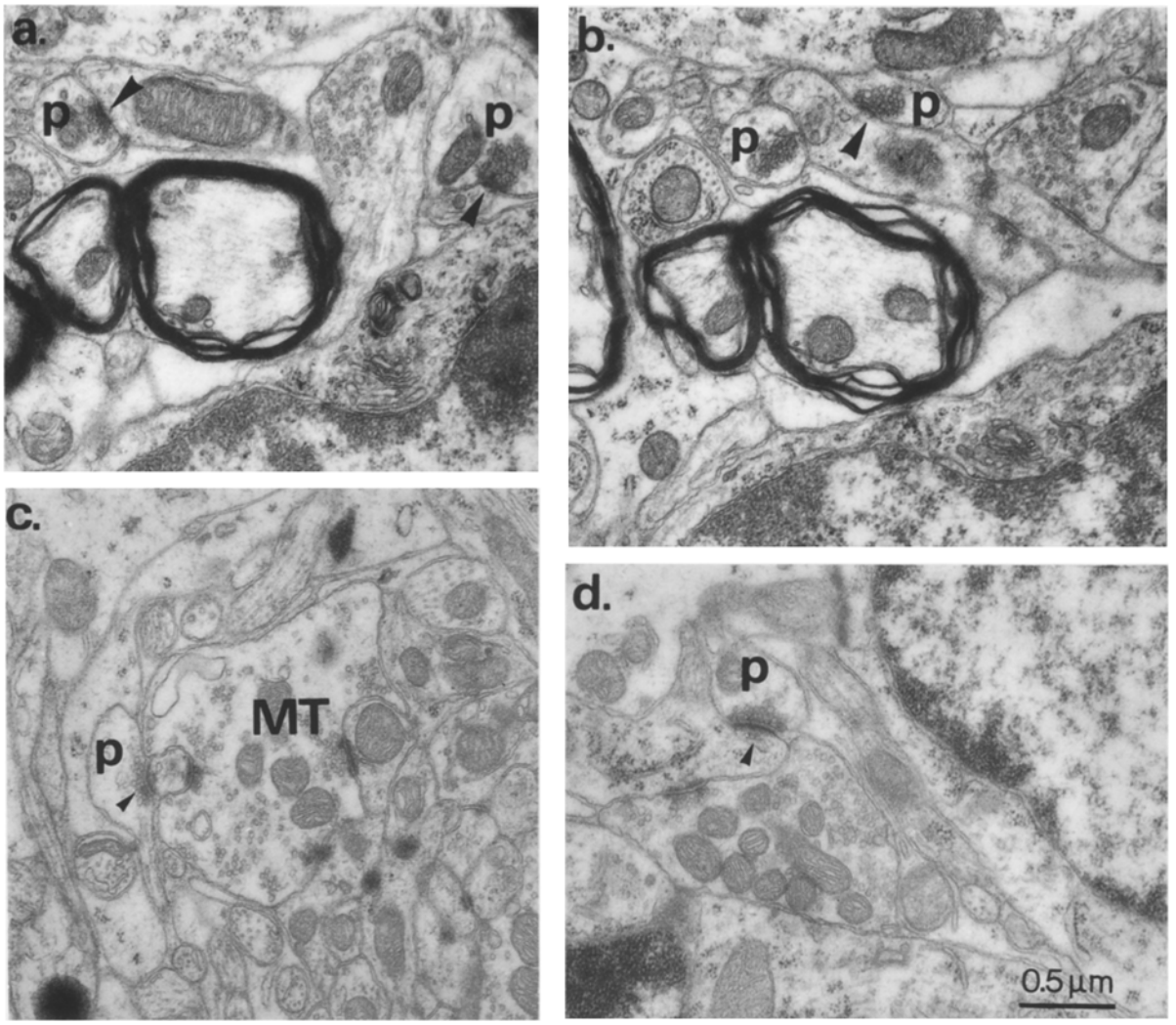

Fig. 3a–d. Parallel fiber-like axon terminals (*p*) synapsing (*arrowheads*) with granule cell dendrites at the periphery of the glomerulus. The synaptic vesicles in these small varicosities are large, empty and round. **a** and **b** are taken from the periphery of glomerulus 4, **c** is from glomerulus 1, **d** from glomerulus 3. ×27000

axis was 14 µm (Palkovits et al. 1972). According to the latter authors, the average light microscopic glomerular volume was about 1500–1800 μm^3. Since in the present study, glomerular volumes were computed from data obtained from electronmicrographs and the sampling of glomeruli was not random, it is difficult to make comparisons with the previous estimations based on light micrographs. Nevertheless, we think, that the cited, light microscopic values are slightly overestimated, because of difficulties in establishing the exact margin of a glomerulus in the light microscope. Low resolution makes inclusion of extraglomerular structures, like glia, ascending, descending axons, inevitable. In addition, two or more tightly neighboured glomeruli, the so called "complex glomeruli" that are not separated by granule cells, might be mistaken for a single glomerulus. The frequent presence of such "protoplasmic islets" composed of more than one simple glomerulus has been described previously (Palay and Chan-Palay 1974). Both of these errors would increase the apparent glomerular volume measured in the light microscope. We suggest, therefore, that the average volume is most likely less than 1500–1800 μm^3.

