ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol Exp 2003, 63: 295-308

Pontocerebellar projection to the rabbit paramedian lobule by means of axonal collaterals: evidence for intralobular connections

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Abstract. In this study, we utilized a double retrograde axonal tracing technique to investigate the possible existence of collateralized axonal projections from the pontine nuclei (PN) to the rostral (rPML) and caudal (cPML) parts of cerebellar paramedian lobule in the rabbit, known to be the forelimb and hindlimb regions, respectively. Following injections of fluorescent tracers Fast Blue (FB) and Diamidino Yellow (DY) within rPML and cPML, respectively, substantial numbers of FB and DY single labeled neurons were found in the dorsolateral, paramedian, lateral and peduncular pontine nuclei bilaterally with a very clearcut contralateral preponderance. No labeling was observed in the ventral pontine nucleus. Extensive areas of overlap of FB or DY labeled neurons indicated that no somatotopical relationship existed in projection from PN to the two functionally different PML target regions. In addition, a small number of double FB + DY labeled neurons was detected in the common areas of FB and DY single labeling in PN. These neurons give rise to pontocerebellar projections to rPML and cPML simultaneously by way of axonal collaterals and thus they may play a role in the coordination of unilateral forelimb and hindlimb movements.

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Key words: pontine nuclei, cerebellar paramedian lobule, collateral projection, rabbit, retrograde fluorescent tracing

INTRODUCTION

The projection that connects the cerebral cortex to the cerebellum is one of the most important pathways through the central nervous system. This connection is realized by fibers system that involves the pontine nuclei (PN), as the major precerebellar intercalated structure. Judging by the number of axons, the cerebropontocerebellar pathway is one of the largest pathways in the brain of mammalian species. In human, about 20 million neurons on one side project from the cerebral cortex to PN and about 10 million neurons project from PN to the cerebellar cortex (Schwarz and Their 1999, Tomasch 1969). PN are targets of afferents from widespread areas of motor, sensory and limbic cortex (Brodal 1978, 1979, 1983, Brodal and Bjaalie 1997, Distler et al. 2002, Giolli et al. 2001, Lee and Mihailoff 1990, Leergaard et al. 2000a,b, Legg et al. 1989, Lui and Aldon 1997, Mihailoff et al. 1978, 1985, Schmahmann and Pandya 1997, Schwarz and Mőck 2001, Schwarz and Thier 1995) and from other sources of non-cortical origin including the cerebellar deep nuclei (Lee and Mihailoff 1990, Mihailoff et al. 1981, Voogd 1964, Watt and Mihailoff 1983), pretectum and zona incerta (Mihailoff 1995), superior and inferior colliculi (Kawamura 1975, Matsuzaki and Kyuhou 1997), dorsal column and spinal trigeminal nuclei as well as spinal cord (Kosinski et al.1986, Swenson et al. 1984, Van Ham and Yeo 1992, Yamada et al. 1985). PN output is directed exclusively to the cerebellum. PN contain neurons which axons distribute to most of the cerebellar cortex regions as mossy fibers ending in its granular layer as well as to the cerebellar deep nuclei (Mihailoff 1993, see also Brodal and Bjaalie 1992 for other references). Organization of projection from PN to the cerebellar cortex has been demonstrated both with anatomical and electrophysiological methods in the cat (Bjaalie et al. 1991, Brodal 1983, Brodal and Hoddevik 1978, Brodal and Walberg 1977, Hoddevik and Walberg 1979, Kawamura and Hashikawa 1981, Matsuzaki and Kyuhou 1997, Rosina and Provini 1981), rat (Azizi et al. 1981, Eisenman 1980, 1981, Eisenman and Noback 1980, Huang et al. 1990, Mihailoff et al. 1981, Päällysaho et al. 1991), monkey (Brodal 1979, Xiong et al. 2002) and opossum (Mihailoff et al. 1980). Only few data are available on these projections in the rabbit. Brodal and Jansen (1946) have observed degenerated neurons in all PN as a result of extensive lesions of the cerebellar cortex. Hoddevik (1977) has showed bilateral projections from all PN to the flocculus, paraflocculus and nodulus with the retrograde HRP technique.

Double labeling studies have revealed that some pontocerebellar neurons may send collaterals to both hemispheres as well as to different lobules within the same hemisphere (Mihailoff 1983, Payne 1983, Rosina and Provini 1984, Rosina et al. 1980) and to widely separated folia within one lobule (Bjaalie and Brodal 1997) in the cat and rat. In our laboratory we have indicated PN neurons which give off axonal collaterals to the cerebellar paramedian lobule (PML) of both sides in the rabbit (Zguczyński 1998). The present study in the rabbit is focused on the intrahemispheric collateral branchings of pontocerebellar projection to PML, a major part of the intermediate zone of the cerebellum, which plays an important role in motor control.

There is ample evidence that the rostral PML (rPML) sublobules receive afferents related primary to the forelimb and face, whereas the mainly hindlimb receiving area has been identified in more caudal PML (cPML) folia (Apps 1998, Armstrong et al. 1973, Atkins and Apps 1997, Cooke et al. 1972, Inui 1989, Oscarsson and Sjőlund 1977, Trott and Apps 1993).

In this context, the present investigation is made to identify cells of origin for pontocerebellar projection to the unilateral rPML and cPML. Moreover, it is addressed the issue of the possible existence of pontocerebellar collateralization distributed to somatotopically non-homologous cortical target regions of rPML (forelimb) and cPML (hindlimb). To answer the question the method of double retrograde fluorescent tracing was employed in the rabbit. Such connections have not been so far studied in any species.

