ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol. Exp. 1995, 55: 35-47

Cerebellovestibular projection from the posterior lobe cortex in the rabbit: an experimental study with the retrograde HRP method. II. Zonal organization

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Abstract. The mediolateral distribution of neurones of origin of the corticovestibular projection from the cerebellar posterior lobe in the rabbit was studied with the retrograde horseradish peroxidase (HRP) tracing method. After iontophoretic injections confined to various subdivisions of the vestibular nuclear complex (VNC) labelled Purkinje neurones were found ipsilaterally in widespread mediolateral cortical regions of vermal lobules from VI to IX, as well as in crus I and crus II of the ansiform lobule, the copula pyramidis, lobule HV and the ventral paraflocculus. However, when projections from individual sublobules were examined, a clearly visible zonal pattern was found. Thus, Purkinje neurones projecting to VNC were arranged in longitudinal bands with medial and lateral boundaries quite well demarcated. These bands had a different width and were found to be located at different distances from the midline. The present findings constitute the first indication of a zonal organization of corticovestibular projections from individual sublobules of the cerebellar posterior lobe in the rabbit. This zonal arrangement of VNC afferents is discussed with the special emphasis on the cerebellar longitudunal zones and related to previous studies on other species.

Key words: vestibular afferents, cerebellar cortex, zonal organization, HRP nd WGA-HRP retrograde tracing, rabbit

INTRODUCTION

Classical anatomical investigations indicated that each half of the mammalian cerebellar cortex consists of three longitudinal zones that do not overlap: (1) a medial, vermal zone projecting to the fastigial nucleus; (2) an intermediate, paravermal zone projecting to the interposite nucleus; and (3) a lateral hemispheral zone projecting to the dentate nucleus (Jansen and Brodal 1942, Walberg and Jansen 1961). Based on the myeloarchitecture and organization of efferent connections seven major longitudinal zones were delineated in the cerebellar cortex (Voogd 1964, Van Rossum 1969, Voogd and Bigaré 1980). The medial zone was divided into A zone (which is subdivided into three compartments in the caudal vermis) projecting to the fastigial nucleus as well as to the medial vestibular nucleus (MV) and B zone which sends axons to the lateral vestibular nucleus (LV). In the paravermal zone, three zones C1, C2 and C3 were distinguished, connecting with the interposite nuclei. Finally, zones D1 and D2 fall within the lateral zone, which projects differentially to the dentate nucleus.

Most authors agree that the vermal B and A zones are the richest sources of corticovestibular projections. These zones were clearly described in the anterior lobe, but they have not been established in the posterior lobe. Generally, it has been suggested that the region of vestibular projection is very narrow or nonexistent in lobules VI and VII, but is wider and more complexly arranged in lobules VIII and IX (Walberg and Jansen 1961, Voogd 1964, Angaut and Brodal 1967, Van Rossum 1969, Haines 1975a,b, Voogd and Bigaré 1980, Balaban 1984, Klinkhachorn et al. 1984, Epema et al.1985, Thunnissen et al. 1989). On the other hand, Dietrichs et al. (1983) observed wide mediolateral distribution of corticovestibular neurones. Vestibular afferents arising laterally to B zone (C and D zones) were reported as a sparse only from crus I and crus II of the ansiform lobule (Eager 1963, Haines 1975a). Although the general organization of the corticovestibular projection was revealed by these studies in various species, detailed information on the mediolateral arrangement of the cells of origin is still unknown. Thus, the present investigation was undertaken with the retrograde horseradish peroxidase (HRP) tracing method in the rabbit in order to identify precisely the zonal arrangement of Purkinje neurones in terms of its corticovestibular projections, not only from lobules but also from individual sublobules of the posterior lobe vermis and hemisphere.

METHODS

The results presented in this report are based on 25 experiments. Adult rabbits were injected iontophoretically with HRP (Sigma, type VI) or wheat germ agglutinin-horseradish peroxidase (WGA-HRP, Sigma) in various regions of the vestibular nuclear complex (VNC) on the right side. Details of the method of tracer administration as well as histochemical procedure were described in a corresponding report (Bukowska 1995). The location of labelled Purkinje neurones in the cerebellar posterior lobe was plotted from each section and transferred to diagrams of sagittal section of the cerebellum from the midline to 7.2 mm laterally. In four cases labelled neurones were identified on transversal sections according to description of Brodal (1940). The nomenclature of the cerebellar posterior lobe was reffered to Van Rossum (1969). However, in this study several additional vermal sublobules (VIa1, VIb1, VIIb1 and VIIIb1) were distinguished. In order to establish the location and extent of labelling zones, the medial and lateral borders of distribution of labelled Purkinje neurones in the individual sublobules were plotted on diagrams of the horizontal view of the cerebellar posterior lobe vermis and hemisphere, including lobule HV.

RESULTS

The experimental material was classified into groups with similar injections within VNC. Detailed descriptions and diagrams of the injection sites were provided in a corresponding paper (Bukowska 1995).

