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CEREBELLO-VESTIBULAR CONNECTIONS OF THE ANTERIOR VERMIS. A RETROGRADE TRACER STUDY IN DIFFERENT MAMMALS INCLUDING PRIMATES

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INTRODUCTION

Projections of Purkinje cells of the vermis of the anterior lobe and the simple lobule (28, lobule VI), subsequently to be called the «anterior vermis», to the vestibular nuclei were reported in several mammalian species. They were discovered by Klimoff (25) in experiments on the rabbit, using anterograde tracing of degenerated fibers with the Marchi method. According to this author each half of the «vermis» projects to the ipsilateral fastigial nucleus, and to the large cells in Deiters' nucleus. The «hemisphere» is connected with the interposed and lateral cerebellar nuclei. We do not know exactly how much of the rabbit cerebellum was included in Klimoff's «vermis» because some early anatomists often used the term «anterior vermis» in small mammals for the entire anterior lobe. The demarcation of the vermis from the hemisphere of the anterior lobe and the simple lobule is not such a simple matter. Bolk (4) concluded from his comparative anatomical studies of the mammalian cerebellum that there is no valid reason to distinguish between a vermis and a hemisphere in the anterior lobe, and introduced the term «lobulus simplex» to stress the absence of such a division also in this lobule. Bolk's statement was criticized by Riley (33), who pointed out that embryological and pathological studies favoured the distinction of an anterior vermis and that it was present in cetaceans. Riley was right, of course, but none of his arguments are very helpfull to the neuroscientist who wants to identify the anterior vermis in laboratory animals. Brodal (5) in his studies of the olivocerebellar projection in rabbit and cat, defined the anterior vermis by extrapolation of the borders of the well-defined vermis of the posterior lobe. He concluded that there existed transients in the projection of the accessory olives to the anterior vermis and the hemispere, which did not allow a sharp demarcation of these structures. In their subsequent studies Jansen and Brodal (23, 24) developed their three-zonal hypothesis, in which they defined vermis, pars intermedia and hemisphere as longitudinal zones, characterized by their corticonuclear projection. The medial, vermal zone was defined by its projection to the fastigial and vestibular nuclei. They assumed that the corticovestibular fibers originated from the entire vermis, with

a major contribution of the anterior lobe and the nodule, a moderate projection from the uvula and the pyramis and few or none from the lobules VII and VI (43).

A difference in origin of the vestibular and the cerebellar nuclear projections from the anterior vermis was suggested by Hohman (22) who distinguished two bundles of degenerated Purkinje cell fibers in the white matter after lesions of the anterior vermis in the cat: the medially located «anterior vermis — fastigial bundle» and, lateral to it and separated by a degeneration-free gap, the «anterior vermis — Deiters bundle». Later these bundles were found to occupy two separate compartments in the white matter of the anterior vermis in cat and ferret, which could be recognized in sections stained with Häggqvist's-myelin stain (37, 38). The medial A-compartment is located next to the midline and contains Purkinje cell fibers entering the fastigial nucleus, the lateral B-compartment leads its fibers, between the fastigial and interposed nuclei to Deiters' nucleus. Thin, myelinated fibers accumulate at the midline and at the borders of the compartments. These «raphes» apparently correspond to the gap, separating Hohman's (22) degenerated bundles of Purkinje cell fibers. Voogd (37, 38) concluded that the anterior vermis consisted of two parallel projection zones A and B, which send their Purkinje cell axons through corresponding compartments to their target nuclei. It was assumed that the lateral border of the B-zone coincided with the shallow furrow which demarcates the vermis of the anterior lobe in the cat from the hemisphere.

The termination of the corticovestibular fibers of the anterior vermis is limited to Deiters' nucleus (25, 36, rabbit; 11, 32, 37, 43, cat; 23, 24, rabbit, cat, monkey; 18-20, prosimian primates; 26, 27, opossum). The giant cells of Deiters' nucleus occupy the dorsal part of the lateral vestibular nucleus as delimited by Brodal and Pompeiano (6) in the cat, and are located within the juxtarestiform body. Cells of the ventral part of the lateral vestibular nucleus are of all sizes and are located outside the juxtarestiform body. They should be included with the medial vestibular nucleus, as its magnocellular portion (15, 16, 37). It is clear from most papers that their authors did not observe termination of corticovestibular fibers in the magnocellular part of the medial vestibular nucleus, but some described a slight extension of the terminal area into the dorsal part of the descending vestibular nucleus. The projection has never been studied in any detail in the rat and has been denied in the monkey (12).

The differences in projection of the A and B-zones of the anterior vermis have been verified in anterograde and retrograde tracing studies. Haines and Rubertone (20) concluded that degenerated axons from the lateral B-zone in *Galago* terminated in the nucleus of Deiters and in the medial part of the posterior interposed nucleus. The A-zone was found to project to the fastigial nucleus. Retrograde tracing with injections of horseradish peroxidase (HRP) in the vestibular nuclei of the cat resulted in the labelling of Purkinje cells in a single area roughly corresponding to the B-zone (9, 10). Voogd and Bigaré (41), however, found labelling in two, sharply delimited bands in the dorsal part of the anterior vermis of the cat, which fuse into a single band in the ventral part of the anterior lobe. A similar configuration was described by Balaban (2) in the rabbit. The medial strip of labeled Pur-

kinje cells is located within the A-zone and their axons pass through the fastigial nucleus to reach the vestibular nuclei. Selective retrograde labelling of Purkinje cells in the lateral A-zone was obtained following HRP injections in the magnocellular medial vestibular nucleus. Complete labelling of the A-zone resulted from injections of HRP in the fastigial nucleus and selective labeling of the B-zone was found after injections of the dorsolateral part of Deiters' nucleus (40, 41, cat; 14 rabbit). This indicates that the B-zone projects exclusively to Deiters' nucleus, whereas the A-zone projects both to the fastigial nucleus and the magnocellular portion of the medial vestibular nucleus.

