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THE CEREBELLAR OLIVO-CORTICONUCLEAR CONNECTIONS IN THE RAT

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1. INTRODUCTION

The cerebellum, which receives information from sensory pathways, about peripheral events, and from motor centres, co-ordinates voluntary as well as reflex movements, and in this way supports posture and motor behaviour. It has been concluded (Llinas and Hillman, 1969) that the cerebellar cortex has two levels of morphological and functional organization: one termed the "basic cerebellar circuit" (Blanks, 1988) and another one related to the organization of the cortical interneurones (which are out of the scope of the present review).

The basic cerebellar circuit is composed of the afferent and efferent connections of the Purkinje cells (PCs) of the cerebellar cortex. There are two main input systems: (i) the mossy fibre–granule cell system, which provides a disynaptic excitatory input to the distal dendrites of the PCs. Mossy fibre afferents have their origin in a variety of cephalic and spinal regions; (ii) the climbing fibre (CF) system which, as commonly agreed (Larramendi and Victor, 1967; Desclin, 1974), exclusively arises from the contralateral inferior olive (IO), to form excitatory synapses with the proximal dendrites of the PCs.

The CFs represent a unique system of innervation whose functional significance is still far from being understood (Montarolo *et al.*, 1981). In order to understand the role played by the IO in motor control, a knowledge of its cytoarchitecture as well as of the topographic organization of its afferent and efferent connections constitutes an essential step.

The diversity of afferent fibres to the IO suggests that this structure is of considerable functional complexity. Abundant anatomical and physiological data (see De Zeeuw, 1990, for a review) have shown that a number of afferent systems, from the cerebral cortex, mesodiencephalic areas, brain stem, spinal cord and cerebellum, affect IO neurones. Each pathway carries information to specific olivary subnuclei (see review of the literature in Brodal, 1981). Different neurotransmitters would be specifically used at their synapses by the various afferent pathways; among these neurotransmitters, GABA, substance P and serotonin may be the most widely distributed (De Zeeuw, 1990).

Histological (Ramon y Cajal, 1909) and ultrastructural investigations of the IO have been performed on a variety of mammalian species, including monkeys (Bowman and Sladek, 1973; Rutherford and Gwyn, 1980; see also Whitworth and Haines, 1986), cat (Walberg, 1963, 1964, 1966; Sotelo *et al.*, 1974; Bozhilova and Ovtscharoff, 1979; De Zeeuw, 1990), rabbit (Mizuno *et al.*, 1974), rat (Gwyn *et al.*, 1977) and opossum (Bowman and King, 1973; King, 1980). On a cytoarchitectural basis, the olivary complex is classically sub-divided into (i) three major subdivisions: the principal olive (PO), the medial (MAO) and the dorsal (DAO) accessory olive, and (ii) four minor sub-divisions: the nucleus beta, the dorsal cap (dc), the ventrolateral outgrowth (vlo) and the dorsomedial cell column (dmcc). Cytoarchitecturally, in all the subdivisions of the IO the neuronal somata are gathered in clusters scattered in a dense neuropil. Direct casual appositions without any ultrastructural membrane specialization have been observed between neighbouring cells or between several dendrites (dendritic thickets). However, the most characteristic feature of this neuropil is the presence, either in non-specialized zones of the neuropil or within "glomeruli" (or synaptic clusters), of dendrodendritic "gap junctions", which establish electrotonic coupling between olivary neurones. This intercellular coupling as well as ionic properties of the neuronal membrane have been implicated in oscillatory mechanisms and synchronous firing of the olivary neurones (Llinas *et al.*, 1974; Llinas and Yarom, 1981). Recently, physiological and morphological evidence has been brought forward (Sotelo *et al.*, 1986; Llinas and Sasaki, 1989) that synchronous firing in the IO can be modulated by GABAergic afferents. The bulk of GABAergic afferents corresponds to cerebello-olivary projections (Angaut and Sotelo, 1989; De Zeeuw, 1990).

The olivocerebellar projections disclose a high degree of organization in the connections they establish with parasagittal strips of PCs (see Brodal and Kawamura, 1980, for a review). In adult mammals, each PC is provided with one single CF (Ramon y Cajal, 1911; Eccles *et al.*, 1966). As each olivocerebellar axon collaterally innervates some six PCs in the rat (Schild, 1970), and over twice as many in man (Escobar *et al.*, 1968), the number of PCs amounts to six times or more that of olivary neurones in the same species (Eccles *et al.*, 1967). Aspartate has been suspected by several scholars to be the neurotransmitter of the CFs (Wiklund *et al.*, 1982, 1984; Toggenburger *et al.*, 1983; Kimura *et al.*, 1985; Campistron *et al.*, 1986; Matute *et al.*, 1987; Cuénod *et al.*, 1989). However, according to the recent observations of Zhang *et al.* (1990), the most likely neurotransmitter at the olivocerebellar endings would not be aspartate but, as first proposed by Foster and Roberts (1983), a "glutamate-like" substance. Besides PCs, collaterals of olivocerebellar fibres also reach neurones of the central cerebellar nuclei (Latham *et al.*, 1970; Eccles *et al.*, 1971, 1974a,b; Kitai *et al.*, 1977; Groenewegen *et al.*, 1979; Dietrichs *et al.*, 1985; Dietrichs and Walberg, 1985, 1986; Andersson *et al.*, 1987; Gibson *et al.*, 1987; Gravel *et al.*, 1987; Llinas and Mühlethaler, 1988; Ikeda *et al.*, 1989; Van der Want *et al.*, 1989) and the lateral vestibular nucleus (Ito and Yoshida, 1966; Ito *et al.*, 1966; Allen *et al.*, 1972a,b; Ten Bruggencate *et al.*, 1972; Balaban, 1984, 1988). Consequently, these nuclei will be influenced from the IO both directly via collaterals of olivocerebellar axons, and indirectly via the CF input to the PCs. PC axons have been shown to exert an inhibitory effect upon their nuclear targets (Ito and Yoshida, 1966; Ito *et al.*, 1970).

The topographic patterns of arrangement of the olivocerebellar connections have been documented in numerous mammalian species, whereas information on the rat is still imprecise. An increasing interest is being given to the rat in relation to studies of motor pathways. This phylogenetically "low" species discloses in its motor behaviour an interesting similarity with primates, i.e. some aptitude to move forelimb digits independently, in relation to manipulatory activity (Castro, 1972; Heffner and Masterton, 1975; Elger *et al.*, 1977). Given these similarities, the rat may be a suitable model for the study of the pathways underlying the cerebellar motor control. Indeed, precise, though partial, descriptions have been published of either the olivocerebellar (Chan-Palay *et al.*, 1977; Brown, 1980; Eisenman, 1981, 1984; Hess, 1982; Blanks *et al.*, 1983; Campbell and Armstrong, 1983a,b; Eisenman and Goracci, 1983; Furber and Watson, 1983; Wiklund *et al.*, 1984; Payne *et al.*, 1985; Wharton and Payne, 1985; Akaike, 1985, 1986a,b,c; Gravel *et al.*, 1987) or the corticonuclear projections (Goodman *et al.*, 1963; Achenbach and Goodman, 1968; Armstrong and Schild, 1978a,b; Haines and Koletar, 1979). Only the olivo-cerebellonuclear connections of flocculus and vermian lobules IX and X (Bernard, 1987) have been studied using a tracer transported in both retrograde and anterograde directions (as done, in the cat, by Dietrichs *et al.*, 1985, for the study of olivary connections).

A good knowledge of the organizational patterns of the olivocerebellar and corticonuclear projections is a prerequisite to gaining a functional understanding of the basic cerebellar circuitry in the rat. This was the aim of the present report. It is of utmost interest

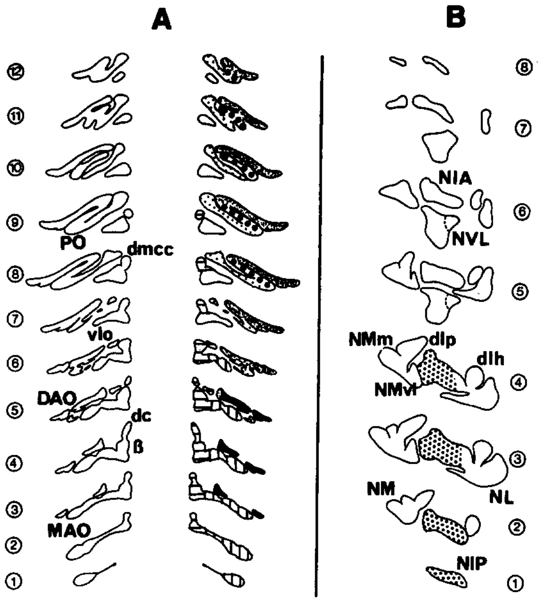

FIG. 1. Subdivision of the inferior olivary complex and cerebellar nuclei of the rat. (A) Subdivision of the inferior olive, on 12 drawings of equally spaced transverse sections from caudal (1) to rostral (12). Left: according to Gwyn *et al.* (1976). Right: according to Azizi and Woodward (1987): shaded: ventral fold of the DAO; black: dorsal fold of the DAO; large dots: dorsal lamella of the PO; small dots: ventral lamella of the PO; white: rostral lamella of the MAO; horizontal lines: vertical lamella of the MAO; vertical lines: horizontal lamella of the MAO. Abbreviations: DAO: dorsal accessory olive; MAO: medial accessory olive; PO: principal olive; β: nucleus beta; dc: dorsal cap; dmcc: dorsomedial cell column; vlo: ventrolateral outgrowth. (B) Subdivision of the cerebellar nuclei (modified from Korneliussen, 1968) and the lateral vestibular nucleus of Deiters (NVL), on 8 drawings of equally spaced transverse sections, from caudal (1) to rostral (8). Abbreviations: NIA: nucleus interpositus anterior; NIP: nucleus interpositus posterior (stippled); NL: nucleus lateralis; dlh: dorsolateral hump; NM: nucleus medialis; NMm: medial subdivision of the nucleus medialis; NMvl: ventrolateral subdivision of the nucleus medialis; dlp: dorsolateral protuberance (of the nucleus medialis).

to compare the results obtained on the rat with those on other mammals, in order to precisely interpret possible interspecies differences. In each species, the specific and consistent arrangement existing between the IO and the cerebellum may represent the anatomical substratum for understanding the role of the IO upon cerebellar functions (Ito, 1984, 1989; Andersson and Hesslow, 1987a,b).

2. METHODOLOGICAL CONSIDERATIONS

Original aspects of our report concern (i) the choice of the rat as a simple experimental model for the study of the topographical organization of the olivocerebellar pathways, and (ii) the use of both retrograde and anterograde transport of the horseradish peroxidase combined to wheatgerm agglutinin (WGA–HRP). The experimental material, described in detail elsewhere (Buisseret-Delmas, 1988a,b; Buisseret-Delmas and Angaut, 1989a,b), consists of rat brain in which a large number of cerebellar sub-lobules had been selectively injected with small amounts of tracer, in order to sample the entire cerebellar surface. WGA–HRP was deposited iontophoretically in the cerebellar cortex; in most cases the injections were very small in order to avoid interzonal diffusion of the tracer. Accordingly, for the same injection site, both the cell bodies at the origin of its afferent CFs and the target regions of PC axon terminals were localized. This differs from previously published studies, in which either the anatomical arrangement of the IO–PC projection, or that of the PC projection to the cerebellar/vestibular nuclei were separately analysed.

