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Cerebellovestibular projection from the posterior lobe cortex in the rabbit: an experimental study with the retrograde HRP method. I. Topographical relationships

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Abstract. The sources of corticovestibular projections from the cerebellar posterior lobe vermis and hemisphere in the rabbit were investigated by the retrograde horseradish peroxidase (HRP) tracing method. Following iontophoretic injections into various subdivisions of the vestibular nuclear complex (VNC), labelled Purkinje neurones were identified ipsilaterally in all vermal lobules (VI through IX) and some regions of the hemisphere. The results indicate that projection is profuse and directed to all four nuclei of VNC. The labelling suggests some topographical relationships between lobules and especially sublobules of the posterior lobe and individual nuclei of VNC. The major projection originates from lobules VI and IX. A moderate projection derives from lobule VIII whereas that from lobule VII is small. Projections from the hemisphere arise mainly from crus I and crus II of the ansiform lobule. Those from the copula pyramidis, lobule HV and the ventral paraflocculus are sparse. In the present study a topographical relationships were more precisely established than before because the technique revealed VNC afferents from individual sublobules of the cerebellar posterior lobe cortex.

Key words: vestibular afferents, cerebellar cortex, topographical relationships, HRP and WGA-HRP retrograde tracing, rabbit

INTRODUCTION

Corticovestibular projections from the cerebellar posterior lobe have been investigated with degeneration and electrophysiological techniques as well as axoplasmic tracing methods in the cat (Walberg and Jansen 1961, Eager 1963, Voogd 1964, Angaut and Brodal 1967, Brodal 1974, Ito et al. 1982, Akaike 1983, Carleton and Carpenter 1983, Dietrichs et al. 1983, Matsushita and Wang 1986, Shojaku et al. 1987), monkey (Carleton and Carpenter 1983, Brodal 1984), opossum (Sreesai 1974, Henkel and Martin 1977, Klinkhachorn et al. 1984), galago (Haines 1975a,b, 1977), tupaia (Haines 1975b, Haines and Whitworth 1978) and rat (Umetani et al. 1986, Umetani and Tabuchi 1988, Tabuchi et al. 1989). Although considerable differences in results were found, general conclusions could be made regarding the arrangement of the projection. Lobules VI and VII contribute to few, if any, corticovestibular projections. Fibres from lobule VIII (pyramis) are sparse to moderate and those from lobule IX (uvula) are the most numerous. The superior (SV) and inferior (IV) vestibular nuclei receive the majority of cortical fibres from the posterior lobe vermis, with the lateral (LV) and medial (MV) vestibular nuclei acquiring a lesser projection. With regard to projections from the hemisphere, most authors agree that the paraflocculus (Angaut and Brodal 1967, Sreesai 1973, Brodal 1974, Haines 1975a, Haines and Whitworth 1978) as well the simple lobule (Umetani et al. 1986) and paramedian lobule (Voogd and Bigaré 1980, Courville and Faraco-Cautin 1986) do not send any Purkinje axons to VNC. The ansiform lobule (crus I and crus II) gives rise to few if any corticovestibular fibres (Eager 1963, Brodal 1967, Sreesai 1974, Haines 1975a, Dietrichs et al. 1983, Umetani et al. 1986). Moreover, no information is available about VNC afferents from the hemispheral part of lobules V (HV) and VIII (copula pyramidis). In many reports projections were found to be ipsilateral. However, some authors found degenerated fibres within bilateral VNC after ipsilateral lesion of the cerebellar cortex (Eager 1963, Sreesai 1975).

There are few reports concerned with VNC afferents arising from the posterior lobe cortex in the rabbit. From the degeneration studies of Van Rossum (1969) it was concluded that sparse projections from lobules VI-VIII were directed to LV. Lobule IX contributes the most significantly to IV and SV and to less extent to MV. In more recent studies HRP injection into SV, MV and LV resulted in labelling Purkinje neurones in lobules VIII and IX (Balaban 1984) or extensive labelling in lobule IX following WGA-HRP injection into VNC (except LV) (Epema et al. 1985). Projections from remaining lobules (VI and VII) and the hemispheral part of the posterior lobe to VNC in the rabbit had not been studied so far. Thus, the present study considers the following questions: (1) Which lobules and especially sublobules of the posterior lobe vermis and hemisphere contribute to the corticovestibular system? (2) Which of the individual nuclei of VNC receive projections from the cerebellar cortex? (3) Is there a topographical pattern in projection from particular lobules and sublobules to the individual nuclei of VNC? (4) What is the laterality of the projection?

METHODS

Experiments were carried out on 35 adult rabbits. The animals were anaesthetized with ketamine hydrochloride (20mg/kg) and diazepam (2mg/kg), and then artificially respirated with the use of 1% halothane. After surgical preparation, single iontophoretic (DC 0.75-3 μA, 7-17min) injections of 10-25% HRP (Sigma, type VI) or 0.5-1,5% WGA-HRP (Sigma) in 0.2 M Tris-HCl (pH 8.6) were made into VNC on the right side through a glass micropipette (tip diameter 5-45 μm). The rabbits survived for 20-46 h and then were sacrificed with an overdose of vetbutal and by transcardiac perfusion with 0.9% NaCl followed by 4% formalin and 10% sucrose in 0.2 M phosphate buffer (pH 7.4). The cerebellum and brainstem were immersed overnight in 30% sucrose in 0.2 M phosphate buffer (pH 7.4) at 4°C. Frozen blocks of tissue were cut into 90 μm-thick sagittal or transverse (cerebellum)

and 40-50 μm-thick transverse (pons and medulla) serial sections. All they were processed histochemically according to the TMB method of Mesulam (1982). The approximate extent of the injection site, including its peripheral zone, was determined basing on the established criteria (Mesulam 1982) and superimposed onto modified diagrams of transverse section and onto horizontal reconstruction of VNC on the right side (Epema et al. 1988). Labelled Purkinje neurones were counted from each sagittal or (in four cases) transversal sections. The subdivisions of VNC were identified according to Meessen and Olszewski (1949), Brodal and Pompeiano (1957), Balaban (1988) and nomenclature of the cerebellar posterior lobe was referred to Van Rossum (1969). Besides of vermal and hemispheral lobules, the copula pyramidis and lobule HV were also taken into account in this paper. Each lobule is classically divided into sublobules, although a few additional sublobules VIa1, VIb1, VIIb1 and VIIIb1 were distinguished in the present study.