The wedge-shaped gap between the A and B-zones in the dorsal part of the anterior lobe seems to correspond to the x-zone, which was identified in electrophysiological and retrograde labelling experiments on the olivocerebellar projection (8, 13). It does not project to the vestibular nuclei, but to the junction of the fastigial and posterior interposed nuclei (35, 40).

In this paper we shall describe the zonal configuration of the Purkinje cells of the anterior vermis with projections to the vestibular nuclei in rat, rabbit, cat and monkey.

METHODS

Wheat-germ coupled HRP (WGA-HRP, Sigma type VI, 5% in saline) was injected with micropipettes, with a tip diameter of 25-30 μm into the vestibular nuclei. Volumes of 0,1 μl were injected in 20 adult Wistar rats, using a caudal, horizontal approach and stereotactic coordinates from the atlas of Paxinos and Watson (31). The position of Deiters' nucleus in two adult monkeys (MR7: *Macaca nemestrina*; MR8: *Macaca fascicularis*) was determined as the maximal antidromic field potential on stimulation of the ipsilateral lateral vestibulospinal tract at C1. A volume of 0.4 μl 7% WGA-HRP subsequently was injected in Deiters' nucleus. The track of the injection pipette passed through and along the caudal brainstem and did not damage the cerebellum. The animals were killed by transcardial perfusion with heparinized saline followed by 1% paraformaldehyde and 1,25% gluteraldehyde in phosphate buffer (pH 7.2) under deep anesthesia. Cerebellum and brainstem were dissected, embedded in 10% gelatine, cut into serial 30 mμ sections on a freezing microtone, and reacted for HRP according to Mesulam (30) using tetramethylbenzidine as a substrate. Alternate sections were incubated for acetylcholinesterase (17) to facilitate identification of the midline in graphical reconstructions. Surgical, injection and histological procedures in cats and rabbits were similar and were specified elsewhere (3, 14, 40, 41). Graphical reconstructions were prepared of the ventral and anterior surface of the anterior lobe, and the dorsal surface of the cerebellum, showing the position of the superficially located labelled Purkinje cells.

ABBREVIATIONS

A , A-zone;
a , labelled Purkinje cell axons;
B , B-zone;
cr , restiform body;

D , dentate nucleus;
Dent , dentate nucleus;
DLP , dorsolateral protuberance;
Dt , Deiters' nucleus;
F , fastigial nucleus;
IA , anterior interposed nucleus;
IP , posterior interposed nucleus;
L , lateral cerebellar nucleus;
LV , lateral vestibular nucleus of Deiters;
m , midline;
MV , medial vestibular nucleus;
SV , superior vestibular nucleus;
X , X-zone.

RESULTS

In cats the distribution of the labelled Purkinje cells in the anterior lobe corresponded closely to previous reports using HRP as a tracer (3, 40, 41). The main difference in the WGA-HRP injected animal (VC6) to be presented in this paper was that the Purkinje cells and their dendrites were impregnated more completely, but that their axons stained only vaguely or not at all.

The injection site in VC6 covers the nucleus of Deiters and the adjoining magnocellular and ventricular portions of the medial vestibular nucleus (Fig. 1). In the lobules I-III a single band of Purkinje cells is labelled. In lobule I this band extends from the midline to 1.3 mm laterally, in the lobules II and III it remains separated from the midline by a space of 0.3-0.4 mm. There is an indistinct subdivision of the band in the lobules II and III into a medial, 0.4 mm wide strip, located in the lateral A-zone and a lateral 0.5-0.7 mm wide B-zone. A wedge-shaped area without labelled cells corresponding to the X-zone separates the labelling in the A and the B-zone in the lobules IV and V (Fig. 2a). The X-zone attains its greatest width in dorsal lobule V. The lateral displacement of the B-zone in dorsal parts of the anterior lobe seems to be due to the intercallated X-zone, rather than to an increase in width of the A and B-zones. The X-zone decreases in width in the ventral part of the primary fissure (Fig. 1e). Caudal to the primary fissure the labelling in the A-zone is sparse or absent and the labelled B zone diverges laterally. It can be traced caudally and laterally over the simple lobule where it ends at the border of the lobules VI and VII, 6 mm lateral to the midline, near the area devoid of cortex in the paramedian sulcus, between lobule VII and the centre of the ansiform lobole (Fig. 1d).

Case C972 is representative for a series of rabbits with injections of WGA-HRP in the vestibular nuclei (14). The injection site covers the nucleus of Deiters and the ventrally and medially adjoining medial vestibular nucleus. It extends rostrally into the superior vestibular nucleus (Fig. 3d, e). The labelled Purkinje cells in the lobules I-III occupy a band extending 1.2-1.5 mm laterally. The region next to the midline contains a strip one or two Purkinje cells wide. The main band