In the following description of the olivo-cerebellonuclear connections, the use of precise nomenclature and delineation for the sub-divisions of the IO, the cerebellar cortex and nuclei is necessary:

(i) The sub-division of the IO made by Gwyn *et al.* (1977) has been classically used (Fig. 1A, left). However, the more recent description of Azizi and Woodward (1987) is more closely fitted by connectional data (Fig. 1A, right). The two nomenclatures will both be used for individual sub-divisions, when necessary.

(ii) The cerebellar cortex is divided into transverse lobules and longitudinal zones.

—*In the rostrocaudal direction*, the ten-lobule sub-division of the cerebellar cortex, which derives from the extensive developmental work of Larsell (for the rat, see Larsell, 1952, 1970), is universally accepted. Larsell's nomenclature and outlining have been applied here (Fig. 2). Developmental studies (analysed by Jansen in his excellent review of 1954) also led to the basic morphological distinction

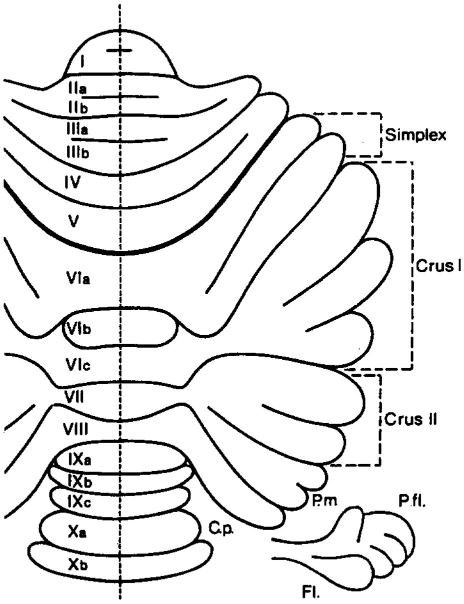

FIG. 2. Diagram of the "unfolded" right half of the cerebellum of the rat, showing the transverse foliation, according to Larsell (1952). Roman numerals, left, refer to Larsell's lobular subdivisions. Vertical hatched line: midline; bold line: fissura prima. Abbreviations: C.p.: copula pyramidis; Fl.: flocculus; P.fl.: paraflocculus; P.m.: paramedian lobule.

between, rostrally, a corpus cerebelli, which comprises the anterior lobe (Larsell's lobules I to V), the posterior lobe (lobules VI to IX) and the flocculonodular lobe (lobule X), caudally. Functionally, the distribution of the main afferent pathways determines (Brodal, 1969): a "spinocerebellum" (anterior lobe and paramedian lobule of the posterior lobe), a "teleceptive cerebellum" (lobules VI and VII of the posterior lobe), and a "vestibulocerebellum", which concerns (Brodal and Høivik, 1964) the caudal parts of lobule IX and lobule X of the vermis, the ventral paraflocculus and the flocculus (i.e. caudal lobule IX and lobule X of the hemisphere, see Jansen, 1954).*

In the rat, we distinguish here the anterior lobe (lobules I to V), the posterior lobe (lobules VI to IXa, including the dorsal paraflocculus) and the "vestibulocerebellum" (vermal lobules IXb, c, and X, the ventral paraflocculus, and the flocculus).

—*In the mediolateral direction*, four main longitudinal zones are classically distinguished within the cerebellar cortex on the basis of both olivocortical and corticonuclear connections. They were named, from medial to lateral, zones A, B, C and D (Voogd, 1964). Concordant observations were obtained in the cat (Voogd, 1967, 1969; Dietrichs, 1981), mouse (Marani, 1982), rabbit (Van Rossum, 1969), ferret (Voogd, 1969) and primates (Haines and Rubertone, 1977–1979). In the rat, this nomenclature has also been adopted (Bernard, 1987; Buisseret-Delmas, 1988a,b; Buisseret-Delmas and Angaut, 1989b), with some adjustments to be dealt with in the next section.

(iii) The anatomical subdivision of the cerebellar nuclei of the rat (Fig. 1B) conforms to the description and nomenclature of Korneliussen (1968). With regard to those of the vestibular nuclei, they concord in the rat with the description of Brodal and Pompeiano (1957) in the cat, to which the reader is referred.

3. ANATOMICAL DATA. COMPARATIVE ASPECTS

In the following description, headings concern the four main zones of Voogd (1964). These zones have been defined on the basis of their corticonuclear efferents. Each of these zones is also characterized by its specific olivocortical afferents. However, the fact that some olivocortical collateral afferents may reach discrete cortical zones mediolaterally (Ekerot and Larson, 1982) induces difficulties of interpretation, and can therefore be the source of apparent discrepancies between data. In the following, the cortical zones are defined in relation to their corticonuclear efferents.

3.1. The A Zone of the Cerebellar Cortex

The A zone is the more medially situated longitudinal strip of the cerebellar cortex. It has been defined (Voogd, 1964, 1969) as projecting to the ipsilateral nucleus fastigius or medialis (NM), which is phylogenetically the eldest cerebellar nucleus (Larsell, 1952). The A zone receives its olivary afferents from the caudal half of the contralateral medial accessory olive (MAOc). Former studies in the cat (Courville and Diakiw, 1976; Groenewegen and Voogd, 1977; Voogd and Bigaré, 1980) showed the existence of two sub-divisions within the A zone: A1 medially and A2 laterally. It is agreed that the CF inputs to the A1 sub-zone are under a spinal influence from the hindlimb whereas those to the A2 sub-zone are under that of the forelimb (Oscarsson, 1969; Brodal, 1980; Brodal and Kawamura, 1980; Armstrong, 1990).

In the rat, we have distinguished three subdivisions within the NM (Fig. 1B) in relation to the distribution of the corticonuclear projections: a medial portion (NMm), a ventrolateral portion (NMvl), and the dorsolateral protuberance (dlp). These subdivisions fit the cytological organization of the NM described in the rat (Korneliussen, 1968; Beitz and Chan-Palay, 1979a,b; Beitz, 1982). In our material, connections corresponding to the above definition of the A zone have been found, as expected, following any injection restricted to the vicinity of the mid-line. Moreover, connections typically fitting those of the A zone have also been found in cases of injections of lobules VI and/or VII more distant from the mid-line (Figs 3 and 9). With regard to the corticonuclear projections from these laterally situated regions onto the NM, our data concord with earlier observations (Goodman *et al.*, 1963; Armstrong and Schild, 1978a,b). However, these groups of authors considered these regions of lobules VI and VII as part of the intermediate or hemispheral cortex. This lateral extension of the A zone through the posterior lobe apparently constitutes a characteristic feature of the rat (Buisseret-Delmas, 1988a). As in other species studied, olivocerebellar and corticonuclear projections of the A zone are topographically organized in the mediolateral and rostrocaudal directions, in spite of some overlapping between the respective projections of the anterior and posterior lobes.

3.1.1. *The A zone in the anterior lobe*

In the rat, the olivary afferents to the A zone of the anterior lobe were always found to come from the lateral region of the MAOc, corresponding to subnuclei a and b of the MAO (Gwyn *et al.*, 1977). These sub-regions coincide with the "horizontal lamella of the MAO" of Azizi and Woodward (1987). In the present material, very little overlapping has been found between the respective origins of the olivocerebellar projections to the medial and to the lateral part of the A zone of the anterior lobe: CFs from the caudal half of the lateral MAOc (levels 1–3) project to the medial aspect of the A zone, whereas CFs from the rostral half of the lateral MAOc (levels 4–6) project to the lateral aspect of the A zone (Fig. 3).

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*Primary vestibulocerebellar projections are, in the cat, markedly less abundant in the hemispheral than in the vermal part of the vestibulocerebellum (Sato *et al.*, 1989). In the rabbit, the presence of primary vestibulocerebellar afferents to the ventral paraflocculus and the flocculus was recently denied by Gerrits *et al.* (1989). This discrepancy may reflect species differences.

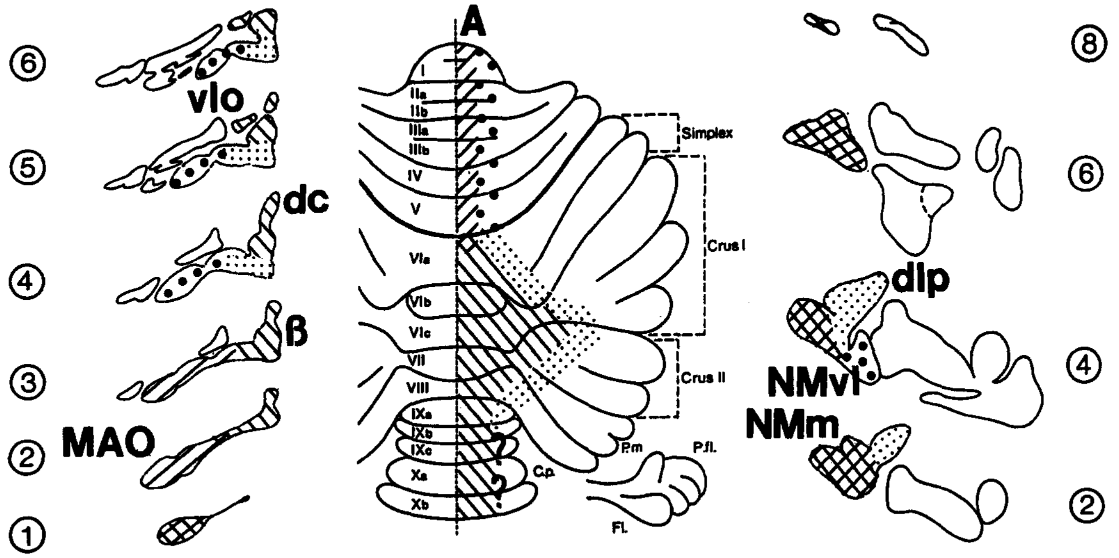

FIG. 3. Topographical arrangement of the connections of the A zone of the rat cerebellum. Middle: cortical extension of the A zone; left: cortical afferent projections from the inferior olive; right: cortical efferent projections onto the medial cerebellar nucleus. Abbreviations: see Figs 1 and 2.

The corticonuclear projections from the two parts of the A zone of the anterior lobe also appear to be topographically segregated: the medial ones reach the NMm, mostly over its rostral two-thirds, whereas the lateral ones reach, more laterally, the NMvl (Fig. 3). On the basis of retrograde tracing studies, Voogd *et al.* (1991) have described in various mammals—including the rat—a projection from the A zone of the anterior lobe onto the lateral vestibular nucleus of Deiters (NVL) and the inferior vestibular nucleus (NVI). No such projections have been found here. Differences in our respective technical approaches may indeed explain the divergence with Voogd *et al.* (1991), whose injections through the NVI may not be free of incident spread of the tracer to the nearby ventral NM. Not so easily explained is our discrepancy regarding the NVL.

We can conclude that a medial and a lateral part may be distinguished in the A zone of the rat on the basis of their respective olivocortical as well as corticonuclear connections. This segregation gets its main functional counterpart from the differential origin of the somatosensory influences that reach the lateral MAOc. Somatosensory afferents from the forelimbs project more rostrally upon the MAOc than do those from the hindlimbs (Swenson and Castro, 1983). Thus, the medial aspect and the lateral aspect of the A zone distinguished here in the rat are likely to correspond to the A1 and A2 zones of the cat, respectively. However, until now, no attempt has been made to correlate anatomical and electrophysiological findings in the rat.