METHODS

Experiments were carried out on 9 adult rabbits weighing 2.7-3.8 kg under general anesthesia with ketamine hydrochloride (50 mg/kg) and promazin (19 mg/kg) injected intramuscularly. The head of animal was fixed in a stereotaxic frame (Narishige) and under aseptic conditions two small craniotomies (maximum 3 mm in diameter) were performed to expose the cortex areas of the dorsal surface of rPML and cPML sublobules on the right side. The glass micropipette (tip diameter 30-60 μm) secured on a 5-μl Hamilton microsyringe was used to deliver the tracer. It was mounted in a micromanipulator and under operating mi-

croscope control, after opening the dura, it was introduced into the cortex just below surface of sublobule. The rPML and cPML sublobules were pressure-injected (1.0-3.0 μl) with 4-5% Fast Blue (FB) and 2% Diamidino Yellow (DY), respectively. Both FB and DY tracers were sonicated for 5 min shortly before use to improve uptake and retrograde transport by axons. After completing the injection, the craniotomy was packed with spongostan and the muscle and skin were closed with sutures.

Following an 8-15 day survival period, the rabbits were reanesthetized and sacrificed by transcardiac perfusion of the whole animal with about 2.4-2.8 liters of 0.9% NaCl mixed with heparin, followed immediately by about 1.5 liter of 20% solution of formalin in 0.2 M phosphate buffer (pH 7.4) and then by cold (4°C) 10% sucrose in the same buffer. The brains were dissected and soaked in 20% sucrose (at 4°C) for approximately 24 h for cryoprotection prior to sectioning. The sagittal (cerebellum) and transverse (pons and medulla) 40-μm-thick frozen serial sections were made and mounted on chrom-alum-gelatinized glass slides, then dehydrated, coverslipped with Fluoromount (Serva) and examined under an epifluorescence microscope (Optiphot-2, Nikon and Jenalumar, Carl Zeiss Jena; 380-nm and 410-nm light excitation wavelength).

For each animal, the extents of FB and DY injection site were superimposed onto diagrams of the unfolded cerebellar cortex adopted from Brodal and Jansen (1946) as well as onto diagrams of sagittal sections of the right PML. In each case, the numbers of both single and double labeled neurons were counted in two out of three mounted serial sections through the entire rostrocaudal extent of PN (average 3,560 μm). Thus, in a single experiment with 40-μm-thick sections, they could be counted in approximately 59 out of 89 sections. To facilitate the comparison of findings between experiments, the distribution of labeled neurons was presented on diagrams of 10 transverse sections through the ventral region of pons (Brodal and Jansen 1946).

The research reported herein was performed under guidelines established by the Declaration of Helsinki concerning the appropriate Care and Use of Animals in Research, and the Polish Law on Animal Protection was also respected.

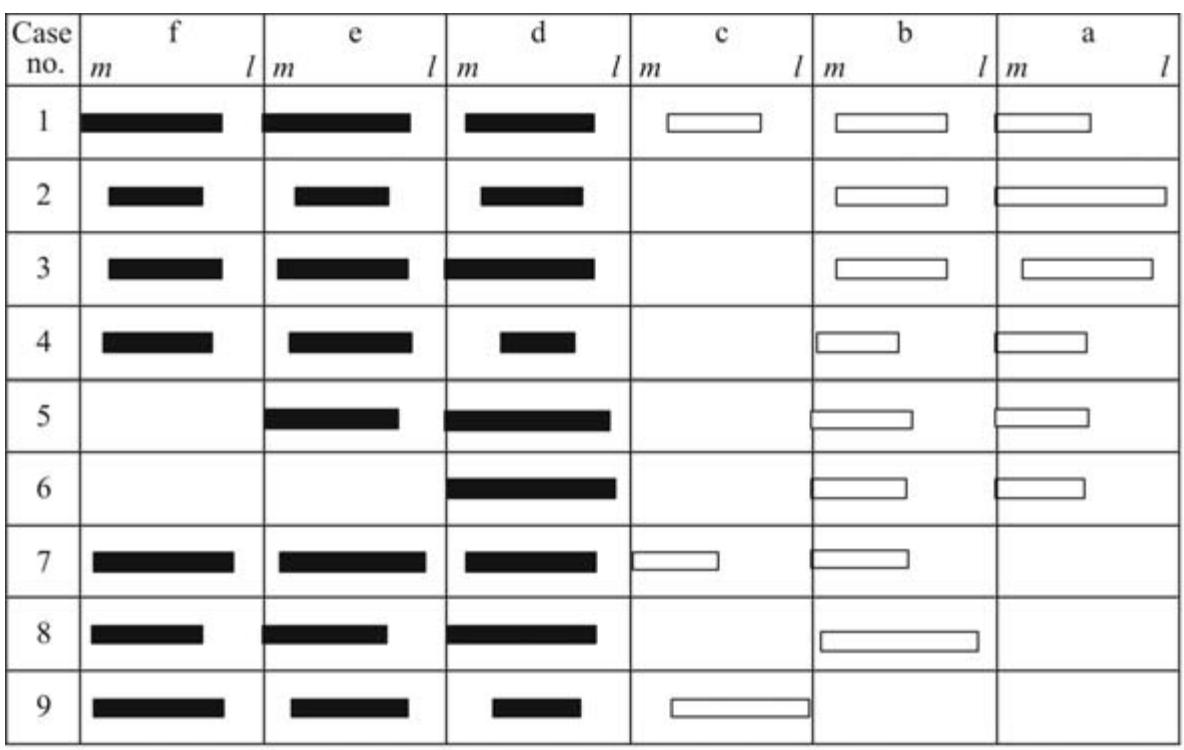

Fig. 1. A schematic representation of the mediolateral extent (length of bars) of FB (black bars) and DY (blank bars) injection sites of each case within the rostral (f, e, d) and caudal (c, b, a) PML sublobules. The rostrocaudal extent of injections is not shown. (*m*) Medial side, (*l*) lateral side.