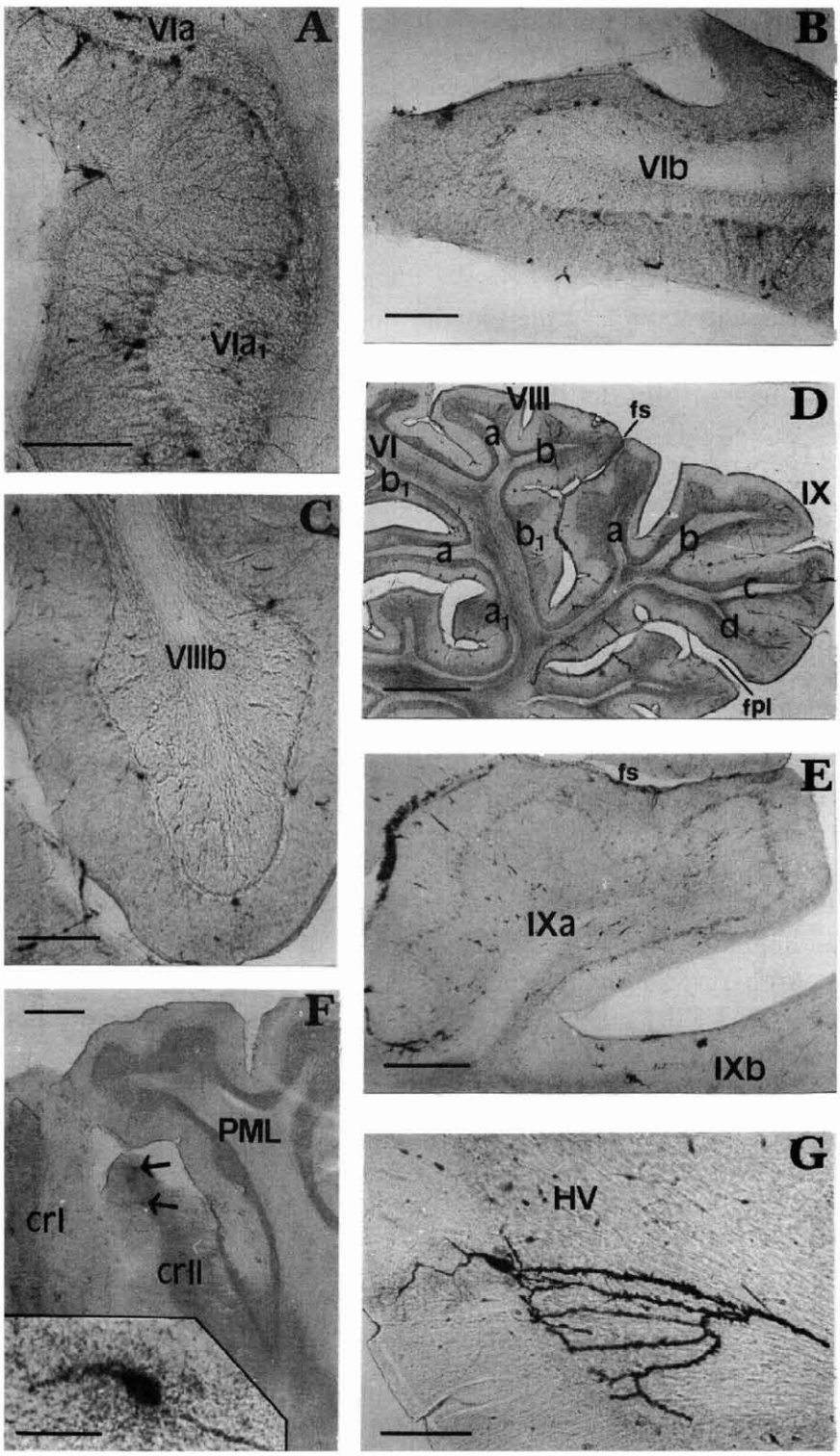

Fig. 1. Photomicrographs of retrogradely labelled Purkinje neurones on sagittal sections through the cerebellar posterior lobe in case No. 200. Labelled neurones in: (A) sublobule VIa1 and on the ventral side of basal part of sublobule VIa, 1.8 mm from the midline, (B) apical part of sublobule VIb, 3 mm from the midline, (C) sublobule VIIIb, 1.8 mm from the midline, (D) sublobule IXa, 180 μm from the midline and (E) their magnification, (F) apical part of crus II, 5.5 mm from the midline, (G) lobule HV, 6.3 mm from the midline. Inset is higher magnification of labelled neurone on the top of crus II. Bars represent 1,500 μm for D, 500 μm for E and F, 250 μm for A-C, 100 μm for G; 50 μm for inset.

Zonal arrangement of labelled Purkinje neurones in the posterior lobe after HRP or WGA-HRP injection into all four vestibular nuclei

In three experiments the tracer was injected into the superior vestibular nucleus (SV), MV, LV and the inferior vestibular nucleus (IV).

In rabbit No. 200 labelled neurones were found ipsilaterally in the entire mediolateral extent of vermis and in the hemisphere, from the midline to about 7.2 mm laterally. In lobule VI distribution of labelled neurones was changing in the mediolateral dimension. They were seen in more ventral sublobules in the medial part of vermis and in more dorsal sublobules in the lateral part. In sublobules VIa1 and VIa labelled neurones were seen at distance of 0-1.9 mm and 540 μm-1.9 mm from the midline, respectively (Fig. 1A). In sublobules VIb1 and VIb they were present more laterally, at distance of 810 μm-2.1 mm and 1.4-3.4 mm from the midline, respectively (Fig.1B). In sublobule VIc few neurones were labelled in a single section, 2 mm from the midline. In lobule VII neurones were labelled exclusivelly in sublobule VIIb1 in a band located 1.9-2.6mm from the midline. In lobule VIII (pyramis) labelled neurones were observed in all sublobules at distance of 900 μm-2 mm (VIIIb), 900 μm-2.3 mm (VIIIb1) and 1.4-2.2 mm (VIIIa) from the midline (Fig. 1C). In lobule IX (uvula), distribution of labelled neurones was changing in the mediolateral dimension. They were present in more dorsal sublobules in the medial part of vermis and in more ventral sublobules in the lateral part. Thus, in sublobules IXa and IXb labelled neurones were seen in a band located 90 μm-2.2 mm from the midline (Fig. 1D and E), in sublobules IXc and IXd they formed two bands at distance of 810 μm-2.4 mm and 810 μm-2.9 mm from the midline, respectively. In the hemisphere three bands of labelled neurones were found in the ansiform lobule. The first was located at distance of 3.5-4.4 mm from the midline in the medial region of crus I, the second one appeared more laterally, 5.3-6.1 mm from the midline in crus II (Fig. 1F) and the third band was identified at distance of 6.5-7.2 mm from the midline in the lateral region of crus I. Few labelled neurones were present in the copula pyramidis at distance of 5.5 mm from the midline to the lateral border of this lobule, as well as in lobule HV, 6.3 mm from the midline and in the ventral paraflocculus (Fig. 1G).

The same specific mediolateral distribution of labelled neurones in vermal sublobules and in the hemisphere was observed after similar extent of injection in rabbit No.189 and after smaller injection in rabbit No.170. (Figs. 2 and 3A-C).

Zonal arrangement of labelled Purkinje neurones in the posterior lobe after HRP or WGA-HRP injection into two vestibular nuclei

INJECTIONS INTO SV AND LV

In one case (No. 210) injection involved SV and LV. In comparison with large injections, the total number of labelled neurones decreased, however, their mediolateral distribution was similar (Fig. 4A). Especially in lobule VI bands of labelling appeared successively in sublobules VIa1-VIb at distance of 0-2.4 mm from the midline. In the uvula bands of labelled neurones were seen in sublobules IXa, IXc and IXd at distance of 360 μm-2 mm, 720 μm-1.4mm and 720 μm-2.7 mm from the midline, respectively. In the hemisphere labelled neurones were located in the lateral region of crus I, copula pyramidis and lobule HV at distance of 6.5-7.3 mm, 5.1 mm and 5.3-5.9 mm from the midline, respectively.

