Anat Embryol (1991) 184:255–268

Anatomy and Embryology

Evidence of an x zone in lobule V of the squirrel monkey (*Saimiri sciureus*) cerebellum: The distribution of corticonuclear fibers*

D.E. Haines[1] **and E. Dietrichs**[2]

[1] Department of Anatomy, The University of Mississippi Medical Center, 2500 North State Street, Jackson, MS 39216, USA
[2] Department of Anatomy, Institute of Basic Medical Sciences and Department of Neurology, National Hospital, University of Oslo, N-0027 Oslo 1, Norway

Accepted January 15, 1991

Summary. The distribution of corticonuclear fibers to medial-most parts of the posterior interposed nucleus (NIP) from lateral areas of the vermis was studied in the squirrel monkey (*Saimiri sciureus*), using a silver impregnation method. The origin and course of degenerated fibers were studied in serial sections. The distribution pattern of corticonuclear fibers from a series of small well localized lesions placed in the vermis and paravermal cortex of lobule V is compatible with the interpretation that an x zone is present in *Saimiri*. A comparison of the positions of lesions and the trajectory of fibers arising therein suggests that corticonuclear input to medial-most parts of the NIP originated from a narrow cortical area (about 0.5–0.7 mm wide) located between a cortical area projecting into the medial cerebellar nucleus (the A zone) and a laterally adjacent area (the B zone) which related to the lateral vestibular nucleus. This NIP-projecting cortical area, located about 1.7 mm to 2.5 mm off the midline in lobule V, is interpreted as the x zone in this primate; it extends from lobule IV into lobule VI in squirrel monkey. Corticonuclear fibers of zone x in this primate form a comparatively small terminal field in the medial-most portions of NIP. This contrasts with the distribution of corticonuclear fibers of the C_2 zone which consistently distribute to terminal fields that are shifted into more central areas of NIP. There appears to be no overlap of the corticonuclear terminal fields in the NIP for zone x versus the C_2 zone. These results were correlated with data from the literature on the distribution of olivocerebellar fibers to the x zone and the C_2 zone and the arrangement of cerebellar nucleoolivary projections into the inferior olive from the NIP. The x zone and the C_2 zone both receive input from the contralateral medial accessory olive (MAO), both zones project into the NIP, and the NIP projects into those regions of the MAO which, in turn, project to these respective cortical zones *and* into the NIP. This suggest that the x zone is a component of the NIP–MAO circuit. Furthermore the proposed function of the x zone would support the view that this sagittal strip may have a more extensive rostrocaudal distribution in primates as compared to the cat.

Key words: Cerebellar cortex – Corticonuclear projections – Cerebellar anterior lobe – Cerebellar zones

Introduction

It is well known that the basic unit of cerebellar cortical organization is one of sagittal zones. These rostro-caudally oriented strips are characterized and defined by the distribution patterns of their ipsilateral cerebellar corticonuclear fibers, and the receipt of olivocerebellar fibers from specific subdivisions of the contralateral inferior olivary complex (e.g., Voogd 1964, 1969, 1989; Haines 1976, 1984, 1989; Chan-Palay et al. 1977; Brodal and Walberg 1977a, b; Groenewegen and Voogd 1977; Haines and Rubertone 1977, 1979; Dietrichs and Walberg 1979, 1980; Groenewegen et al. 1979; Brodal 1980; Oscarsson 1980; Brodal and Kawamura 1980; Walberg 1980; Eisenman 1981; Dietrichs 1981a, b, 1983; Brodal and Brodal 1982; Haines et al. 1982; Beyerl et al. 1982; Trott and Armstrong 1987a, b, c; Trott 1989; and others).

The basic three-zone concept of cerebellar cortical organization (Hohman 1929; see especially Jansen and Brodal 1940, 1942) was further refined by Voogd (1964, 1969), who hypothesized that the vermal cortex was composed of zones A and B, the intermediate cortex of zones C_1, C_2, and C_3, and the lateral cortex of zones D_1 and D_2. Subsequent studies (see above citations) have revealed that these zones have olivocerebellar and corticonuclear connections which are, in general, comparable across mammalian lines. On the other hand, recent studies have also shown that extremely precise representations of body regions are present in the cerebellar cortex (Joseph et al. 1978; Shambes et al. 1978; Robertson

* This paper is dedicated to Professor Fred Walberg on the occasion of his 70th birthday.

Offprint requests to: D.E. Haines

et al. 1982; Robertson 1984). The relationship between these mosaic patterns and the orientation of sagittal zones has not been fully analyzed.

An x zone, located between zones A and B and present primarily in lobule V, has only recently been identified. Our understanding of the connections and potential functions of this specific region of the cerebellar cortex is based, almost exclusively, on studies conducted only in cats. This strip of cortex is about 0.4–0.8 mm wide and receives short-latency input primarily from the ipsilateral forelimb (Ekerot and Larson 1979a, b, 1982; Oscarsson 1980; Campbell and Armstrong 1985; Trott and Armstrong 1987b; Bishop 1988; see also Oscarsson 1969; Oscarsson and Sjölund 1977a, b). Though they were once thought to originate from the dorsal accessory olive (DAO) (e.g., Oscarsson 1980; Ito 1984) there is now convincing evidence that olivocerebellar fibers to the x zone originate from the contralateral medial accessory olive (MAO) (e.g. Voogd 1983; Campbell and Armstrong 1985; Voogd et al. 1987a; Voogd and Hess 1989).

There is not only a paucity of information but also a disparity of opinion concerning the probable distribution of corticonuclear fibers from the x zone. Based on indirect evidence Oscarsson (1980) and Ito (1984) speculated that this zone projected into the anterior interposed nucleus (NIA). On the other hand Voogd (1983-cat) and Trott and Armstrong (1987b-cat) have offered evidence that corticonuclear fibers of the x zone project into the area of the medial nucleus (NM) – posterior interposed nucleus (NIP) interface. However, these authors did not ascribe these terminals to either nucleus with certainty. Haines et al. (1982-primate) reported that lesions in lateral parts of vermal cortex resulted in the simultaneous appearance of degenerated axons in the vestibular complex and in medial NIP. These authors suggested that this may support the view that corticonuclear input to this part of NIP may arise from an x zone. In contrast Yu et al. (1985-cat) in their study of corticonuclear fibers of lobule V did not find a separate projection zone between those cortical regions related to the NM (A zone) and the lateral vestibular nucleus versus those laterally adjacent areas which related to the NIA. Yu et al. (1985-cat) provide no evidence of an x zone and concluded that this zone probably projects into the NM and, therefore, would be part of their fastigial (A) zone.

With the single exception of the recent studies of Voogd et al. (1987a) and Voogd and Hess (1989) on olivocerebellar projections to x and C_2 zones in *Macaca*, a review of the literature reveals no direct evidence for an x zone in the primate cerebellum, and a marked difference of opinion concerning the likely target of corticonuclear fibers arising in this zone in the cat (NIA, NIP–NM interface, NM). To address these points the present study examines the distribution of cerebellar corticonuclear fibers from the vermis-intermediate cortex interface in lobule V of the squirrel monkey (*Saimiri sciureus*). The trajectories of fibers from this region of cortex are examined in serial section, evidence of an x zone projection to NIP offered, and these data correlated with the known patterns of olivocerebellar input to cerebellar cortical zones.

Materials and methods

Eighteen adult male or female squirrel monkeys (*Saimiri sciureus*) were used in this study. Animals were anesthetized with an intravenous injection of sodium pentobarbital (35 mg/ml) through a superficial vein on the posterior surface of the hindlimb until withdrawal reflexes were abolished and the corneal reflex was suppressed. No supplemental anesthesia was required during surgery. The animals were stabilized in a Kopf stereotaxic instrument and monitored during surgery.

Superficial aspects of lobules IV–VI were visualized by removing the overlying occipital lobe on one side and identifying the folia of these lobules through the translucent tentorium cerebelli. Sixteen animals received one lesion each, while two animals received two lesions each for a total of twenty. Small lesions were placed in individual folia from the midline to the lateral margin of lobule V ($n=15$), in medial areas of lobule IV ($n=3$), and in rostral lobule VI ($n=2$) by applying the heated tip of a metal teasing needle to specific spots on the cortex through the unopened overlying tentorium cerebelli. The space of the removed occipital lobe was carefully packed with gelfoam, the dura was closed using 8–0 suture, and muscle and skin sutured over the defect in the skull. Following survival times of 3–5 days the animals were anesthetized via the same intravenous route. A canula was inserted into the left ventricle and secured in the arch of the aorta by a suture just inside the aortic valve. The animals were perfused with 0.9% heparinized saline (about 400 ml) followed by 10% unbuffered formalin (about 1 l). The brainstems and cerebelli were removed intact and stored for several days in additional 10% formalin. Serial sections of the cerebellum and brainstem were made in horizontal and coronal planes at 40 μm; all sections were kept in order. Every other section was impregnated using a modification of the Fink and Heimer (1967-Procedure I) method and the intervening sections were stained with cresyl violet acetate for Nissl substance.

Interpretative comments. The criteria used to identify degenerated axons and their endings are well known (see Heimer 1970; Giolli and Karamanlidis 1978; de Olmos et al. 1981 for reviews). The terms "terminal degeneration" (or debris) or "preterminal degeneration" (or debris) are frequently used to describe the fine-diameter processes found in the neuropil of nuclei or adjacent to neurons. Since use of "terminal" implies an ability to visualize terminal boutons (a level of morphological detail *not* reached in the present study) we have used "preterminal" to designate those tortuous axonal processes found in the cerebellar nuclei; these are areas of potential synaptic contacts between Purkinje cell axons and cerebellar nuclear neurons. Larger diameter degenerated axons arranged in bundles in the white matter are fibers of passage. The extent of the lesion was determined not only by the extent of cortical damage, but also by the fact that degenerated axons were always found in the white matter beneath the lesion, and were followed in serial sections to their target nuclei. It is acknowledged that cerebellar afferent fibers (such as pontocerebellar, olivocerebellar, and others) end in the cortex, and that such terminals would be involved in the lesion. If the degeneration seen in the cerebellar white matter and nuclei were the result of injury to these afferent fibers, one would also see degeneration in the brachium pontis and restiform body; this was *never* the case. Consequently, the degenerated fibers seen in the present study represent the distribution of the axons of Purkinje cells damaged in the cortical lesion.

