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Cerebellar Afferents from the Trigeminal Sensory Nuclei in the Cat

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Summary. The cerebellar afferent projection from the trigeminal sensory nuclei (TSN) was studied by means of retrograde axonal transport of horseradish peroxidase (HRP). The projection is almost exclusively ipsilateral. Three cortical regions, viz., the intermediate-lateral part of lobulus simplex with the adjacent area of lobule V, the rostralmost folia of the paramedian lobule with the surrounding parts of crus I and II, and lobule IX, especially its rostral two folia, are the main targets for the cerebellar afferent fibres. A few fibres reach also the other cerebellar regions, as shown in Fig. 3.

Most of the cerebellar afferent fibres originate in the nucleus interpolaris with nucleus oralis as the second most important region. The projection from the principal nucleus is moderate and reaches primarily the area of the crura bordering on the paramedian lobule and lobule IX. The projections from the nucleus caudalis and nucleus mesencephalicus are scanty. The fibres from the latter reach only the vermal region.

The findings are discussed in relation to previous anatomical and physiological observations.

Key words: Trigeminocerebellar projection – Mammals – Retrograde transport of HRP

Cerebellar afferent fibres from the sensory nuclei of the trigeminal nerve have been described in a variety of species, from cyclostomes through mammals. The fibres have been described to take their origin from the spinal (Huber and Crosby, 1926; Woodburne, 1936; Carpenter and Hanna, 1961; Darian-Smith and Phillips, 1964; Dunn and Matzke, 1968; Karamanlidis, 1968; Faull, 1977), the principal (main) (Huber and Crosby, 1926; Woodburne, 1936; Whitlock, 1952; Darian-Smith and Phillips, 1964; Karamanlidis, 1968; Faull, 1977), and the mesencephalic (Larsell, 1923, 1932, 1936a, b; Weinberg, 1928; Voris and Hoerr, 1932; Woodburne, 1936; Pearson, 1949; Brodal and Saugstad, 1965; Karamanlidis, 1968) nuclei, but it is only with the new tracer techniques that it has been possible to describe details in the connections. Injections of tritiated amino acids have given evidence of a projection from the nuclei to the lobulus simplex (Courville and Faraco-Cantin, 1978, cat) and retrograde transport of horseradish peroxidase (HRP) has demonstrated that cells in one or more of the nuclei project to the cerebellar vermis or hemispheres (Steindler, 1977a, b, mouse; Watson and Switzer, 1978, rat). The most extensive study is that of Ikeda (1979) who with HRP as a tracer in the cat describes a projection mainly to lobulus simplex and the paramedian lobule with the adjacent part of crus II.

The conclusions made in the above mentioned HRP studies are based on a comparison of cases with very large cerebellar injections and few details have therefore been obtained. Because of this we found it of interest to make a systematic investigation of the trigeminocerebellar projection in cats with localized injections of HRP applied to all parts of the cerebellar cortex and nuclei, and including cell counts in all positive cases. The projection from the motor nucleus of the trigeminal nerve will not be described, since it has been dealt with separately (Kotchabhakdi and Walberg, 1977).

As will be seen, several new details have been obtained.