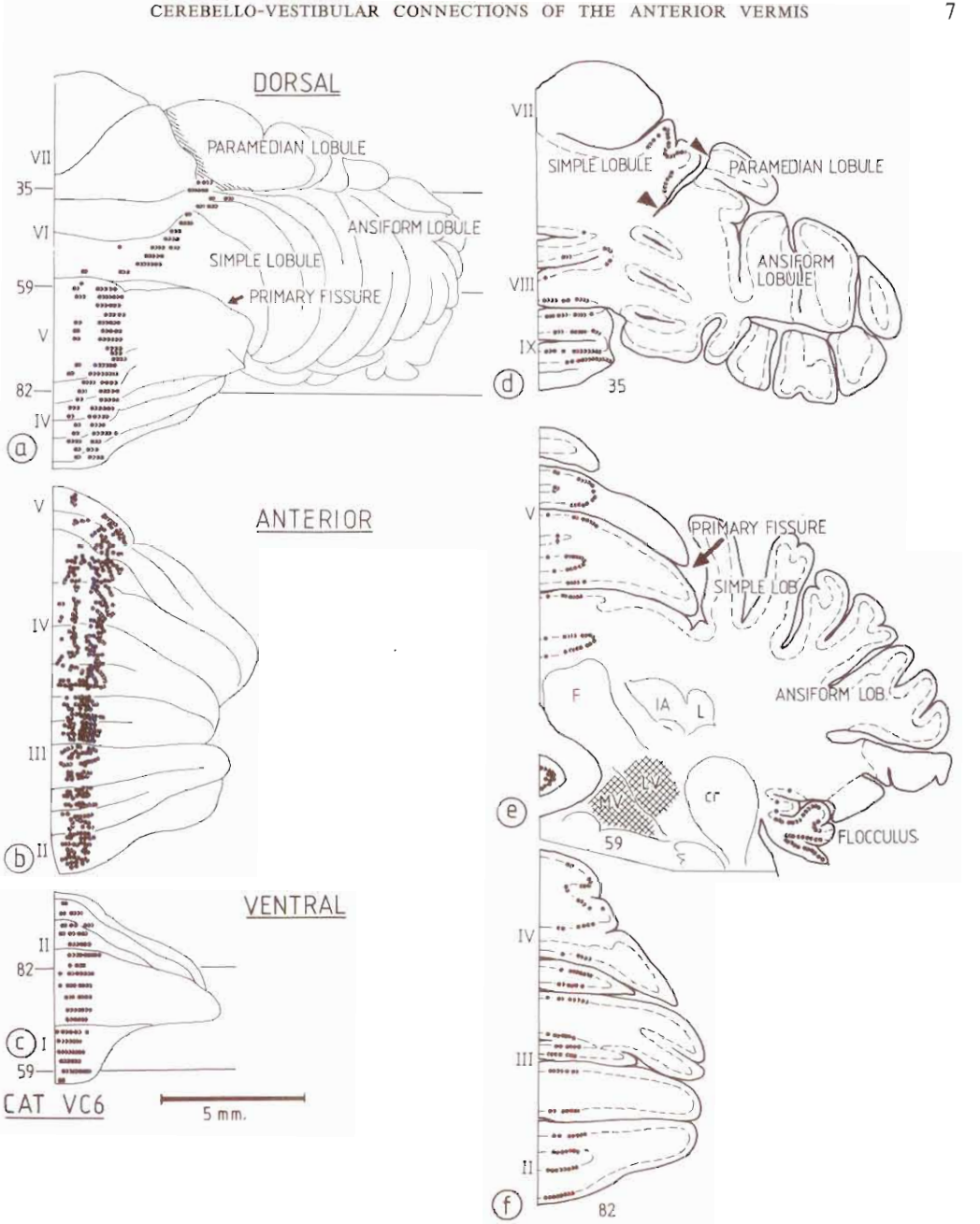

Fig. 1 – *Distribution of labelled Purkinje cells after an injection of the vestibular nuclei in cat VC 6.*

Graphical reconstructions of (*a*) dorsal surface of the cerebellum, (*b*) anterior and (*c*) ventral aspect of the anterior lobe. Level of the sections depicted in *d* - *e* is indicated in (*a*). Area without cortex is hatched in (*a*) and indicated with arrowhead in the sections. Injection site is indicated by double hatching.

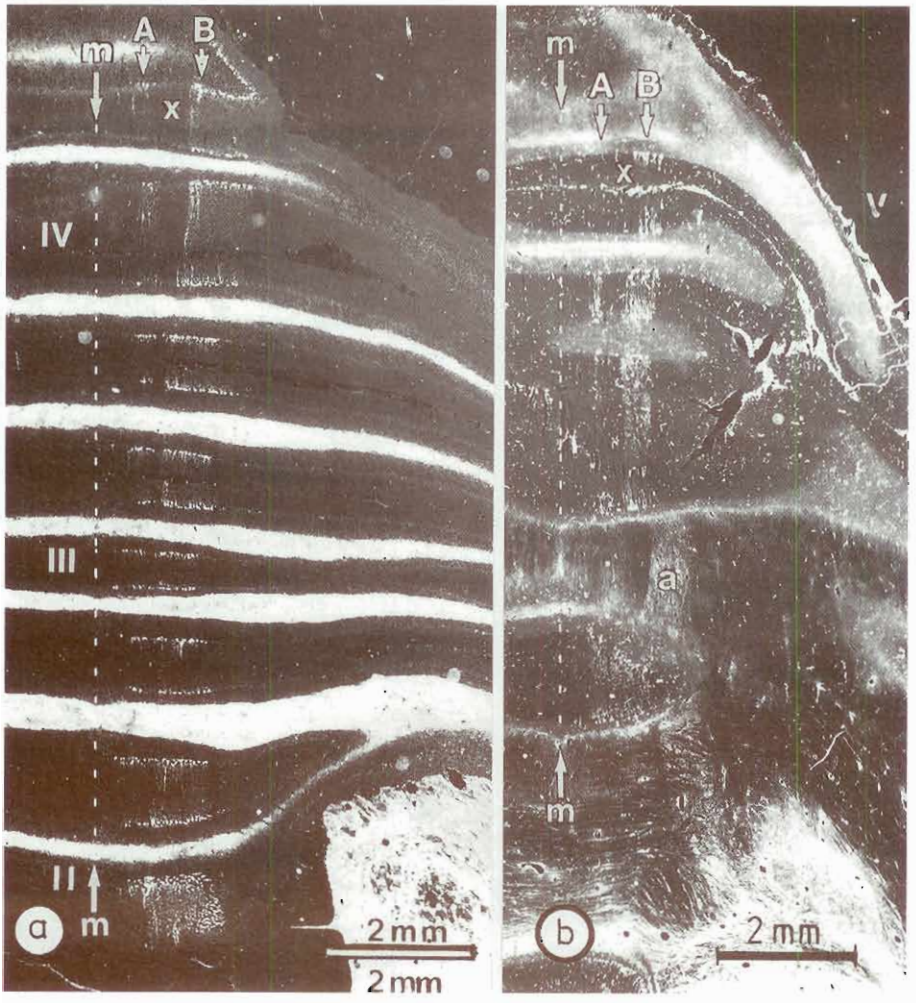

Fig. 2 – *Distribution of labelled Purkinje cells in cat and monkey.*

a) Dark-field photograph of the right half of a section passing through the anterior lobe of the cat VC 6, with retrogradely labelled Purkinje cells. Broken line indicates midline.