Results

Of the twenty lesions placed in the cerebellar cortex of lobules IV–VI in the present study, the ten identified by case numbers in Fig. 1 are particularly relevant to the question at hand. These lesions, as exemplified by

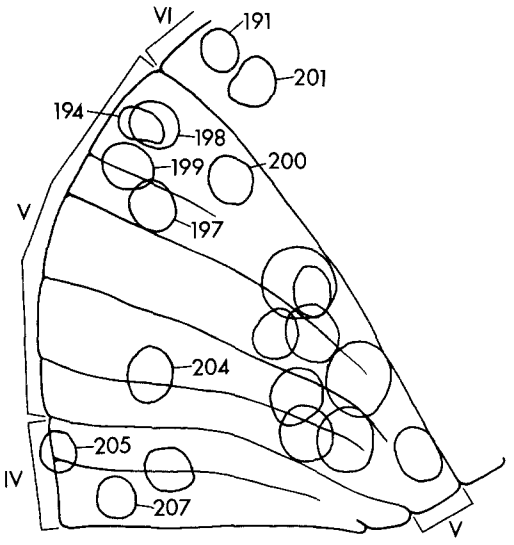

Fig. 1. Drawing to show the relative positions of lesions in lobule V and adjacent areas of lobules IV and VI. Those ten lesions numbered (191, 201, etc.) are specifically relevant to the present study

Abbreviations for all figures: A, zone A; *C*, caudal aspect of medial accessory olive; C_1, zone C_1; C_2, zone C_2; *JRB*, juxtarestiform body; *LVN*, lateral vestibular nucleus; *MVN*, medial vestibular nucleus; *NIA*, anterior interposed nucleus; *mNIA*, medial area of NIA; *NIP*, posterior interposed nucleus; *cNIP*, central area of NIP; *mNIP*, medial area of NIP; *NL*, lateral cerebellar nucleus; *NM*, medial cerebellar nucleus; *RB*, restiform body; *SCP*, superior cerebellar peduncle; *SpVN*, spinal (inferior) vestibular nucleus; *SVN*, superior vestibular nucleus; *x*, zone x

the distribution of their corticonuclear fibers, were located in vermis and intermediate cortices of lobules IV–VI and involved zones A–C_2. Two design factors in this study facilitated the identification of the trajectory of degenerated Purkinje cell axons. First, the lesions were comparatively small and clearly circumscribed; degenerated axons issued *only* from the spot of cortical damage. Second, the fact that every other section was impregnated for degenerated axons allowed a precise delineation of these corticofugal axons as they traversed the white matter and entered their respective nuclei.

Lesions in the A to B zones

In experiments BS198, BS199 (lobule V) and BS191 (rostral lobule VI) small lesions were placed just lateral to the midline (Fig. 1). In all three cases a small area of undamaged cortex (about 300–400 μ wide) was present between the midline and the medial edge of the lesion. The results in all three of these cases were fundamentally the same, therefore case BS198 is described as representative of these experiments.

From the lesion site degenerated Purkinje cell axons course through the white matter in an orderly fashion. The more medially located fibers enter lateral and ventrolateral regions of the NM at *rostral levels*, where they ramify around the cells in this area (Figs. 2A–D, 3A, B). Medial regions of the NM were devoid of axonal debris, and no degeneration was seen in any of the contralateral cerebellar nuclei. In addition to preterminal axonal debris in rostral NM, some larger diameter degenerated fibers of passage continued through ventrolateral NM to join in the formation of the juxtarestiform body (JRB) (Fig. 2B, C). Those degenerated axons that descend through the white matter lateral to the fascicles entering the NM collect to form the JRB between the NM and NIA. These fibers distribute to dorsal and dorsolateral regions of the lateral vestibular nucleus (LVN) as cerebellar corticovestibular axons (Fig. 2B–E). The fact that the medially located fibers enter the NM indicate that the medial portions of the cortical lesion are in the A zone (see Discussion). In like manner, the lateral parts of the cortical lesion invade the B zone, as indicated by the passage of axons from this area into the JRB and ultimately into the LVN. The complete lack of axonal debris in medial NIA (Fig. 3C) shows that this lesion did not involve the medial portions (zone C_1) of the intermediate cortex.

In addition to those larger bundles of degenerated axons which entered the NM and LVN, there were small fasicles of degenerated fibers which turned caudally (Fig. 2C, D) and *were traced in serial section* into the medial NIP. Clusters of preterminal debris were found in the most medial portions of the NIP, while the lateral and ventrolateral areas of the immediately adjacent NM *at caudal levels* contain no significant amounts of degenerated axons (Figs. 2E, F, 3D, E). The exceedingly sparse amounts of axonal debris occasionally seen in ventrolateral NM (e.g., Fig. 2E) are interpreted as preterminal fibers en route to medial NIP. The *trajectory* of these small fascicles is a point of particular emphasis. They descended from the lesion as inconspicuous components of the entire bundle of degenerated corticofugal fibers. However, at the lateral and ventrolateral border of the NM they turned abruptly in a caudal direction from about the middle third of those fibers which were collecting to form the JRB, and coursed directly into the medial NIP (Figs. 2C, D, 4). Since cerebellar corticofugal fibers descend from the cortex in an orderly manner, the fact that these small fasicles coursed into the medial NIP from about the middle third of the JRB indicates that they originated from central portions of the cortical lesion rather than its medial (to NM) or lateral (to LVN) aspects (Fig. 4).

Comparable results to these described above for BS198 (Figs. 2, 3) were also seen in experiments BS191 with a lesion in rostral lobule VI, and in BS199 with a lesion in lobule V (both not illustrated). While the present study does not deal with cerebellar corticonuclear projections in toto, it is appropriate to note that lesions located in more medial portions of the vermis (BS194, BS205; Fig. 1) resulted in axonal debris in only NM. No degenerated fibers were seen in medial NIP or in the LVN.

Lesions in x, B and C_1 zones

On the basis of their distance from the midline the lesions in experiments BS197 and BS201 (Fig. 1) were

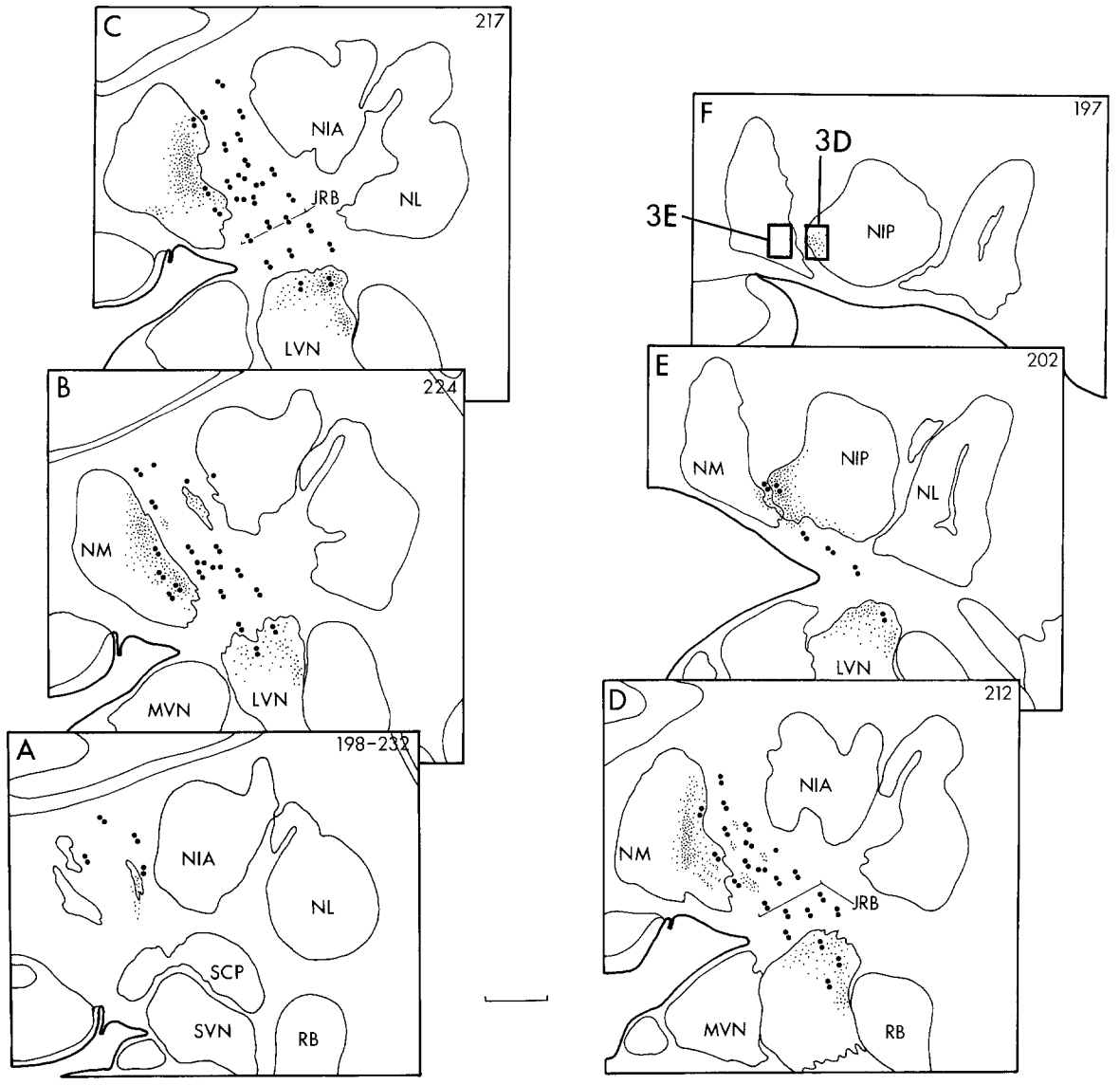

Fig. 2A–F. Tracings, in coronal section, of the cerebellar nuclei of *Saimiri sciureus* (case BS198) from rostral (**A**) to caudal (**F**) showing the distribution of degenerated fibers following a lesion in medial cortex of lobule V. *Small dots* represent the distribution of preterminal degeneration and *large dots* represent the trajectory of degenerated fibers of passage. The case number (198) is shown in **A** and the following numbers (e.g. 232, 224, etc.) are the section number (in serial order) from which each tracing was made. Preterminal axonal debris is present in lateral and rostral NM (**A–D**) and in LVN (**B–D**); the lack of degeneration in NIA indicates that the intermediate cortex is not involved. However, small fascicles of degenerated axons turn caudally (**C, D**) to enter and ramify in medial areas of the NIP (**E, F**). The *sparse* amounts of degeneration in ventrolateral NM (**E**) are fibers en route to medial NIP. The details in **F** are shown in Fig. 3. Scale bar 1.0 mm