RESULTS

Subdivision of PML and PN

PML of the rabbit is composed of six sublobules indicated from rostral to caudal as: f, e, d, c, b and a, according to the original subdivision by Brodal (1940). We refer to sublobules f, e and d as the rostral part of PML, and to sublobules c, b and a as the caudal part of PML.

According to Brodal and Jansen (1946) the basilar PN constitute a complex of five nuclei which appear in the rostrocaudal direction as: the paramedian (PM), ventral (V), peduncular (PD), lateral (L) and dorsolateral (DL) nuclei.

Injection sites

Figure 1 illustrates the mediolateral extent of FB and DY injection sites within sublobules of the right PML. All injections to rPML and cPML were confined exclusively to their sublobules and did not extended onto adjoining regions of the vermis and ansiform lobule. In no case was there an overlap between the two injection sites, including diffusion areas. The injections affected different mediolateral and rostrocaudal regions within corresponding PML sublobules (Figs. 2 and 3A,B).

Location and size of labeled neurons

In each case examined, the large number of single FB or DY and the small number of double FB + DY labeled neurons were consistently detected in DL, PM, L and DL bilaterally, with a clear contralateral preponderance (Table I). No single and double labeling was observed in V. Labeling with FB and/or DY was recognized by blue fluorescence in the neuroplasm and/or yellow fluorescence in the nucleus (Keizer et al. 1983, Kuypers et al. 1980) (Fig. 3C,D). The size of labeled perikarya varied from 20-45 μm in diameter, but there appeared to be no obvious relationship between the size of perikaryon and whether it was single or double labeled.

Distribution pattern of single FB and DY labeled neurons

The present findings indicate that rPML and cPML receive strong projections from the entire rostrocaudal extent of PN except for the rostral part at levels I-II. At level III as well as at level X (caudal pole) projection is weaker (Fig. 4). The ponto-paramedian (PN-PML) connections arise from groups of pontine cells located medially, laterally and ventrolaterally to the peduncle. The medial group comprises neurons of PM, the lateral group is represented by DL and lateral region of PD, and the ventrolateral one is composed of neurons of L. PN-PML fibers are bilateral with a clear contralateral preponderance. This preponderance is over two times in DL and PD, over three times in PM and nearly six times in L.

Considering all cases, the most numerous labeled neurons were found in entire DL (mean 2,120, range 805-3,682 cells), the most frequently in its dorsomedial and dorsolateral regions. In PM the number of labeled cells was nearly half lower (mean 1,187, range 488-2,200 cells). Labeled neurons occupied exclusively the dorsal half of the nucleus but in the caudal part (levels IX-X) they also appeared more ventrally. Labeled cells in L (mean 967, range 256-2,465 cells) were seen from levels IV to IX in the dorsolateral and lateral regions. In PD smaller labeling (mean 596, range 347-985 cells) were found in the caudal three quarters of the nucleus (levels V-X). Distribution of labeled neurons was restricted to its lateral and, rarely, dorsolateral regions. Occasionally some neurons were present also medially at level IX and centrally at level X.

No clearcut topographical relationships were disclosed between injection sites in rPML and cPML, and distribution of FB and DY labeled neurons in PN. In some cases (nos. 1, 3, 6) FB and DY labeled cells in DL tended to form distinct groups with the large interface regions of overlap. Thus, cells showing FB labeling lay laterally and those showing DY labeling lay medially to them. However, considering all analyzing cases labeling areas with FB and DY neurons overlapped in a great extent.

Distribution pattern of double FB + DY labeled neurons

The results presented herein indicate that some neurons within PN may send axonal branchings to terminate in rPML and cPML target regions. These neurons, double labeled with FB + DY, were present bilaterally with a very clear contralateral predominance. Although in the individual cases double labeled cells were numerously on the ipsilateral side (i.e., in PM, case no. 2; in DL and PM, case no. 5; in DL, PM and PD, case no. 7) or they appeared exclusively ipsilaterally (in DL, PM and L, case