RESULTS

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

In three experiments (Nos. 170, 189 and 200) the tracer was injected into all four nuclei of VNC to determine possible sources of afferent projection from various parts of the posterior lobe cortex (Fig. 1).

In rabbit No.200 the injection involved the caudal half of SV, the rostral portion of the medial vestibular nucleus (MVr), the rostral 1/3 of the caudal portion of the medial vestibular nucleus (MVc), as well as LV and the rostral half of IV. Moreover, HRP spread to the medial regions of the acoustic tubercle (TA) and marginally to the inferior cerebellar peduncle (PCI). A great number of labelled Purkinje cells were present ipsilaterally in all lobules of the posterior lobe vermis (Fig. 2A) and in some regions of the hemisphere. In lobule VI abundant labelling was found in sublobules VIa1, VIa (Fig. 2B), VIb1 and VIb, with light labelling in sublobule VIc. No neurones were labelled in sublobule VId. In lobule VII heavy labelling was seen in sublobule VIIb1 but sublobules VIIa and VIIb were free of labelled neurones. A large number of neurones were labelled in all sublobules of the pyramis (VIIIa, VIIIb and VIIIb1) as well as in all sublobules of the uvula (IXa through IXd) (Fig. 2A and C). In the hemisphere labelled neurones were found in the medial and lateral regions of crus I, in the apical part of crus II, with few in the copula pyramidis, lobule HV and the ventral paraflocculus.

Comparable distribution of labelled neurones was observed after similar extent of injection in rab-

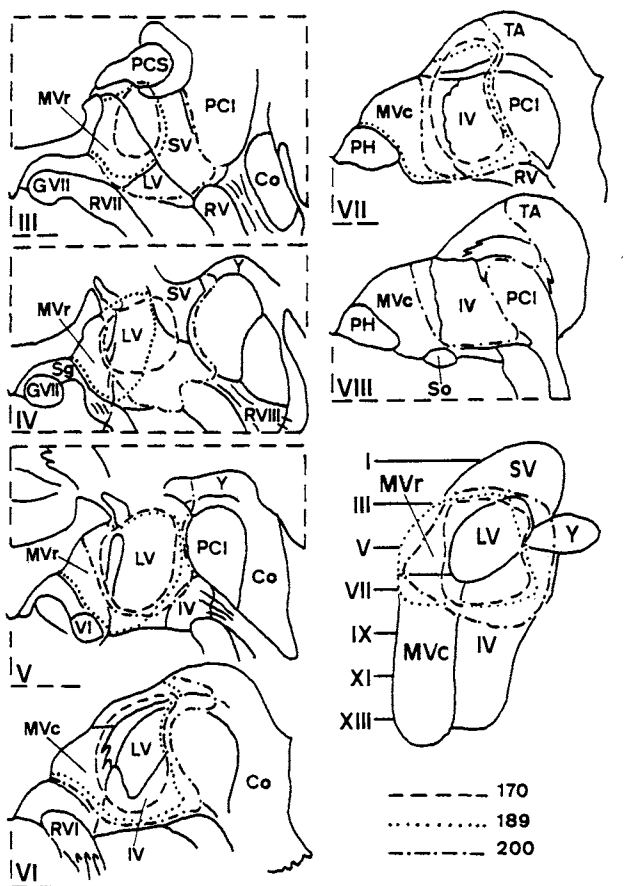

Fig. 1. Extent of the HRP and WGA-HRP injection sites in SV, LV, MV and IV (cases Nos. 170, 189 and 200) on diagrams of transverse section through the vestibular nuclear complex and horizontal reconstruction of the vestibular nuclear complex obtained by dorsal projection of the boundaries between the individual main vestibular subdivisions on right side. The same diagrams apply to Figs. 4-8.