placed so that their medial areas overlapped the same sagittal strip of cortex involved in the lateral parts of those lesions described above for BS198 and BS199. These areas of cortical damage were in lobule V (BS197) and in lobule VI (BS201). In both of these experiments the results were essentially the same, consequently case BS197 is described as representative.

Degenerated axons exit the lesion site and descend through the subcortical white matter toward dorsomedial and dorsal aspects of the NIA (Fig. 5A). Many degenerated fibers from the lateral portions of this bundle ramify in the medial-most portions of the NIA where they form a somewhat crescent-shaped terminal field (Fig. 5B–D). Degenerated fibers of passage from the medial portions of this bundle descend medial to those which enter the NIA, and course between the NM and NIA to form the JRB; these axons continue into the LVN, where they ramify in the neuropil and adjacent to cells of this nucleus (Figs. 5E–G, 6D). The distribution pattern of degenerated axons indicate that this cortical lesion involved the B zone (fibers to LVN) and the laterally adjacent C_1 zone (fibers to medial NIA).

In case BS197 (lobule V; and in BS201, lobule VI, see Fig. 1) a small cluster of axonal debris was found in the most medial regions of the NIP where it abuts against the ventrolateral portions of the NM (Figs. 5G–

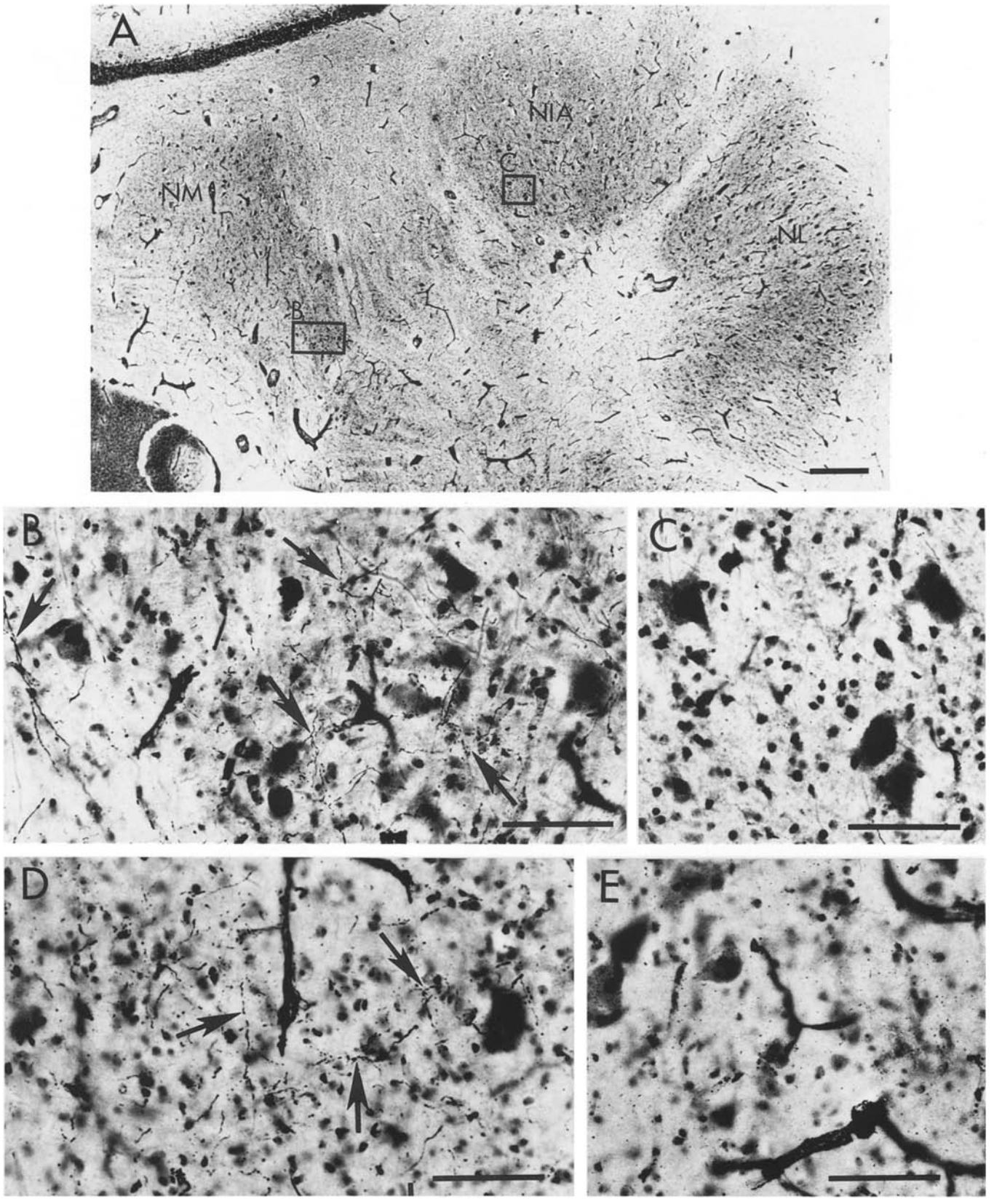

Fig. 3A–E. Low power (**A**) and high power (**B–E**) photomicrographs showing the distribution of degenerated axons in the cerebellar nuclei (case BS198). **A** is a photograph of section 224 from Fig. 1. Axonal debris (examples shown at *arrows*) is present in ventrolateral NM (**B** – detail from **A**) at *rostral levels* but lacking in medial NIA (**C** – detail from **A**). The medial NIP (**D**) contains a concentrated cluster of degenerated axons while the adjacent ventrolateral areas of NM (**E**) at *caudal levels* are devoid of degeneration; **D** and **E** are details from section 197 (see Fig. 1F). Scale bar 1.0 mm for **A**; 50 μm for **B–E**

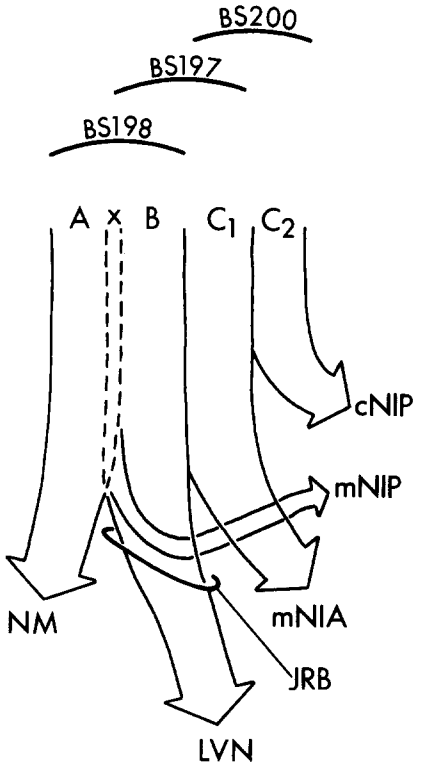

Fig. 4. Diagrammatic representation of the trajectory of fibers into the cerebellar nuclei and the lateral vestibular nucleus from representative lesions. Note that those fibers to medial NIP arise between those going to NM and LVN, and turn caudally out of those fibers which are collecting to form the JRB. See text for additional discussion

I, 6A, B). The adjacent lateral and ventrolateral portions of the NM contained no degenerated fibers (Fig. 6C). An examination of serial sections revealed that these degenerated axons to medial NIP originated from the medial fascicles located between NM and NIA that were collecting to form the JRB (Fig. 4). These small fascicles of caudally directed fibers did not constitute a noticeable separate bundle in the white matter between the lesion and the dorsal aspect of the cerebellar nuclei. However, as the degenerated axons between NM and NIA consolidated to form the JRB, small fascicles from the *medial aspect* of this larger bundle turned caudally to enter the medial NIP (Fig. 4). Based on the orderly arrangement of cerebellar corticofugal fibers and on their trajectory in these cases, it is apparent that those fibers to the medial NIP (x zone) originated from the most medial parts of the lesion, those to the medial NIA (C_1 zone) from its lateral aspect, and those to LVN (B zone) from the intervening cortical area (Fig. 4). It should be noted that the course of these medial NIP-directed fibers in case BS197 (lesion in B–C_1 zones) is closely comparable to the same bundle seen in case BS198 (A–B lesion; see Fig. 4). Essentially identical patterns of projections into LVN, medial NIP, and medial NIA were seen in experiment BS201. This lesion, while located in rostral lobule VI, was in the same sagittal plane as that in case BS197 (Fig. 1).