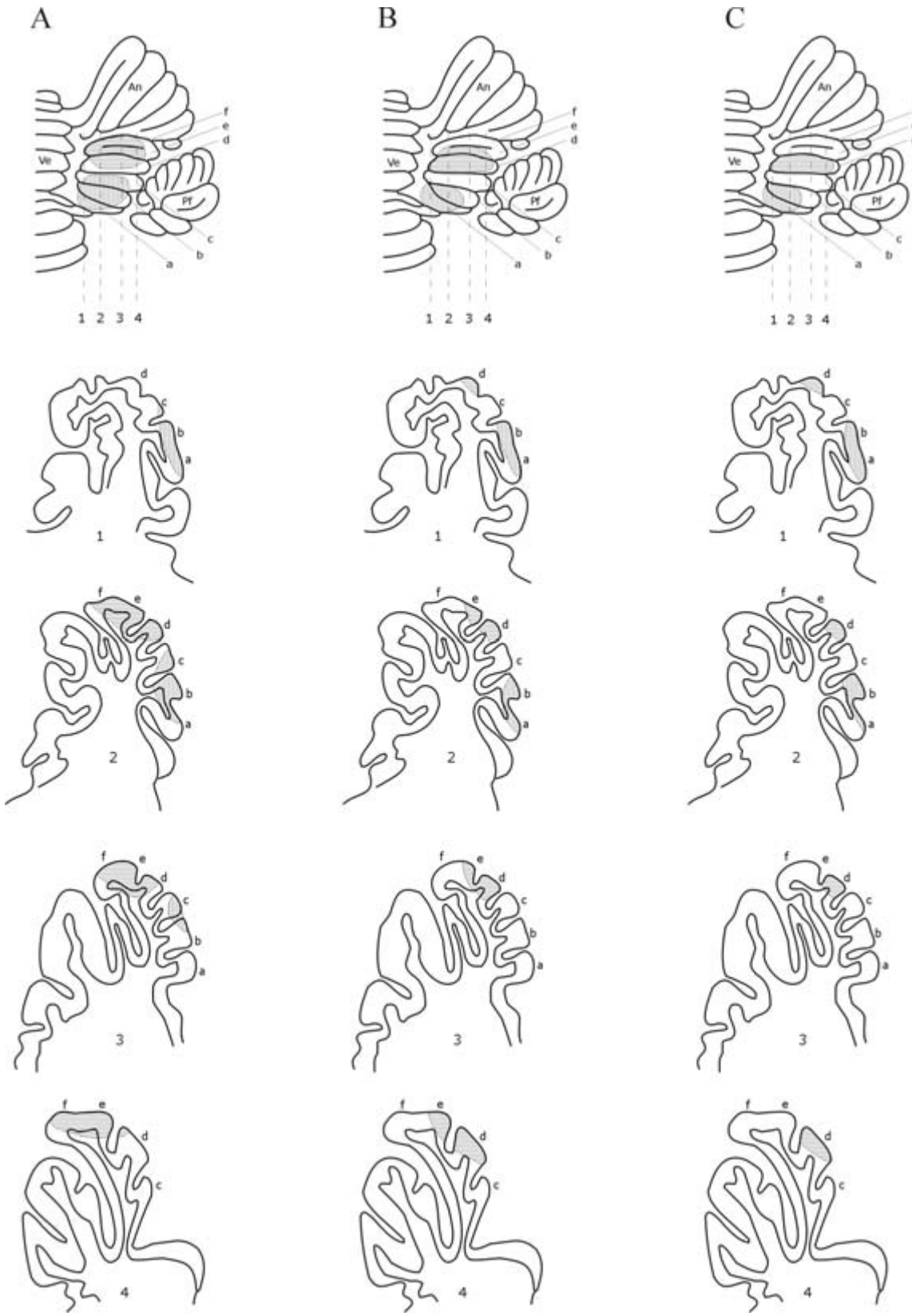

Fig. 2. Diagrams of the cerebellar dorsal view of the right side (upper) and four sagittal sections through PML illustrating injection sites in its rostral f, e, d (FB- horizontal lines) and caudal c, b, a (DY- vertical lines) sublobules in cases no. 1 (A), 5 (B) and 6 (C).