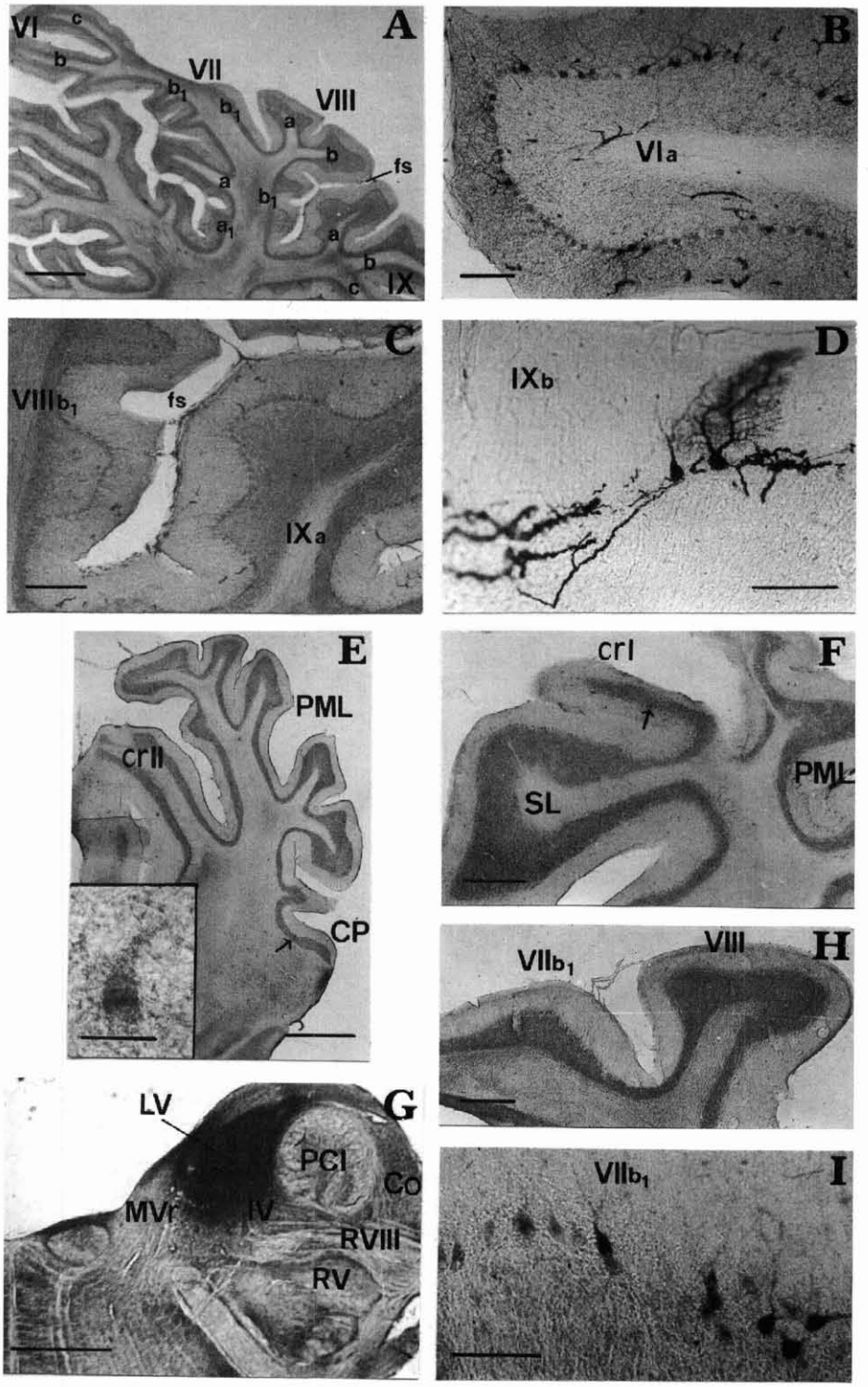

Fig. 2. Photomicrographs of retrogradely labelled Purkinje neurones on sagittal sections through the cerebelllar posterior lobe and transverse section through the injection site in the vestibular nuclear complex. (A) Labelled neurones in the vermal lobules VI, VII, VIII and IX, and (B) higher magnification of labelled neurones in sublobules VIa, (C) VIIIb1 and IXa from A, in case No. 200. (D) Labelled neurones in sublobule IXb, (E) the copula pyramidis and (F) crus I, in case No. 189. (G) WGA-HRP injection in VNC between levels V and VI and (H) labelled neurones in sublobule VIIb1 and (I) their magnification, in case No. 170. Inset is higher magnification of labelled neurone indicated by arrow. Bars represent 1,500 μm for A, E and G, 500 μm for C, F and H , 100 μm for B, D and I; 50 μm for inset.

bit No.189 and after smaller injection in rabbit No.170 (Fig. 2D-I).

Distribution of labelled Purkinje neurones in the posterior lobe after HRP injection into two vestibular nuclei

INJECTIONS INTO SV AND LV

In one case (No. 210) the injection involved the caudal 2/3 of SV and the dorsal region of the rostral half of LV. Labelled neurones were seen mostly in sublobule IXd, along the posterolateral fissure and at its bottom. In the hemisphere several neurones were labelled in the lateral region of crus I, the copula pyramidis and lobule HV.

INJECTIONS INTO MV AND LV

In five cases (Nos. 160, 162-not illustrated, 188, 192 and 195) injection was made into various regions of MV and LV (Fig. 3).

For rabbits Nos. 160, 162 and 195, the most representative is that No. 162. The injection covered the dorsolateral region of MVr and the dorsomedial region of the caudal 2/3 of LV. Labelled neurones were identified mainly in sublobules VIa1-VIb (Fig. 4A and B), VIIb1, in the pyramis and on the dorsal side of sublobule IXd (along the posterolateral fissure). In the hemisphere several neurones were labelled in the medial region of crus I, in the apical part of crus II and the ventral paraflocculus.

In the next two rabbits, Nos. 188 and 192, similar WGA-HRP injections involved mainly the ventrolateral region of MVr and ventromedial region of LV. Moreover, the tracer spread to the root of the facial nerve (RVII) (case No.188). Labelled neurones were seen only in sublobules VIa1-VIb1 in case No.188.

INJECTIONS INTO LV AND IV

In seven experiments, Nos. 151, 156, 196, 209 (Fig. 5) and Nos. 149, 158,164 (not illustrated), the injection was made into various regions of LV and IV. Moreover, the tracer spread to neighboring lat-

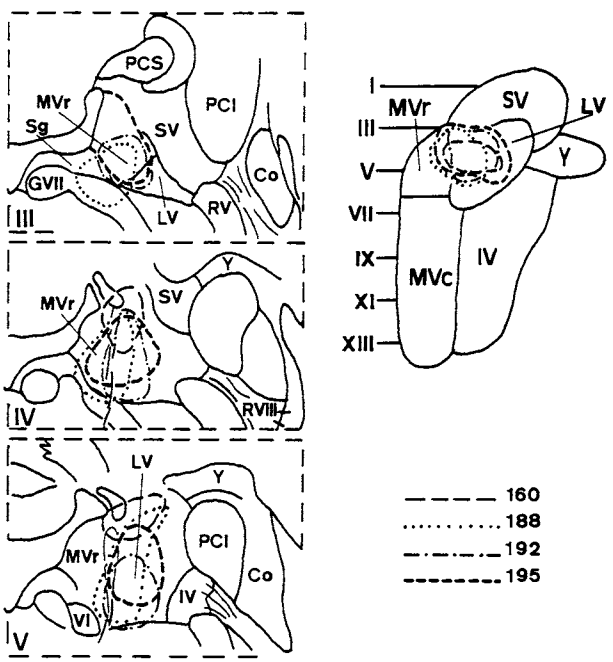

Fig. 3. Extent of the HRP and WGA-HRP injection sites in MV and LV (cases Nos. 160, 188, 192 and 195).

eralmost region of MVc and to TA in cases Nos. 149 and 151.

In all these rabbits labelled neurones were seen in sublobules VIa1-VIb. In most cases they were found in sublobule VIIb1, the pyramis and the uvula, mainly on the dorsal (along the second fissure) and ventral (along the posterolateral fissure) sides of sublobules IXa and IXd, respectively. In the hemisphere labelled neurones occurred sparsely in the lateral region of crus I, the apical part of crus II, the copula pyramidis, lobule HV and the ventral paraflocculus.

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

INJESTIONS INTO SV

In four experiments (Nos. 94, 179-not illustrated, 201 and 206) the enzyme was injected into SV (Fig. 6).