3.1.2. *The A zone in the posterior lobe*

According to classical data in the cat, the A zone extends throughout the posterior lobe.

In the rat, the A zone appears to be more complexly organized mediolaterally and rostrocaudally in the posterior lobe than in the anterior lobe.

3.1.2.1. *Lobules VI and VII*

The olivary afferents to the A zone of lobules VI and VII were found to come from the medial region of the MAOc, corresponding to part of the sub-nucleus b, the sub-nucleus c, and the nucleus beta. The latter two olivary sub-regions (which have been considered by some authors as representing a single cell group (see Whitworth and Haines, 1986) are included within the "vertical lamella of the MOA" of Azizi and Woodward (1987). Cells in the caudal half of the medial MAOc (with the exception of its caudal-most tip: Fig. 3, left, level 1) project to the medial aspect of zone A whereas cells in the rostral half of the medial MAOc project to its lateral aspect. The corticonuclear projections from the medial A zone of lobules VI and VII are directed to the NMm. Corticonuclear projections from the lateral A zone of lobules VI and VII reach the dlp (Fig. 3). Therefore, the vermal part of lobules VI and VII can be subdivided into a medial and a lateral sub-division. These apparently continue the A1 and A2 sub-zones of the anterior lobe, respectively.

3.1.2.2. *Lobules VIII and IX*

The olivocortical projections to the A zone of lobules VIII and IX not only come from the medial MAOc but also from cells of the lateral MAOc (Fig. 3, left, level 1), corresponding to subnuclei a and b. The corticonuclear projections massively concern the caudoventral part of the NMm (Fig. 3, right). Scarce projections are also observed in the NMvl following injections of lobule VIII whereas injections limited to lobule IX show corticonuclear projections through the NMm only. Therefore, the origin of the olivocerebellar projections to the medial aspect of the A zone in lobules VIII and IX corresponds to both that of the anterior lobe and that of lobules VI and VII of the posterior lobe. On the other hand, no corticonuclear fibres from lobule IX reach either the NMvl or the dlp. This is to be reconciled with some observations in the cat from Voogd and Bigaré (1980), who mentioned that "in lobule IX, the A1 and A2 zones either fuse or A2 disappears". We believe that ony A1 persists in lobule IX of the rat.

Our results confirm, as suggested by Tabuchi *et al.* (1989), that uvulovestibular projections do not arise from the dorsal uvula (lobule IXa). These exclusively arise from lobules IXb and c. Functionally, the dorsal uvula must be considered as part of the posterior lobe. The ventral uvula (lobules IXb, c) is functionally part of the vestibulocerebellum. This segregation fits the distinction established on the basis of mossy afferents to these sub-lobules.

3.1.3. *The A zone in the vestibulocerebellum*

On the basis of both its mossy vestibular afferents and PC efferents (Brodal *et al.*, 1962), the vermis of the vestibulocerebellum includes the caudal lobule IX (uvula) and lobule X (nodulus). It has been considered that the dorsal part of the uvula, lacking primary vestibular afferents (Dow, 1936; Brodal and Høivik, 1964; Mehler and Rubertone, 1985; Sato *et al.*, 1989) is not identical to its ventral part. These anatomical differences would therefore correspond to functional dissimilarities between the dorsal and ventral sub-lobules of the uvula. As stated above, only the ventral uvula is considered here.

It has been well accepted since the work of Dow (1936, 1938) that, besides fibres to restricted regions of the cerebellar nuclei, the vestibulocerebellum essentially sends off projections onto the nuclei of the vestibular complex (cat: Angaut and Brodal, 1967; Carleton and Carpenter, 1983; Shojaku *et al.*, 1987; monkeys: Carleton and Carpenter, 1983; Haines, 1987; rabbit: Balaban, 1984).

In the ventral uvula and nodulus, an orderly arrangement of the olivocerebellar projections has been observed in the cat (Brodal, 1976; Brodal and Kawamura, 1980; Walberg, 1980; Kanda *et al.*, 1989), opposum (Linauts and Martin, 1978), mouse (Eisenman *et al.*, 1983) and rabbit (Sato and Barmack, 1985), as well as in primates (Brodal and Brodal, 1982; Whitworth *et al.*, 1983).

In the rat, our results show that the medial aspect of the ventral uvula receives CFs from the MAOc and nucleus beta, whereas the medial aspect of the nodulus is primarily related to the dc and the vlo, in agreement with previous studies (Furber and Watson, 1983; Eisenman, 1984; Azizi and Woodward, 1987; Bernard, 1987; Apps, 1990). These olivary sub-regions are included by Azizi and Woodward (1987) in their "vertical lamella of the MAO". As in other mammals, both the ventral uvula and the nodulus send off PC axons to the NM as well as to the vestibular complex. The uvular projections onto the NM appear quantitatively abundant, whereas those from the nodulus would be scanty. The projections from the medial uvula to the vestibular nuclear complex concern the NVI and the superior vestibular nucleus (NVS). However, the existence of uvular projections onto the medial vestibular nucleus (NVM) cannot be deduced from our material. Massive projections to the NVM have been described (Bernard, 1987); nevertheless, according to Tabuchi *et al.* (1989) projections to the NVM were observed only when the nodulus was also involved. The absence of an uvula–NVM projection would be concordant with observations made in other species (Angaut and Brodal, 1967; Shojaku *et al.*, 1987). Nodular projections to the vestibular complex are found to be rather heavy within the NVS, NVM and NVI, and mild within the NVL (Bernard, 1987; Tabuchi *et al.*, 1989).

In conclusion (Fig. 3), having adopted to define, according to the general view, the cerebellar cortical zones with respect to their corticonuclear projections (the cerebellar output), we may consider that, in the rat, the *medial part of the A zone*, traced throughout the anterior lobe, the posterior lobe and the vestibulocerebellum, constitutes a unique sagittal band, which receives CFs from the "horizontal lamella of the MAO" of Azizi and Woodward (1987) and projects to the NMm. This would correspond to Voogd's A1. A *lateral aspect of the A zone*, which receives CFs from the "vertical lamella of the MAO" and projects to the NMvl and dlp, has only been found through lobules I–VIII. In the anterior lobe, the lateral A zone, which projects to the NMvl, may correspond to Voogd's A2. In the posterior lobe, the dlp is the nuclear target of the lateral A zone through lobules VI, VII and VIII. Homology between the dlp and the NMvl is hazardous, both on cytoarchitectural and hodological grounds. Therefore, on the basis of corticonuclear connections, the lateral part of the A zone in the posterior lobe would not correspond to the lateral part of the A zone in the anterior lobe.

Besides the A zone, three other cortical strips, located more laterally in the anterior lobe, the posterior lobe, and in the caudal flocculus, receive their CFs from sub-regions of the "vertical lamella of the MAO", which is a major source of olivary afferents to the A zone. On the other hand, their cortical efferents respectively reach a region wedged between the NM and the posterior interposed nucleus (NIP), a medial region of the NIP, and the parvocellular region of the nucleus lateralis (NL) (Table 1). Having adopted to define cortical zones with respect to their corticonuclear projections, these three cortical strips

Table 1. Diagrammatic Representation of the Olivo-corticonuclear Connections of the X Zone, CX Sub-zone, and Caudal Flocculus

Vertical lamella of the MAO	CEREBELLAR CORTEX	CEREBELLAR NUCLEI
	X ZONE	
Subnucleus c →	Lobules V-VI	→ NM - NI
dmcc →	Lobules IX-X	→
	CX Subzone	
Subnucleus c →	Lobule V	→ NI
dmcc →	Lobules IX-X	→
dc →	Caudal FLOCCULUS	→ Slp

slp: small-celled part of the NL. Other abbreviations: see Fig. 1.

are considered below as the X zone, the CX sub-zone, and the floccular component of the D2 sub-zone.

3.2. THE X ZONE OF THE CEREBELLAR CORTEX

The existence of a narrow strip of cortex located between the A and B zones was first defined electrophysiologically, in the cat, in lobule V of the anterior lobe, by Ekerot and Larson (1977) (see also Oscarsson, 1980). They called this strip, where they found somaesthetic afferents from the forelimbs, the "X" zone. Further studies (Andersson and Ericksson, 1981; Ekerot and Larson, 1982) reported that the X zone extended over lobules V and VI. Voogd and Bigaré (1980) suggested the presence of an X-like compartment in the vestibulocerebellum.

An anatomical delineation of the X zone was first noticed, in the cat, by Voogd (1983). The origin of the olivocortical projections to, as well as the target of the corticonuclear projections from, the X zone have been extensively detailed, both anatomically and electrophysiologically (Campbell and Armstrong, 1985; Trott and Armstrong, 1987a,b; see also review in Armstrong, 1990): the X zone receives its CFs from a row of cells of the MAOc. Its corticonuclear efferents distribute within a nuclear region wedged between the NM and the nucleus interpositus (NI). In a primate (the squirrel monkey), Haines and Dietrichs (1991) defined, on the basis of its projections onto the medialmost NIP, an X zone extending from lobule IV to lobule VII.

3.2.1. *The X zone in the anterior and posterior lobes*

In the rat, the presence of a narrow strip of cortex corresponding to the X zone of the cat has been observed recently (Apps, 1990; Voogd *et al.*, 1991). In our material, selective identification of this narrow strip was not obtained. However, in two cases of injections in the B zone (to be commented on in the next section), we observed (i) olivary cells within the sub-nucleus c (Fig. 4A) i.e. within the rostral end of the "vertical lamella of the MAO" of Azizi and Woodward (1987), and some through a more lateral part of the MAO, including the "sub-nucleus b1" of Apps (1990); (ii) corticonuclear terminals sandwiched between the NM and the NIP. This pattern of olivocerebellar and corticonuclear connections fits that described in the cat for the X zone. Therefore, as previously suggested by Voogd *et al.* (1991), our observations indicate the existence of an X zone in the rat.

3.2.2. *The X zone in the vestibulocerebellum*

In the cat, Voogd and Bigaré (1980) described an "A3 zone" in the lateral part of the lobules IX and X, which they interpreted as homologous to the X zone.

In the rat, the CF afferents to the intermediate aspect of the uvula (Eisenman, 1984; Azizi and Woodward, 1987; Bernard, 1987) and nodulus (Bernard, 1987) originate within a small group of cells medial and dorsal to the MAOr referred to, by most authors, as the dorsomedial cell column (dmcc) by analogy with the description of the dmcc made by Walberg (1956) in the cat. This dorsomedial olivary region in the rat is included in the "vertical lamella of the MAO" of Azizi and Woodward (1987). The cortical efferents from the intermediate part of the uvula and nodulus reach the medial aspect of the NIP, the NVI, NVS and NVL (Bernard, 1987; Tabuchi *et al.*, 1989).