Lesions in C_1 and C_2 zones

A detailed description of corticonuclear fibers of the intermediate and lateral cortices is beyond the scope of the present study. However, it is appropriate to consider briefly the projection from the medial areas of the intermediate cortex, as these data relate directly to what is interpreted above as the terminal field in medial NIP for the presumed x zone.

In three experiments, BS200, BS204, and BS207 (Fig. 1), lesions were placed in medial areas of the intermediate cortex. Based on the distribution pattern of corticonuclear fibers these lesions were located in zones C_1 and C_2. Experiment BS200 (Fig. 7) is discussed as representative of these cases. A bundle of degenerated axons coursed from the lesion toward the interposed nuclei. Fibers in the medial parts of this bundle entered medial and rostral NIA where they terminate (Fig. 7A, B). Degenerated fibers in the lateral portions pass over the top of the NIA then drop down to enter the NIP; axonal debris was present in rostral and more central areas of this nucleus. No degeneration was seen in the NM or in the lateral cerebellar nucleus. This tendency for the C_2 zone to project into dorsal, rostral and/or more central areas of the NIP (Fig. 7A, B) is similar in its essential features to other reports detailing the corticonuclear projections from this area of cortex (e.g., Voogd 1964; Haines and Rubertone 1977, 1979; Dietrichs 1983; Trott and Armstrong 1987a; see Discussion).

It is important, at this point, to comment on the distribution of axonal debris in the NIP following lesions of the C_2 zone, versus what is interpreted here as an x zone projection to this nucleus. Corticonuclear fibers from the C_2 zone tend to occupy terminal fields, which are shifted laterally in the nucleus and are usually described as being more centrally, dorsally or rostrally located. In contrast, lesions in the lateral vermis resulted in terminal fields in the NIP which were characterized by two features. First, this area of axonal debris was small, relatively compact, and found in the medial-most portions of the NIP. Second, it occupied an area of the nucleus which was clearly separate from the C_2 terminal field; the latter is located more laterally in the NIP. In addition, the trajectory of fibers to the medial NIP as they course through the beginnings of the JRB, clearly indicate that they arise lateral to those fibers going to NM (the A zone) but medial to those fibers passing into the LVN (the B zone).

Discussion

The results of this study show that the most medial region of the NIP receives a corticonuclear projection from intermediate parts of the vermal cortex. A close examination of serial sections (every other section impregnated) through the cerebellum revealed that those fibers to the medial NIP arose lateral to the area which projected into the NM (zone A) but medial to the sagittal

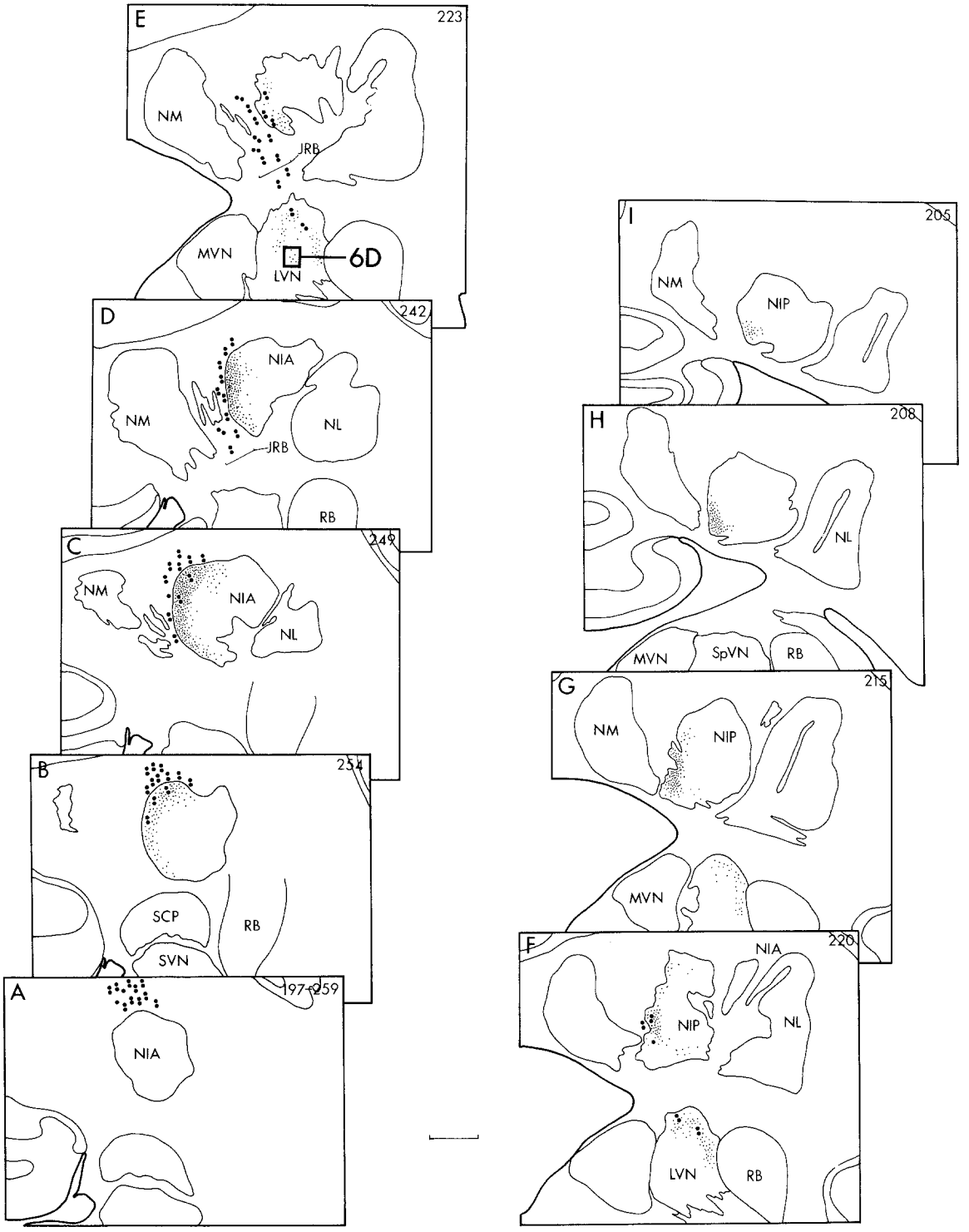

Fig. 5A–I. Tracings, in coronal section, of the cerebellar nuclei of *Saimiri sciureus* (case BS197) from rostral (**A**) to caudal (**I**) showing the distribution of degenerated axons in the cerebellar and vestibular nuclei. Axonal debris is present in medial NIA (**A–D**), in the LVN (**E, F**) and in medial NIP (**F–I**). Those degenerated fibers which enter NIP course through the medial portions of the JRB (see also Fig. 4). General points of presentation are as in Fig. 2. Scale bar 1.0 mm

strip which projected mainly into the LVN (zone B). This is interpreted as evidence for an x zone in lobule V of the squirrel monkey (*S. sciureus*) and suggests that this area projects into medial NIP. A comparison of cortical lesion sites in the present study suggests that the x zone in *Saimiri* is about 0.5–0.7 mm wide, and extends from about 1.7–2.5 mm off the midline of lobule V. This width and location are comparable to reports in cat (Ekerot and Larson 1979a, b; Campbell and Armstrong 1985; Trott and Armstrong 1987b).