b) Dark-field photograph of the right half of a section passing through the anterior lobe of monkey M8, with retrogradely labelled Purkinje cells. Bundle of retrogradely labelled Purkinje cell axons in B-compartment (a) is seen to emerge from the periphery of the injection site Broken line indicates midline.

is subdivided by a narrow space in medial and lateral zones. In the lobules IV and V the space between the two strips of labelled neurons widens into a 0.3 mm wide gap, corresponding to the X-zone of the cat. The two 0.5 mm wide strips of Purkinje cells can be traced over the anterior and posterior surface of the primary fissure, which reaches far caudally into the cerebellum (Fig. 3d, e and 5b). On the ventral surface of lobule VI the two strips and the X-zone which separates them, are still present between 1.6 and 2.6 mm lateral to the midline.

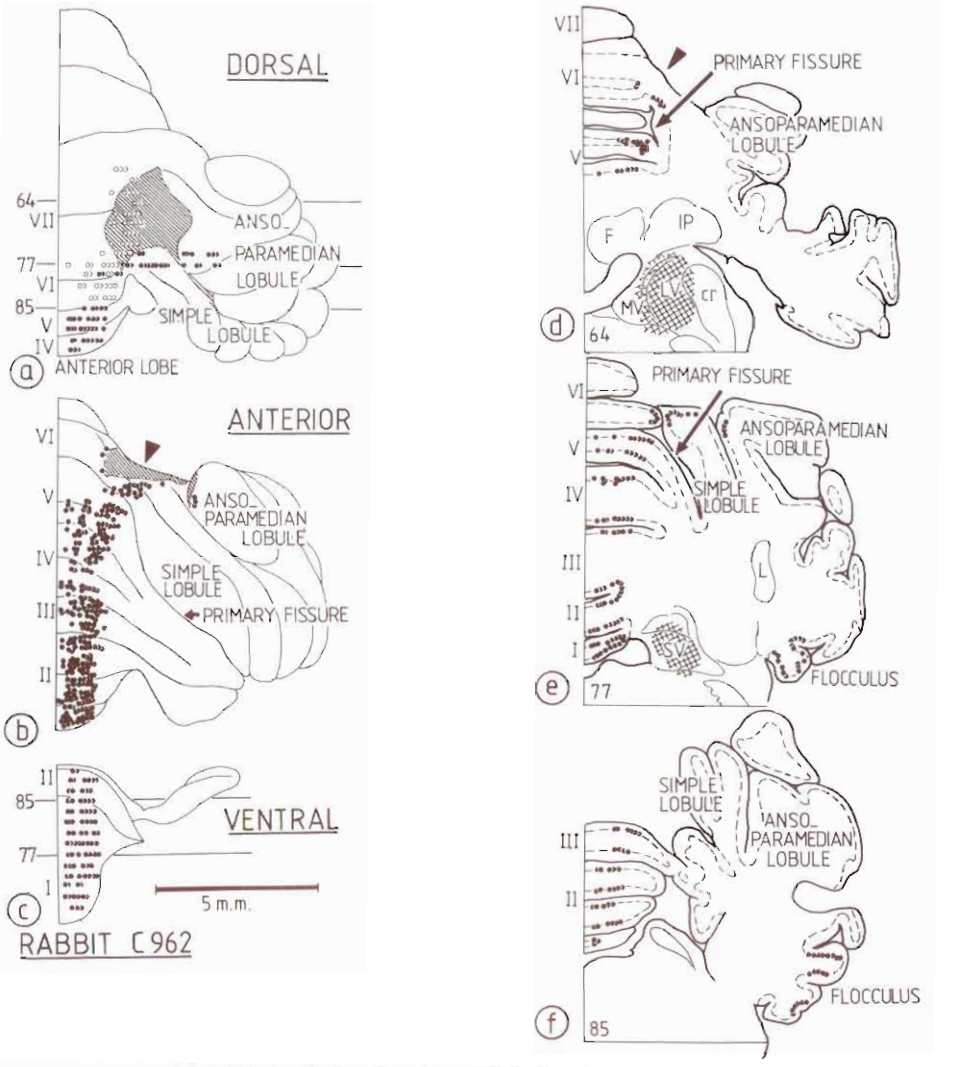

Fig. 3 – *Distribution of labelled Purkinje cells after an injection of the vestibular nuclei in rabbit C 962.*

Graphical reconstructions of (*a*) dorsal and (*b*) anterior surface of the cerebellum and (*c*) ventral aspect of the anterior lobe. Level of the sections depicted in *d* - *f* is indicated in (*a*). Area without cortex is hatched in (*a*) and (*b*) and indicated with arrowhead in the sections. Injection site is indicated by double hatching. Filled circles in *a-b* represent superficially located labelled Purkinje cells, open circles indicate labelled cells in the walls of the primary fissure.

At the anterior surface of the cerebellum, labelled Purkinje cells of the lateral of the two zones emerge from the primary fissure and turn laterally, rostral to the extensive area devoid of cortex, where they are found at the roots of the radiating folia of the ansoparamedian lobule.