In our material, in a case of selective injection of the intermediate part of lobule IX (Figure 4B), the olivary projections were found to essentially arise from the dmcc. Corticonuclear projections were found in a region homologous to the terminal field of

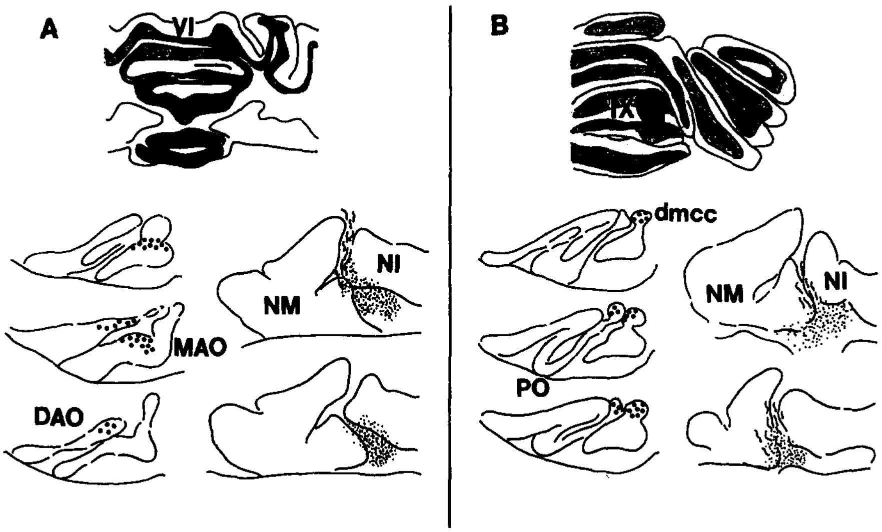

FIG. 4. Olivocortical and corticonuclear connections of the X zone. A: injection in lobule VI; B: injection in lobule IX (black areas on the drawings of transverse sections through the cerebellar cortex). For A and B, left: olivary levels showing retrogradely labelled cells (large dots), right: cerebellar nuclear levels showing anterogradely labelled passing (wavy lines) and terminal (small dots) fibres. Abbreviations as in Fig. 1.

the X zone (compare Fig. 4A and 4B). We believe that this cortical strip is a caudal continuation of the X zone over the vestibulocerebellum of the rat. This strip would be homologous to the A3 zone described, in the cat, by Voogd and Bigaré (1980). As already noted, it is worth mentioning here that the olivary region projecting to the X zone is included within that projecting to the A zone. On the other hand, the cortical efferents from the X zone might apparently be related to those of the A zone, to those of the C1 sub-zone (see Section 3.4.1), or to a mixture of both (Table 1). Indeed, the output of the X zone needs to be further investigated, and this strip of cortex to be more closely defined.

Some olivary afferents to this "vestibulocerebellar X zone" have also been found here to arise from the medial aspect of the PO ventral lamella. Most likely, this observation reflects the existence of a contingent of CF afferents to this caudal X zone collateral of CFs to the D0 sub-zone (to be considered in Section 3.5).

3.3. THE B ZONE OF THE CEREBELLAR CORTEX

The B zone has been defined in the cat according to its projections to the NVL (Voogd, 1964, 1967). It runs lateral to the A zone over lobules I–IV, and lateral to the X zone over lobules V and VI. In the rabbit, the B zone was found to extend as caudal as lobule VIII (Van Rossum, 1969).

The PC axons of the B zone impinge upon the NVL (Voogd, 1964; Voogd *et al.*, 1991). It is generally described that the B zone projects to the dorsal half of the NVL (Brodal *et al.*, 1962; Ito, 1984) and, to a lesser degree, to the NI (see Brodal and Kawamura, 1980). Climbing fibre afferents to the B zone arise in the caudal DAO.

In the rat, connections that may be selectively related to the B zone, in our experiments, may be described as follows: olivary neurones projecting to zone B are located in the lateral two-thirds of the caudal DAO (levels 3–5), in agreement with earlier HRP (Furber and Watson, 1983) and autoradiographic (Campbell and Armstrong, 1983a,b) reports. The region involved corresponds to the "dorsal fold of the DAO" in the description of Azizi and Woodward (1987). With regard to the corticonuclear projections, some have been found throughout the whole dorsoventral extent of the NVL in the rat (Buisseret-Delmas, 1988a), in agreement with immunocytochemical data (De Camilli *et al.*, 1984; Mugnaini and Oertel, 1985). This is concordant with observations made in the rabbit (Van Rossum, 1969). In our material, PC fibre endings within the dorsal part of the NVL were found to arise in the B zone of either the anterior or the posterior lobe. Only for injections of the tracer involving lobule VI did a significant additional amount of PC axons terminate in the ventral part of the NVL (Fig. 5). We do not subscribe to the existence of a projection from zone B onto the NI as, in our material, all the corticonuclear fibres reaching the NI could be attributed to the involvement of the C zone. In conclusion, zone B extends in the rat from lobule I to lobule VI. It receives its CFs from the "dorsal fold of the DAO" of Azizi and Woodward (1987) and exclusively projects onto the NVL (Fig. 9).

3.4. THE C ZONE OF THE CEREBELLAR CORTEX

The C zone has been defined, in the cat (Voogd, 1964, 1969) as the region of the cerebellar cortex whose PC axons terminate in the NI. The NI is sub-divided into an anterior (NIA) and a posterior (NIP) sub-division (see Voogd, 1964). Three longitudinal sub-zones (C1, C2 and C3) have been classically described within the C zone in all species studied. The C1 and C3 sub-zones extend from lobule II to lobule VIII (the paramedian lobule in the cat), and the C2 sub-zone from lobule II to lobule IX (Kawamura and Hashikawa, 1979; Brodal and Kawamura, 1980). The olivocortical afferents to the C1 and C3 sub-zones come from the rostral part of the DAO, those to the C2 sub-zone come from the

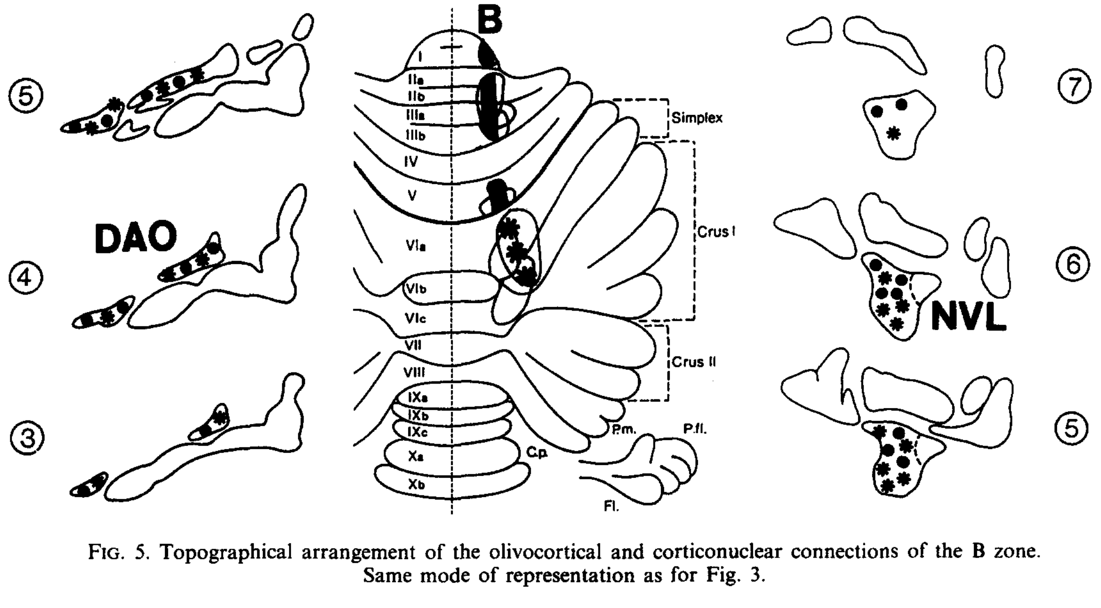

FIG. 5. Topographical arrangement of the olivocortical and corticonuclear connections of the B zone. Same mode of representation as for Fig. 3.

rostral part of the MAO (Brodal and Kawamura, 1980). More recently, anatomical and physiological investigations delimited a "CX zone" between the C1 and C2 sub-zones, through lobule V of the anterior lobe (Campbell and Armstrong, 1985; Armstrong, 1990; see also Trott and Apps, 1991). This strip of cortex, here named "CX sub-zone", receives its CFs from the medial portion of the MAO and projects to the medial aspect of the NIP (see Armstrong, 1990). It must be stressed that the CX sub-zone and the X zone receive CFs from the same olivary region (Andersson and Eriksson, 1981; Ekerot and Larsson, 1982; Apps *et al.*, 1991).

In the rat, the NI is, on its medial aspect, contiguous to the NM; on its lateral aspect, the NI abuts the mass of NL and the dorsolateral hump (dlh), which is considered here as part of the NL (Angaut and Cicirata, 1982; see also Angaut and

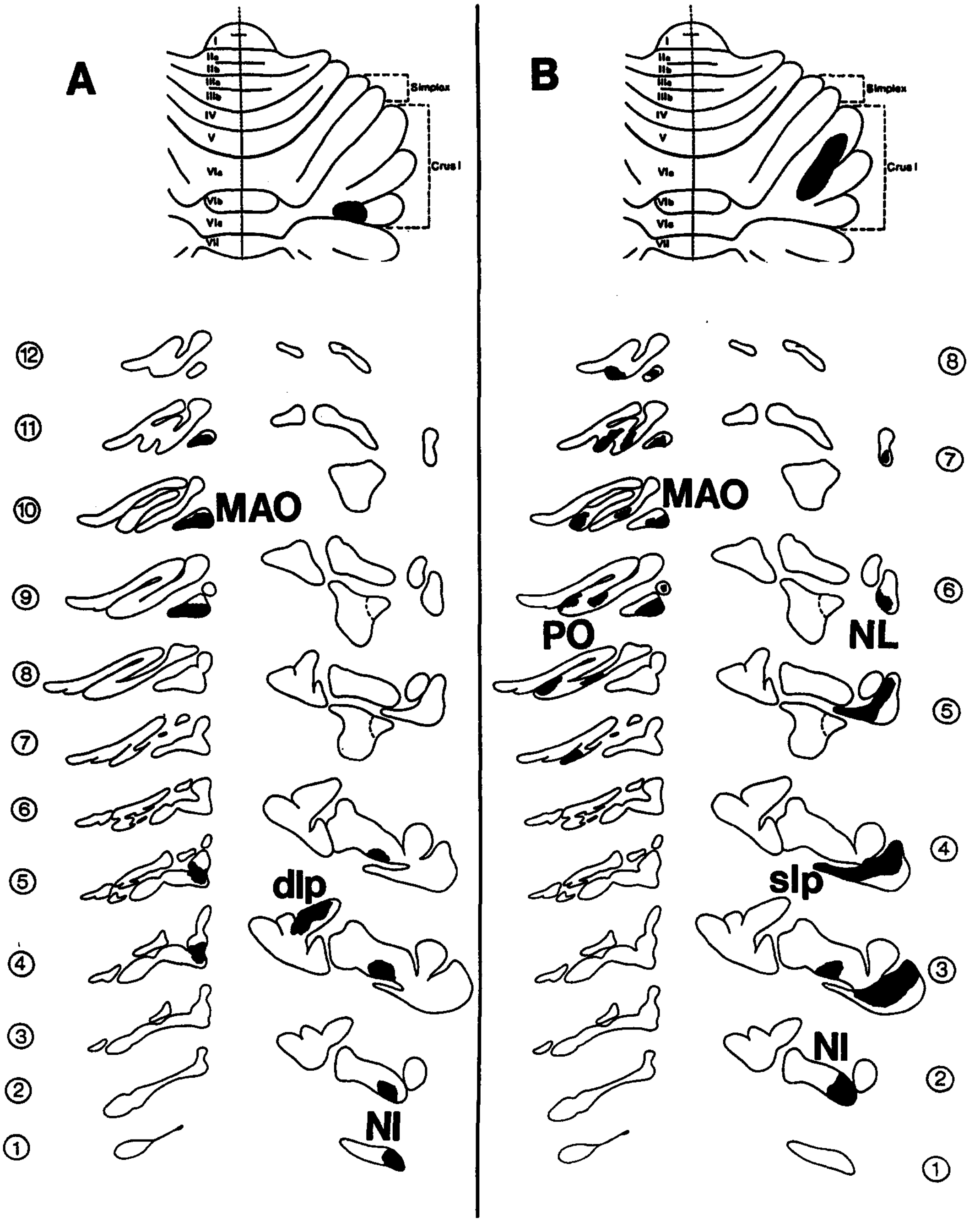

FIG. 6. Two cases of injection in lobule VI involving, in A: zone A and sub-zone C2, and in B: sub-zones C2, D1 and D2. For A and B, the corresponding afferent and efferent connections are represented, in black, respectively on the inferior olive (left) and on the cerebellar nuclei (right). Notice, in A, the absence of C1-like connections and, in B, of C3-like and/or D0-like connections. Abbreviations: see Fig. 1.