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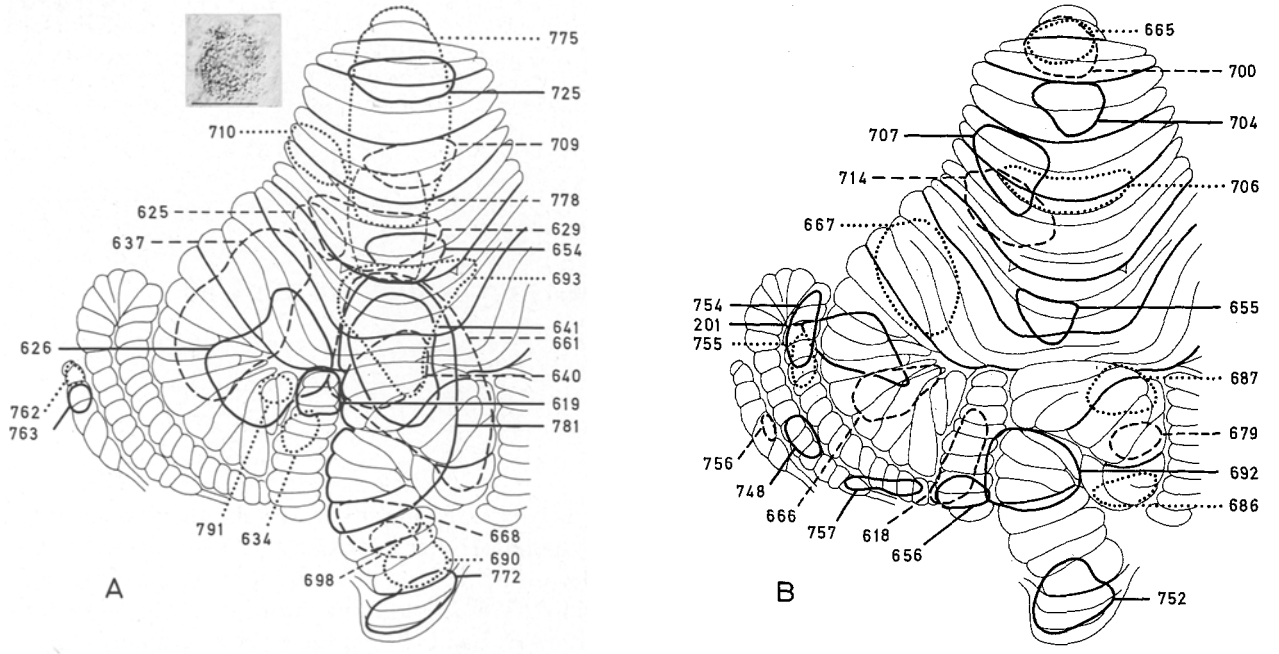

Fig. 1A and B. Diagrams of the cerebellar folia in the cat, imagined unfolded (Larsell, 1970), showing the extent of the HRP injections in the positive (**A**) and negative (**B**) cases. Inset shows large HRP labelled cell in left mesencephalic nucleus of cat B.St.L. 661. Scale line 20 μ

Material and Methods

The material consists of brains from 52 operated and 3 normal cats. Most of the injected animals have been used in our other studies on cerebellar afferent projections from the brain stem nuclei.

Details concerning the type and amount of HRP used, the weight and survival times of the animals, the experimental technique for injection of HRP, and the procedure followed for processing of the sections are found in other publications (Walberg et al., 1976; Pierce et al., 1977; Kotchabhakdi et al., 1978; Dietrichs and Walberg, 1979).

The presence of HRP-labelled neurons in the trigeminal sensory nuclei was from every fifth section studied in bright and dark field and with interference contrast microscopy. The location of each positive cell was entered as a dot in drawings taken at equal intervals through the nuclei, and the maps obtained from the individual cases were transferred to standard diagrams of equally spaced transverse sections. The identification of the injection sites in the cerebellar cortex was also made on the histological sections and transferred to a diagram of the cat cerebellum imagined unfolded (Larsell, 1970).

No endogenous peroxidatic activity was found in cells of the trigeminal sensory nuclei in the normal control animals.

Results

Main Features of the Topography of the Cat Trigeminal Sensory Nuclei (TSN)

The subdivision of the TSN referred to in this study is based on the description given by Taber (1961). For details (also concerning cell sizes), the reader is referred to this publication. Here only the major points will be outlined.

The TSN constitutes a column of cells beginning at the rostral end of the dorsal horn of the first cervical segment and terminating at the beginning of the posterior commissure. The spinal sensory nucleus (Vsp) in the cat is subdivided in a nucleus caudalis (Vc), nucleus interpolaris (Vi), and nucleus oralis (Vo). The Vi extends from the Vc at the level of the obex and continues as Vo just anterior to the rostral pole of the hypoglossal nucleus. The rostral part of Vo merges rostrally with the ventral subdivision of the principal nucleus (Vpv of Vp) at the rostral pole of the facial nucleus, and the Vpv blends with the dorsal subdivision of Vp (Vpd) to end at the caudal pole of the medial parabrachial nucleus. The mesencephalic nucleus (Vme) is situated somewhat more medially, begins at the rostral pole of the trigeminal motor nucleus (Vmo), and can be followed as a gradually thinner strand of cells to the rostral end of the complex.