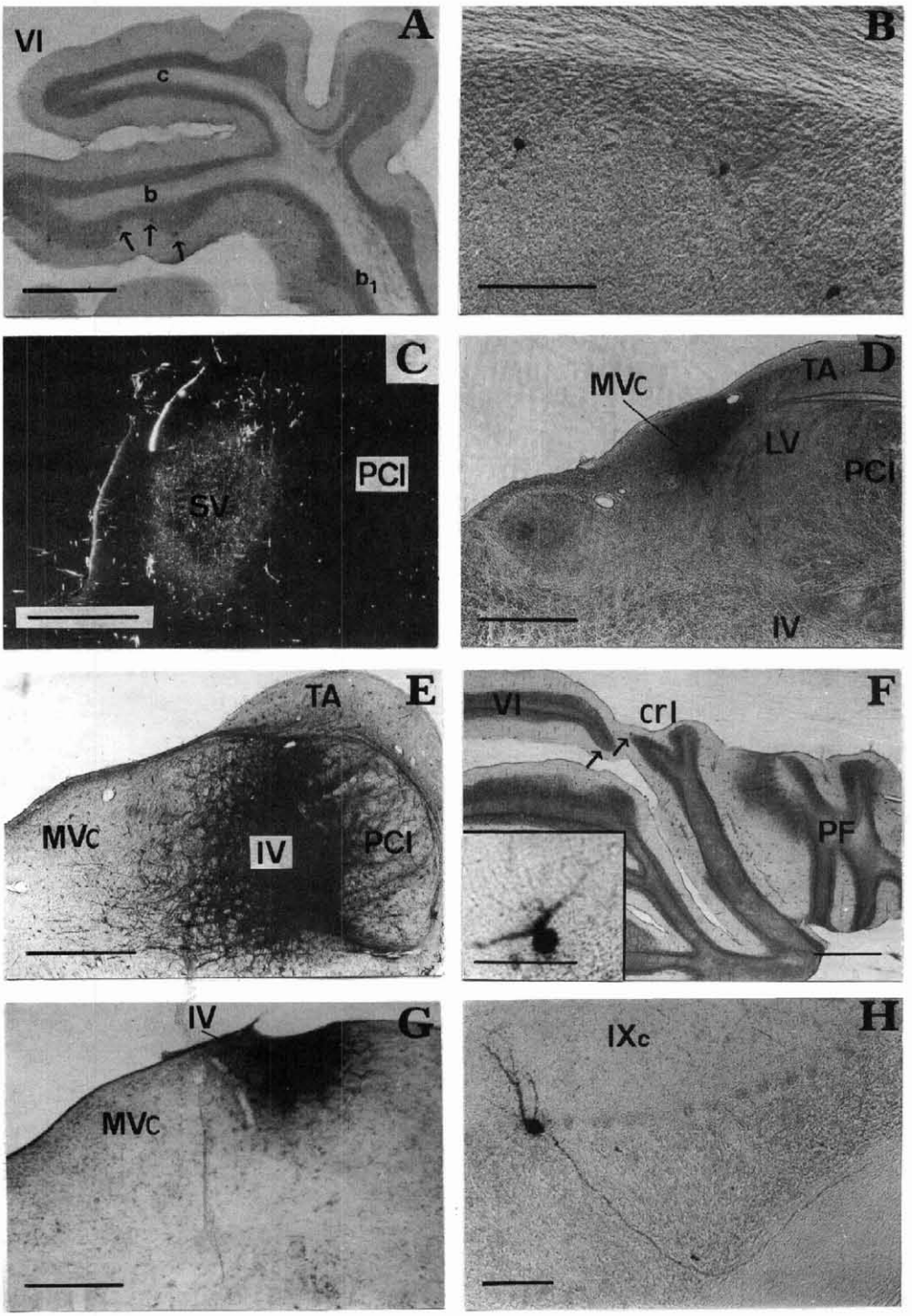

Fig. 4. Photomicrographs of retrogradely labelled Purkinje neurones in the cerebellar posterior lobe and transverse sections through the injection site in the vestibular nuclear complex. (A) Labelled neurones in sublobule VIb on sagittal section and (B) magnification of labelled neurones (interference contrast microscopy) indicated by arrows, in case No. 162. (C) WGA-HRP injection in SV between levels II and III, in case No. 206 (polarized illumination). (D) HRP injection in MV at level VI, in case No. 163. (E) HRP injection in the rostral part of IV at level VIII, in case No. 199. (F) Labelled neurones in lobule VI and crus I on transverse section through the cerebellum, in case No. 140. (G) WGA-HRP injection in the caudal part of IV at level X and (H) labelled neurone in lobule IXc, in case No. 203. Inset is higher magnification of labelled neurone in crus I indicated by arrow. Bars represent 1,500 μm for F, 1,000 μm for A and C-E, 500 μm for G, 250 μm for B, 100 μm for H; 100 μm for inset.

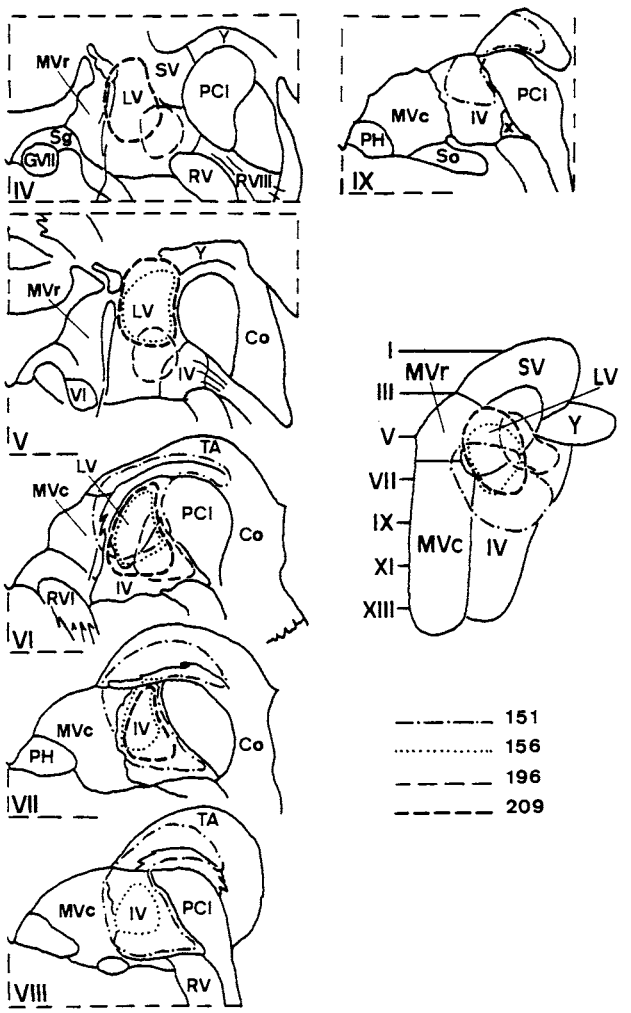

Fig. 5. Extent of the HRP injection sites in LV and IV (cases Nos. 151, 156, 196 and 209).