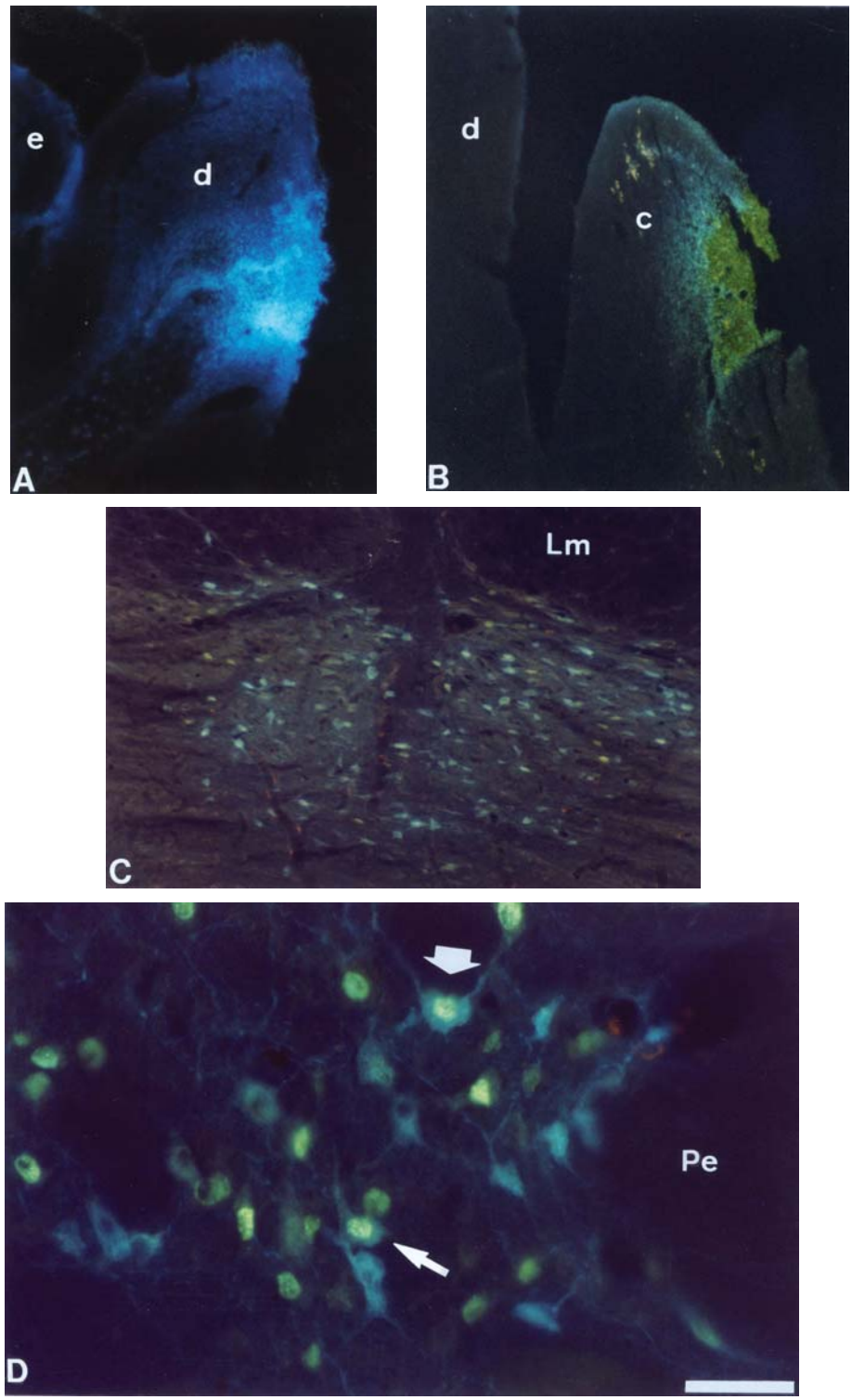

Fig. 3. Photomicrographs of sagittal sections through injection sites into rPML and cPML and resulting retrograde labeling of neurons in PN showed on transverse sections. (A) FB injection site in sublobule d, in case no. 2; (B) DY injection site in sublobule c, in case no. 9; (C) an intermingled population of FB and DY single labeled neurons in bilateral PM at level IX, in case no. 3; (D) an intermingled population of contralaterally FB and DY single labeled neurons located laterally to the peduncle (Pe) containing two FB + DY double labeled neurons in PD (block arrow) and L (thin arrow) at level VI, in case no. 1. Scale bars are: 600 μm for A, 500 μm for B, 400 μm for C and 100 μm for D.

Table I

Number of PN single and double labeled neurons as a result of FB and DY injection into rostral and caudal PML sublobules of one side

	DL							PM							L							PD						
	single			double				single			double				single			double				single			double			
	i	c	total	i	c	total	%	i	c	total	i	c	total	%	i	c	total	i	c	total	%	i	c	total	i	c	total	%
1	911	2,345	3,256	21	30	51	1.6	908	1,292	2,200	15	21	36	1.6	14	2,151	2,465	7	22	29	1.2	237	672	909	5	6	11	1.2
2	636	1,721	2,357	9	35	44	1.9	340	492	832	9	6	15	1.8	158	1,019	1,177	0	17	17	1.4	83	387	470	2	3	5	1.1
3	940	2,742	3,682	11	25	36	1.0	847	1,316	2,163	18	33	51	2.3	246	1,499	1,745	4	14	18	1.0	44	303	347	0	1	1	0.3
4	571	747	1,318	4	8	12	0.9	336	465	801	2	5	7	0.9	102	266	368	0	1	1	0.3	195	292	487	1	3	4	0.8
5	452	706	1,158	5	4	9	0.8	407	334	741	6	2	8	1.1	116	348	464	0	1	1	0.2	202	239	441	0	1	1	0.2
6	884	1,224	2,108	8	0	8	0.4	670	742	1,412	1	0	1	0.1	160	280	440	1	0	1	0.2	264	437	701	0	0	0	0
7	339	466	805	4	2	6	0.7	203	285	488	1	0	1	0.2	53	203	256	0	0	0	0	145	292	437	3	2	5	1.1
8	904	1,893	2,797	3	36	39	1.4	637	801	1,438	3	6	9	0.6	173	1,020	1,193	0	13	13	1.1	277	708	985	0	5	5	0.5
9	348	1,248	1,596	5	21	26	1.6	256	350	606	0	9	9	1.5	4	590	594	0	4	4	0.7	129	456	585	1	11	12	2.0
Total after all injections	5,985	13,092	19,077	70	161	231	1.2	4,604	6,077	10,681	55	82	137	1.2	1,326	7,376	8,702	12	72	84	1.0	1,576	3,786	5,362	12	32	44	0.8
Mean			**2,120**			**26**	**1.1**			**1,187**			**15**	**1.1**			**967**			**9**	**0.7**			**596**			**5**	**0.8**

In each rabbit the number of both single and double labeled neurons was counted in two out of three serial sections of PN: (i) ipsilateral; (c) contralateral; (total) sum of ipsilaterally and contralaterally labeled neurons; (%) percentage of the total number of double labeled neurons in relation to the total number of single labeled neurons.

no. 6) in total, contralateral predominance was over two times in DL, one and half times in PM, six times in L and nearly three times in PD. In comparison with single labeled neurons, the number of double ones was very small. As might be expected, such neurons were found almost exclusively in the regions of overlap, most fre-