Observations in two rats with injections in the vestibular nuclei are very similar. The injection site in rat R11 (Fig. 4e) is large and covers the nucleus of Deiters

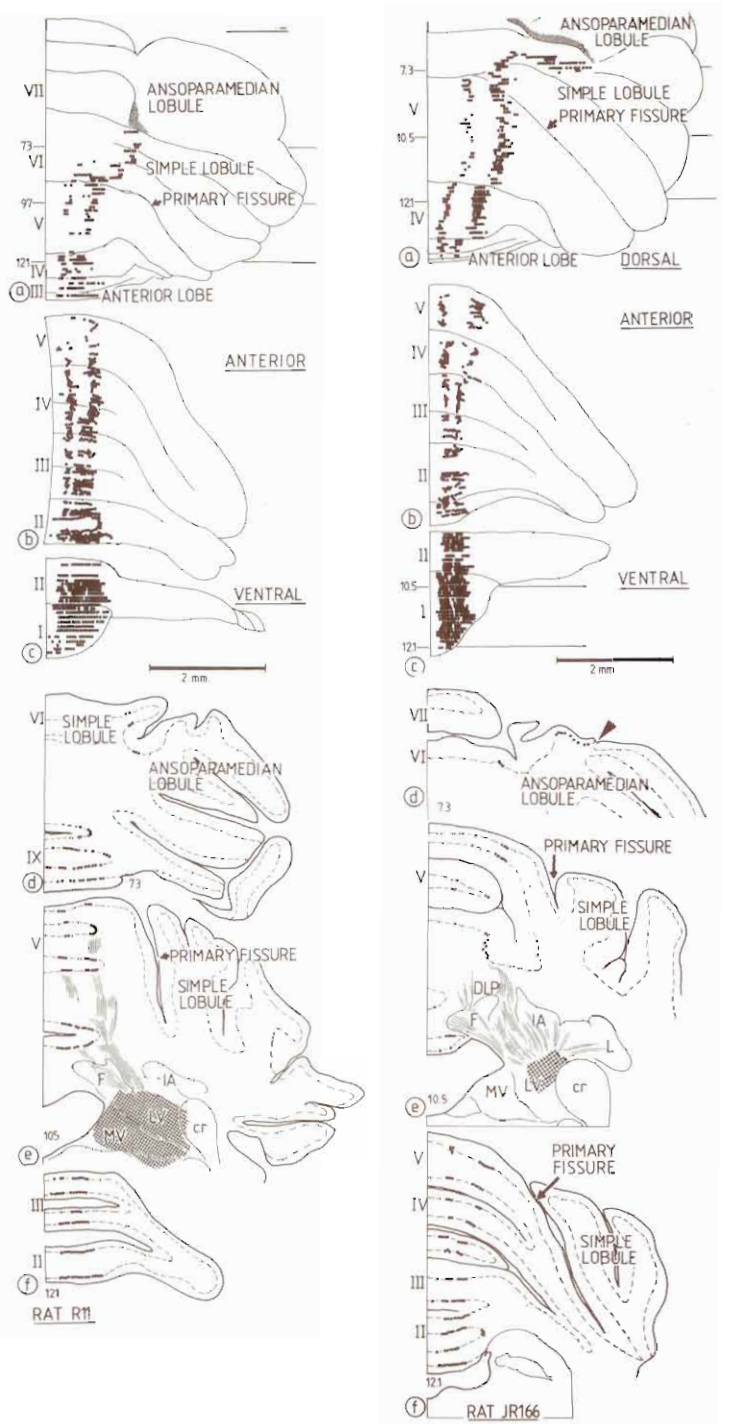

Fig. 4 – *Distribution of labelled Purkinje cells after an injection of the vestibular nuclei in rat R11 (left column) and rat JR166 (right column).*

Graphical reconstructions of (*a*) dorsal surface of the cerebellum, (*b*) anterior and (*c*) ventral aspect of the anterior lobe. Level of the sections depicted in *d* - *f* is indicated in (*a*). Area without cortex is hatched in (*a*) and indicated with arrowhead in the sections. Injection sites are indicated by double hatching.