Experimental Findings

In the description given below, the operated animals are subdivided into the following groups: those with injections in the (1) vermis, (2) intermediate-lateral

Table 1

	Left side						Right side						Both sides
Cat B.St.L.	Vc	Vi	Vo	Vp	Vme	Total	Vc	Vi	Vo	Vp	Vme	Total	Total
Vermis													
775	20	19	5	25[a]	7	76	35	44	15	23[a]	9	126	202
725	2	2	6	0	0	10	8	3	3	0	0	14	24
709	5	1	3	4[a]	0	13	2	2	3	0	0	7	20
778	0	2	7	3[a]	3	15	0	5	4	8[a]	3	20	35
654	0	3	0	0	0	3	0	0	0	0	0	0	3
693	0	7	0	0	0	7	0	6	0	4[b]	0	10	17
641	0	1	0	0	0	1	0	2	0	0	0	2	3
661	0	44	0	10[a]	12	66	0	53	0	4[a]	9	66	132
781	0	13	7	19[a]	2	41	0	13	17	8[a]	3	41	82
640	0	2	0	0	0	2	0	0	0	0	0	0	2
668	0	244	13	27[b]	0	284	1	92	0	15[b]	0	108	392
698	0	22	11	24[b]	0	57	0	10	4	22[b]	0	36	93
690	0	40	0	0	0	40	0	6	0	0	0	6	46
772	0	2	3	0	0	5	2	0	2	1[b]	0	5	10
Intermediate-lateral													
710	0	1	0	0	0	1	0	0	0	0	0	0	1
629	0	1	6	0	0	7	0	0	4	0	0	4	11
625	0	28	14	0	0	42	0	0	0	0	0	0	42
637	0	10	0	0	0	10	0	0	0	0	0	0	10
626	0	135	45	53[b]	0	233	0	0	0	1[b]	0	1	234
791	0	17	9	0	0	26	0	0	0	0	0	0	26
619	1	146	7	0	0	154	0	1	0	0	0	1	155
634	0	3	0	0	0	3	0	0	0	0	0	0	3
762	0	0	3	1[b]	0	4	0	0	0	0	0	0	4
763	0	3	0	0	0	3	0	0	0	0	0	0	3
Nuclei													
695 (N.f.)	0	2	0	0	0	2	0	0	0	0	0	0	2
649 (N.i.)	0	4	0	0	0	4	0	0	0	0	0	0	4
652 (N.i.)	0	9	0	0	0	9	0	0	0	0	0	0	9
777 (N.l.)	0	1	0	0	0	1	0	0	1	0	0	1	2
708 (N.l.)	0	1	0	0	0	1	0	0	0	0	0	0	1

[a] Labelled cells in Vpv and Vpd
[b] Labelled cells in Vpv only

part of the anterior lobe and lobulus simplex, (3) crus I, II and the paramedian lobule, (4) paraflocculus and flocculus, and (5) cerebellar nuclei.

Most of the HRP labelled cells found in Vsp and Vp are medium-sized, the positive cells in the Vme are mostly of the large type. Table 1 gives the number of labelled cells of all sizes found in the various subdivisions of the left and right TSN in the positive cases.

1. Vermis

As shown in Fig. 1A and B, only three cases with small injections in the anterior lobe vermis were positive (cats B.St.L. 725, 709, 654, and Table 1), but extensive anterior lobe vermis injections (cats B.St.L. 778 and 775) resulted in a greater number of labelled cells in the TSN, especially in the latter case where the staining included all lobules. Only in this case were labelled cells found in all subdivisions of the TSN (Fig. 2; for details, see Table 1).

All the cases with small injections in the vermal lobules VI–VIIIB were negative[2], but larger injections in these lobules (cats B.St.L. 693, 641, 661, 781, Fig. 1A) resulted in labelled cells in the TSN. However, Table 1 shows that it was only in the two latter cases that a substantial number of positive cells were observed. The first of these (cat B.St.L. 661) had an injection encroaching upon the rostralmost two folia of the paramedian lobule, the other (cat B.St.L. 781) had a spreading of the HRP fluid to the rostralmost folium of lobule IX. We will return to the observation in these two cases in the interpretation of the findings.