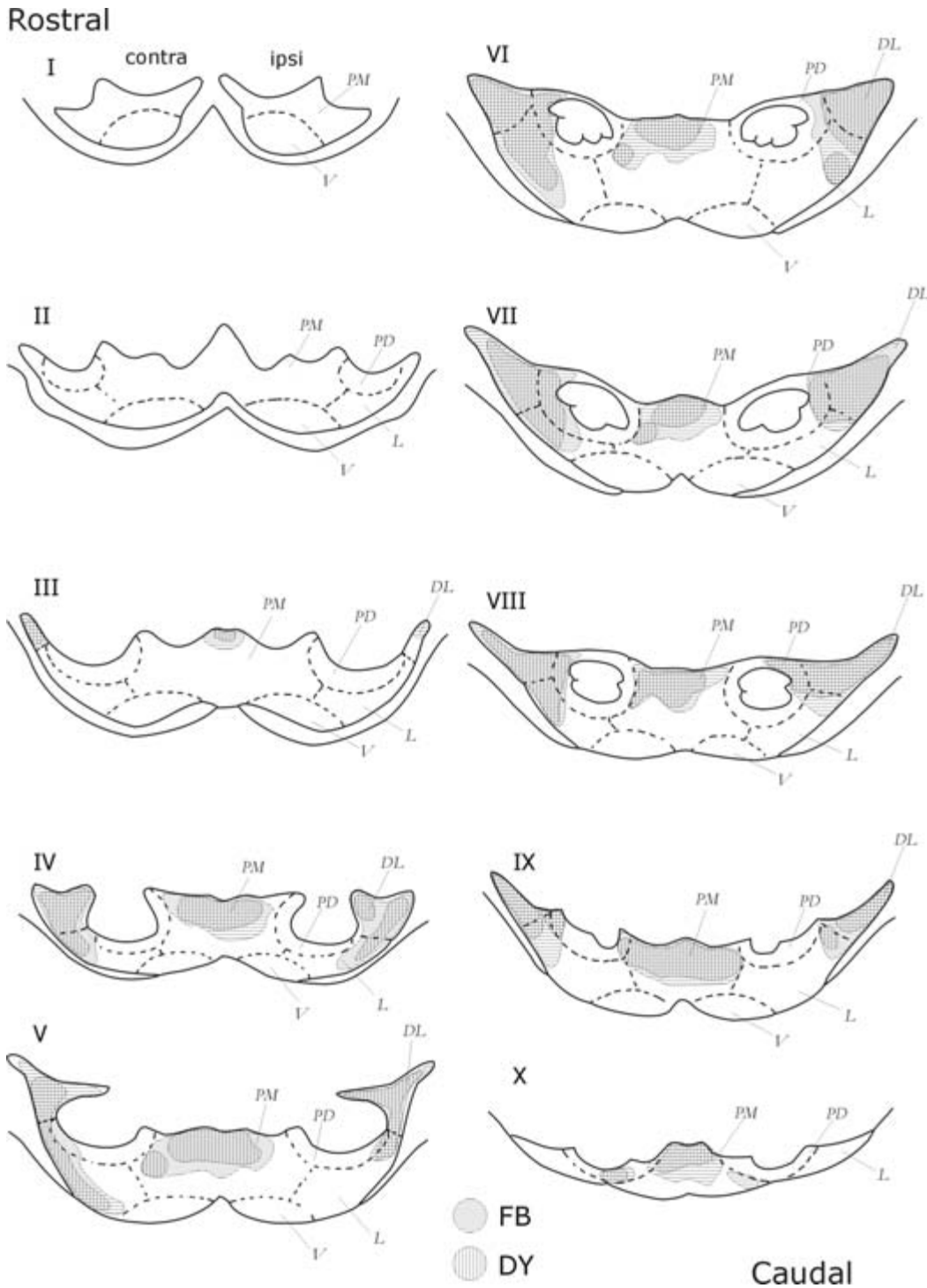

Fig. 4. Summarizing diagram of transverse sections through the ventral region of pons illustrating the areas occupied by single FB (horizontal lines) and DY (vertical lines) labeled neurons in PN, i.e., neurons projecting to rPML and cPML, respectively. The common areas are cross hatched. They correspond to most extreme localization of individual FB or DY labeled neurons, but not to density of their distribution.

quently in DL (n = 231), and in the lower number in PM (n = 137), L (n = 84) and PD (n = 44). In relation to the total number of single labeled neurons in PN in individual cases, double labeled neurons constituted 0.4-1.9% in DL (mean 1.1%; 6-51 cells per rabbit), 0.1-2.3% in PM (mean 1.1%; 1-51 cells per rabbit), 0.0-1.4% in L