Cicirata, 1990). In a schematic representation of the NI through eight transversal levels (Fig. 1B), NIA and NIP are shown to coexist through levels 3 and 4, whereas NIA fully occupies rostral levels 5–8, and NIP caudal levels 1 and 2. The C1, C2 and C3 sub-zones have all been distinguished (Buisseret-Delmas, 1988b). The existence of a CX sub-zone in the cerebellum of the rat has not yet been mentioned in the literature.

3.4.1. *The C zone in the anterior and posterior lobes*

3.4.1.1. *The C1 sub-zone*

In the rat, as seen in other species, the CF afferents to the C1 sub-zone come from the lateral DAO (levels 6–10 in Fig. 1A). This region is included in the "ventral fold of the DAO" in the description of Azizi and Woodward (1987). The corticonuclear projections of the C1 sub-zone reach the medial third of the NI throughout its rostrocaudal extent. Both NIA and NIP receive an equal amount of afferents from the anterior and posterior lobes. Whereas, in most species, the C1 sub-zone has been found to project onto the NIA only (Brodal and Kawamura, 1980), in the rat, C1 corticonuclear projections appear to distribute more extensively in the rostrocaudal direction.

The C1 sub-zone extends from lobule I to lobule VIII. However, in all our injections restricted to lobules VIb and/or VIIa, the olivocortical and corticonuclear connections did not correspond to those of the C1 sub-zone as described above. They most often combined the features of those of the A zone (CF afferents from the MAOc and PC efferents to the dlp, Fig. 6A) and those of the C2 sub-zone (CF afferents from the MAOr and PC efferents to the NI, Fig. 6A). Therefore, sub-zone C1 is interrupted at this rostrocaudal level. Afferent and efferent connections of the rostral and caudal segments of sub-zone C1 widely overlap at both the olivary and the interposed nuclear level.

3.4.1.2. *The CX sub-zone*

Our material does not permit selective identification a CX sub-zone in the rat. However, several of our observations favour its existence. Thus, cases of injections involving lobule V in which both C1 and C2 sub-zones were concerned showed a retrograde labelling of neurones within the rostral part of the "vertical lamella of the MAO". The cells concerned were interpreted as projecting onto the C2 sub-zone (Buisseret-Delmas, 1988b, see her Fig. 5). However, this labelling would more likely be due to the involvement of the CX sub-zone. Moreover, in the same material, terminal labelling observed within the medialmost NIP was attributed to corticonuclear fibres from the C1 sub-zone. This terminal labelling would actually reflect the concomitant involvement of the CX sub-zone.

Therefore, the CX sub-zone may be regarded as a strip of cortex whose (i) CF afferents come from the "vertical lamella of the MAO", that projects to the A zone, and (ii) corticonuclear efferents reach the NIP, which receives corticonuclear efferents from the C1 sub-zone. It is worth pointing out that the CX sub-zone and the X zone have (i) a common source of CF afferents within the "vertical lamella of the MAO", and (ii) strictly contiguous nuclear targets for their efferents (Table 1).

3.4.1.3. *The C2 sub-zone*

In the rat, the C2 sub-zone runs as a continuous strip of cortex, through the anterior and posterior lobes, from lobule II to lobule IXa. As shown in Fig. 7 (compare Fig. 7, A and B), the C2 sub-zone extends caudally onto the dorsal paraflocculus. The olivary afferents to the C2 sub-zone originate in the MAOr (levels 7–12 in Fig. 1A), which corresponds to the "rostral lamella of the MAO" of Azizi and Woodward (1987). The nuclear efferents from C2 terminate throughout the rostrocaudal development of the NI. Mediolaterally, they concern the central

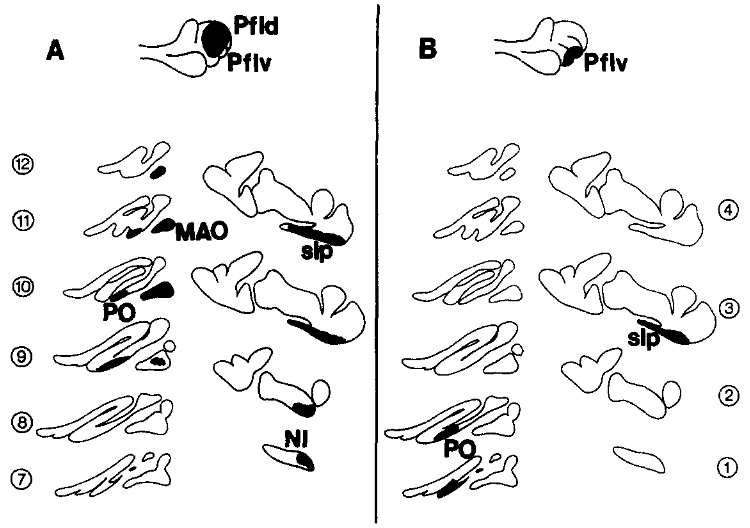

FIG. 7. Two cases of injection in the paraflocculus involving, in A, the dorsal and ventral paraflocculus and, in B, the ventral paraflocculus only. Same mode of representation as for Fig. 6.

third of the NIA and the lateral half of the NIP (levels 1 and 2 in Fig. 1B). From a comparison between cases of diversely placed injections, no clear rostrocaudal arrangement has been detected within the olivary afferents to C2; on the other hand, some rostrocaudal topographic organization is found within its nuclear efferents. The fibres from the anterior lobe as well as lobules VIa and VIII of the posterior lobe mainly project to the NIA, whereas those from lobule VIb, c and VII, and those from the dorsal paraflocculus (Fig. 7A), essentially reach the NIP.

It is of interest to mention here that, in some cases of selective injections of the D2 sub-zone, a scant retrograde labelling has also been observed within the "rostral lamella of the MAO", in conjunction with labelling in the ventral lamella of the PO. The most likely interpretation of this finding is that CF afferents to the C2 sub-zone give off colaterals to some regions of the D2 sub-zone, and specifically to lobule VI.

3.4.1.4. *The C3 sub-zone*

In the rat, none of our injection sites has been found to be exclusively centred to sub-zone C3. The tracer had always spilled medially and/or laterally. The presence of retrograde and anterograde labelling respectively in the "rostral lamella of the MAO" and in the central aspect of the NI witnessed the involvement of the C2 cortex; the presence of retrograde and anterograde labelling in the principal olive (PO) and NL and/or dlh corresponded to the encroachment of zone D (see next section). It can be deduced from the present material that the olivocerebellar projections to the C3 sub-zone originate from the medial aspect of the rostral DAO (Fig. 9). The region involved corresponds to the "ventral fold of the DAO" of Azizi and Woodward (1987). In concordance with previous data from other species, the zones of projection to sub-zones C1 and C3 largely overlap within the DAO. This may account for the presence of collateral olivocerebellar projections to C1 and C3 in the rat, as has also been observed in several other mammals (Brodal *et al.*, 1980; Rosina and Provini, 1983).

The corticonuclear projections concern the lateral third of the NI. Although the NIA is difficult to distinguish from the NIP on frontal sections, the projection of sub-zone C3 is most likely confined inside the limits of the NIA. The C3 sub-zone extends from lobule II to lobule VIII. However, following injections restricted to lobules VIb–c and VII in which the tracer had spread lateral to the C2 sub-zone, olivocortical and corticonuclear connections (Fig. 6B) always combined features of the C2 sub-zone (CF afferents from the MAOr and PC efferents to the NI) with some typical of the D zone (CF afferents from the PO and PC efferents to the NL). None showed connections corresponding to those of the C3 sub-zone. Therefore, sub-zone C3 is, like sub-zone C1, interrupted at this rostrocaudal level.

3.4.2. *The C zone in the vestibulocerebellum*

All four subdivisions of the C zone do not seem to be represented within the vestibulocerebellum.

Connections typically fitting those of the CX sub-zone have been found in relation to lobules IX–X of the vestibulocerebellum: the cortical strip concerned receives its CF afferents from the dmcc, in the "vertical lamella of the MAO", and projects to the medial aspect of the NIP (Bernard, 1987). In our opinion, this may represent a caudal extension of the CX sub-zone over the vermis of the vestibulocerebellum, in the rat.

In concordance with observations made in the cat (Kanda *et al.*, 1989) and rabbit (Gerrits, 1985), CFs from the MAOr to the lateralmost uvula have also been described in the rat (Eisenman, 1984). These data would favour the existence of the C2 sub-zone. However, such olivocerebellar projections have not been confirmed by Bernard (1987) to the lateral edge of lobule IX, and corticonuclear projections from this strip of cortex have, as yet, not been investigated. No evidence of an extension of the C2 sub-zone to lobule X has been obtained.

Our observations (Fig. 7A) show a caudal extension of the C2 sub-zone through the ventral paraflocculus (CF afferents from the MAOr and PC efferents to the lateral NIP), in agreement with previous data (Armstrong and Schild, 1978b; Blanks *et al.*, 1983). To date, no C2-like connections have been found in relation to the flocculus.

In the vestibulocerebellum of the rat, cortical regions having CF afferent and nuclear efferent connections typically matching those of the C1 and C3 sub-zones have not been observed.

In conclusion, in the rat, the C zone is made up of four sub-zones, C1, CX, C2 and C3. Sub-zone C2 extends from lobule II to the ventral paraflocculus. The C1 and C3 sub-zones are interrupted through lobules VI and VII. The CX sub-zone is made of two compartments, one in lobule V and one in lobules IX–X. The rostrocaudal outlines of zone C in the anterior and posterior lobes are by no means rectilinear (Fig. 9). At the level of lobules VIb and c, and VIIa, where the lateral expansion of zone A is maximal (Buisseret-Delmas, 1988a), zone C undergoes (i) an abrupt lateral flexure around zone A, and (ii) a marked decrease of its mediolateral thickness. In cases of encroachment of the C zone through these sub-lobules, sub-zone C2 was directly apposed to zone A medially and to sub-zone D1 laterally.