The difference between the average digit-volume measured in this study (0.20 μm^3) and in that by Palkovits et al. (1972) in cat (0.83 μm^3) may be due to the different methods of calculation that were used, (particularly the lack of direct quantitative EM measurements of digits in Palkovits et al.'s study), or may be real, that is, that the dendritic digits in cat are larger than those in the rat. Similar deviations in the size of cerebellar glomeruli among different species (in this case between rat and cat) are also possible. However there is no evidence of size differences in the literature on mammals. Cerebellar glomeruli of the turtle (long and short axis 20–60 µm and 7–20 µm respectively) serve as example of extreme sizes (Mugnaini et al. 1974). The mossy fiber terminal, the granule cell dendrites and the Golgi axons filled 30–39%, 46–58% and 7–15% of the glomerular volume, respectively. In the cat cerebellar glomerulus (Palkovits et al. 1972) only 31% of the glomerular volume was occupied by granule cell dendrites. Similarly, this difference may be the result of species differences, or differences that result from the techniques used. Considering the larger volume of this digits in the cat (and the larger number of dendrites per glomerulus) one would also expect a proportionally larger volumetric representation for the granule cell dendrites in the cat cerebellar glomerulus.

2) Convergence and divergence in the glomerulus

Since the sample studied here includes glomeruli of smaller size, the number of dendrites per glomerulus probably represents the lower limit. This means, that in an average glomerulus in the rat the granule cell dendrite: glomerulus ratio must be greater than 50:1. Since each dendrite in a glomerulus originates from a different granule cell, the ratio between granule cell dendrites and the mossy terminal represents the ratio between individual granule cells and a mossy terminal. Estimations made by Fox et al. in monkey (1967) and Eccles et al. (1967), in the rat, suggesting that 15 to 20 dendrites would participate in a glomerulus in average are most likely underestimates. Palkovits et al. (1972), assumed the glomerulus: granule cell ratio to be 1:28, based on planimetric measurements in the granular layer of the cat cerebellum. Since each granule cell has, on the average, 4 dendrites (Palkovits et al. 1972), an average of $28 \times 4 = 112$ dendrites would be expected to participate in the cat cerebellar glomerulus. Although the possibility of species differences cannot be excluded, both values appear to be overestimates.

The question, as to whether Golgi axon varicosities of a glomerulus originate from one or from different Golgi cells, cannot be decided by methods used in this study.

3) Synaptic connections

The surfaces of the four mossy fiber swellings varied between 170 and 270 μm^2, and were occupied by 113 to 176 synapses. The synapse density, however, was found to be remarkably constant (0.682 ± 0.015 synapses/μm^2), and the area of the synaptic surface was 5.45% (± 0.029 S.E.M.), in good agreement with the synaptic surface area of mossy terminals (5.7%), found by Hámori and Somogyi (1983a) in the rat cerebellar cortex. The number of Golgi axon varicosities belonging to one single glomerulus varied between 12 and 28. Although a precize correlation between varicosity number and the size of the glomeruli plus the number of Grd-s could not be established, the number of synapses per varicosity was found to be constant: 4.48 (± 0.30 S.E.M.) axodendritic synapses per varicosity.

The relatively large number (43 to 145 within one glomerulus) of the inhibitory Golgi axon synapses is notable, and suggests the existence of an extremely strong postsynaptic inhibitory potential. The innervation of 33% of all dendritic digits by Golgi axon varicosities may be a maintenance factor for the survival of granule cell dendrites in mossy fiber deafferented glomeruli. In previous descriptions of chronically isolated cerebellar cortex (Hámori and Szentágothai 1966), dendritic digits, although reduced significantly in number, did survive chronic mossy fiber deafferentation. It was suggested that only those dendrites and dendritic digits survived, which maintained synaptic contact(s) with surviving Golgi axons. Studies utilizing 3D reconstruction and quantitative analysis of cerebellar glomeruli chronically deafferented of mossy fibers are presently being made in our laboratory to investigate this hypothesis.

At the periphery of the glomeruli studied, there was observed, in addition to mossy terminals and Golgi axons, a third type of axon terminal that was not continuous with mossy terminals and which contained large spheroid synaptic vesicles. These small axon terminals established synaptic contacts with granule cell dendrites, or dendritic digits. These axonal elements may represent:

a) ascending part of granule cell axon (parallel axon)
b) monoaminerg fibers
c) Purkinje-axon collaterals
d) Lugaro-cell axon collaterals
e) climbing fiber collaterals

Considering synaptic vesicle size and shape, the unknown glomerular axon terminals do not appear to be noradrenergic (Kimoto et al. 1981) or serotoninergic (Chan-Palay 1975) fibers. Aside from mossy terminals, empty round vesicles are characteristic of parallel and climbing fibers in the cerebellar cortex. However, the vesicles in climbing fibers (Palay and Chan-Palay 1974) are crowded and embedded into a dense matrix, while the glomerular small axon terminal is more similar to the parallel axon terminals in the molecular layer, with their loosely organized synaptic vesicles and light matrix. Although final proof for these axons being ascending granule cell axons can only be provided by Golgi-EM studies, the previous observation appears to strenghten, although indirectly, this notion. "Parallel"-axon varicosities, i.e. ascending granule cell axons, were observed to synapse in both deafferented and normal cerebellar cortex with the axon hillock of Golgi cells in the granular layer (Hámori 1981). It is also remarkable that granule cell-to-granule cell dendritic synaptic contacts can be induced by mossy fiber deafferentation (Hámori and Somogyi 1982).

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