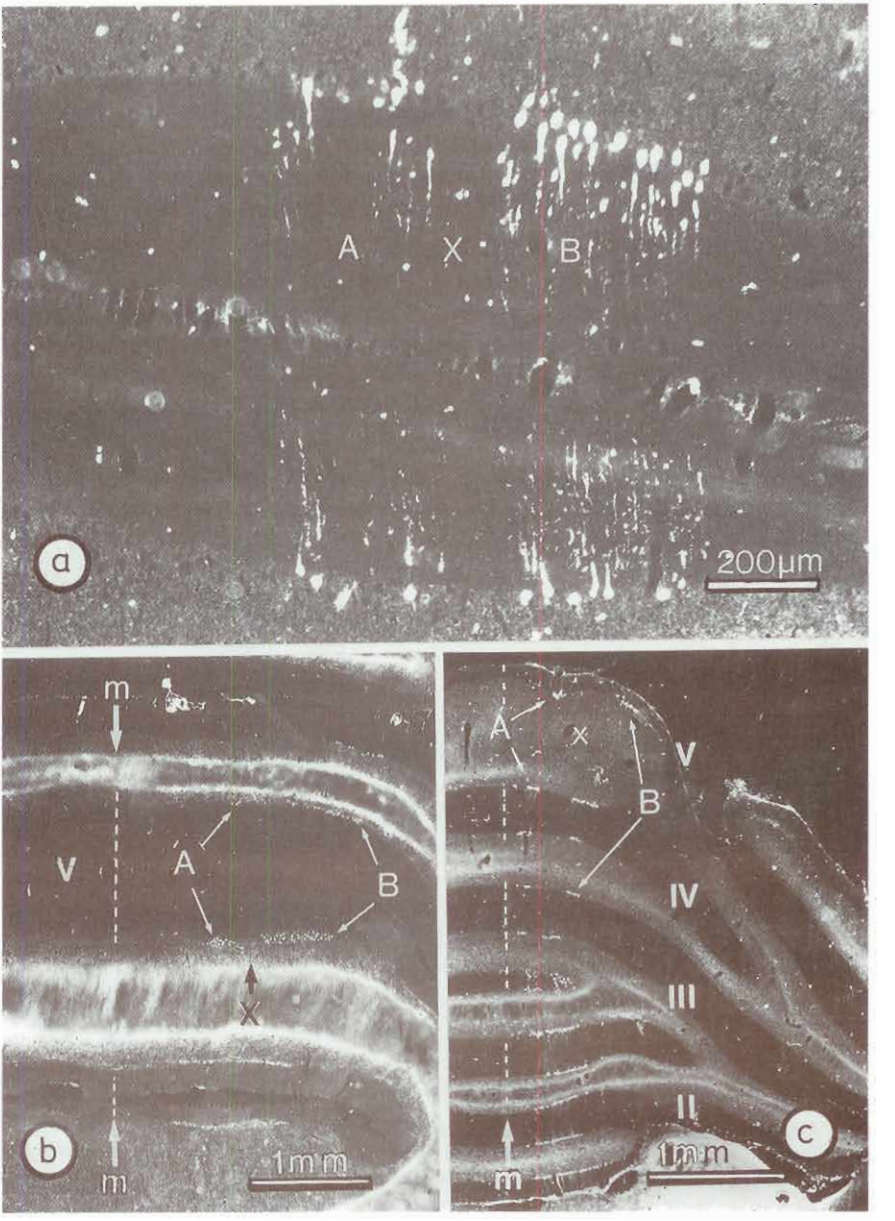

Fig. 5 – *Distribution of labelled Purkinje cells.*

a) Labelled Purkinje cells in lobule V (monkey M7, same level as Fig. 7*f*). Medial two strips are located in A-zone, lateral strip corresponds to B-zone. Darkfield.

b) Labelled Purkinje cells in section through the primary fissure in the rabbit (C 962, same level as Fig. 2*d*). Dark-field.

c) Dark-field photograph of the right half of a section passing through the anterior lobe of rat JR166 (Fig. 4*f*, right column) with retrogradely labelled Purkinje cells. Broken line indicates midline.

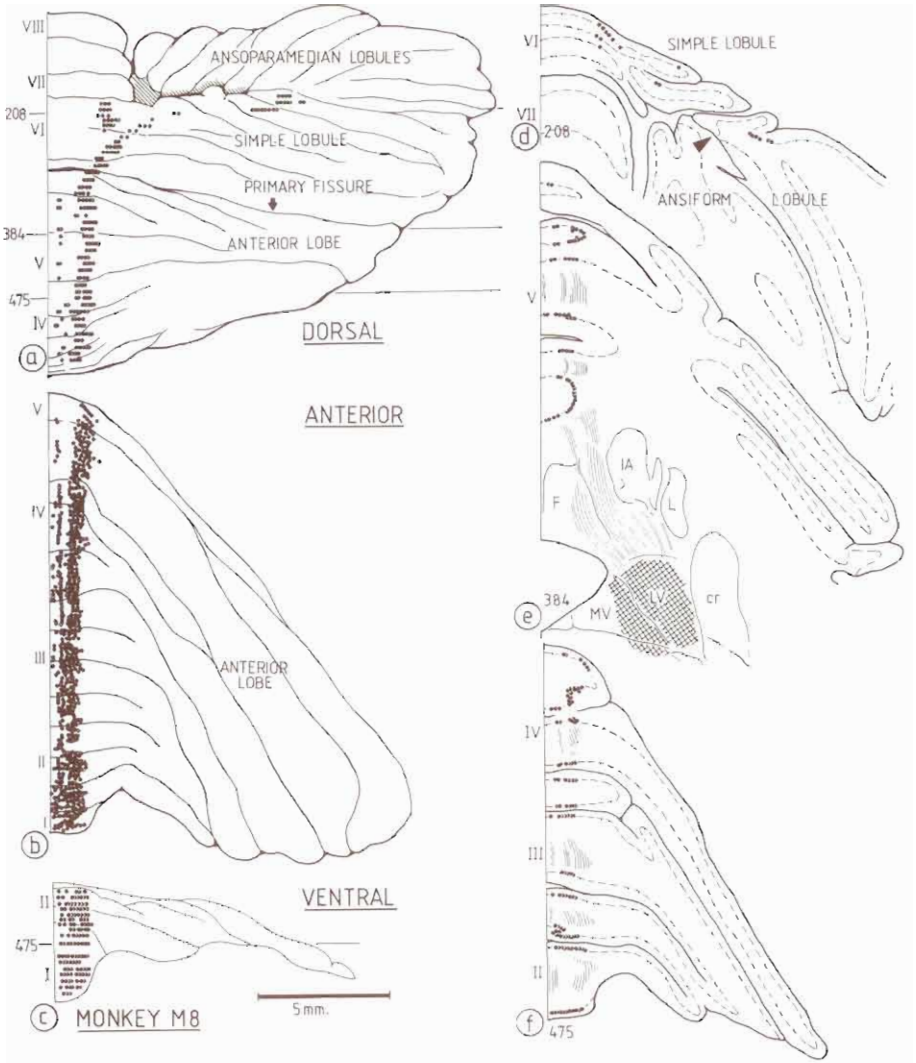

Fig. 6 – *Distribution of retrogradely labelled Purkinje cells and their axons after an injection of the vestibular nuclei, in monkey M8.*

Graphical reconstructions of (*a*) dorsal surface of the cerebellum, (*b*) anterior and (*c*) ventral aspect of the anterior lobe. Level of the sections depicted in *d* - *f* is indicated in (*a*). Area without cortex is hatched in (*a*) and indicated with arrowhead in the sections. Injection sites are indicated by double hatching.

and adjoining parts of the superior and medial vestibular nuclei. Labelled Purkinje cells in the lobules I-III constitute a broad, undivided band, which extends 1.1-0.8 mm laterally. It almost reaches the lateral margin of lobule I. In lobule III the band divides in medial and a lateral zones. On the dorsal surface of lobule V the gap between the two labelled Purkinje cell zones has widened and the lateral zone is located 1.0 mm. lateral to the midline. A few neurons located in the A-zone are still present in the simple lobule, caudal to the primary fissure. The

labeled B-zone diverges laterally and ends along the caudal border of the simple lobule, 1.6 mm laterally, near the border of lobule VII and the ansoparamedian lobule (Fig. 4d).