In two rabbits the injection was confined to the medial region (case No. 201) or the dorsal half (case No. 94) of the central aspect of SV and diffusion involved marginally MVr. In both cases labelled neurones were found only in the uvula, especially on the ventral side of sublobule IXd, along the posterolateral fissure. In the hemisphere several neurones were labelled in lobule HV and in the copula pyramidis (case No. 94).

In rabbits with the injection restricted to the very small dorsomedial region of SV (case No. 179) or the central SV (case No. 206) (Fig. 4C), the posterior lobe cortex was free of labelling.

INJECTIONS INTO MV

In three cases (Nos. 163, 168 and 173) injection was confined to MV (Fig. 6).

In rabbits No. 163 (Fig. 4D) and No.168 the injection was centred in the dorsal regions of the caudal half of MVr and the rostral part of MVc with small involvement of adjacent IV and TA. Labelled neurones occurred in sublobules VIIIa, VIIIb, on the dorsal side of sublobule IXa and the ventral side of sublobule IXd, mainly at the bottom of the posterolateral fissure.

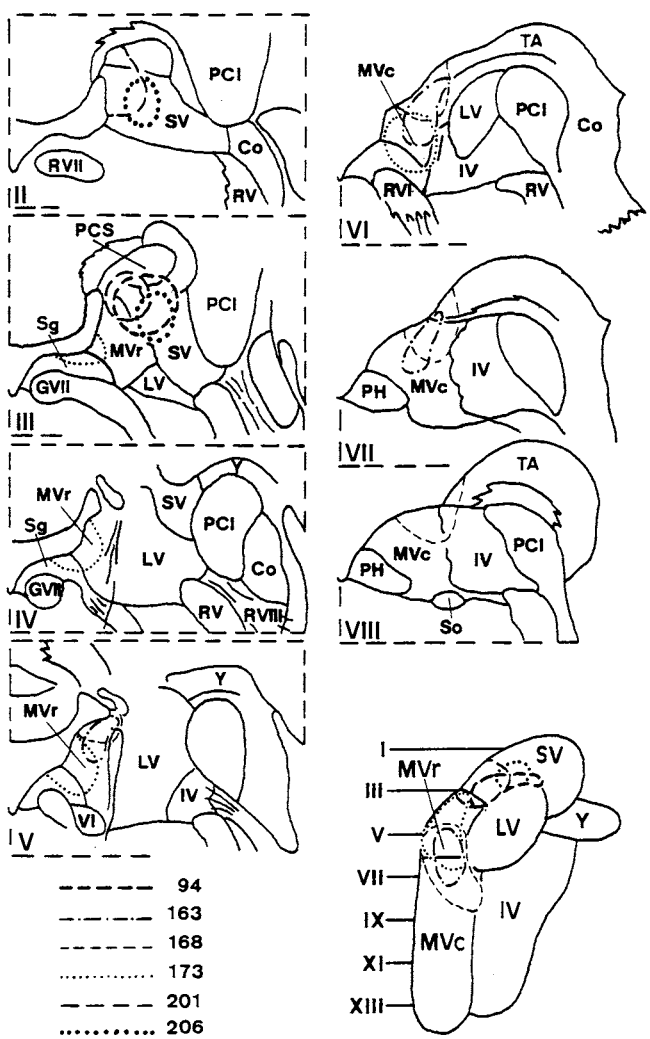

Fig. 6. Extent of the HRP and WGA-HRP injection sites in SV (cases Nos. 94, 201 and 206) and MV (cases Nos. 163, 168 and 173).

In rabbit No. 173 with the WGA-HRP injection in the medial and ventral regions of MVr and MVc, no labelled neurones were observed in the posterior lobe cortex.

INJECTIONS INTO LV

In five experiments (Nos. 148, 159, 187-not illustrated, 197 and 211) the tracer was injected into LV (Fig. 7).

For two rabbits, No. 159 and No. 211, with the injection made in the dorsal region of the caudal part of LV, the representative case is that No. 159. Labelled neurones were found in sublobules VIa1-VIc, VIIIb and VIIIb1 as well as on the dorsal side of sublobule IXa (mainly at the bottom of the second fissure) and on the ventral side of sublobule IXd (mainly at the bottom of the posterolateral fissure).

In rabbit No. 148 a small injection was placed in the caudal pole of LV. Only few neurones were labelled in sublobule VIb1.

In rabbits No. 187 and No. 197 no labelled neurones were found after WGA-HRP injection into the ventral region of LV or very small HRP injection into the lateralmost region of LV, respectively.

INJECTIONS INTO IV

In five experiments, Nos. 140, 194, 202 (Fig. 8), No. 199 (Fig. 4E) and No. 191 (not illustrated), the enzyme activity was identified in the rostral area within IV.

In rabbits No. 140 and No. 199 almost identical injections covered the rostral half of IV, and the tracer spread to small neighbouring regions of LV, MVc and cell group x. In rabbits No.194 and No. 202 injections were smaller. In these cases small number of labelled neurones appeared mainly in sublobules VIa1, VIa, VIIIb1 and in the uvula, as well as in the medial region of crus I (Fig. 4F) and the ventral paraflocculus. In rabbit No. 191 a small WGA-HRP injection, limited to the ventromedial

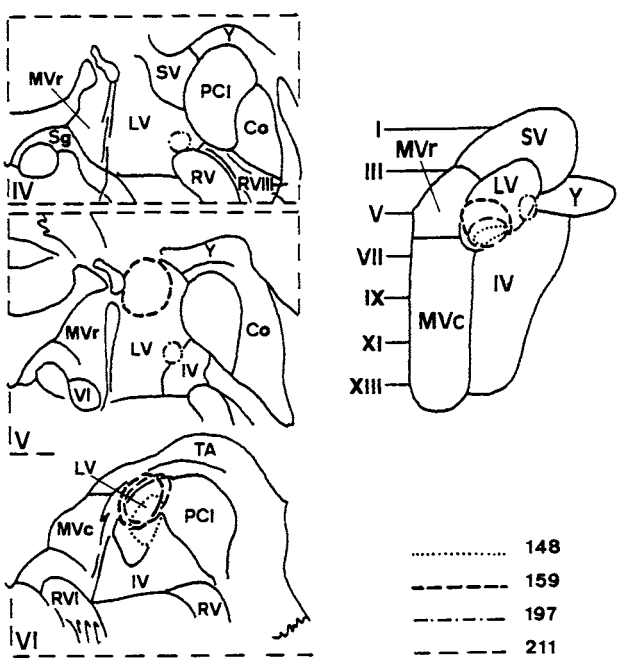

Fig. 7. Extent of the HRP injection sites in LV (cases Nos. 148, 159, 197 and 211).