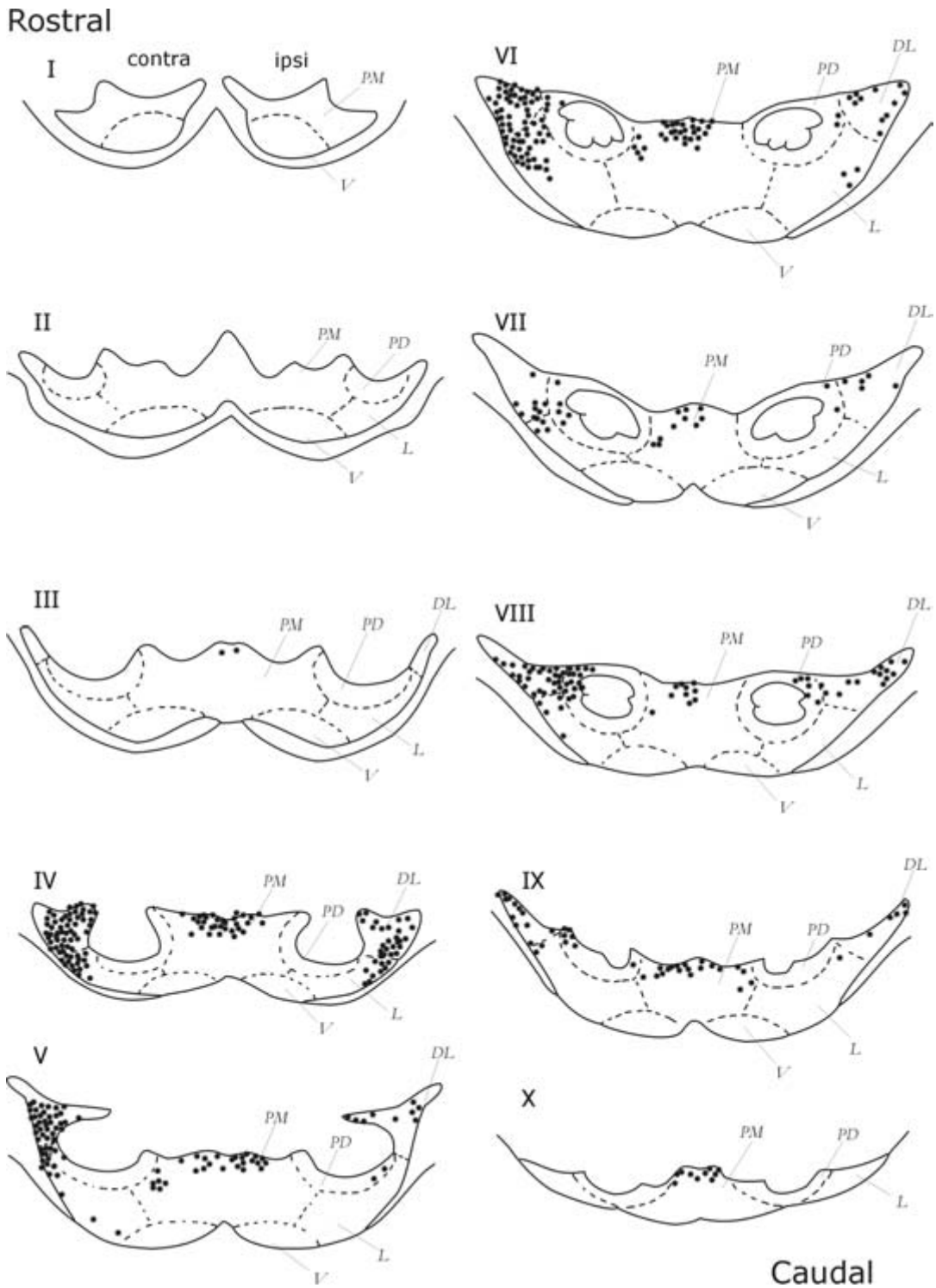

Fig. 5. Summarizing diagram of transverse sections through the ventral region of pons illustrating distribution of double FB + DY labeled neurons, i.e., those projecting by way of axonal collaterals to the forelimb (rPML) and hindlimb (cPML) regions of the unilateral PML as recognized in the present study. Each asterisk represents one double labeled cell body (n = 496).

(mean 0.7%; 0-29 cells per rabbit) and 0.0-2% in PD (mean 0.8%; 0-12 cells per rabbit).

In DL double labeled neurons were distributed in entire nucleus without tendency to clustering (levels IV-IX). The most frequently they appeared in its rostral half, apart from the rostral pole (level III). In PM double labeled neurons were observed in the dorsomedial (levels III-VIII) and dorsal (levels IX-X) regions and, in addition, they formed separate group in the lateral region on the contralateral side (levels V-VIII). Out of all PN, double labeling in PM exhibited the largest rostrocaudal extent. FB + DY labeled cells in L were present in the dorsolateral and lateral regions (levels IV-IX) with two cells laying ventrally (level V). Labeling in PD concerned the lateral (levels V-IX) and also dorsolateral (level VIII) regions. Figure 5 illustrates the exact distribution of all double labeled neurons (n = 496) recognized in the present study.

DISCUSSION

The present study using FB and DY as retrograde axonal tracers reveals profuse projections from PN to PML in the rabbit. Moreover, the findings are the first to demonstrate the existence of intralobular axonal branchings in pontocerebellar projection to PML. PN-PML connections are bilateral with a very clearcut contralateral preponderance.

Estimation of the number of labeled neurons

It is not unlikely that the number of labeled neurons indicated herein may be a little overestimation of the real number of neurons projecting to the injection sites. Probability of an overestimation appears from the fact that double-counting of labeled neurons in the border of sections is difficult to be entirely avoided. However, this may affect the total number of labeled neurons, but does not affect the population ratio of labeled neurons in various nuclei. In this paper only FB labeled neurons with a visible nucleus, i.e., the central non-labeled region of perikaryon were counted (Kolta et al. 2000). This method appears minimize the mistake of double-counting on adjacent sections. With regard to DY labeled neurons, it seems that thickness of section and nuclear diameter of a cell limit to a large extent the possibility of counting the same neurons twice. As concerns double FB + DY labeled neurons, rarity of their appearance (from 0-4 cells on one side per section) caused that such neurons were likely counted only once. On the other hand, it can be taken into account that with the technique of retrograde tracing not all neurons which axons terminate in the injection site are labeled, because effectiveness of uptake and retrograde transport is influenced by many factors (Keizer and Kuypers 1984, Macchi et al. 1984).

Origin of pontocerebellar projections

PN-PML projections originate from pontine nuclei through their entire rostrocaudal extent apart from the rostral parts. The strongest projection is derived from DL, mainly from the dorsomedial and dorsolateral regions. Prominent connections originate also from the dorsal half of PM and the dorsolateral and lateral regions of L. PD sends less numerous fibers arising from its lateral and, occasionally, dorsolateral regions. No evidence is given for projection from V. Extensive areas of overlap of PN neurons with axons terminating in the rPML and cPML indicate that no somatotopic correspondence exists in projection from PN to the two functionally different PML regions.