INJECTIONS INTO MV AND LV

For three cases of injections into various regions of MV and LV (Nos. 160, 162 and 195) the most representative is that No. 162 (Fig. 5). In lobule VI distribution of labelled neurones was changing in the mediolateral dimension from more ventral to more dorsal sublobules at distance of 1.4 mm (VIa1) to 2.9 mm (VIb) from the midline. Several neurones were labelled in sublobule VIc in a single section, 2.2 mm from the midline. In lobule VII labelled

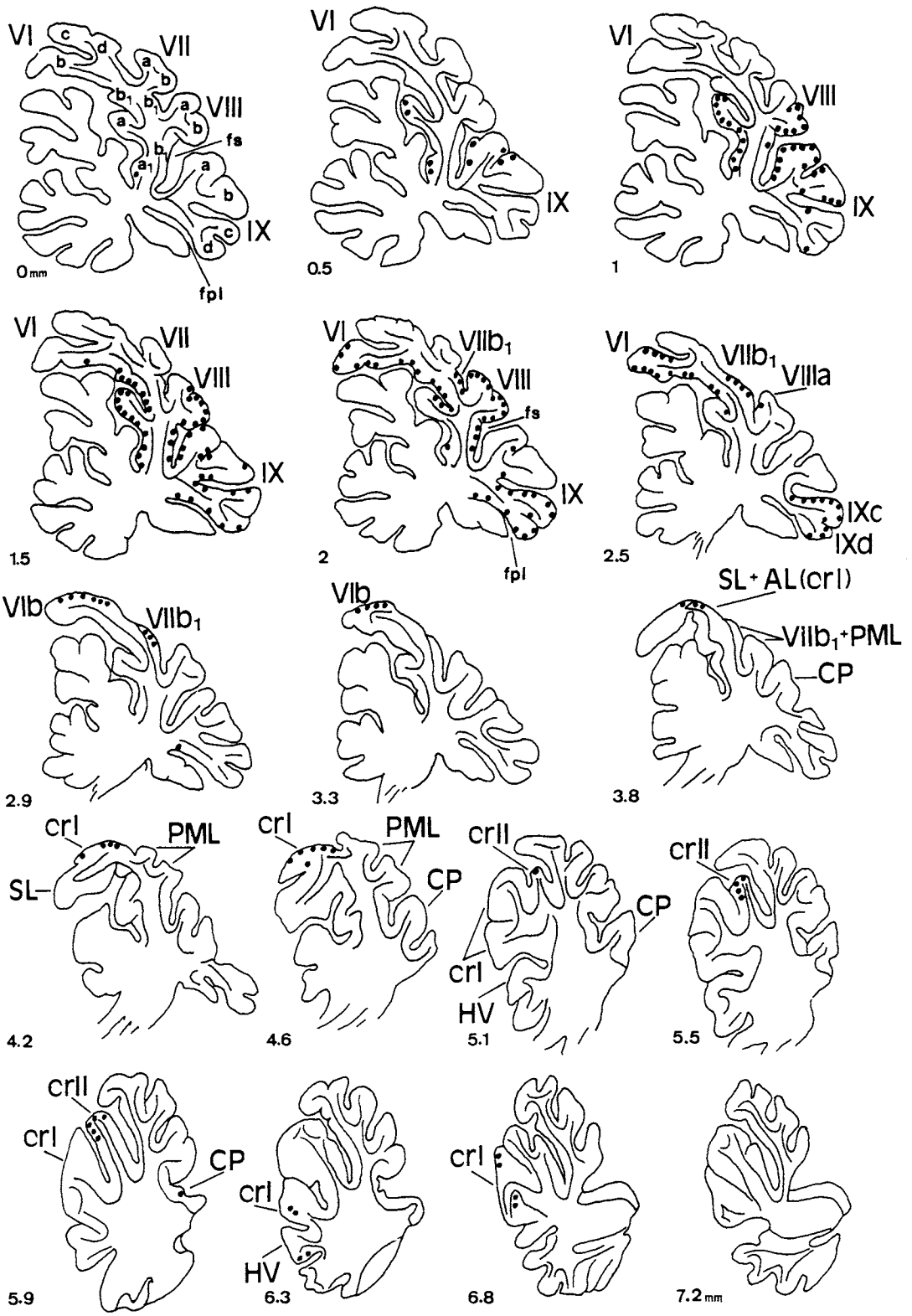

Fig. 2. Case No. 189. Distribution of retrogradely labelled Purkinje neurones on the diagram of sagittal sections through the cerebellum from the midline to 7.2 mm laterally. One dot represents 20-40 labelled neurones in the vermis and 5-10 labelled neurones in the hemisphere.