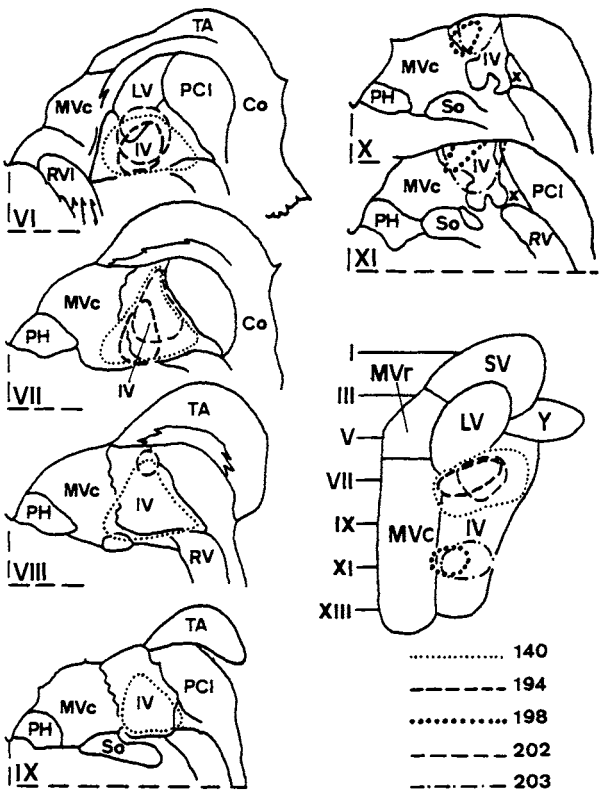

Fig. 8. Extent of the HRP and WGA-HRP injection sites in the rostral (cases Nos.140, 194 and 202) and caudal (cases Nos. 198 and 203) parts of IV.

region of the rostral part of IV, produced no labelled neurones in the posterior lobe cortex.

In two cases small HRP (No. 198) or WGA-HRP (No. 203) injections were made into the caudal part of IV (Fig. 8).

In rabbit No. 198 light labelling was seen in sublobules VIIb1, VIIIa and IXd. In rabbit No. 203 relatively great number of neurones were labelled in all sublobules of the uvula. They were also seen in sublobules VIIIb, VIIIb1 and in the ventral paraflocculus.

DISCUSSION

Methodological remarks

It has been suggested that only the dark central core represents the real site of the tracer uptake (Vanegas et al. 1978, Horton et al. 1979, FitzGibbon et al. 1983), although the peripheral diffusion zone and even intact passing fibres could also be the effective uptake area (Walberg et al. 1980, Ahlsén 1981). In few cases of injections into VNC, HRP spread to a small medial regions of TA and to the dorsal region of RF. In five control experiments, HRP injection was restricted to TA or the dorsal region of RF (data not shown). Absence of labelling in the cerebellar cortex in all control cases suggests that in the present study the tracer has not been taken up by any corticofugal axons passing through the injection site within VNC.

Origin of cerebellar corticovestibular projections

The present report with the retrograde HRP and WGA-HRP techniques has revealed profuse cortical ipsilateral projections from all lobules of the cerebellar posterior lobe vermis and from some lobules of hemisphere to all four nuclei of VNC in the rabbit. The different patterns of labelling suggest that there are some topographical relationships between individual nuclei of VNC and lobules or even sublobules of the posterior lobe. The greater number of afferents to the vestibular nuclei originate from the vermal lobules VI and IX. A smaller projection derives from lobule VIII and fibres from lobule VII are moderately frequent. Afferents from the hemisphere originate mainly from crus I and crus II of the ansiform lobule. Those from the copula pyramidis, lobule HV and the ventral paraflocculus are sparse. Main targets of corticovestibular fibres are IV and the dorsal region of LV. A lesser projection is directed to SV and MV.

Corticovestibular projections from individual sublobules of the posterior lobe including sublobules distinguished in this study (VIa1, VIb1, VIIb1 and VIIIb1) have not been described thus far.

Lobule VI gives rise to great number of axons to LV from sublobules VIa1-VIc and less to IV from sublobules VIa1 and VIa. No fibres terminate in SV and MV. Van Rossum (1969) used axonal degeneration method in the rabbit and found sparse projection to the dorsal region of LV. More recent HRP study of Balaban (1984) revealed projection only from sublobule VIa to LV and MV. The present findings suggest that the projection is more profuse and in addition originates from more dorsal sublobules VIb1-VIc. The projection from lobule VI to IV in the rabbit has been described for the first time here. Moreover, only the rostral part of IV receives afferents from lobule VI. A small or no projection from lobule VI to LV and IV was observed in other species (Voogd 1964, Haines 1975a,b, Carleton and Carpenter 1983, Klinkhachorn et al. 1984, Umetani et al. 1986).

Projection from lobule VII takes origin only from sublobule VIIb1 and it is directed to LV and IV. The projection to IV in the rabbit is reported here for the first time . There is a general agreement that projection from lobule VII is very sparse to LV, IV and SV (Walberg and Jansen 1961, Van Rossum 1969, Klinkhachorn et al. 1984, Umetani et al. 1986) or even absent to LV and IV (Haines et al. 1976, Carleton and Carpenter 1983).

Lobule VIII gives rise to projections that end in LV and IV, and in the dorsal region of MV. Sublobules VIIIa and VIIIb send axons to all these nuclei, and sublobule VIIIb1 projects to LV and IV. There are different opinions on terminal areas within VNC

of Purkinje axons arrising from the pyramis (Voogd 1964, Angaut and Brodal 1967, Van Rossum 1969, Sreesai 1974, Henkel 1977, Carleton and Carpenter 1983, Dietrichs et al. 1983, Klinkhachorn et al. 1984, Umetani and Tabuchi 1988). The present results are in agreement with those of Balaban (1984) in the rabbit showing that lobule VIII projects to LV and MV, but do not confirm projections to SV. Moreover, projection from the pyramis to IV in the rabbit has not been described so far.