The findings presented herein are in general agreement with neuroanatomical studies on the PN-PML projections in other species, although some differences have been observed. These differences concerned primarily the rat where retrograde labeled neurons after HRP injections into PML occupied mainly the ventral peduncular and central ventral regions being absent in the lateral perimeter of the pontine gray (Mihailoff et al. 1981) or where anterograde labeled fibers projecting to PML originated in the rostroventral, centroventral peduncular and caudolateral regions of basilar PN (Serapide et al. 2001). Unlike the present paper and that in the opossum (Mihailoff et al. 1980), some degree of topographical organization for dorsal regions of PM and L projecting to rPML and for their ventral regions projecting to more cPML folia have been disclosed with HRP method in the cat (Hoddevik 1975, Hoddevik and Walberg 1979). Moreover, some differences concern the rostrocaudal extent of PN-PML projecting neurons. Such neurons were distributed in the entire extent of PN in the cat (Enger and Brodal 1985, Hoddevik 1975, Hoddevik and Walberg 1979, Kawamura and Hashikawa 1981) and monkey (Brodal 1979), in the rostral two thirds in the opossum (Mihailoff et al.1980) and in the entire PN apart from the caudal pole in the rat (Mihailoff et al. 1981) as well as except for the rostral part in the rabbit (present study). In

comparison to our findings and those in other species PN-PML projection is the weakest differentiated in the monkey where mainly neurons of lateral pontine gray supply PML (Brodal 1979).

Axonal branching of pontocerebellar neurons

The possibility of pontocerebellar connections to give off axonal collaterals to the cerebellar cortex have been studied so far as regard to different lobules of the same or both hemispheres rather than to different regions of a single lobule in the unilateral hemisphere. To our knowledge the only one paper concerns the divergence in pontocerebellar pathway reaching individual folia of unilateral paraflocculus in the cat (Bjaalie and Brodal 1997). Intrahemispheric and interhemispheric pontocerebellar projections by divergent axons have been indicated in the rat. Combined injections of Nuclear Yellow, Propidium Iodide and FB into different pairs of hemispheral lobules including PML and paraflocculus, PML and crus I, PML and lobulus simplex as well as into homotopic regions of the left and right PML have resulted in double labeling of cells in PN (Mihailoff 1983). Employment the same double fluorescent labeling technique has revealed that specific regions of the left and right PN project to symmetrical target areas of two hemispheres, i.e., crus I-II (Rosina and Provini 1984) as well as crus II or to crus II and vernal lobule VIIa,b (Rosina et al. 1980) in the cat. Recently in our laboratory we have disclosed that some PN neurons, mainly those of DL and PD, may bifurcate to terminate in PML sublobules of both sides in the rabbit (Zguczyński 1998). The studies referred to above (see Bjaalie and Brodal 1997 for other references) have shown that pontocerebellar mossy fibers are highly collateralized and that on way to the cerebellar cortex they give off collaterals to supply also the deep cerebellar nuclei (Mihailoff 1994, Shinoda et al. 1992). In addition, there is evidence on collateralization in the other cerebellar mossy fiber system. Payne (1983) has found that the lateral reticular nucleus, pontine tegmental reticular nucleus and nucleus praepositus hypoglossi have neurons which axons branch to terminate in the lobulus simplex of both sides in the rat. In our report (Bukowska et al. 1998) we have provided evidence of bilateral projections from neurons of the trigeminal sensory nuclear complex to homotopic and heterotopic sublobules of both PML by way of axonal collaterals. Moreover, we have proved that collateralization exists also within the olivocerebellar climbing fibers system terminating in PML (Bukowska et al. 2002).

It is well known that the rPML sublobules are targets for forelimb and face afferents, whereas the cPML folia receive inputs from hindlimb (see Introduction for references). The present results indicate that rPML (forelimb region) and cPML (hindlimb region) receive bilateral projections from particular parts of PN and that some pontine neurons may send branching axons that terminate in these two somatotopically non-corresponding cerebellar target regions. PN neurons indicated herein to supply both rPML and cPML are known to receive inputs from functionally heterogeneous sources. Most of their afferents arise from widespread regions of cerebral cortex including motor, primary sensory as well as associative sensory areas of several modalities, limbic areas as well as cerebellar nuclei, subcortical structures and other brain regions, and even spinal cord (see Introduction). It seems that PN neurons might integrate and pre-process these various signals and then send the information by way of axonal collaterals to rPML and cPML. Besides those from PN, PML is influenced directly by other projections, e.g., secondary vestibular (Grottel et al. 1991), trigeminal (Bukowska 1996, Bukowska and Grottel 1997) as well as those originating from the nucleus praepositus hypoglossi and nucleus "k" known to play a role in the control of ocular movements (Grottel et al. 1986, Zimny and Grottel 1995), and from pontine reticular tegmental nucleus mediating optokinetic signals (see Grottel et al. 1988 for references). In light of above it is possible that PN neurons indicated herein to form a link between rPML and cPML by way of axonal collaterals may plays a role in the coordination of unilateral forelimb and hindlimb movements with simultaneous adjustment of eye and head position, in response to heterogeneous PN inputs.

CONCLUSIONS

The present findings show that the rabbit rPML and cPML receive strong, mainly contralateral, projections from defined regions of pontine nuclei, i.e., DL, PM, L and PD. Moreover, a small number of neurons in these nuclei send axonal collaterals to the two functionally different PML regions.

ACKNOWLEDGEMENT

This study was supported by the State Committee for Scientific Research grant.

ABBREVIATIONS

a - f	-	sublobules of paramedian lobule
An	-	ansiform lobule
DL	-	dorsolateral nucleus
DY	-	Diamidino Yellow
FB	-	Fast Blue
L	-	lateral nucleus
Lm	-	medial lemniscus
PD	-	peduncular nucleus
Pe	-	peduncle
Pf	-	paraflocculus
PM	-	paramedian nucleus
PML	-	paramedian lobule
V	-	ventral nucleus
Ve	-	vermis

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Received 23 December 2002, accepted 15 July 2003