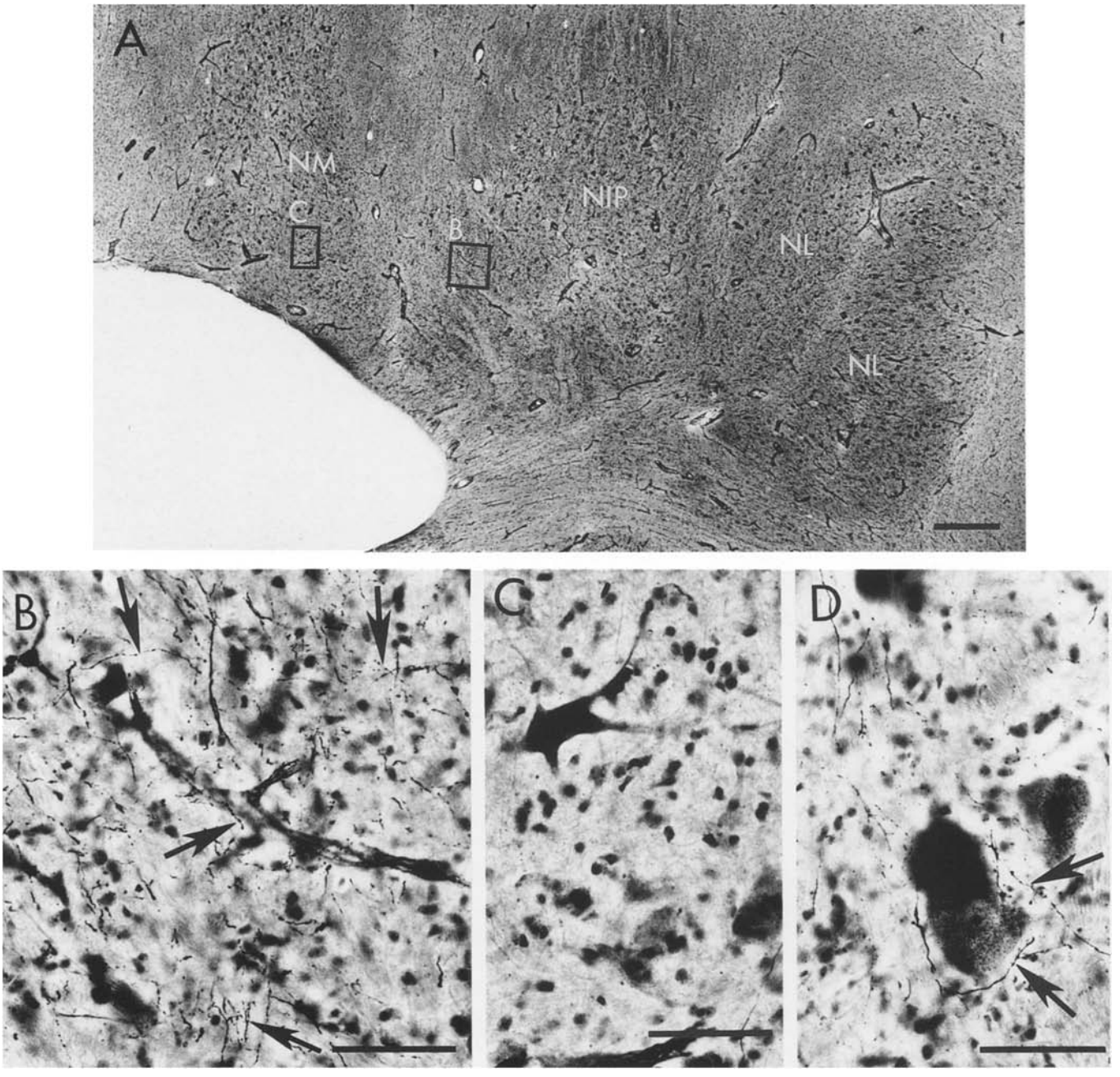

Fig. 6A–D. Photomicrographs showing the cerebellar nuclei (**A** – from section 215, Fig. 5), degenerated axons in medial NIP (**B** – detail from **A**), the lack of axonal debris in lateral and ventrolateral NM (**C** – detail from **A**), and the characteristic appearance of axonal debris in the LVN (**D** – detail from Fig. 5E). In **B** and **D** examples of degenerated axons are shown at *arrows*. Scale bar 1.0 mm for **A**; 50 μm for **B–D**

Corticonuclear fibers of the x zone

For two reasons, our knowledge of the organization of corticonuclear fibers of the x zone is quite limited. First, few studies have directly studied this connection and, second, the only animal to be investigated to date is the cat. Voogd et al. (1987b) have identified an x compartment in the *Macaca* cerebellum based on the patterns of acetylcholinesterase staining (see also Voogd et al. 1987a; Voogd and Hess 1989). Oscarsson (1980) and Ito (1984) speculated that the x zone projected into the NIA. This view was predicated on the prevailing opinion at the time that the dorsal accessory olive was the main source of climbing fibers to zones C_1 and C_3 *and to this general region* of the lateral vermis (Groenewegen and Voogd 1977; Groenewegen et al. 1979; Brodal and Kawamura 1980; Ekerot and Larson 1982; see also Brodal and Brodal 1982). The fact that zones C_1 and C_3 projected, via their corticonuclear fibers, into the NIA (Voogd 1964; van Rossum 1969; Haines 1976; Haines and Rubertone 1977, 1979; Voogd and Bigaré 1980; Haines et al. 1982; see also Dietrichs 1981a) gave

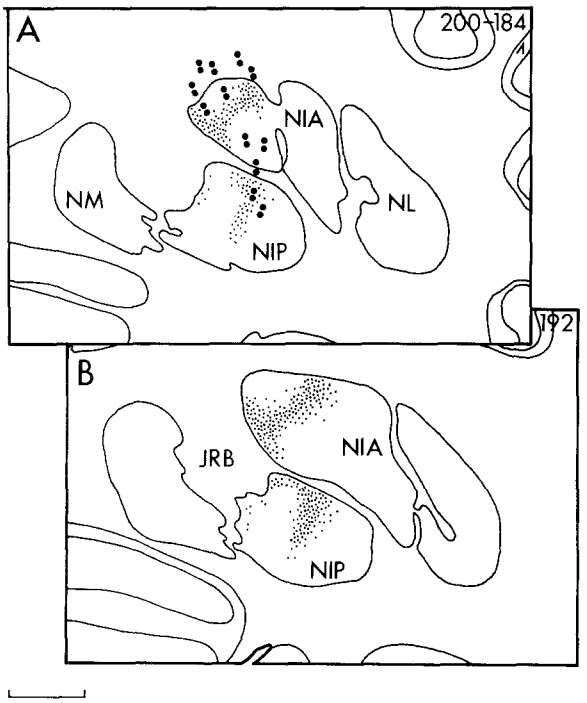

Fig. 7A, B. Tracings in horizontal section, of the cerebellar nuclei of *Saimiri sciureus* (case BS200) showing the distribution of degenerated fibers of passage and preterminal debris in the NIA and NIP. Note that degeneration in the NIP (from the C_2 zone) is concentrated in more central areas of this nucleus (compare with Figs. 2E, F and 5G–I). Scale bar 1.0 mm

some credence to this interpretation. In general it was assumed that since C_1 and C_3 received input from DAO and projected into NIA, then that small area in the lateral vermis which presumably received a DAO projection must also project into NIA.

Recent studies have provided evidence that the Purkinje cells of the x zone do not relate to the NIA. Following injections of horseradish peroxidase into the NM–NIP interface Voogd (1983) described labeled Purkinje cells in the x zone. He also noted that the Purkinje cell bodies (and axons) of the x and C_2 zones (and compartments) were smaller than those in the adjacent A and B or C_1 and C_3 zones. Trott and Armstrong (1987b, c) used ^{3}H-leucine injections into the electrophysiologically identified x zone (short latency input from the ipsilateral forelimb) and arrived at similar conclusions. These authors described an x zone projection into the junction of NM with the NIP, but noted that it was not possible to determine, with certainty, which of these two nuclei was the primary target. The present study confirms and extends these observations of Voogd (1983) and Trott and Armstrong (1987b, c). Although the present results corroborated the view that the x zone projects into the general area of the NM–NIP junction, it further suggests that these fibers in *Saimiri* terminate exclusively in medial NIP. What appear to be differences between cat (Voogd 1983; Trott and Armstrong 1987a, c) and primate (present study) may actually be a reflection of the morphology of the cerebellar nuclei. Flood and Jansen (1961) in their detailed study of the cat cerebellar nuclei noted that the NM and NIP fuse "...in a way which renders it impracticable in certain places to draw definite borders between the two nuclei". In contrast, the NM and NIP in many primates (e.g., Courville and Cooper 1970; Riche et al. 1971; Haines 1986; and others), while apposing each other, are more obviously separated into two distinct cell groups.

In contrast to the data of Voogd (1983) and Trott and Armstrong (1987b, c), which offered evidence of an x zone projection into the NM-NIP junction, other investigators have not seen a comparable pattern. Bishop et al. (1979) described longitudinal populations of labeled Purkinje cells in the intermediate cortex of the anterior lobe following injections of horseradish peroxidase into NIA and NIP which corresponded, in general, to zones C_1, C_2 and C_3. These authors did not report Purkinje cell labeling in a part of the lateral vermis that would correlate with the x zone, even in cases with HRP placement in more medial areas of NIP. However, in their autoradiography experiments, Bishop et al. (1979) reported anterogradely labeled axons coursing into "...the caudal pole of the NIP..." following injections in the "...medial three-fourths of lobule III...". Yu et al. (1985) antidromically drove Purkinje cells in the vermis and intermediate cortex following placement of electrodes in NM, NIA and NIP. These authors described a distinct medial area related to the NM (an A zone), an adjacent lateral area related to the NIA (probable C_1 zone), and an overlap in the lateral vermis of cells projecting to NM and LVN. In other words they did not see a "...spatially isolated..." B zone. Yu et al. (1985) concluded that corticonuclear connections of the x zone were a component of their fastigial zone (A zone) as there were data suggesting (Voogd 1983) that these fibers may end in the NM.

In their anterograde tracer studies in the cat Dietrichs and Walberg (1979; see also Dietrichs 1981a) described two distinct corticonuclear termination areas in between the NM (A zone) and lateral NIP (C_2 zone); one area was located medially in NIP and the other was found in medial NIA. These authors, who did not comment on a possible x zone, suggested that the former terminal area (to medial NIP) belonged to zone C_1. However, when the now substantial evidence for a C_1 termination in medial NIA (see above) is taken into account, it is reasonable to assume that the terminal labeling in medial NIP as reported by Dietrichs and Walberg (1979) and Dietrichs (1981a) actually represented corticonuclear fibers of the x zone.

Extent of the x zone

There is general agreement that the x zone is a narrow sagittal strip of cortex in lateral areas of the vermis of lobule V (Ekerot and Larson 1979a, b; Oscarsson 1980; Andersson and Eriksson 1981; Trott and Armstrong 1987b, c) and that it may extend into rostral parts of lobule VI and the caudal area of lobule IV (Voogd 1983; Voogd et al. 1987a, b; see also Bishop 1988). The present study offers evidence of a projection into medial NIP

from intermediate to lateral areas of vermis lobules IV–VI in a primate. Based on the apparent origin of these fibers from cortical areas located between those projecting to NM versus those related to LVN, their trajectory through the white matter, and their termination in the most-medial NIP, these fibers are interpreted as the corticonuclear fibers of the x zone. In this respect these data (on a primate) are in general agreement with studies on the cat as regards the location of zone x in lobule V and its probable extent into lobules IV and VI. Assuming that this zone may relate more to medial NIP than to NM (see above) it is appropriate to note that corticonuclear projections into medial NIP have been reported from vermis lobule IV (Eager 1963-cat; Goodman et al. 1963-rat; Armstrong and Schild 1978a-rat) and lobules III–IV (Dietrichs 1981a-cat). In a detailed study of corticonuclear fibers of the anterior lobe and posterior vermis in a prosimian primate (*Galago*) Haines (1975, 1976) and Haines and Rubertone (1977, 1979) described persistent projections into medial NIP from vermis lobules III–VI, with occasional sparse input from lobule II. Without knowledge, at that time, of zones in the vermis other than A or B (Voogd 1969) it was suggested that these vermis-to-medial NIP fibers may originate from zone B (Haines and Rubertone 1979). After further experimentation, and when comparing the course of fibers from lesions which crossed the midline to encroach on progressively more lateral areas of vermal cortex, Haines et al. (1982) noted that degenerated axons appeared first in NM then, at about the same time, in medial NIP *and* LVN. These authors speculated that this may indicate an x zone-to-medial NIP corticonuclear projection.