Afferents from lobule IX terminate in all nuclei of VNC, mainly in SV and IV, to a lesser extent in LV and rather sparsely in MV. Lobule IX is the only part of the posterior lobe vermis that sends axons to SV. Most fibres to SV arise from the ventral side of sublobule IXd (along the posterolateral fissure). This corresponds to the findings of Epema et al. (1985) and Shojaku et al. (1987). The present study confirms the previous results that only peripheral region of SV receives afferents from the uvula (Voogd 1964, Angaut and Brodal 1967, Van Rossum 1969, Walberg 1972, Brodal 1974, Haines 1977, Carpenter and Cowie 1985). Selective injections into IV (present study) support the existence of afferents from lobule IX reported with the degeneration method (Van Rossum 1969) or extensive HRP injection into the caudal part of VNC (Epema et al. 1985) in the rabbit. The present findings has shown that unlike the rostral part of IV, the caudal part receives greater number of Purkinje axons from the uvula. The observation, for the first time made in the rabbit, confirms those made in other species (Angaut and Brodal 1967, Walberg 1972, Brodal 1974, Haines 1977, Henkel 1977). Moreover, the present results support observation that the largest projections to IV arise from lobule IX (Carleton and Carpenter 1983, Matsushita and Wang 1983, Shojaku et al. 1987, Tabuchi et al. 1989).The main source of the uvular afferents to LV seems to be the dorsal side of sublobule IXa (mainly the bottom of the second fissure) and the ventral side of sublobule IXd (mainly the bottom of the posterolateral fissure). Sublobules IXb and IXc give rise to few afferents to LV. The present results confirm the existence of the uvular projection to LV (Akaike 1983, Carleton and Carpenter 1983, Balaban 1984, Tabuchi et al. 1989) and precisely determine the origin of that projection. MV is supplied by fibres from the uvula in a lesser extent. It is likely that the projection is limited to the dorsal region of MV. Epema et al. (1985) achieved in the rabbit profuse labelling in lobule IX after injection into VNC. In the present study selective injections into MV have revealed that the uvular projection to MV arise from the dorsal side of sublobule IXa (along the second fissure) and the ventral side of sublobule IXd (mainly from the bottom of the posterolateral fissure). There is no agreement whether fibres from the uvula terminate in MV or not. Some authors obtained negative results (Walberg and Jansen 1964, Brodal 1974), others indicated scarce (Voogd 1964, Haines 1975a, 1977, Klinkhachorn et al. 1984, Shojaku et al. 1987) or relatively profuse projections (Carpenter 1988, Tabuchi et al. 1989).

In the present study projections from the hemispheral part of the posterior lobe arise mainly from the ansiform lobule. The medial region of crus I sends axons to IV and to a less extent to LV and MV. The lateral region of crus I seems to supply SV and LV. Smaller projection from crus II, especially the apical part, has been shown to MV, LV and IV. Projection from the ansiform lobule to VNC in the rabbit has not been studied so far. Few afferents from crus I to LV (Eager 1963) or to VNC (Dietrichs et al. 1983) are revealed in the cat. Fibres from crus II were not reported to terminate in VNC (Angaut and Brodal 1967, Sreesai 1974, Umetani et al. 1986) or the projection was extremely sparse (Haines 1975a). The scanty projection from the copula pyramidis at least to SV revealed in the present report has not been shown before. Umetani and Tabuchi (1988) found no connection to VNC in the rat. Sparse afferents from lobule HV directed at least to SV and from the ventral paraflocculus directed at least to IV (present study) have not been reported until now (Angaut and Brodal 1967, Brodal 1974, Haines 1975a, Haines and Whitworth 1978, Umetani et al. 1986). In the present study absence of projections from the simple lobule and paramedian lobule to VNC is consistent with previous observations

(Voogd and Bigaré 1980, Courville and Faraco-Cautin 1986, Umetani et al. 1986, Grottel et. al. 1991).

The present report provides new data on the corticovestibular projections from the cerebellar posterior lobe in the rabbit. Some discrepancies in the results between the rabbit and other mammals may reflect differences in the species and/or the techniques used by previous authors.

ABBREVIATIONS

CP	copula pyramidis
Co	ventral cochlear nucleus
cr I	crus I
cr II	crus II
fs	second fissure
GVII	genu of facial nerve
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
PCI	inferior cerebellar peduncle
PCS	superior cerebellar peduncle
PH	prepositus hypoglossi nucleus
PML	paramedian lobule
RV	root of trigeminal nerve
RVII	root of facial nerve
RVIII	root of vestibular nerve
Sg	supragenual nucleus
So	solitary tract and its nucleus
SV	superior vestibular nucleus
SL	simple lobule
TA	acoustic tubercle
x	group x
Y	group Y
VI	abducens nucleus

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REFERENCES

Akaike T. (1983) Electrophysiological analysis of cerebellar corticovestibular and fastigovestibular projections to the lateral vestibular nucleus in the cat. Brain Res. 272: 223-235.

Ahlsén G. (1981) Retrograde labelling of retinogeniculate neurones in the cat by HRP uptake from the diffuse injection zone. Brain Res. 223: 374-380.

Angaut P., Brodal A. (1967) The projection of the "vestibulocerebellum" onto the vestibular nuclei in the cat. Arch. Ital. Biol. 105: 441-479.

Balaban C.D. (1984) Olivo-vestibular and cerebello-vestibular connections in albino rabbits. Neuroscience 12: 129-149.

Balaban C.D. (1988) Distribution of inferior olivary projections to the vestibular nuclei of albino rabbits. Neuroscience 24: 119-134.

Brodal A. (1974) Anatomy of the vestibular nuclei and their connection. In: Handbook of sensory physiology (Ed. H.H. Kornhuber). Chapter VI. Springer Verlag, New York, p. 239-352.

Brodal A. (1984) The vestibular nuclei in the macaque monkey. J. Comp. Neurol. 227: 252-266.

Brodal A., Pompeiano O. (1957) The vestibular nuclei in the cat. J. Anat. 91: 438-454.

Carleton S.C., Carpenter M.B. (1983) Afferent and efferent connections of the medial, inferior and lateral vestibular nuclei ih the cat and monkey. Brain Res. 278: 29-51.