2 Cat B.St.L. 640 with an injection in lobule VIIA had two labelled cells (Table 1)

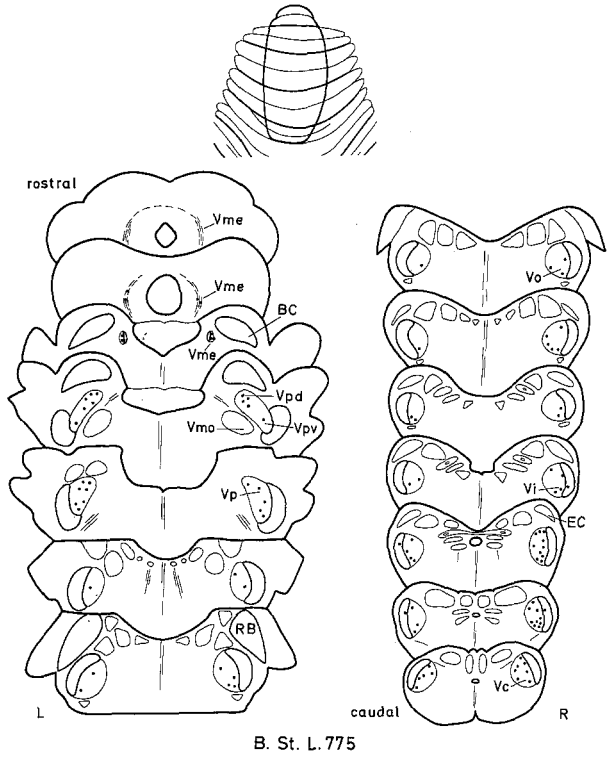

Fig. 2. Diagrams showing the injection site in cat B.St.L. 775 and the distribution of labelled cells indicated by dots (one dot does not represent one labelled cell) in the various subdivisions of the sensory trigeminal nuclei. Abbreviations: BC, brachium conjunctivum; EC, external cuneate nucleus; RB, restiform body; Vc, nucleus caudalis of spinal sensory nucleus; Vi, nucleus interpolaris of spinal sensory nucleus; Vme, mesencephalic nucleus of trigeminal nerve; Vmo, motor nucleus of trigeminal nerve; Vo, nucleus oralis of spinal sensory nucleus; Vp, principal (main) trigeminal nucleus; Vpd, Vpv, dorsal and ventral subdivision of principal trigeminal nucleus

Lobule IX, especially its rostral two folia, has a very strong connection with the TSN. This is learnt from a comparison of cases B.St.L. 668, 698 and 690 (Fig. 1A and Table 1). In the first of these cases the large majority of positive cells were restricted to the Vi (Table 1). The observations furthermore show that an injection into lobule X and the adjacent caudalmost part of lobule IX (cat B.St.L. 772, Fig. 1A) results in a few labelled cells in the TSN.

2. The Intermediate-Lateral Part of the Anterior Lobe and Lobulus Simplex[3]

Injections in the intermediate-lateral part of lobules IV and V were either negative (cats B.St.L. 707, 714, Fig. 1B) or gave only one labelled cell in the ipsilateral Vi (cat B.St.L. 710, Fig. 1A), but a larger injection in the intermediate part of lobule V (including its vermal area, cat B.St.L. 629) showed a restricted number of labelled cells bilaterally, especially in the Vo. However, a localized injection a little more caudally including lobulus simplex (cat B.St.L. 625, Fig. 1A) gave a large number of labelled cells in the ipsilateral Vi and Vo (Table 1).