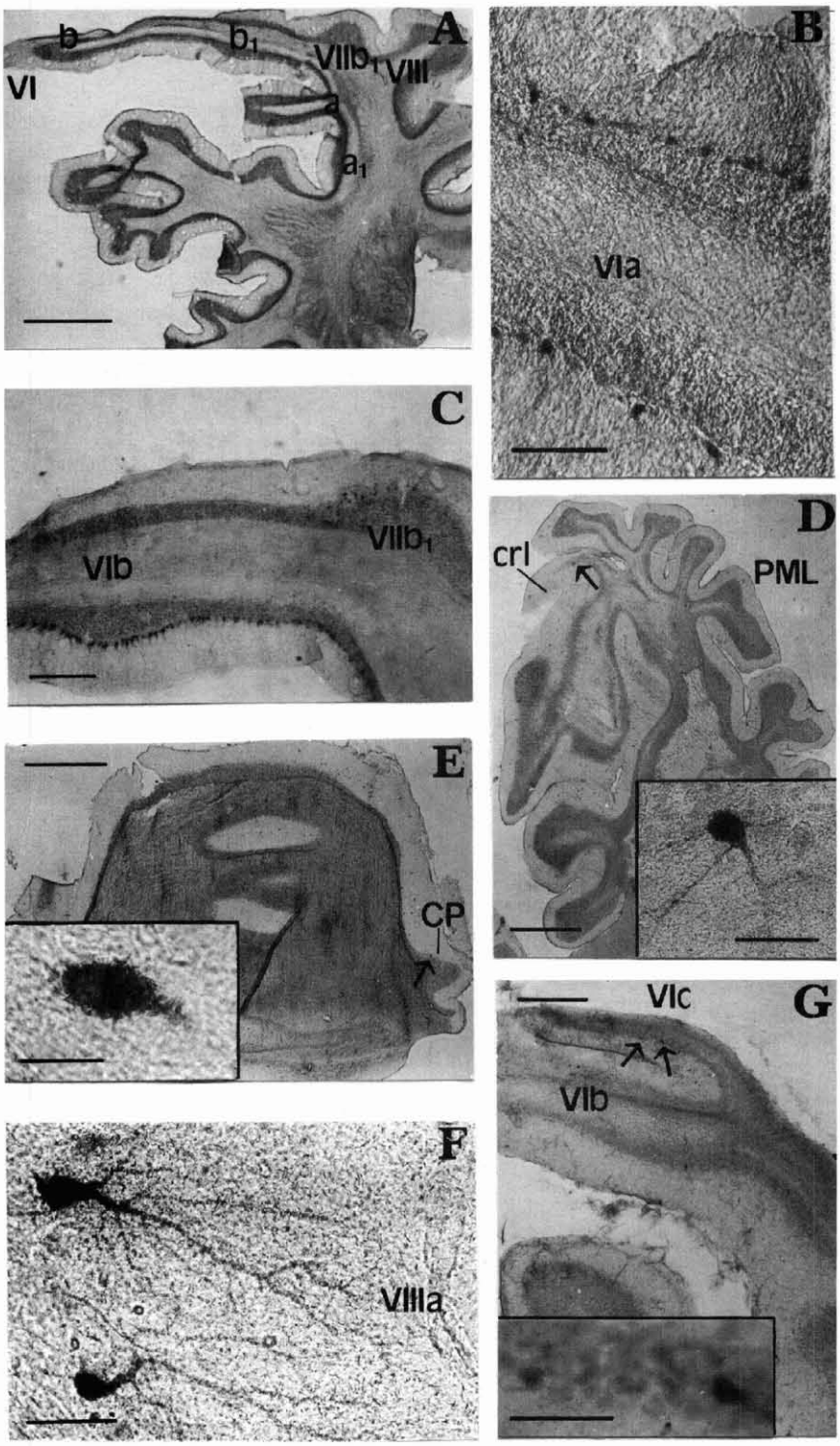

Fig. 3. Photomicrographs of retrogradely labelled Purkinje neurones on sagittal sections through the cerebellar posterior lobe. Labelled neurones in: (A) sublobules VIa-VIb and VIIb1, 2.7 mm from the midline, and (B) their magnification in a basal part of sublobule VIa (interference contrast microscopy), (C) ventral side of sublobule VIb and sublobule VIIb1, 2.4 mm from the midline, in case No. 170. Labelled neurones in: (D) crus I, 4.8 mm from the midline in case No. 162, (E) copula pyramidis (transversal section) in case No. 94, (F) sublobule VIIIa, 1.3 mm from the midline in case No. 163, (G) ventral side of sublobule VIc, 2.7 mm from the midline in case No. 159. Insets are higher magnification of labelled neurones indicated by arrows. Bars represent 1,500 μm for A, D and E, 500 μm for C and G, 250 μm for B, 50 μm for F; 25 μm for insets in E, 50 μm in D, 100 μm in G.

neurones were found in sublobule VIIb1 at distance of 1.9-2.8 mm from the midline. In the pyramis they appeared medialmost in sublobule VIIIb, then in VIIIb1 and next in sublobule VIIIa at distance of 990 μm-2.3 mm, 1.4-2.4 mm and 2.2-2.8 mm from the midline, respectively. In the uvula labelling was observed medialmost in sublobule IXa, and more laterally in sublobules IXc and IXd, at distance of 450 μm-2.3 mm from the midline. In the hemisphere labelled neurones were located in the medial (4.2-4.8 mm from the midline) (Fig. 3D) and lateral (6.7mm from the midline) regions of crus I, in crus II (5.6-5.9 mm from the midline) and the ventral paraflocculus.

INJECTIONS INTO LV AND IV

In seven experiments the enzyme was injected into various regions of LV and IV.

For three cases (Nos. 156, 158 and 209) the most representative mediolateral distribution of bands of labelling in vermal sublobules was that in case No. 209 (Fig. 4B). In the hemisphere, however, no labelled neurones were seen in this case, in contrast to cases Nos. 156 and 158 with weak labelling in the lateral region of crus I and in crus II (7.2 mm and 5.5 mm from the midline, respectively), as well as in the copula pyramidis and lobule HV (6.1 mm and 5.7 mm from the midline, respectively) and in the ventral paraflocculus.

In case No. 196 representative also for other rabbits (Nos. 149, 151, 164 and 196), bands of labelled neurones in lobule VI appeared successively in sublobules VIa1 through VIb at distance of 1-3.1 mm from the midline. In lobule VII neurones were labelled in sublobule VIIb1 at distance of 1.9-3.1mm from the midline. In the pyramis labelled neurones were found in sublobules VIIIb and VIIIb1 at distance of 810 μm-2.2 mm and 1 mm-2.3 mm from the midline, respectively. In sublobule VIIIa they formed band of labelling located 1.3-2.8 mm from the midline. In the uvula labelled neurones were seen medialmost in the dorsal sublobules (IXa and IXb) at distance of 270 μm-1mm, more laterally in