Taken collectively these data suggest that the x zone, as the source of corticonuclear fibers to medial NIP, may have more extensive rostrocaudal limits in primates (II or III-rostral VI) than in the cat (caudal IV-rostral VI). Based on the potential functional responsibilities of Purkinje cells of the x zone, as recently suggested by Bishop (1988), it is entirely possible that this zone may be more restricted in quadrupeds (cat) than in primates; the latter have hindlimb dominated locomotor patterns, and forelimbs that are extensively used to manipulate objects and food in the environment (see Functional considerations).

Olivocerebellar, corticonuclear, and nucleoolivary circuits related to zone x

The relationships of cerebellar cortical zones are determined not only by their corticonuclear projections, but also by their receipt of a highly-ordered input from specific divisions of the contralateral inferior olivary complex. Consequently, the observation of a corticonuclear projection from an area of cortex interpreted as the x zone into the medial-most areas of NIP (present study) must be considered in this larger context. While earlier studies concluded that the DAO was the source of olivary input to the x zone (Oscarsson 1980; Ekerot and Larson 1982; Ito 1984) recent evidence suggests that this area of the cerebellar cortex receives climbing fiber input

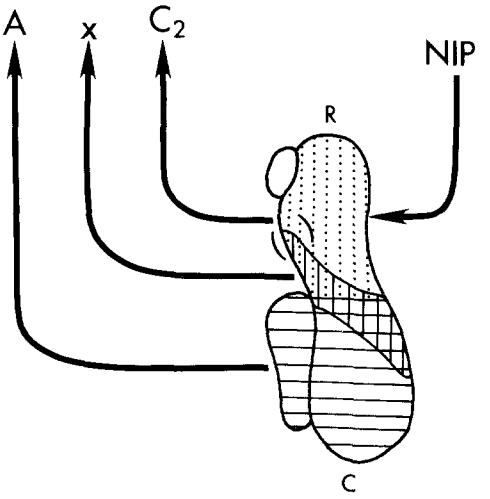

Fig. 8. Semidiagrammatic representation of olivocerebellar projections to zones A, x, and C_2 from the MAO, and of cerebellar nucleoolivary projections from the NIP into rostral MAO. Data modified from Groenewegen et al. 1979; Campbell and Armstrong 1985; and Dietrichs and Walberg 1986. See text for discussion

from the MAO (Voogd 1983; Campbell and Armstrong 1985; Voogd et al. 1987a; Voogd and Hess 1989). Campbell and Armstrong (1985) electrophysiologically identified the x zone as a strip of cortex about 0.6 mm wide in lobule Vc that received short latency (about 15–18 ms) input following stimulation of the ipsilateral forepaw. It was bordered on either side by sagittal zones (A and B) with longer latency (+30 ms) responses (see also Trott and Armstrong 1987a, b, c; Bishop 1988). Following identification of the x zone Campbell and Armstrong (1985) injected small amounts of horseradish peroxidase, and reported that olivary neurons which projected to this specific region of cerebellar cortex were located in the MAO in an oblique band extending across the nucleus from mid-rostromedial to mid-caudolateral (Fig. 8 – vertical lines). In comparison[1] the C_2 zone, which also projects into the NIP (see Dietrichs 1981a; Haines et al. 1982), receives input from the rostral half of the MAO (Groenewegen et al. 1979; Brodal and Kawamura 1980). This creates an overlap of areas of MAO which project to zones x and C_2 (Fig. 8 – vertical lines/dots). This point is further corroborated by Voogd et al. (1987a) and Voogd and Hess (1989) who reported anterograde labeling of olivocerebellar fibers in the x and C_2 compartments and zones following injections of H^3-leucine into "...the middle portion..." of the MAO in *Macaca*.

[1] An accurate comparison of the positions of olivary cells in the MAO that project to the x and/or C_2 zone (or to their corresponding cerebellar nuclei) is expedited by the fact that most investigators (i.e. Groenewegen et al. 1979; Brodal and Kawamura 1980; Campbell and Armstrong 1985; Dietrichs and Walberg 1985, 1986, 1989) illustrate their results on the unfolded horizontal view of the inferior olivary complex as developed by Brodal (for example see Fig. 1 of Brodal et al. 1975). Consequently, one can superimpose these various results to gain an accurate appreciation of the position of cells (olivocerebellar projections) or terminals (nucleoolivary fibers) in the MAO

The results of the present study suggest that the x zone sends corticonuclear fibers into the most-medial NIP. It is well known that the C_2 zone of the anterior lobe (Voogd 1964; van Rossum 1969; Haines and Rubertone 1977, 1979; Voogd and Bigaré 1980; Dietrichs 1981a) and of the posterior lobe hemisphere (Voogd 1964; Walberg and Jansen 1964; Brodal and Courville 1973; Courville et al. 1973; Haines and Whitworth 1978; Armstrong and Schild 1978b; Dietrichs and Walberg 1979, 1980; Voogd and Bigaré 1980; Dietrichs 1981b; Haines and Patrick 1981; Haines et al. 1982, Umetani et al. 1986; Umetani and Tabuchi 1988; Umetani 1989) project into what are usually described as central and/or more lateral regions of the NIP. Medial NIP appears to receive an inconsistent projection from posterior vermis lobules VII and VIII (Armstrong and Schild 1978b; Umetani and Tabuchi 1988; Umetani et al. 1986); most reports do not describe such a connection (e.g., Walberg and Jansen 1964; Haines 1975; Courville and Diakiw 1976; Haines et al. 1982; Dietrichs 1983; Umetani 1989; and others). In contrast, Angaut and Brodal (1967), Haines (1977), Bernard (1987), and Tabuchi et al. (1989) have described a modest, yet consistent, projection into medial NIP from intermediate and lateral regions of lobule IX. This same region of the uvula (lobule IX) receives olivary input from rostral MAO, including the dorsomedial cell column (Groenewegen et al. 1979; Brodal and Kawamura 1980; Whitworth et al. 1983; Bernard 1987).

Taking these data together it is evident that areas of the cerebellar cortex which receive input from middle and rostral levels of MAO (x zone, C_2 zone, lateral lobule IX) send corticonuclear fibers into the NIP; C_2 into its more central and lateral regions and zone x, and lateral IX into its medial areas. In turn, the NIP projects to rostral areas of the contralateral MAO (Fig. 8). Dietrichs and Walberg (1986, 1989), after implanting horseradish peroxidase in the NIP, reported anterogradely labeled fibers coursing into the contralateral MAO. They *specifically* described anterogradely labeled NIP axons *and* retrogradely filled MAO cells in the *same area* of MAO (see Fig. 8–brackets)[2] that contains olivary neurons known to project to the x zone and the C_2 zone (Groenewegen et al. 1979; Campbell and Armstrong 1985). The correlation of x zone (present study) and C_2 zone (see above references) projections into NIP, NIP projection to the contralateral middle and rostral MAO, and projections back to the x and C_2 zones (and their associated cerebellar nucleus – the NIP) from about the middle third of MAO supports the interpretation that the x zone is related, through its efferent fibers, to the NIP. Regions of the MAO which project to the x zone also overlap into areas of the MAO which are related primarily to the A zone (Fig. 8, horizontal + vertical lines; Groenewegen et al. 1979; Brodal and Kawamura 1980; Voogd et al. 1987b, Voogd 1989). We acknowledge that there may not be a precise cortico-nucleo-olivary alignment for all cerebellar zones. However, if the x zone were related primarily to the NM (and the A zone) one would expect to see a significant fastigioolivary projection to those areas of MAO which, in turn, are related to the A zone. Dietrichs and Walberg (1985, 1989) have reported fastigial projections into caudal MAO – the source of olivary projections to the A zone and NM – following horseradish peroxidase implants in the NM. However, the patterns described by these authors indicate that anterogradely labeled axons, and retrogradely labeled cells, largely or exclusively *avoid* those middle regions of MAO from which olivary projections to the x zone arise. Also, Voogd et al. (1987a) have reported that "middle portions" of the MAO projected to x and C_2 zones *and*, via collaterals, *into only the NIP*. The apparent lack of collateral projections into NM in their study (Voogd et al. 1987a) further supports the interpretation that the x zone is related to NIP rather than NM.

[2] See footnote 1 (p. 264)

Functional considerations

The x zone receives short latency (12–20 ms) inputs from the ipsilateral forelimb and forepaw, relayed primarily through the dorsal funiculus-spinoolivocerebellar pathway (e.g., Ekerot and Larson 1979a, b, 1982; Campbell and Armstrong 1985; Trott and Armstrong 1987a, c). While acknowledging a predominant input from the ipsilateral forelimb, Bishop (1988) has offered evidence that x zone Purkinje cells in lobule V also receive input from the contralateral forelimb and the hindlimb. Of the six Purkinje cells in the x zone which responded to hindlimb stimulation (Bishop 1988), three responded bilaterally, two ipsilaterally, and one contralaterally. In this respect Oscarsson and Sjölund (1977a, b) and Robertson (1984, 1987; see also Robertson et al. 1982) have also reported forelimb and hindlimb representation in this same general area of cortex. Bishop (1988) also reported that the recurrent collaterals of x zone Purkinje cells had a greater extent in the transverse plane, and a wider distribution of fibers with varicosities in molecular and granular layers, than did collaterals of Purkinje axons from cells in the medially adjacent A zone or the laterally adjacent B zone (see also Bishop et al. 1987). Individual Purkinje cells of the x zone appear to receive input from flexor and extensor aspects of the same limb, from both forelimbs, or from the hindlimb and forelimb on the same side (Bishop 1988). Based on these structural/functional characteristics Bishop (1988) suggested that Purkinje cells of the x zone compare input from different aspects of the same limb, or from different limbs, and function in the regulation of "...overall tone during movement rather than controlling specific actions...".