3. Crus I, II, and the Paramedian Lobule

Injections confined to the lateral part of the crura (cats B.St.L. 667, 666, C.Co.L. 201)[4] or to the caudal part of the paramedian lobule (cats B.St.L. 618, 656) gave no labelling in the TSN (Fig. 1B). However, a very circumscribed injection in the medial part of crus II (cat B.St.L. 791, Fig, 1A) resulted in many labelled cells in the nuclei, and a larger injection covering the medial parts of the crura with the adjacent area of the rostralmost two paramedian folia (cat B.St.L. 626, Fig. 1A) gave a very high number of labelled cells (Table 1). Numerous positive cells were also observed in a case where the injection covered the two rostralmost folia (with a slight spreading to the third folium) of the paramedian lobule (cat B.St.L. 619), but an injection comprising the third to fifth folia of the paramedian lobule (cat B.St.L. 634) resulted only in a labelling of three cells in the TSN (Fig. 1A and Table 1).

4. Paraflocculus and Flocculus

All the paraflocculus injected cases were negative (cats B.St.L. 754, 755, 757, 748, C.Co.L. 201) as was also the case with an injection in the medial part of the flocculus (cat B.St.L. 756, Fig. 1B), but two cases with localized injections in the lateral part of the flocculus (cats B.St.L. 762, 763, Fig. 1A) showed a few labelled cells in the TSN.

5. Cerebellar Nuclei

Our material comprises six cases, all with injections on the left side. Table 1 shows that all except one (cat B.St.L. 702, fastigial nucleus) were positive, but that the nuclear afferent projection is very moderate.

Interpretation of Findings

A comparison of HRP-injected cases is not suited for conclusions concerning quantitative differences.

3 We have no cases with injections restricted to lobules II and/or III without involvement of the cerebellar nuclei or adjacent structures

4 The series C.Co.L. 201 was prepared by Dr. P. Brodal. We acknowledge his permission to use this series

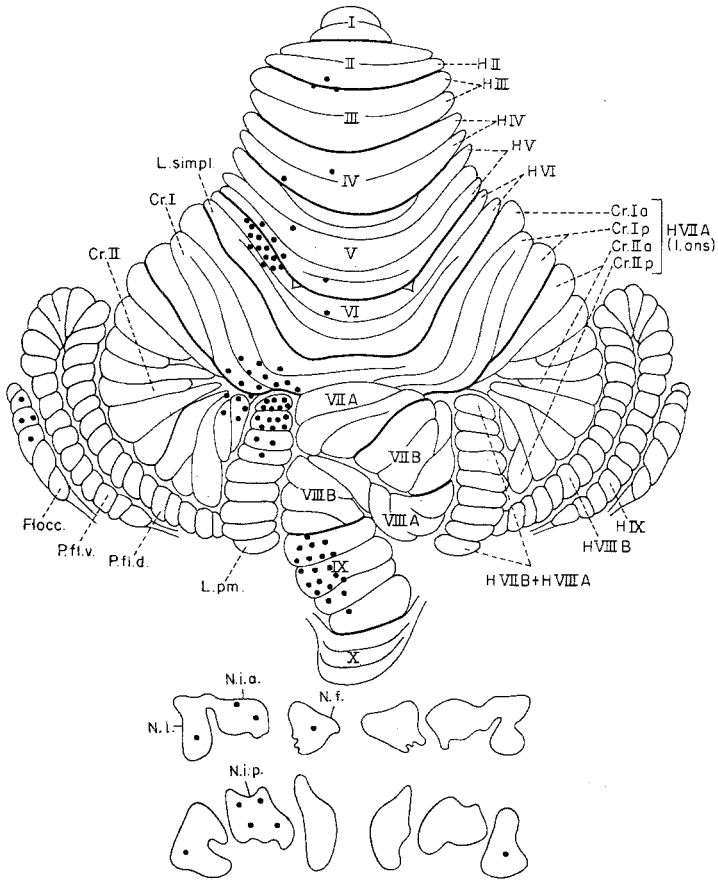

Fig. 3. Diagram showing the projections from the sensory trigeminal nuclei to the various parts of the cerebellar cortex and nuclei. Variation in the density of dots indicates the relative density of the projections. Abbreviations: Cr.I, crus I; Cr.II, crus II; Flocc., flocculus; HII– HVI, hemispheral lobules II–VI; HVIIA(l.ans.)Cr.Ia,p,Cr.IIa,p, anterior and posterior folia of crus I and II of the ansiform lobule; HVIIB, HVIIIA,B, sublobules A and B of hemispheral lobules VII and VIII; HIX, hemispheral lobule IX; L.pm., paramedian lobule; L.simpl., lobulus simplex; N.f., nucleus fastigii; N.i.a., nucleus interpositus anterior; N.i.p., nucleus interpositus posterior; N.l., nucleus lateralis; P.fl.d., P.fl.v., dorsal and ventral paraflocculus; I–VI, vermal lobules I–VI; VIIA,B, VIIIA,B, anterior and posterior sublobules of lobules VII and VIII; IX, uvula; X, nodulus