3.5. THE D ZONE OF THE CEREBELLAR CORTEX

The D zone has been defined (Voogd, 1964, 1969) as the cortical region whose PCs project to the NL. Zone D receives its climbing fibre afferents from the principal olive (PO). This cortical zone, which extends from lobule IV to lobule IX (Voogd and Bigaré, 1980), is classically sub-divided into two sub-zones: D1 medially and D2 laterally.

In the rat, all our cases showing olivary projections from the PO also disclosed corticonuclear projections within the NL and/or the dlh. On the basis of these olivary and nuclear connections, we have distinguished three sub-zone within the D zone of the rat: from medial to lateral these were called sub-zones D0, D1 and D2 (Buisseret-Delmas and Angaut, 1989b).

3.5.1. *The D zone in the anterior and posterior lobes*

3.5.1.1. *The D0 sub-zone*

The D0 sub-zone receives it olivary afferents from the medial half of the PO ventral lamella, and sends off its PC axons onto the dlh (Buisseret-Delmas and Angaut, 1989a, b). This sub-zone consists of a sagittal band of cortex lateral to the C3 sub-zone and medial to the D1 sub-zone in the anterior and the posterior lobe (Fig. 8). However, the D0 sub-zone is not continuous rostrocaudally; it is interrupted at the level of the crus I, where sub-zones C2 (CF afferents from the MAOr and PC efferents to the NI) and D1 (CF afferents from the PO and PC efferents to the NL) are contiguous (Fig. 6B). This discontinuity, as those observed in the C1 and C3 sub-zones, lines the region where the lateral extension of the A zone is maximal. Thus, the D0 sub-zone consists of two segments, one rostral through the anterior lobe and lobule VIa and one caudal through lobule VII. A comparison between cases of injections diversely placed rostrocaudally suggests that a rostrocaudal arrangement of either olivary or cerebellar nuclear connections of the D0 sub-zone is unlikely.

3.5.1.2. *The D1 sub-zone*

In agreement with observations made in the cat (Brodal and Kawamura, 1980), this sagittal band of cortex projects onto the main, magnocellular, part of the NL in the rat. It receives its olivary afferents from the dorsal lamella of the PO (Fig. 9). We found no clear cut rostrocaudal organization of either the olivary or the nuclear connections of the D1 sub-zone. Rostrocaudally, sub-zone D1 extends from lobule III to lobule VIII as a continuous band of cortex (Buisseret-Delmas and Angaut, 1989b). It abuts D0 through the anterior lobe. Through the posterior lobe its medial neighbour, sub-zone D0, is, as noted in the previous paragraph, discontinued at the level of crus I, where D1 is directly apposed to C2.

3.5.1.3. *The D2 sub-zone*

In the cat, the olivary afferents to the D2 sub-zone come from the PO ventral lamella (Brodal and Kawamura, 1980). According to the same authors, the D2 sub-zone projects onto the *subnucleus lateralis parvocellularis* (slp) of Flood and Jansen (1961).

In the rat, our results show that the olivary origin of the CF afferents to the D2 cortex is restricted to the lateral half of the PO ventral lamella; the cortical efferents terminate in the ventral, small-celled, region of the NL, which corresponds in the rat (Korneliussen, 1968) to the slp of Flood and Jansen (1961). There does not seem to exist a clear rostrocaudal arrangement of either olivary or nuclear connections of the D2 sub-zone. Such connections have been observed following the involvement of the lateral aspect of lobules III to VIII, and of the dorsal paraflocculus (Fig. 7A), in agreement with Armstrong and Schild (1978b). In addition, the D2 sub-zone may also extend onto the lateral part of the lobule IX (Bernard, 1987). As schematically reported on Fig. 9, D2 appears as a strip of cortex lateral to D1 through lobules III–VIII, and lateral to C2 in the dorsal paraflocculus.

3.5.2. *The D zone in the vestibulocerebellum*

In the cat, various regions of the PO have been found to project to the hemispheral part of the vestibulocerebellum: lateral flexure, central regions of the dorsal lamella and/or the ventral lamella (Walberg *et al.*, 1979; Kawamura and Hashikawa, 1979; Balaban, 1984). The efferents from the paraflocculus seem to distribute selectively onto the

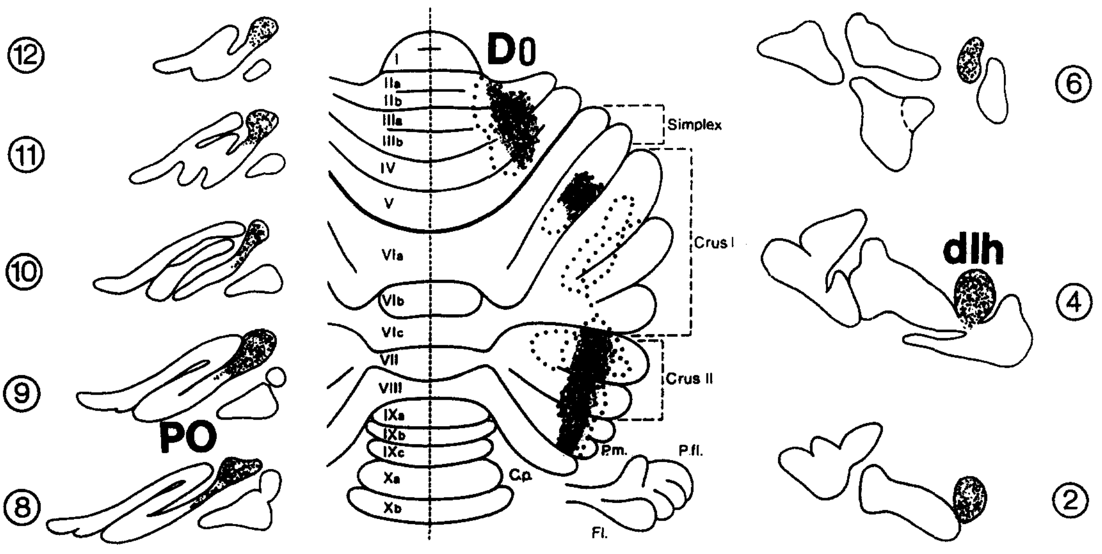

FIG. 8. Topographical arrangement of the olivocortical and corticonuclear connections of the D0 sub-zone. Same mode of representation as for Fig. 3. Notice the absence of D0-like connections in relation to crus I.

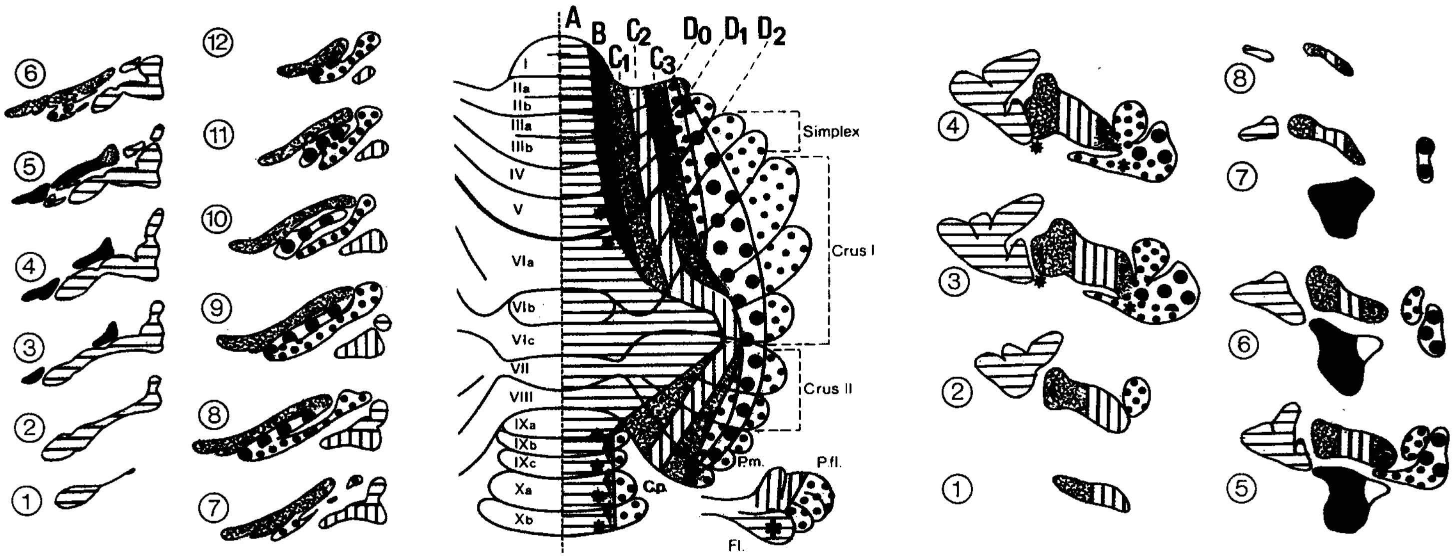

FIG. 9. Topographical arrangement of the olivo-corticonuclear connections of the cerebellum in the albino rat. Stars, arrow heads and asterisks correspond to the three zones detailed in Table 1.

lateral aspect of the NL (Angaut and Brodal, 1967; Blanks, 1988), and not to the vestibular complex (see literature in Blanks *et al.*, 1983 and Langer, 1985). The cortical efferents from the flocculus (Angaut and Brodal, 1967; Sato *et al.*, 1982a,b; Sato and Kawasaki, 1984) reach regions in both cerebellar and vestibular nuclei; whereas some were traced to the slp, the bulk of the efferents distribute over the NVS, NVM and NVI and group y of Brodal and Pompeiano (1957).

In the rat, our results show that the D2 sub-zone extends over a lateral zone of the ventral paraflocculus (Fig. 7B), as previously suggested by observations of Armstrong and Schild (1978b) and of Blanks *et al.* (1983). Furthermore, it would also extend, more medially, over the lateral aspect of the ventral uvula and the nodulus (Bernard, 1987).

It is worthy of note that D2-like corticonuclear projections have also been found in the flocculus (Bernard, 1987). However, as mentioned above, the cortical strip concerned receives its CF afferents from the dc (i.e. the "vertical lamella of the MAO"), and not from the PO ventral lamella. Thus, this floccular strip of cortex is "atypical" in its connections. If its corticonuclear efferents correspond to those of sub-zone D2, its CF afferents resemble those of zone A (Table 1).

In conclusion, in the rat the D zone is made of three sub-zones, D0, D1 and D2. Contrary to the lateral D1 and D2 sub-zones, the D0 sub-zone is rostrocaudally discontinued at the level of the crus I. The D0 and D1 sub-zones are present within the anterior and posterior lobes, through lobules III–VIII. The D2 sub-zone, on the other hand, extends caudally over lobules IX and X, as two separate strips of cortex, one vermal (over lobules IXa, b, c, and lobule X), and one hemispheral (over the dorsal and the ventral paraflocculus).

4. SYNTHESIS. FUNCTIONAL CONSIDERATIONS

The olivocerebellar pathway is, in the rat, topographically organized in strict relation to the sagittal organization of its target, the cerebellar cortex. The compartmentation of the inferior olive of the rat, as we deduce it from our analysis of the olivocerebellar projections, closely follows the outlining of the sub-nuclei due to Azizi and Woodward (1987). This intraolivary outlining has its counterpart at the level of the target of the cerebellocortical efferent, the cerebellar nuclei. As a consequence, the cortical sagittal sub-divisions appear, on the basis of their CF afferent and nuclear efferent connections, as functional entities segregated from one another. Interestingly, the loops generated by the projections from the cerebellar nuclei onto not only the overlying cortex but also distant cortical sub-zones (Buisseret-Delmas and Angaut, 1987, 1989a) might exert a regulatory effect to this interzonal segregation. Functionally, this coherent topographical arrangement of the cerebellar cortex draws its significance from the targets of the cerebellar nuclear outputs, essentially the motor centres they control.