Carpenter M.B. (1988) Vestibular nuclei: afferent and efferent projections. Progr. Brain Res. 76: 5-15.

Carpenter M.B., Cowie R.J. (1985) Connections and oculomotor projections of the superior vestibular nucleus and cell group "y". Brain Res. 336: 265-287.

Courville J., Faraco-Cautin F. (1986) Cerebellar corticonuclear projection demonstrated by the horseradish peroxidase method. Neurosci. Abstr. 12: 108.

Dietrichs E., Zheng Z.-H., Walberg F. (1983) The cerebellar corticovestibular projection in the cat as studied with retrograde transport of horseradish peroxidase. Anat. Embryol. 166: 369-383.

Eager R.P. (1963) Efferent cortico-nuclear pathways in the cerebellum of the cat. J. Comp. Neurol. 120: 81-103.

Epema A.H., Gerrits N.M., Voogd J. (1988) Commissural and intrinsic connections of the vestibular nuclei in the rabbit: a retrograde labeling study. Exp. Brain Res. 71: 129-146.

Epema A.H., Gouldemond J.M, Voogd J. (1985) Reciprocal connections between the caudal vermis and the vestibular nuclei in the rabbit. Neurosci. Lett. 57: 273-278.

FitzGibbon T., Kerr L., Burke W. (1983) Uptake of horseradish peroxidase by axons of passage and its modification by poly-L-ornithine and dimethylosulphoxide. J. Neurosci. Meth. 7: 73-88.

Grottel K., Zimny R., Jakielska D., Ostrowska A. (1991) Non-reciprocal connections between the vestibular nuclei and cerebellar paramedian lobule, with special reference to the climbing fiber zones: an analysis in the rabbit using the retrograde horseradish peroxidase method. Neurosci. Res. 12: 185-200.

Haines D.E. (1975a) Cerebellar corticovestibular fibers of the posterior lobe in a prosimian primate, the lesser bushbaby (Galago senegalensis). J. Comp. Neurol. 160: 363-398.

Haines D.E. (1975b) Cerebellar cortical efferents of the posterior lobe vermis in a prosimian primate (Galago) and tree shrew (Tupaia). J. Comp. Neurol. 163: 21-40.

Haines D.E. (1977) Cerebellar corticonuclear and corticovestibular fibers of the flocculonodular lobe in a prosimian primate (Galago senegalensis). J. Comp. Neurol. 174: 607-630.

Haines D.E., Whitworth R.H. (1978) Cerebellar cortical efferent fibers of the paraflocculus of tree shrew (Tupaia glis). J. Comp. Neurol. 182: 137-150.

Henkel C.K., Martin G.F. (1977) The vestibular complex of the american opossum Didelphis virginiana. II. Afferent and efferent connections. J. Comp. Neurol. 172: 321-348.

Horton J.C., Greenwood M.M., Hubel D.H. (1979) Nonretinotopic arrangement of fibres in cat optic nerve. Nature 282: 720-722.

Ito M., Sasa M., Matsuoka I., Takaori S. (1982) Afferent projection from reticular nuclei, inferior olive and cerebellum to lateral vestibular nucleus of the cat as demonstrated by horseradish peroxidase. Brain Res. 231: 427-432.

Klinkhachorn P.S., Haines D.E., Culberson J.L. (1984) Cerebellar cortical efferent fibers in the north american opossum, Didelphis virginiana. II. The posterior vermis. J. Comp. Neurol. 227: 439-451.

Matsushita M., Wang C.L. (1986) Cerebellar corticovestibular projection from lobule IX to the descending vestibular nucleus in the cat. A retrograde wheat germ agglutinin-horseradish peroxidase study. Neurosci. Lett. 66: 293-298.

Meessen H., Olszewski J. (1949) A cytoarchitectonic atlas of the rhombencephalon of the rabbit (Ed. S. Karger). Basel, New York.

Mesulam M.-M. (1982) Principles of horseradish peroxidase neurohistochemistry and their application for tracing neural pathways - axonal transport, enzyme histochemistry and light microscopic analysis. In: Tracing neural connections with horseradish peroxidase (Ed. M.-M. Mesulam). John Wiley and Sons, New York, p.1-151.

Shojaku H., Sato Y., Ikarashi K., Kawasaki T. (1987) Topographical distribution of Purkinje cells in the uvula and the nodulus projecting to the vestibular nuclei in cats. Brain Res. 416: 100-112.

Sreesai M. (1974) Cerebellar cortical projections of the opossum (Didelphis marsupialis virginiana). J. Hirnforsch. 15: 529-544.

Tabuchi T., Umetani T. Yamadori T. (1989) Corticonuclear and corticovestibular projections from the uvula in the albino rat: differential projections from sublobuli of the uvula. Brain Res. 492: 176-186.

Umetani T., Tabuchi T. (1988) Topographic organization of the corticonuclear and corticovestibular projections from the pyramis and copula pyramidis in the albino rat. An autoradiographic orthograde tracing study. Brain Behav. Evol. 32: 160-168.

Umetani T., Tabuchi T., Ischimura R. (1986) Cerebellar corticonuclear and corticovestibular fibers from the posterior lobe of the albino rat, with comments on zones. Brain Behav. Evol. 29: 54-67.

Vanegas H., Hollander H., Distel H. (1978) Early stages of uptake and transport of horseradish-peroxidase by cortical structures, and its use for the study of local neurons and their process. J. Comp. Neurol. 177: 193-212.

Van Rossum J. (1969) Corticonuclear and corticovestibular projections of the cerebellum: an experimental investigation of the anterior lobe, the simple lobule and the caudal vermis in the rabbit. Van Gorcum and Comp. N.V., Assen, 169 p.

Voogd J. (1964) The cerebellum of the cat. Structure and fibre connexions. Van Gorcum and Comp. N.V., Assen, 215 p.

Voogd J., Bigaré F. (1980) Topographical distribution of olivary and corticonuclear fibers in the cerebellum: a review. In: The inferior olivary nucleus: anatomy and physiology (Eds. J. Courville, C. Montigny and Y. Lamarre). Raven Press, New York, p. 207-234.

Walberg F., Jansen J. (1961) Cerebellar corticovestibular fibers in the cat. Exp. Neurol. 3: 35-52.

Walberg F., Nordby T., Dietrichs E. (1980) A note on the anterograde transport of horseradish peroxidase within the olivocerebellar fibers. Exp. Brain Res. 40: 233-236.

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