However, when a material comprises a high number of animals it is in our opinion permissible to draw certain conclusions concerning differences in the density of a projection.

Firstly, it is quite clear from Table 1 that the trigeminocerebellar projection is almost exclusively ipsilateral. Secondly, three cortical regions are the main targets for the cerebellar afferents, viz., the intermediate-lateral part of lobulus simplex with the adjacent area of lobule V, the rostralmost folia of the paramedian lobule with the surrounding parts of crus I and II, and lobule IX, especially its rostral two folia (Fig. 3). The projections to the two latter regions are the heaviest (Table 1).

More moderate contingents from the TSN reach the vermal lobules II–IV, the cerebellar nuclei and the lateral part of the flocculus, but the greater parts of the crura and the paraflocculus are devoid of a connection. This is probably also the case for the vermal lobules VI–VIII.

Most of the cerebellar afferents originate from the Vi, with the Vo as the second most important part. The projection from the Vp is relatively moderate and appears primarily to reach the two crura (the area bordering the paramedian lobule) and lobule IX. It is furthermore noteworthy that in six of the injected cases (cats B.St.L. 626, 668, 693, 698, 762, 772) labelled neurons in Vp were restricted to the Vpv.

The projections from the Vc and Vme are sparse (Table 1), and labelled cells were in the latter found only following very large injections in the vermis (Table 1).

Discussion

Our demonstration of a heavy projection from the TSN to the lobulus simplex and to the paramedian lobule with the apposed crus II is in full agreement with the observations of Ikeda (1979). Our cell counts give further details and show that of the two mentioned regions it is the rostral part of lobulus simplex with the adjacent area of lobule V (our cases B.St.L. 625, 637 and 629, Table 1) and the rostralmost folia of the paramedian lobule (cats B.St.L. 619, 634, 618, 656, Table 1) that receive the bulk of the projection (Fig. 3). The very heavy projection to the uvula (lobule IX), especially its rostral part (Fig. 3) was not described by Ikeda (1979), she had no cases with injections into this cortical region. For the

same reason she was also unable to comment upon a projection to the cerebellar nuclei.

There are certain discrepancies between Ikeda's (1979) findings and those made by us. We found a moderate projection to the cerebellar lobules II–IV and to the flocculus. Ikeda concluded that the anterior portion of the anterior lobe and the flocculus were devoid of a connection with the TSN. As concerns the flocculus, her injections were made in rabbits (not illustrated) and it may well be that they were restricted to the medial part which in the cat lacks a connection with the TSN (our Fig. 1A and B). Our findings are likewise at variance with her observations as regards the projection from the Vp; she places labelled cells in all her illustrated cases only in Vpv, many of our positive cases had labelled cells also in Vpd (Table 1). A further difference between the findings is that we, unlike Ikeda, found labelled cells in the Vc only after vermal injections.[5]

The demonstrated heavy TSN projection to lobulus simplex correlates well with the results obtained in studies with anterograde tracers (Courville and Faraco-Cantin, 1978) and with physiological observations in the cat (Adrian, 1943; Snider, 1943, 1950; Snider and Stowell, 1944; Darian-Smith and Phillips, 1964; Miles and Wiesendanger, 1975a, b; Cody and Richardson, 1977, 1978a, 1979). Snider (1943) furthermore showed that gentle mechanical stimulation of hairs in the face area of the cat gave well localized potentials not only in the posteromedial part of the anterior lobe and the anterior two folia of lobulus simplex, but also in the ipsilateral paramedian lobule and the medial folia of the crura. This finding correlates well with Ikeda's (1979) and our studies in the same species, and with anatomical (Watson and Switzer, 1978) and physiological (Shambes et al., 1978) observations in the rat.