Viewing the hypothesis of Bishop (1988) in relation to the extent of the x zone, one sees the following. The cat, with an x zone located primarily in lobule V and probably extending into rostral VI and caudal IV, is an animal with stereotypical movements of hindlimb with forelimb, and forelimbs which function in toilet behavior and in catching and restraining prey, but not in the manipulation of food or objects. Based on the evidence of an x zone projection into medial NIP, this zone in squirrel monkey (*Saimiri*; present study) extends from lobule IV into lobule VI; more rostral lobules were

not explored. However, in *Galago* (a prosimian primate) there is clear evidence of a projection into medial NIP from vermis lobule VI through III, and possibly from lobule II. This would indicate, based on the interpretation of an x zone relationship to medial NIP (see above), that this zone in *Galago*, and probably *Saimiri* (see Voogd et al. 1987a, b for some data on *Macaca*), has a longer rostrocaudal extent than in cat. In the light of the hypothesis of Bishop (1988), that the x zone may function to coordinate forelimb with hindlimb and forelimb with forelimb movements, this zone in *Galago* (and probably other primates) *should* be more extensive. *Galago* has a saltatory hindlimb-dominated style of locomotion, frequently assumes an upright stance, and may even walk upright for short distances, and routinely uses its hands to handle food, manipulate objects in its environment, and to groom its mate (Napier and Napier 1967; Napier and Walker 1967; Martin et al. 1974; personal observations). Such behavioral activities would require a more elaborate cerebellar zone (Bishop 1988) to integrate the various inputs for the coordinated interactions between the forelimb and hindlimb and between the two forelimbs. This would argue in favor of the probability that the x zone in primates is more extensive in the sagittal plane as compared to cat and rat.

Acknowledgments. The author is indebted to Ms A Carr for technical help, Ms G Rainer for typing the manuscript and to Mr L Bird for some editorial help. The work was supported, in part, by USPHS Grant NS 11327.

Professor Walberg, through his numerous contributions, has greatly influenced our concept of cerebellar structure and function. The senior author (DEH), as a young neuroscientist in the early 1970's, boldly wrote to Professor Walberg soliciting his opinion on a manuscript. The high-quality of our interaction continues to this very day, and I will always appreciate and value his friendship and wise scientific counsel. The coauthor of this paper (ED) was a pupil of Professor Walberg and has ever since enjoyed a most fruitful collaboration with him.

References

Andersson G, Eriksson L (1981) Spinal, trigeminal, and cortical climbing fiber paths to the lateral vermis of the cerebellar anterior lobe in the cat. Exp Brain Res 44:71–81

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

Armstrong DM, Schild RF (1978a) An investigation of the cerebellar cortico-nuclear projections in the rat using an autoradiographic tracing method. I. Projections from the vermis. Brain Res 141:1–19

Armstrong DM, Schild RF (1978b) An investigation of the cerebellar corticonuclear projections in the rat using an autoradiographic tracing method. II. Projections from the hemisphere. Brain Res 141:235–249

Bernard J-F (1987) Topographical organization of olivocerebellar and corticonuclear connections in the rat – An WGA-HRP study: I. Lobules IX, X, and the flocculus. J Comp Neurol 263:241–258

Beyerl BD, Borges LF, Swearingen B, Sidman RL (1982) Parasagittal organization of the olivocerebellar projection in the mouse. J Comp Neurol 209:339–346

Bishop GA (1988) Quantitative analysis of the recurrent collaterals derived from Purkinje cells in zone x of the cat's vermis. J Comp Neurol 274:17–31

Bishop GA, McCrea RA, Lighthall JW, Litai ST (1979) An HRP and autoradiographic study of the projection from the cerebellar cortex to the nucleus interpositus anterior and nucleus interpositus posterior of the cat. J Comp Neurol 185:735–756

Bishop GA, Blake TL, O'Donoghue DL (1987) The distribution pattern of Purkinje cell axon collaterals: Variations on a theme. In: King JS (ed) New concepts in cerebellar neurobiology. Alan R Liss, New York, pp 29–56

Brodal A (1980) Olivocerebellar projection in the cat as determined with the method of retrograde axonal transport of horseradish peroxidase 2. Topographical pattern in relation to the longitudinal subdivision of the cerebellum. In: Courville J, deMontigny C, Lamarre Y (eds) The inferior olivary nucleus, anatomy and physiology. Raven Press, New York, pp 187–205

Brodal P, Brodal A (1982) Further observations on the olivocerebellar projection in the monkey. Exp Brain Res 45:71–83

Brodal A, Courville J (1973) Cerebellar corticonuclear projection in the cat. Crus II. An experimental study with silver methods. Brain Res 50:1–23

Brodal A, Kawamura K (1980) Olivocerebellar Projection: A Review. Adv Anat Embryol Cell Biol 64:1–140

Brodal A, Walberg F (1977a) The olivocerebellar projection in the cat studied with the method of retrograde axonal transport of horseradish peroxidase IV. The projection to the anterior lobe. J Comp Neurol 172:85–108

Brodal A, Walberg F (1977b) The olivocerebellar projection in the cat studied with the method of retrograde axonal transport of horseradish peroxidase VI. The projection onto longitudinal zones of the paramedian lobule. J Comp Neurol 176:281–294

Brodal A, Walberg F, Hoddevik GH (1975) The olivocerebellar projection in the cat stained with the method of retrograde axonal transport of horseradish peroxidase. J Comp Neurol 164:449–470

Campbell NC, Armstrong DM (1985) Origin in the medial accessory olive of climbing fibres to the x and lateral C_1 zones of the cat cerebellum: a combined electrophysiological/WGA-HRP investigation. Exp Brain Res 58:520–531

Chan-Palay V, Palay SL, Brown JT, Van Itallie C (1977) Sagittal organization of olivocerebellar and reticulo-cerebellar projections: Autoradiographic studies with ^{35}S-methionine. Exp Brain Res 30:561–576

Courville J, Cooper CW (1970) The cerebellar nuclei of *Macaca mulatta:* a morphological study. J Comp Neurol 140:241–254

Courville J, Diakiw N (1976) Cerebellar corticonuclear projection in the cat. The vermis of the anterior and posterior lobes. Brain Res 110:1–20

Courville J, Diakiw N, Brodal A (1973) Cerebellar corticonuclear projections in the cat. The paramedian lobule. An experimental study with silver methods. Brain Res 50:25–45

Dietrichs E (1981a) The cerebellar corticonuclear and nucleocortical projections in the cat as studied with anterograde and retrograde transport of horseradish peroxidase III. The anterior lobe. Anat Embryol 162:223–247

Dietrichs E (1981b) The cerebellar corticonuclear and nucleocortical projections in the cat as studied with anterograde and retrograde transport of horseradish peroxidase IV. The paraflocculus. Exp Brain Res 44:235–242

Dietrichs E (1983) The cerebellar corticonuclear and nucleocortical projections in the cat as studied with anterograde and retrograde transport of horseradish perxodiase V. The posterior lobe vermis and the flocculonodular lobe. Anat Embryol 167:449–462

Dietrichs E, Walberg F (1979) The cerebellar corticonuclear and nucleocortical projections in the cat as studied with anterograde and retrograde transport of horseradish peroxidase I. The paramedian lobule. Anat Embryol 158:13–39

Dietrichs E, Walberg F (1980) The cerebellar corticonuclear and nucleocortical projections in the cat as studied with anterograde