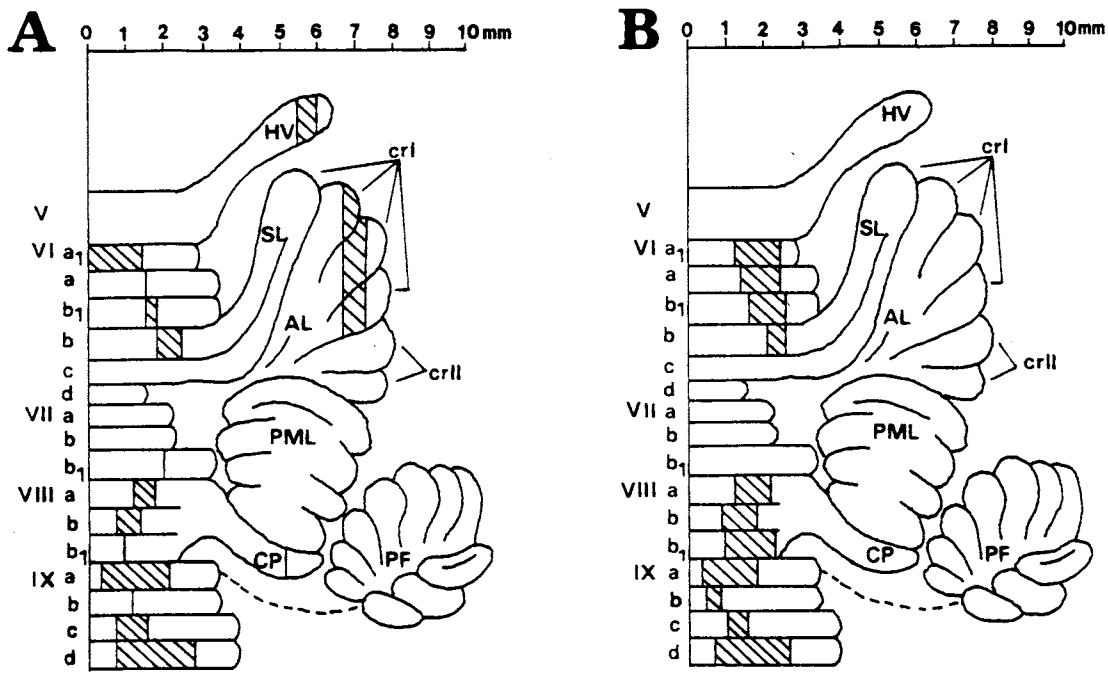

Fig. 4. Mediolateral extent of zones of labelling (hatched area) in the vermal sublobules and in the hemisphere on diagrams of horizontal sight of the cerebellar posterior lobe in cases No. 210 (A) and No. 209 (B). Vertical lines in sublobule VIa and the copula pyramidis in A designate labelling in a single section.

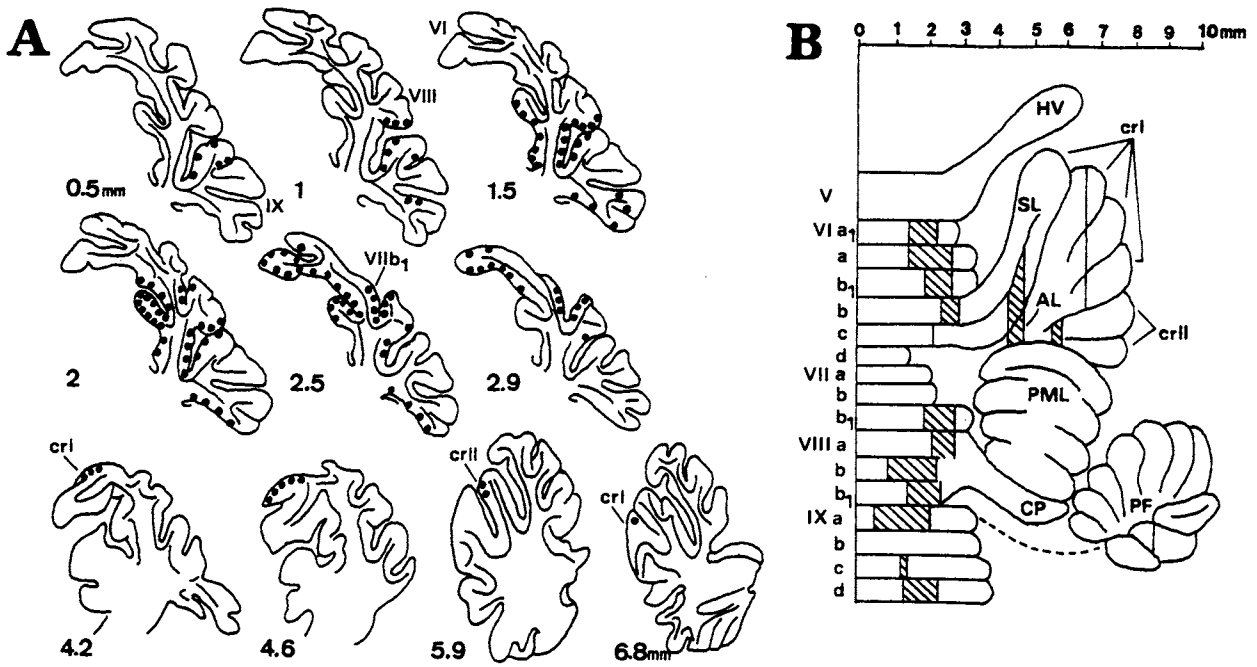

Fig. 5. Case No. 162. (A) Distribution of retrogradely labelled Purkinje neurones on diagram of sagittal sections through the posterior lobe vermis and hemisphere. One dot represents 15-20 labelled neurones in the vermis and 1-4 labelled neurones in the hemisphere. (B) Mediolateral extent of zones of labelling (hatched areas) in the vermal sublobules and in the hemisphere on diagram of horizontal sight of the cerebellar posterior lobe. Vertical lines in sublobule VIc, crus I and the ventral paraflocculus designate labelling in a single section.