Our demonstration that the TSN send a heavy contribution of fibres to lobule IX is not paralleled with other observations in the cat. However, it should be noted that in the rat an HRP injection in the posterior vermis including lobule IX (their case 78865) results in labelled cells in the trigeminal complex (Watson and Switzer, 1978) and that evoked potentials have been observed in lobule IXa (the rostral folium of the uvula) of the same species after gentle mechanical stimulation of hairs in the face area (Joseph et al., 1978). This part of the cat cerebellum has been shown to receive proprioceptive impulses after stimulation of the triceps brachii and quadriceps femoris muscles (Dow and Andersen, 1942) and it might therefore be speculated whether in the cat the rostral part of lobule IX represents a proprioceptive area for the head region.

Our demonstration of a projection from the TSN to the cerebellar nuclei (Fig. 3) agrees with the previous observation in the monkey (Carpenter and Hanna, 1961) and shows that in the cat the interposite nucleus, especially its posterior part, is the main recipient for the fibres. A projection to the interposite nucleus has also been demonstrated in physiological studies (Cody and Richardson, 1978b; Richardson et al., 1978), but no data have been given as to a possible termination within the other two cerebellar nuclei, and a projection to the flocculus likewise appears not to have been shown.

Turning now to the cerebellar afferents from the various nuclear subdivisions, there are contradictory findings concerning the Vc cerebellar projection. With anterograde degeneration techniques Dunn and Matzke (1968) demonstrated cerebellar afferent fibres from this region in the marmoset, but Steindler (1977b, mouse) and Watson and Switzer (1978, rat), using retrograde transport of HRP, failed to find such a projection. Similarly Stewart et al (1963) and Kawamura (1971) reported negative findings in the cat following Vc lesions. The reason for the mentioned discrepancies in the cat probably is due to the paucity of the connections (Table 1), but it remains to be seen whether species differences exist. That this actually may be the case is shown by our own and previous observations (Ikeda, 1979) that in the cat the Vi, and to a lesser extent the Vo, are the main regions of origin of the cerebellar afferent fibres, whereas in the rat and mouse (Steindler, 1977a, b; Watson and Switzer, 1978) also the Vp is an important nuclear region for the afferents.

We were only able to show labelled cells in Vme after vermal injections (Fig. 1A, Table 1), and the positive cells were usually restricted to the caudal part of the Vme. Brodal and Saugstad (1965) reported a similar restriction of retrogradely changed cells following large lesions of the cerebellar cortex including the superior cerebellar peduncle. However, the cerebellar projection from the Vme may actually be somewhat stronger than appears from our Table 1. This is due to the fact that the border between Vme and locus coeruleus can be given only arbitrarily, especially at the caudal part of the former nucleus. In this region it is very difficult with certainty to decide whether the small border cells lie in one nucleus or the other. Because of this we have preferred to include only medium-sized and large labelled cells as belonging to the Vme.

With the presently used technique it is impossible to draw conclusions as to whether the main axons from the TSN cells or only collaterals from such

5 Cat B.St.L. 619 (Fig. 1A and Table 1) had one labelled cell in Vc

axons terminate within the cerebellum. Likewise, our findings have little bearing on the problem whether a cerebellar afferent fibre branches to supply different regions of the cortex and nuclei with collaterals from a stem fibre. It is of some importance that as concerns the Vp, labelled cells are present only in the Vpv following injections in the medial part of the crura and in the uvula[6], but that they are present also in the Vpd in the other positive cases (Table 1). This might indicate that the distribution of the cerebellar afferents from Vpv is rather restricted, but that the fibres from the Vpd divide more abundantly within the cerebellum. However, definite conclusions as regards a possible branching of axons from the TSN cells can only be made in animal where different types of tracers are injected (see especially Hayes and Rustioni, 1978, 1979).

The connection from the TSN to the cerebellum demonstrated in the present study is an example of the complexity in the connections from the brain stem nuclei to this part of the central nervous system. Further details and an even higher degree of differentiation will presumably be demonstrated in studies with more sensitive tracer techniques.

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