and retrograde transport of horseradish peroxidase II. Lobulus simplex, Crus I and II. Anat Embryol 161:83–103
Dietrichs E, Walberg F (1985) The cerebellar nucleoolivary and olivocerebellar nuclear projections in the cat as studied with anterograde and retrograde transport in the same animal after implantation of crystalline WGA-HRP II. The fastigial nucleus. Anat Embryol 173:253–261
Dietrichs E, Walberg F (1986) The cerebellar nucleoolivary and olivocerebellar nuclear projections in the cat as studied with anterograde and retrograde transport in the same animal after implantation of crystalline WGA-HRP III. The interposed nuclei. Brain Res 373:373–383
Dietrichs E, Walberg F (1989) Direct bidirectional connections between the inferior olive and the cerebellar nuclei. In: Strata P (ed) The olivocerebellar system in motor control. Springer, Berlin, pp 61–81
Eager RP (1963) Efferent corticonuclear pathways in the cerebellum of the cat. J Comp Neurol 120:81–104
Eisenman LM (1981) Olivocerebellar projections to the pyramis and copula pyramidis in the rat: Differential projections of parasagittal zones. J Comp Neurol 199:65–76
Ekerot C-F, Larson B (1979a) The dorsal spinoolivocerebellar system in the cat I. Functional organization and termination in the anterior lobe. Exp Brain Res 36:201–217
Ekerot C-F, Larson B (1979b) The dorsal spinoolivocerebellar system in cat II. Somatotopical organization. Exp Brain Res 36:219–232
Ekerot C-F, Larson B (1982) Branching of olivary axons to innervate pairs of sagittal zones in the cerebellar anterior lobe of the cat. Exp Brain Res 48:185–198
Fink RP, Heimer L (1967) Two methods for selective silver impregnation of degenerating axons and their synaptic endings in the central nervous system. Brain Res 4:369–374
Flood S, Jansen J (1961) On the cerebellar nuclei in the cat. Acta Anat 46:52–72
Giolli RA, Karamanlidis AN (1978) The study of degenerating nerve fibers using silver-impregnation methods. In: Robertson RT (ed) Neuroanatomical research techniques. Academic Press, New York, pp 211–240
Goodman DC, Hallett RE, Welch RB (1963) Patterns of localization in the cerebellar cortico-nuclear projections of the albino rat. J Comp Neurol 121:51–67
Groenewegen HJ, Voogd J (1977) The parasagittal zonation within the olivocerebellar projection I. Climbing fiber distribution in the vermis of cat cerebellum. J Comp Neurol 174:417–488
Groenewegen HJ, Voogd J, Freedman SL (1979) The parasagittal zonation within the olivocerebellar projection II. Climbing fiber distribution in the intermediate and hemispheric parts of cat cerbellum. J Comp Neurol 183:551–602
Haines DE (1975) Cerebellar cortical efferents of the posterior lobe vermis in a prosimian primate (*Galago*) and the tree shrew (*Tupaia*). J Comp Neurol 163:21–40
Haines DE (1976) Cerebellar corticonuclear and corticovestibular fibers of the anterior lobe vermis in a prosimian primate (*Galago senegalensis*). J Comp Neurol 170:67–95
Haines DE (1977) Cerebellar corticonuclear and corticovestibular fibers of the flocculonodular lobe in a prosimian primate (*Galago senegalensis*). J Comp Neurol 174:607–630
Haines DE (1984) Organizational principles of cerebellar cortical systems. In: Davis R, Bloedel JR (eds) Cerebellar stimulation for spasticity and seizures. CRC Press, Boca Raton, pp 15–34
Haines DE (1986) The primate cerebellum. In: Swindler DR, Erwin J (eds) Comparative primate biology, Vol 1, Systematics, evolution, and anatomy. Alan R Liss, New York, pp 491–535
Haines DE (1989) HRP study of cerebellar corticonuclear-nucleocortical topography of the dorsal culminate lobule – lobule V – in a prosimian primate (*Galago*): with comments on nucleocortical cell types. J Comp Neurol 282:274–292
Haines DE, Patrick GW (1981) Cerebellar corticonuclear fibers of the paramedian lobule of tree shrew (*Tupaia glis*) with comments on zones. J Comp Neurol 201:99–119
Haines DE, Rubertone JA (1977) Cerebellar corticonuclear fibers: evidence of zones in the primate anterior lobe. Neurosci Lett 6:231–236
Haines DE, Rubertone JA (1979) Cerebellar corticonuclear fibers of the dorsal culminate lobule (anterior lobe – lobule V) in a prosimian primate, *Galago senegalensis*. J Comp Neurol 186:321–342
Haines DE, Whitworth RH (1978) Cerebellar cortical efferent fibers of the paraflocculus of tree shrew (*Tupaia glis*). J Comp Neurol 182:137–150
Haines DE, Patrick GW, Satrulee P (1982) Organization of cerebellar corticonuclear fiber systems. Exp Brain Res [Suppl 6]:320–371
Heimer L (1970) Selective silver-impregnation of degenerating axoplasm. In: Nauta WJH, Ebbesson SOE (eds) Contemporary research methods in neuroanatomy. Springer, New York, pp 106–131
Hohman LB (1929) The efferent connections of the cerebellar cortex; investigations based upon experimental extirpations in the cat. Res Publ Assoc Res Nerv Ment Dis 6:445–460
Ito M (1984) The cerebellum and neural control. Raven Press, New York
Jansen J, Brodal A (1940) Experimental studies on the intrinsic fibers of the cerebellum. II. The cortico-nuclear projection. J Comp Neurol 73:267–321
Jansen J, Brodal A (1942) Experimental studies on the intrinsic fibers of the cerebellum. The corticonuclear projection in the rabbit and the monkey (*Macaca rhesus*). Skr Norske Vidensk, Akad I Math Nat Kl, Vol 11:1–50
Joseph JW, Shambes GM, Gibson JM, Welker W (1978) Tactile projections to granular cells in caudal vermis of the rat's cerebellum. Brain Behav Evol 15:141–149
Martin RD, Doyle GA, Walker AC (eds) (1974) Prosimian biology. Duckworth, London
Napier JR, Napier PH (1967) A handbook of living primates; morphology, ecology and behavior of nonhuman primates. Academic Press, London
Napier JR, Walker AC (1967) Vertical clinging and leaping, a newly recognised category of locomotor behaviour among primates. Folia Primatol 6:180–203
Olmos de JS, Ebbeson SOE, Heimer L (1981) Silver methods for the impregnation of degenerating axoplasm. In: Heimer L, Robards MJ (eds) Neuroanatomical tract-tracing methods. Plenum Press, New York, pp 117–170
Oscarsson O (1969) The sagittal organization of the cerebellar anterior lobe as revealed by the projection patterns of the climbing fiber system. In: Llinás R (ed) Neurobiology of cerebellar evolution and development. AMA-ERF, Chicago, pp 525–537
Oscarsson O (1980) Functional organization of olivary projection to cerebellar anterior lobe. In: Courville J, de Montigny C, Lamarre Y (eds) The inferior olivary nucleus, anatomy and physiology. Raven Press, New York
Oscarsson O, Sjölund B (1977a) The ventral spinoolivocerebellar system in the cat. I. Identification of five paths and their termination in the cerebellar anterior lobe. Exp Brain Res 28:469–486
Oscarsson O, Sjölund B (1977b) The ventral spinoolivocerebellar system in the cat. III. Functional characteristics of the five paths. Exp Brain Res 28:505–520
Riche D, Courville J, Massion J, Nieoullon A (1971) Stereotaxic anatomy of the cerebellar nuclei of the baboon (*Papio papio*). J Physiol (Paris) 63:793–837
Robertson LT (1984) Topographic features of climbing fiber input in the rostral vermal cortex of the cat cerebellum. Exp Brain Res 55:445–454
Robertson LT (1987) Organization of climbing fiber representation in the anterior lobe. In: King JS (ed) New concepts in cerebellar neurobiology. Alan R Liss, New York, pp 281–320
Robertson LT, Laxer KD, Rushmer DS (1982) Organization of climbing fiber input from mechanoreceptors to lobule V vermal cortex of the cat. Exp Brain Res 46:281–291

Rossum van J (1969) Corticonuclear and corticovestibular projections of the cerebellum. An experimental investigation of the anterior lobe, the simple lobule and the caudal vermis in the rabbit. Dissertation, University of Leiden

Shambes GM, Gibson JM, Welker W (1978) Fractured somatotopy in granular cell tactile areas of rat cerebellar hemisphere revealed by micromapping. Brain Behav Evol 15:94–140

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

Trott JR (1989) The olivocerebellar input to the medial and lateral halves of the C1 and C3 zones of the cat anterior lobe. In: Strata P (ed) The olivocerebellar system in motor control. Springer, Berlin, pp 20–25

Trott J, Armstrong DM (1987a) The cerebellar corticonuclear projection from lobule Vb/c of the cat anterior lobe: a combined electrophysiological and autoradiographic study I. Projections from the intermediate region. Exp Brain Res 66:318–338

Trott J, Armstrong DM (1987b) The cerebellar corticonuclear projection from lobule Vb/c of the cat anterior lobe: a combined electrophysiological and autoradiographic study II. Projections from the vermis. Exp Brain Res 68:339–354

Trott JR, Armstrong DM (1987c) Olivocorticonuclear organization within lobule V of the anterior lobe of the cat cerebellum. In: King JS (ed) New concepts in cerebellar neurobiology. Alan R Liss, New York, pp 221–238

Umetani T (1989) Topographic organization of the corticonuclear fibers from the tuber vermis and paramedian lobule in the albino rat. Brain Behav Evol 33:334–341

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

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

Voogd J (1964) The cerebellum of the cat. Structure and fibre connexions. Dissertation, University of Leiden

Voogd J (1969) The importance of fiber connections in the comparative anatomy of the mammalian cerebellum. In: Llinás R (ed) Neurobiology of cerebellar evolution and development. AMA-ERF, Chicago, pp 493–514

Voogd J (1983) Anatomical evidence for a cortical x zone in the cerebellum of the cat. Soc Neurosci Abstr 9:1091

Voogd J (1989) Parasagittal zones and compartments of the anterior vermis of the cat cerebellum. In: Strata P (ed) The olivocerebellar system in motor control. Springer, Berlin Heidelberg New York, pp 3–19

Voogd J, Bigaré F (1980) The topographical distribution of olivary and corticonuclear fibers in the cerebellum. A review. In: Courville J, de Montigny C, Lamarre Y (eds) The inferior olivary nucleus, anatomy and physiology. Raven Press, New York, pp 207–234

Voogd J, Hess DT (1989) Identification of A, X, and B cortical zones and white matter compartments in the anterior vermis of the cerebellum of the monkey (*Macaca fascicularis*). Soc Neurosci Abstr 15:611

Voogd J, Gerrits NM, Hess DT (1987a) Parasagittal zonation of the cerebellum in Macaques: an analysis based on acetylcholinesterase histochemistry. In: Glickstein M, Yeo C, Stein J (eds) Cerebellum and neuronal plasticity. NATO AS1 Series, Life Sciences, Vol 148, Plenum Press, New York, pp 15–39

Voogd J, Hess DT, Marani E (1987b) The parasagittal zonation of the cerebellar cortex in cat and monkey: topography, distribution of acetylcholinesterase, and development. In: King JS (ed) New concepts in cerebellar neurobiology. Alan R Liss, New York, pp 183–220

Walberg F (1980) Olivocerebellar projection in the cat as determined with the method of retrograde axonal transport of horseradish peroxidase 1. Topographical pattern. In: Courville J, de Montigny C, Lamarre Y (eds) The inferior olivary nucleus, anatomy and physiology. Raven Press, New York, pp 169–186

Walberg F, Jansen J (1964) Cerebellar corticonuclear projection studied experimentally with silver impregnation methods. J Hirnforsch 6:338–354

Whitworth RH, Haines DE, Patrick GW (1983) The inferior olive of a prosimian primate, *Galago senegalensis*. II. Olivocerebellar projections to the vestibulocerebellum. J Comp Neurol 219:228–240

Yu Q-X, Ebner TJ, Bloedel JR (1985) Electrophysiological study of the corticonuclear projection in the cat cerebellum. Brain Res 327:121–134