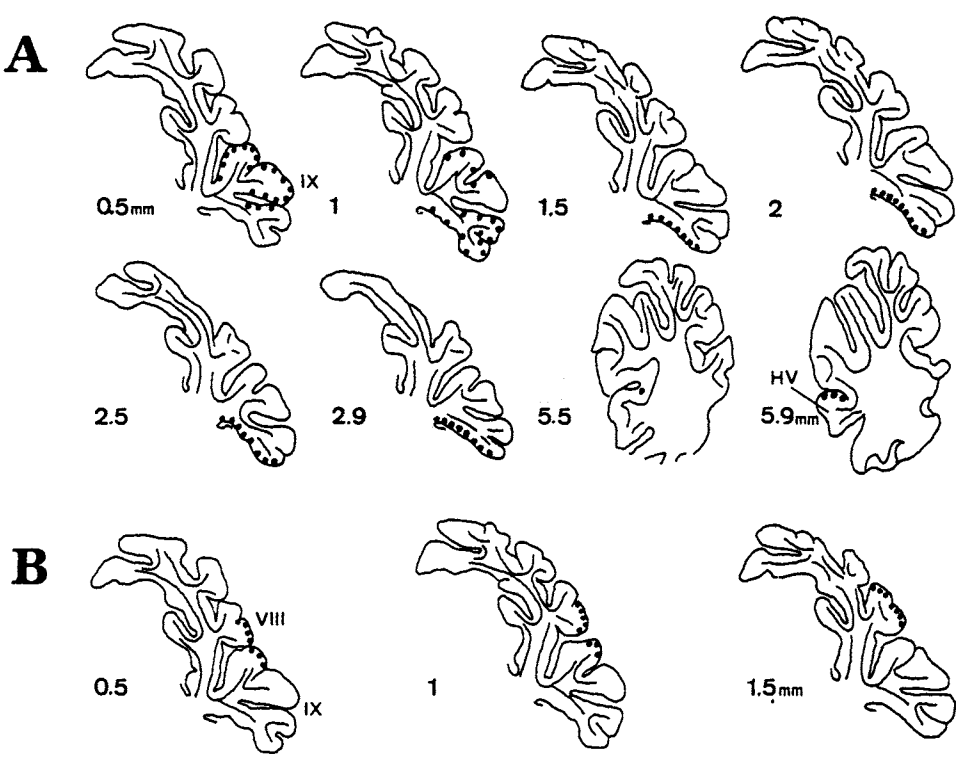

Fig. 6. Distribution of retrogradely labelled Purkinje neurones on diagrams of sagittal sections through the posterior lobe vermis and hemisphere in cases No. 201 (A) and No. 163 (B). One dot represents 2-3 labelled neurones in A, and 6-7 labelled neurones in B.

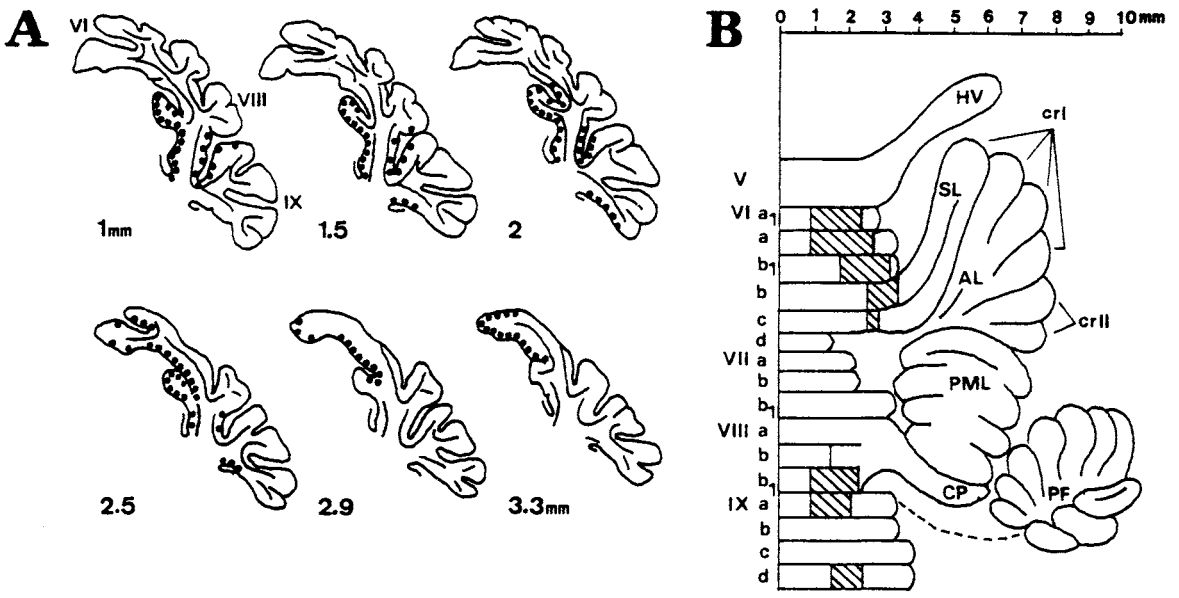

Fig. 7. Case No. 159. (A) Distribution of retrogradely labelled Purkinje neurones on a diagram of sagittal sections through the posterior lobe vermis. One dot represents 5-10 labelled neurones. (B) Mediolateral extent of zones of labelling (hatched areas) in the vermal sublobules on a diagram of horizontal sight of the cerebellar posterior lobe. Vertical line in sublobule VIIIb designates labelling in a single section.

the ventral sublobules at distance of 720 μm-1.6 mm (IXc) and 720 μm-3 mm (IXd) from the midline. In the hemisphere light labelling was seen in the medial region of crus I, 5 mm from the midline, in crus II, 6.1 mm from the midline (case No. 149) and the ventral paraflocculus (case No. 151).

Zonal arrangement of labelled Purkinje neurones in the posterior lobe after selective HRP or WGA-HRP injection into individual vestibular nuclei

INJECTION INTO SV

In two experiments injection into various regions of SV caused labelling in lobule IX at distance of 0.5-3 mm (case No. 201) and 1.2-1.7 mm (case No. 94) from the midline. In case No. 201 distribution of labelled neurones was changing in mediolateral dimension in the specific manner (Fig. 6A). Thus, medialmost they appeared in the more dorsal sublobules (IXa, IXb and on the dorsal side of sublobule IXc). Centrally the number of labelled neurones in sublobules IXa and IXb decreased, and they were mainly seen in the ventral sublobules (IXc and IXd). Laterally labelled neurones were densely located on the ventral side of sublobule IXd, along the posterolateral fissure. In the hemisphere few neurones were labelled in lobule HV (5.5-6 mm from the midline) in both cases (Fig. 3E) and in the copula pyramidis (5.3 mm from the midline) in case No. 94.

INJECTIONS INTO MV

In two experiments HRP or WGA-HRP injections caused labelling of neurones in sublobules VIIIa, VIIIb and IXa at distance of 0.5-1.5 mm from the midline (case No. 163) (Fig. 3F and 6B) and in sublobule IXd, 1-2.5 mm from the midline (case No. 168).