4.1. THE A ZONE

As shown in "higher" species, the CF projection to the A zone arises in the rat from the caudal half of the MAO, i.e. from the "horizontal" and the "vertical lamella of the MAO" of Azizi and Woodward (1987). The A zone discloses in the rat a conspicuous lateral swelling onto the "hemisphere" at the level of lobules VI and VII. This swelling seems to be a peculiarity of the rat cerebellum. This point has been considered elsewhere (Buisseret-Delmas, 1988a).

The projection of the caudal MAO onto the A zone appears to be highly organized. We have observed a right-angle rostrocaudal arrangement between the location of the neurones within the caudal MAO and the distribution of their projection over the A zone; the more caudal the cells within the MAO the more medial their cortical projection, the more rostral the cells in the MAO the more lateral their projection. Along the mediolateral direction, on the other hand, olivovermal projections seem to be more complexly arranged; cells of the—laterally situated—"horizontal lamella" project onto the anterior lobe, but also onto lobules VIII–IXa of the posterior lobe. Cells of the—medially situated—"vertical lamella" project onto the posterior lobe as well as the vestibulocerebellum. The twinned projections from the "horizontal lamella of the MAO" may correspond to a functional coupling between zones of the anterior lobe and lobules VIII–IXa: although not proven, the collateral nature of these twinned projections is likely, by analogy with observations made in the cat (Brodal *et al.*, 1980; Rosina and Provini, 1983).

All the way from lobules I–X, the A zone projects onto the NM (Fig. 9). In the *rostrocaudal direction*, a clear distinction has been made between a rostral part and a caudal part of the NM on the basis of their respective corticonuclear connections. The rostral NM stands as a major output of the "spinocerebellum" (i.e. mainly the anterior lobe), whereas the caudal NM is one of the main outputs of the "teleceptive" cerebellum (i.e. essentially lobule VI) and, to some degree, of the medial vestibulocerebellum (Bernard, 1987). In the *mediolateral direction*, on the other hand, only the medial part of the A zone is, throughout the *corpus cerebelli* and lobule X, the source of a projection onto the NMm, whereas the lateral parts of the A zone of the anterior and posterior lobes project onto the NMvl and the dlp, respectively.

Functionally, the efferent projections of the NM have been best documented in the cat; the rostral NM essentially projects to the ipsilateral medulla, whereas the caudal NM mainly projects to the contralateral medulla (Flood and Jansen, 1966) but also, to a lesser degree, to higher brain levels (Angaut and Bowsher, 1970). The bulk of the fastigiomedullary projections control the NVL and the reticular formation (Walberg *et al.*, 1962a, b). From the available data, fastigiomedullary connections do not significantly differ in the rat and in the cat. These pathways are the substratum for the role of the A zone on stance and equilibrium. With regard to the projections to higher brain levels, the caudal NM of the rat gives rise to a crossed fastigiothalamic projection (Angaut *et al.*, 1985b). Individual efferents from the three sub-divisions of the NM have not been thoroughly scrutinized. However, the dlp, which would mainly project to the brain stem reticular formation (Rubertone *et al.*, 1990), also sends off fibres to the superior colliculus and thalamus (Bentivoglio and Kuypers, 1982). Through the latter pathway, "teleceptive" regions of the A zone will influence the cortical motor control of the axial and/or proximal musculature.

4.2. The X Zone and CX Sub-zone

These two topographically distinct strips of cerebellar cortex are remarkable in having a strictly colocalized (and partly collateral: Apps *et al.*, 1991) origin of CF afferents, and contiguous, if not largely overlapping, nuclear efferent targets. Furthermore, it is generally agreed that: (i) both cortical strips receive somaesthetic influences from forelimb territories (see Armstrong, 1990), and (ii) their source of CF afferents is narrowly connected with the mesencephalic visual centres as well as the vestibular nuclear complex (Maekawa and Takeda, 1979; Takeda and Maekawa, 1980; Saint-Cyr and Courville, 1982; Swenson and Castro, 1983; Kyuhou and Matsuzaki, 1991a,b). The latter data suggest important connections of zone X and sub-zone CX with oculomotor mechanisms. For these reasons, the two bands are considered here under the same heading.

In the rat (Table 1), the X zone is apparently fractured into a rostral component, in the anterior lobe and lobule VI, and a caudal component, in the vermal lobules of the vestibulocerebellum. The existence of a continuity between these two components through the posterior lobe is not excluded, but is unlikely according to the current experimental data. The nuclear target of the X zone, interposed ventrally between the NM and the NI, is ill-defined cytoarchitecturally in the rat.

The CX sub-zone also discloses a rostral component over lobule V of the anterior lobe, and a caudal component within the vermal lobules of the vestibulocerebellum (Table 1). The source of CF afferents to CX lays in the "vertical lamella of the MAO". The corticonuclear projections from CX and those from C1 reach regions in the medial-most NIP that can hardly be distinguished from one another. Thus, the CX sub-zone appears as a composite strip, with A-like CF afferents and C1-like nuclear efferents.

Functionally, the output from the NM-NI junctional region remains to be made precise. Consequently, the role of the X zone is still conjectural. The output from the medial NIP affects the medial part of the red nucleus (Angaut, 1970, in the cat; Daniel *et al.*, 1987, in the rat), and strands of neurones mediodorsally adjacent to the red nucleus (Angaut, 1970, in the cat; unpublished observations in the rat). Through its rubral connection, the CX sub-zone is involved in cervical motor activity; through its other mesencephalic connections—essentially with accessory oculomotor nuclei—the CX sub-zone would be related to the control of oculomotor mechanisms. The extent to which the former and the latter efferent connections concern the anterior lobe compartment and the vestibulocerebellar compartment, respectively, of CX is not clearly defined yet.

4.3. The B Zone

The band of cortex that receives its CFs from the dorsal DAO and projects onto the NVL extends, in the rat (Fig. 9), over the anterior lobe and lobule VI (Buisseret-Delmas, 1988a). Corticonuclear projections onto the NVL span out throughout the dorsoventral extent of the nucleus. This corticovestibular projection is topographically arranged, only fibres from lobule VI reach the ventral part of the NVL.

As in the cat (Pompeiano and Brodal, 1957a), the ventral part of the NVL of the rat (Leong *et al.*, 1984) is the source of vestibulospinal projections to the cervical cord, whereas the vestibulolumbar projections arise from the dorsal part of the NVL. Spinal influences to lobule VI would, in the rat as in other mammals, be conveyed through both (i) CF afferents relaying within the DAO (see literature in Molinari, 1984) and (ii) mossy afferents, selectively coming from cervical levels (Matsushita and Ikeda, 1987; Matsushita, 1991). Functionally, this indicates a highly consistent organization of the cerebellar control, through the B zone, of the activity of the lateral vestibulospinal pathway upon spinal motoneurones.

4.4. The C Zone

Three cortical strips, corresponding to the classical C1, C2 and C3 sub-zones, are observed in the cerebellum of the rat, besides a minute CX sub-zone (Fig. 9). Sub-zones C1 and C3 receive their CF afferents from the "ventral fold of the DAO", whereas those to C2 come from the "rostral lamella of the MAO"; each of the three sub-zones projects onto specific regions of the NI. Some features of the C zone in the rat are at variance with those described in other species. These features concern the cortical outlines of the three sub-zones (i), and the nuclear targets of their respective PC axons (ii): (a) rostrocaudally, the C2 sub-zone extends throughout the *corpus cerebelli*, whereas both C1 and C3 are interrupted at the level of crus I, i.e. where the A zone expands laterally. This fractured character of C1 and C3 might be a specific feature of the rodents' cerebellum; (b) the C3 sub-zone appears to send corticonuclear projections selectively onto the NIA. On the contrary, C1 and C2 project onto both NIA and NIP. Therefore, on the basis of their cortical connections, three sub-regions are delimited mediolaterally within the NIA, and only two within the NIP.

Functionally, the NI is an essential source of cerebellar control over the rubrospinal pathway (Courville, 1966, in the cat; Daniel *et al.*, 1987, in the rat). In the rat, interpositorubral fibres arise throughout the whole extent of the NIA, and selectively from the medial half of the NIP. The interpositorubral contingent from the NIA will convey influences from C1, C2 and C3 onto rubrospinal projection cells, whereas that from the NIP will convey influences from C1 only. It should be kept in mind that the NIA projects heavily all over the red nucleus, whereas the NIP projects in a restricted way onto the medial aspect of the red nucleus (Angaut, 1970, in the cat; Daniel *et al.*, 1987, in the rat) and the adjacent medial accessory oculomotor nuclei (Angaut, 1970 in the cat; unpublished observations in the rat). As a consequence to this organization, the rubrospinal actions upon spinal motoneurones will be controlled from the whole C zone, whereas neurones involved in specific motor activities, like ocular regulatory mechanisms, will be selectively controlled from C1 (and possibly the CX compartment of the vestibulocerebellum: see Section 4.2).

Both the NIA and NIP also contribute contingents to the cerebello-thalamocortical pathway (Angaut *et al.*, 1985b; Cicirata *et al.*, 1986). The influences conveyed through these contingents could derive from all three sub-zones of the C zone. They would mainly concern those regions of the motor cortex responsible for pyramidal motricity of head, trunk and forelimb. The specific case of the C2 compartment of the vestibulocerebellum is considered in Section 4.6.

4.5. THE D ZONE

At variance with the classical sub-division of the D zone into two sub-zones (see Brodal and Kawamura, 1980), we can distinguish three sub-zones within the D zone in the rat (Fig. 9), on the basis of their corticonuclear interrelations (Buisseret-Delmas and Angaut, 1989a, b). Each of these sub-zones selectively projects onto a cytoarchitecturally individualized sub-division of the NL. The lateral two sub-zones, which respectively project onto the magnocellular part of the NL and onto the slp, correspond to D1 and D2 of the cat, respectively. Medial to D1, we have identified (Buisseret-Delmas and Angaut, 1989b) a strip of cortex by its projection onto the dlh (the relation of dlh to the NL has been documented in Angaut and Cicirata, 1982, and Umetani *et al.*, 1986). This medial sub-zone has been named D0.

The presence of this third sub-zone has obvious implications on the arrangement of CF afferents to the D zone. The origin within the PO dorsal lamella of the olivary projections to sub-zone D1 conforms to that observed in cat (Brodal and Kawamura, 1980). At variance, the CFs to sub-zone D2 in the rat do not come, as in the cat, from the whole development of the PO ventral lamella but solely from its lateral half: the medial half of the PO ventral lamella gives rise to the CFs to sub-zone D0. These two halves of the PO ventral lamella of the rat are not distinguishable from one another cytoarchitecturally. However, they could be differentiated on ontogenetic grounds (Bourrat and Sotelo, 1991).