In the other case (rat JR166) the injection site is smaller and confined to the nucleus of Deiters (Fig. 4e). The labelling is less profuse than in the previous case and the bands are generally narrower (Fig. 5c). It is possible to separate the labelled Purkinje cells in the lobules I and II in a paramedian and a more lateral strip. At the caudal margin of the simple lobule the lateral zone turns laterally to terminate next to the area without cortex in the centre of the folial loop of the ansoparamedian lobule (Fig. 4a, d). In both cases Purkinje cell axons are retrogradely labeled. One bundle of retrogradely labelled axons passes from the injection site, between the dorsolateral protuberance of the fastigial nucleus and the anterior interposed nucleus to the labelled Purkinje cells of the lateral zone. Other fibers which turn more medially, through the fastigial nucleus, can be traced back to the labelled Purkinje cells located more medially (Fig. 4e).

Similar results were obtained in two monkeys (MR8, Fig. 6; MR7 Fig. 7). The injection sites in both cases included Deiters' nucleus and parts of the superior, medial and descending vestibular nuclei. Labelling in the lobules I and II is present in a single, wide band with a width of 1.4 mm. Occasionally it can be subdivided into a medial and a lateral strip. This subdivision becomes more distinct in the lobules III, IV and V. In MR7 three strips can be distinguished ventrally in III and IV, and in ventral V in the rostral wall of the primary fissure (Fig. 6b, f, 5a), a narrow medial strip consisting of one or two Purkinje cells, a wider, paramedian strip, which does not diverge laterally and attenuates in the dorsal part of the anterior lobe and a lateral zone. At the crest of lobule V the width of the B-zone is approximately 0.7 mm and it is separated by a 0.8 mm wide x-zone from the paramedian strip of labelled Purkinje cells which is located at 0.5 mm from the midline. In the simple lobule the labelled Purkinje cells of the lateral zone turn laterally. Labelled cells which are present as far laterally as 9 mm from the midline, are located at the roots of folia where the emerge from the intercrural sulcus with its area without cortex in the centre of the folial loop of the ansiform and paramedian lobules. Retrogradely labelled Purkinje cell axons, located in bundles corresponding to the labelled Purkinje cell zones were observed in case MR8 (Figs. 6e, f and 2b).

DISCUSSION

Purkinje cells of the anterior vermis projecting to the vestibular nuclei are arranged in parallel strips. This zonal pattern was found to be very constant among the different species studied in this paper. Our observations confirm previous studies in cat (7, 40, 41), and rabbit (2), and prosimian primates (20) and extend these to the rat and the monkey. It seems justified, therefore, to apply the nomenclature for the cortical zonation of the anterior vermis of carnivores (37, 38, 40, 42)

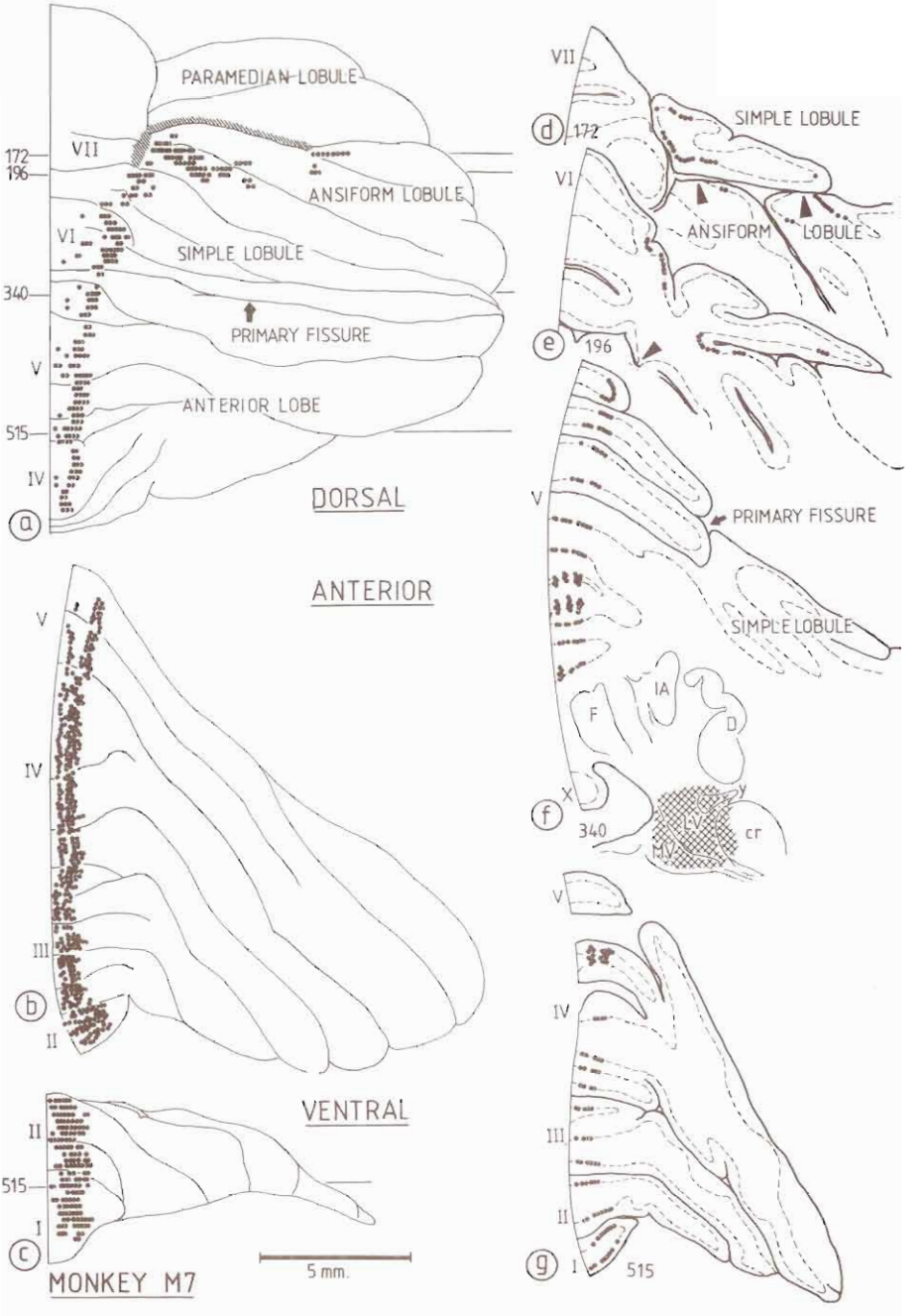

Fig. 7 – *Distribution of labelled Purkinje cells after an injection of the vestibular nuclei in monkey M7.*