INJECTIONS INTO LV

For two cases (Nos. 159 and 211) with similar injections the most representative mediolateral distribution of labelled neurones was that in rabbit No. 159 (Fig. 3G and 7). In lobule VI labelled neurones appeared successively in sublobules VIa1 through

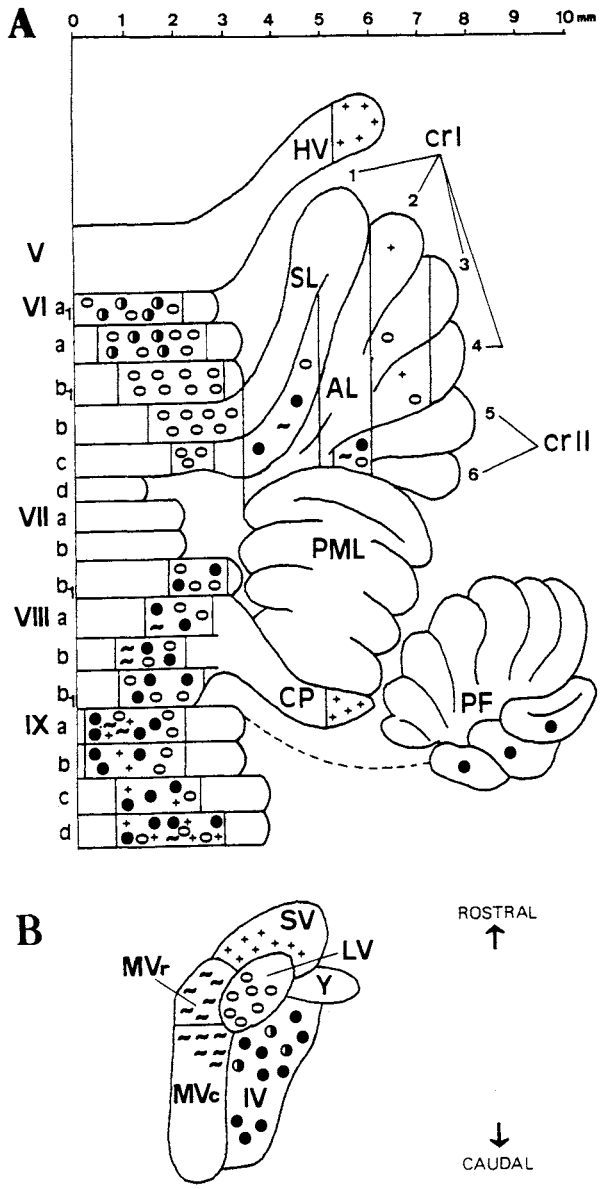

Fig. 8. Diagram summarizing zonal organization of cerebellovestibular projection from the posterior lobe cortex in the rabbit as recognized in the present study with including topographical relationships determined in the previous report (Bukowska 1995). (A) Mediolateral extent of projection zones in the vermal sublobules and hemisphere on diagram of horizontal sight of the cerebellar posterior lobe on right side. (B) Terminal regions of projection within individual vestibular subdivisions on horizontal reconstruction of the vestibular nuclear complex on right side. Origin and terminal regions of the projection are indicated by the same symbols.

VIb at distance of 900 μm-3.4 mm and in sublobule VIc, 2.5-2.9 mm from the midline. In the pyramis wide band of labelled neurones was located in sublobule VIIIb1, 900 μm-2.3 mm from the midline. In the uvula two bands of labelling were seen in sublobules IXa and IXd at distance of 900 μm-2 mm and 1.6-2.4 mm from the midline, respectively.

INJECTIONS INTO IV

In five experiments (Nos. 140, 194, 199, 202 and 203) injections involved various regions of IV.

For the first four cases with injection into the rostral part of IV the most representative mediolateral distribution of labelled neurones was that in rabbit No. 199. In lobule VI labelled neurones were observed in sublobules VIa1 and VIa at distance of 450 μm-1.4 mm and 810 μm-1.6 mm from the midline, respectively.In the pyramis they were present in sublobule VIIIb1, 1.2-1.3 mm from the midline. In the uvula labelled neurones were found in the dorsal sublobules (IXa and IXb) at distance of 450-990 μm and in the ventral sublobules (IXc and IXd) more laterally, 720 μm-1.5 mm from the midline. In the hemisphere narrow strip of labelling was seen in the medial region of crus I (4.6-4.8 mm from the midline).

In rabbit No. 203 with injection into the caudal part of IV labelled neurones in the pyramis formed narrow bands in sublobules VIIIb and VIIIb1 at distance of 720 μm-1.2 mm and 810 μm-1.3 mm from the midline, respectively. In the uvula labelled neurones in the dorsal sublobules were present more medially (180 μm-1.2 mm from the midline) but those in the ventral sublobules occurred more lateraly (900 μm-1.9 mm from the midline). In the hemisphere few neurones were labelled in the ventral paraflocculus.

DISCUSSION

The present study has shown that vestibular afferents from the cerebellar posterior lobe in the rabbit originate from widespread ipsilateral cortical region. Most of the retrogradely labelled Purkinje neurones were found in the lateral region of vermis at distance of about 1-2.5 mm from the midline. However, some labelled neurones were observed in

the midline, others were located in the paravermal region or even in the hemisphere. On the other hand, when projections from individual sublobules were examined, a clearly visible zonal pattern was revealed. Thus, Purkinje neurones projecting to VNC were arranged in quite well demarcated longitudinal bands. These bands had a different width and were found to be located at the various distance from the midline (Fig. 8).

In lobule VI the projection zone was wide, but within individual sublobules a clear arrangement of longitudinal projection bands in mediolateral dimension was observed. These bands were located in sublobules VIa1 at distance of 0-2.3 mm, VIa 540 μm-2.7 mm, VIb1 810 μm-3.1 mm and in sublobule VIb 1.4-3.4 mm from the midline. The narrow projection strip in sublobule VIc was seen 2-2.9 mm from the midline. No projection arrises from sublobule VId. Thus, projection bands located medially in more ventral sublobules tended to shift laterally in more caudal sublobules. It is likely that vestibular afferents from sublobule VIa1 take origin mainly from A zone projecting to the fastigial nucleus and those from sublobule VIa are included partially both in A and B zones. The projection band in sublobule VIb1 seems to represent mainly B zone, but that in sublobule VIb corresponds to B zone and to the medial aspect of C1 zone projecting to the anterior interposite nucleus. The projection band in sublobule VIc appears to be included within B zone (Voogd and Bigaré 1980). In the present material projection bands in the ventral sublobules correspond with projections from A and B zones of sublobule VIa to MV and LV in the rabbit (Balaban 1984). However, in contrast to Balaban (1984) projection bands from remaining sublobules (VIb1-VIc) have been shown here.