Functionally, the D zone, which corresponds to the neocerebellum, is most important in the control of "cortical motricity". The three sub-zones distinguished in the rat participate to this function. Each of them would be involved in the control of specific types of motor behaviours (Angaut and Cicirata, 1990; Cicirata *et al.*, 1992). As noted above, the lateral two sub-zones (i.e. D1 and D2) are analogous to the classical two sub-divisions of the cerebellar hemisphere described in other species. In the following they are individually considered briefly. On the contrary, the medially located sub-zone D0, of which no analogy has so far been described in "higher" mammals, deserves special emphasis.

—The nuclear output of the D1 sub-zone, the magnocellular NL, gives off a large component to the ascending *brachium conjuctivum*. This component, which primarily ends within the ventrolateral nucleus of the thalamus, also projects onto the parvocellular red nucleus. These two target structures are involved in limb motor activity: (i) the dentato-thalamocortical projections of D1 affect large regions of the cerebral motor cortex (Angaut *et al.*, 1985b; Cicirata *et al.*, 1986), which command movements of the limbs (Cicirata *et al.*, 1992), involved in ambulatory mechanisms; (ii) the dentatorubral projections, which would be collaterals of dentatothalamic fibres (Ramon y Cajal, 1911), essentially concern the parvocellular red nucleus (Caughell and Flumerfelt, 1977; Angaut *et al.*, 1987). In the rat, the parvocellular red nucleus is mainly, if not exclusively, the source of a contingent to the rubrospinal tract (Shieh *et al.*, 1983). Therefore, dentatorubral connections represent a further substrate to the influence of the D1 sub-zone upon limb—predominantly forelimb—motor behaviours.

—The nuclear output of the D2 sub-zone, the slp, gives off a moderately developed component to the ascending *brachium conjuctivum*. Through it, the D2 sub-zone is involved in the control of fine cortical motor mechanisms, namely individual digital movements of the forelimb (Cicirata *et al.*, 1986; Cicirata *et al.*, 1992). The region of the cerebral cortex involved (the "rostral motor area" of Neafsey and Sievert, 1982), which is responsible for movements of individual digits, is in close vicinity of a cortical zone responsible for eye movements (Cicirata, unpublished observations). Whether the slp also controls this pseudo-frontal eye field of the rat is being investigated.

—The nuclear output of the D0 sub-zone, the dlh, is the source of a component to the ascending *brachium conjunctivium*. This pathway would more specifically influence regions of the motor cortex involved in oral and peri-oral motricity (Cicirata *et al.*, 1992). On the other hand, the dlh is the nearly exclusive source of fibres running in the ipsilateral descending limb of the *brachium conjuctivum* (Woodson and Angaut, 1984; Bentivoglio and Molinari, 1986; Rubertone *et al.*, 1990), whose termination concerns medullary regions involved in buccopharyngeal motor mechanisms. Thus, the dlh appears to control muzzle motor behaviours (likely related to feeding mechanisms) through both a cortical loop and a very direct pathway.

The D0 sub-zone has not been described in "higher" mammalian forms. This—apparently older—strip of the neocerebellum could (i) persist, as a medial fringe of the neocerebellar cortex. Such an evolution of D0 might explain the fact that, in the cat, CFs arising from the ventral lamella of the PO have been found to project onto sub-zone D1 (Voogd and Bigaré, 1980); (ii) alternately, this strip of cerebellar cortex, and the related nuclear sub-region, might have undergone total regression in "higher" mammals. This would imply a reorganization of the ventral lamella of the PO, and particularly of its medial portion, along the phylogenetic scale.

4.6. THE VESTIBULOCEREBELLUM

The ventral uvula, the ventral paraflocculus and the flocculonodular lobe, known together as the vestibulocerebellum, receive their CF afferents from four neighbouring neuronal subgroups of the inferior olive: the dc, the vlo, the nucleus beta, and the dmcc (Groenewegen and Voogd, 1977; Kawamura and Hashikawa, 1979; Brodal and Kawamura, 1980).

These four neuronal sub-groups, all localized dorsally and medially to the MAO, have first been clearly described by Brodal (1940) in his pivotal analysis of the inferior olive in the cat and rabbit. Brodal delineated the nucleus beta, and identified the presence in the rabbit and cat of three other entities already observed in human: the dc and the vlo, first described by Kooy (1917), and the dmcc, first described by Mareschal (1934). Due to their respective topographical relation to the neighbouring olivary subnuclei, Brodal considered the dmcc and nucleus beta as connected to the MAO, and the vlo and dc as connected to the PO. This classification has since been followed by most scholars working on cats, rabbits and rats (see literature in Brodal, 1980). However, in the rat, Gwyn *et al.* (1976) related the nucleus beta, dc and vlo to the MAO, but included the dmcc to the ventral lamella of the PO. More recently, Azizi and Woodward (1987), on the basis of (i) the topographical vicinity of the four olivary sub-groups, in the mediodorsal IO, and (ii) the close similarity of their cerebellar target (i.e. the vestibulocerebellum) considered the four sub-groups as belonging to their "vertical lamella of the MAO". The "vertical lamella"—which corresponds to the subnucleus c of the caudal MAO in the nomenclature of Gwyn *et al.* (1976)—has been shown to receive the bulk of its inputs from visual centres (Maekawa and Takeda, 1979; Takeda and Maekawa,1980; Saint-Cyr and Courville, 1982; Swenson and Castro, 1983; Kyuhou and Matsuzaki, 1991a, b). From this unicity in afferent as well as efferent connections, Azizi and Woodward (1987) concluded that "the medial MAO is mostly, if not completely, involved in the visual and vestibular function". The statement is largely supported by our results.

Extensive regions of the vestibulocerebellum are known to directly project onto the vestibular nuclear complex, through which they influence oculomotor centres. Moreover, strips of the vestibulocerebellar cortex also project onto several cerebellar nuclear regions, particularly within the NM, NIP and slp. On the basis of these corticonuclear efferents, the related strips of cortex could be considered as belonging to the A zone, the C2 and the D2 sub-zones respectively. How directly these cortico-cerebellonuclear projections are related to visuoceptive and/or oculomotor centres may be questioned:

—The "oculomotor region" observed in the NM of several mammalian species receives its main afferent from the vermal lobules VI and VII, i.e. the "visual cerebellar cortex" (Noda *et al.*, 1990, in the monkey; Kawamura *et al.*, 1990, in the cat), but also from lobules IX and X (Blanks, 1988). In the rat, we have seen that the corticonuclear projections from lobules VI–VII and from lobules IX–X converge upon a ventral region of the NM (see Fig. 3). How far this region of the NM of the rat corresponds to the "oculomotor" fastigial region of "higher" mammals is still to be made precise.

—The lateral NIP, which is the target of the lateral—C2—strip of the ventral paraflocculus, sends off fibres to the ventromedial thalamic nucleus (Angaut *et al.*, 1985b), but would not participate to the interpositorubral pathway (Daniel *et al.*, 1987). Thus, the control exerted upon pyramidal motricity of the head and forelimb by the lateral NIP (Angaut *et al.*, 1985b; Cicirata *et al.*, 1986) would likely reflect vestibular, and possibly visual, influences.

—The slp, which is the target of the D2 strip of the ventral paraflocculus and the flocculus, is considered as controlling fine cortical motor behaviours (see Section 4.5). The participation of vestibulocerebellar compartments to this control of manipulatory activities would also implicate visual and vestibular influences upon the elaboration of "skilled" movements.

4.7. CONCLUDING REMARKS

The olivocerebellar system appears to be topographically arranged in such a way that segregated strips in the cerebellar cortex are strictly associated to neuronal aggregates in the IO and the cerebellar nuclei. How far a corresponding segregation is reflected along the cerebellar output is a question of crucial functional bearing. The cerebellar output is mainly directed to five targets: the IO, the pontine grey, the cerebral motor cortex (through a relay in the ventrolateral thalamus), the red nucleus and the vestibular complex.

—*The cerebello-olivary projection.* Its topographical arrangement (Angaut and Cicirata, 1982; Ruigrok and Voogd, 1990) is totally concordant to that of the longitudinal organization of the olivocerebellar system: each olivary sub-region is selectively under the influence of the cerebellar strip upon which it projects. As the cerebello-olivary pathway controls the rate of electrotonic coupling between the olivary neurones, its activity is determinant for the spatial patterning of the olivocerebellar discharge (Angaut and Sotelo, 1989). Therefore, the olivocerebello-olivary loop might be responsible for the functional patterning of the cerebellar output.

—*The cerebellopontine projection.* Together with the IO, the pontine grey represents a major "precerebellar" structure (Mihailoff *et al.*, 1981). The cerebellopontine projection mainly arises from the NL but also, to a lesser degree, from the NI and the NM (Cicirata *et al.*, 1982; Angaut *et al.*, 1985a). Current anatomical data do not permit to correlate the topographical arrangement of the cerebellopontine projection with the longitudinal organization of the olivocerebellar system.

—*The cerebello-thalamocortical projection.* In relation to the arrangement of the dentato-thalamocortical projection, three sub-divisions are distinguished within the NL. Each of these sub-divisions corresponds to one cytoarchitectonic subdivision of the NL (Angaut and Cicirata, 1990). As a consequence (see Section 4.5), the D0 sub-zone appears to be involved in oral motor mechanisms, the D1 sub-zone in the displacement in space of the body, or segments of the body, and D2 in distal, "skilled", motricity. Finally, each of the three sub-divisions defined within the PO of the rat on the basis of their respective olivocerebellar connections will be selectively related to one of the above pyramidal activities. Therefore, a topographical consistency exists between the functional organization of the dentato-thalamocortical pathway and the longitudinal organization of the olivocerebellar system. Whether a similar topographical consistency also exists within the pathways conveying influences from the NM and NI upon pyramidal motricity needs further investigations.

—*The cerebellorubral projection.* In the rat, the rubrospinal projection arises from both the magno and the parvocellular subdivision of the red nucleus (Shieh *et al.*, 1983), and is therefore influenced not only from the NI, but also from the NL. Thus, the cerebellorubral projection would convey influences from the C1, C2 and C3 sub-zones, but also the D0, D1 and D2 sub-zones. At variance with what we have seen for the dentato-thalamocortical pathway, a topographical consistency between the functional organization of the rubral motor output (Daniel *et al.*, 1987; Angaut *et al.*, 1987) and the longitudinal arrangement of the olivo-cerebellonuclear system has not been clearly demonstrated.

—*The cerebellovestibular projection.* As is well known, part of this cerebellar output arises from cells of the NM, and another part directly from PCs of the B zone and the vestibulocerebellum. Anatomical analyses have not yet established any clear cut topographical consistency between the functional organization of the vestibulospinal/vestibulo-oculomotor pathways and the longitudinal arrangement of the olivocerebellar system.

Hence, a strict topographical correspondence exists between specific regions of the IO, corresponding to the "lamellae" of Azizi and Woodward (1987), longitudinal sub-zones of the cerebellar cortex and specific regions in each of the cerebellar nuclei. More importantly, this topographical correspondence is reflected along one cerebellar output, the control pathway from the neocerebellum upon the pyramidal tract. As yet, no such correspondence has been demonstrated along any other major cerebellar output, although its existence is most possible. Thinner functional entities have been defined within the IO as "rostrocaudally oriented columns of olive cells" (Apps, 1990), which would supply "microzones" of the cortex (Oscarsson, 1980; Armstrong *et al.*, 1982). It remains to be shown whether a fine organization exists within the cerebellar nuclei, and consequently along the cerebellar output, in relation to the columnar organization of the IO.

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