Graphical reconstructions of (*a*) dorsal surface of the cerebellum, (*b*) anterior and (*c*) ventral aspect of the anterior lobe. Level of the sections depicted in *d* - *f* is indicated in a. Area without cortex is hatched in (*a*) and indicated with arrowhead in the sections. Injection sites are indicated by double hatching.

to these species. The presence of two strips of labelled Purkinje cells with projections to the vestibular nuclei is clearly visible in the dorsal part of the anterior lobe, where they are separated by a wedge-shaped area. The medial (sometimes double) strip of labeled Purkinje cells is located within the A-zone, the lateral strip corresponds to the B-zone, the intervening area to the x-zone of Ekerot and Larson (13; see also 8, 34, 35, 39, 40). Labelling in the A-zone diminishes in the dorsal part of the anterior lobe and is scarce or absent in the simple lobule. In the ventral part of the anterior lobe, where the X-zone is either absent or extremely narrow, the labelling in the A and B-zones fuses into a single band. In some of our cases, however, a subdivision into two zones is even present in the lobules I and II. When acetylcholinesterase is used to stain alternate sections, it is possible to verify the presence of labelling in separate A and B-zones in cat (29,40) and monkey (21) on the basis of the characteristic banding of this enzyme in the molecular layer of the cerebellar cortex and the presence of a distinct compartmentation of the cerebellar white matter. The lateral displacement of the B-zone in the simple lobule and its termination near the centre of the folial loop of the ansoparamedian lobule was found in all four species. The present study does not answer the question whether A and X-zones also continue into the simple lobule.

When the lateral border of the B-zone is taken as the lateral border of the anterior vermis this means that the vermis extends far into the territory usually assigned to the hemisphere (Fig. 8). It could be argued that the vermis corresponds to the A-zone only and that the B-zone should be included with the hemisphere. This denomination, however, is incompatible with the correspondence between the lateral border of the B-zone and the vague depression which delimits the anterior vermis in cat and monkey and which contains the paravermal vein (34, 35). We should accept the fact that zonal borders do not conform to the classical borders between vermis and hemisphere.

The efferent connections of the A and the B-zone with the vestibular nuclei have only been studied with retrograde methods in cat (41) and rabbit (14), and the conclusions that the A-zone projects both to the fastigial and the medial vestibular nucleus, and the B-zone to Deiters' nucleus still need to be verified with anterograde axonal tracing methods. In fact Andersson and Oscarsson (1), who studied these connections with electrophysiological methods, found the units which received inhibition from Purkinje cells of the a-zone and the b-zone to be intermingled in Deiters' nucleus.

Both the pattern and the width of the cerebellovestibular projection zones is very similar in the different species. The main difference between the species is the length of the anterior vermis and its component zones. When the length of the Purkinje cell layer of the lobules I-VI is determined slightly lateral to the sagittal plane in the different species it turns out that it increases from 46 mm in the rat and 75 mm in the rabbit to 153 mm in the cat to 180 mm in the monkey. Apart from allometrical factors, the differences in length of the anterior vermis may indicate that the number of parallel fibers and, consequently, the

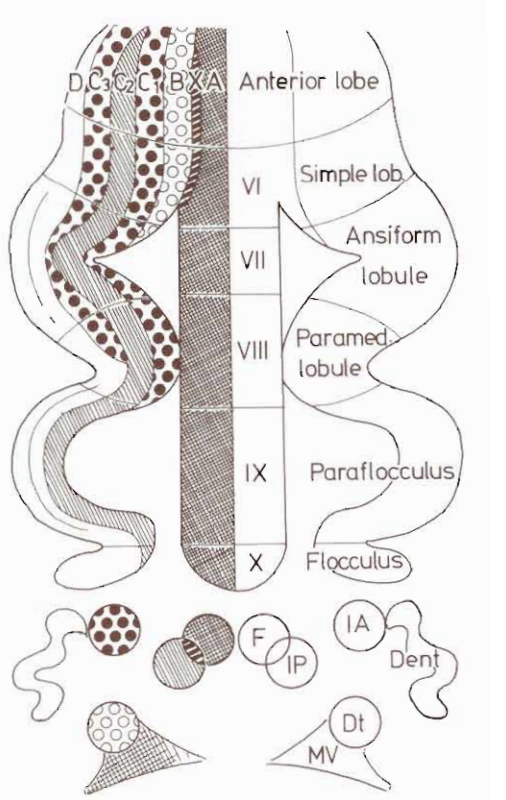

Fig. 8 – *Diagramatic representation of the corticonuclear and corticovestibular projection zones of the mammalian cerebellum.*

Zones A-D and their target nuclei are indicated with the same symbols (reproduced from Ref. 42).

number (and the diversity) of the mossy fibers which have access to the zonally organized efferent system of the anterior vermis, is much greater in primates and carnivores than in lagomorphs and rodents.

SUMMARY

Purkinje cells were retrogradely labelled from large injections of wheatgerm-coupled horseradish peroxidase in the vestibular nuclei, including Deiters' nucleus. The labelled Purkinje cells were located in two parallel strips in the anterior vermis; the medial strip is located within the A-zone, the lateral strip corresponds to the B-zone. In the ventral part of the anterior lobe the two strips fuse into a single band, in the dorsal part of the anterior lobe they are separated by a wedge-shaped area, corresponding to the X-zone. The B-zone proceeds in the simple lobule, where it deviates laterally and where it terminates at the centre of the

ansoparamedian lobule. Identical zonal patterns were observed in cat, rabbit, rat and monkey. The demarcation of the anterior vermis by the lateral border of the B-zone, and the differences in the projection of the A and B-zone are briefly discussed.

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