In lobule VII the band of vestibular afferents located in the lateral region of sublobule VIIb1 (1.9-3.1 mm from the midline) corresponds to A zone (Voogd and Bigaré 1980). So far, zone of vestibular afferents from lobule VII has not been described in the rabbit. Van Rossum (1969) found only a few degeneration fibres in LV and Balaban (1984) obtained negative results. Dietrichs et al. (1983) observed labelled Purkinje neurones in lobule VII about 2-3 mm from the midline after large HRP injection into VNC in the cat.

In lobule VIII most of the vestibular projecting neurones were found in the lateral region. Projections originating from sublobules VIIIb and VIIIb1 appeare medialmost about 800 μm from the midline and disappear 2.3 mm and 2.6 mm from the midline, respectively. The projection band in sublobule VIIIa is located more laterally (1.3-2.8 mm from the midline). This pattern suggests that afferents from sublobule VIIIa and VIIIb arise mainly from A3 and A2 zones, respectively. The widest projection band in sublobule VIIIb1 apparently corresponds to A2 and A3 zones of Voogd and Bigaré (1980). Moreover, corticovestibular neurones in the lateralmost region of sublobules VIIIa and VIIIb1 are intermingled with corticonuclear neurones in the medialmost aspect of C1 zone (Voogd and Bigaré 1980). Corticovestibular neurones found here in lobule VIII seem to correspond to the lateral half of A zone in the rabbit (Balaban 1984), cat (Dietrichs et al. 1983), opossum (Klinkhachorn et al. 1984), galago (Haines et al. 1976) and rat (Umetani et al. 1986, Umetani and Tabuchi 1988). It is possible, that these neurones can form from two to three longitudinal strips in lobules VIII in the rabbit (Thunnissen et al. 1989).

In lobule IX mediolateral distribution of corticovestibular neurones in the dorsal and ventral sublobules was considerably different. Projection bands in sublobules IXa and IXb were located more medially at distance of 90 μm-2.2 mm from the midline. In sublobules IXc and IXd, the medial border of projection bands was seen 720 μm from the midline, but lateral border was shifted to 2.5 mm and 3 mm from the midline, respectively. Thus, projection bands in the dorsal sublobules appeared to lie within A1 and A2 zones, but those in the ventral sublobules within A2 and A3 zones of Voogd and Bigaré (1980). Moreover, corticovestibular neurones located most laterally on the ventral side of sublobule IXd, along the posterolateral fissure, probably belong to C2 zone projecting to the posterior interposite nucleus (Voogd and Bigaré 1980).

The observation that the intermediate third of uvula (A2 zone) contributes most significantly to vestibular projection supports results of Balaban (1984) and Van Rossum (1969) in the rabbit. The present results are consistent with those reported by Epema et al. (1985) and Shojaku et al. (1987) that the lateralmost region of uvula is a free zone in terms of vestibular projection, but do not support findings of other authors (Haines 1975b, Umetani et al. 1986). This region corresponds to D zone projecting to the dentate nucleus in the rabbit (Van Rossum 1969) and rat (Bernard 1987). Corticovestibular neurones in the uvula had tended to segregate into three longitudinal strips (Epema et al. 1985) or two to three longitudinal strips in sublobules IXa-IXc and formed small clusters in sublobule IXd (Thunnissen et al. 1989) in the rabbit. They were arranged in two longitudinal areas in the cat i.e. one located medially comprising A1 and A2 zones, and the other located laterally corresponding to A3 zone of Voogd and Bigaré (1980) (Matsushita and Wang 1986, Shojaku et al. 1987). In contrast to that, Dietrichs et al. (1983) and Carpenter and Cowie (1985) showed in the cat labelled neurones throughout mediolateral extent of the uvula without separate strips.

The results which describe projection from hemispheral part of the cerebellar posterior lobe in the rabbit are reported here for the first time. In the ansiform lobule three longitudinal projection bands were identified. The medial band in crus I seemed to be a lateral prolongation of projection from sublobule VIb and it extended to 5 mm from the midline. The central narrow band was present in crus II and the lateral band in crus I at distance of 5.3-6.1 mm and 6.1-7.3 mm from the midline, respectively. It is possible that medial and central bands are located within C1, C2 and C3 zones projecting to the interposite nuclei. However, the lateral band corresponds to D1 zone which projects to the medial part of dentate nucleus (Voogd and Bigaré 1980). The lateralmost region of the ansiform lobule projecting to the lateral part of dentate nucleus (D2 zone) (Dietrichs and Walberg 1980) was not found in the present study to send projections to VNC. Some corticovestibular neurones in both crus I and crus II (Eager 1963, Haines 1975a, Dietrichs et al. 1983) were described in the cat and galago, however, with no conclusions on the mediolateral location of corticovestibular neurones. Small projections from the lateralmost aspect of hemispheral part of pyramis, i.e. the copula pyramidis at distance of 5.1 mm to its lateral border (6.1 mm) and from lobule HV at distance of 5.3 mm to its lateral border (6.4 mm), have not been earlier reported in any species. Projections bands in the copula pyramidis and lobule HV are probably included within C2 and D, and C3 and D1 zones, respectively (Voogd and Bigaré 1980). Corticovestibular neurones scattered in all folia of the ventral paraflocculus in the present material seem to be intermingled with those projecting to the cerebellar nuclei (C2 and D zones) (Haines and Whitworth 1978, Voogd and Bigaré 1980, Dietrichs 1981).

In conclusion, the results suggest that cerebellar corticovestibular system in the posterior lobe is more precisely organized than previously expected. Further investigations are required to explain whether there exist some relationships between longitudinal cortical zones in individual sublobules and the cerebellar afferent system of climbing and mossy fibres in the rabbit.

ABBREVIATIONS

AL	ansiform lobule
CP	copula pyramidis
cr I	crus I
cr II	crus II
fpl	posterolateral fissure
fs	second fissure
IV	inferior vestibular nucleus
LV	lateral vestibular nucleus
MV	medial vestibular nucleus
MVc	caudal portion of medial vestibular nucleus
MVr	rostral portion of medial vestibular nucleus
PF	paraflocculus
PML	paramedian lobule
SL	simple lobule
SV	superior vestibular nucleus

ACKNOWLEDGEMENTS

The author is greatly indebted to Prof. Roman Zimny and Prof. Kazimierz Grottel for their valuable suggestions and criticism during preparation of this paper. This study constitutes a part of the doctor thesis submitted by the author. The study was partly supported by KBN Grant No. 4 1387 91 01.

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Received 7 June 1994, accepted 15 November 1994