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CEREBELLOTECTAL PROJECTION IN THE RAT: ANTEROGRADE AND RETROGRADE WGA-HRP STUDY OF INDIVIDUAL CEREBELLAR NUCLEI

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ABSTRACT

Cerebellotectal projections were studied in the rat by the anterograde and retrograde tracing methods using wheat-germ-agglutinin-conjugated horseradish peroxidase. The pathway arises from all four cerebellar nuclei on the contralateral side; mainly from the posterior interpositus nucleus and lateral nucleus and to a lesser extent from the medial nucleus and anterior interpositus nucleus. The fibers arising from the medial nucleus and the posterior interpositus nucleus terminate mainly in the deeper zone of layer IV and in layer VI throughout the entire rostrocaudal extent of the contralateral superior colliculus. Those arising from the anterior interpositus nucleus and the lateral nucleus terminate mainly in the superficial zone of layer IV in the rostral three-fourths of the contralateral superior colliculus. In addition, the fibers from the lateral nucleus terminate densely in a zone extending from the deep part of layer III through layer VII in the lateral portion of the rostral half of the superior colliculus. In comparison with data on other species the present findings are discussed with respect to the evolutional changes from monocular to binocular vision.

INTRODUCTION

Many papers have described cerebellotectal projections in various animal species, including the cat (Thomas et al., 1956; Cohen et al., 1958; Angaut, 1969; Angaut, 1970; Angaut and Bowsher, 1970; Edwards et al., 1979; Roldan and Reinoso-Suarez, 1981; Sugimoto et al., 1982; Kawamura et al., 1982; Hirai et al., 1982), monkey (Carpenter, 1959; Batton III et al., 1977; Stanton, 1980; Carpenter and Batton III, 1982; Gonzalo-Ruiz et al., 1988; May et al., 1990), opossum (Foltz and Matzke, 1960; Walsh and Ebner, 1973; Martin et al., 1974), hedgehog (Earle and Matzke, 1974), rabbit (Uchida et al., 1983), squirrel (May and Hall, 1986), and rat (Chan-Palay, 1977; Faull and Carman, 1978; Gonzalo-Ruiz et al., 1990). A comparison of the descriptions in these papers indicates the presence of species differences in the origin and termination of these projections, particularly between animals with extensive binocular overlap (frontally placed eyes) and those with little binocular overlap (temporally placed eyes). These differences may be associated with evolutional changes from monocular to binocular vision.

Of the species with temporally placed eyes, cerebellotectal projections have been studied in detail in the opossum (Martin et al., 1974) by the anterograde degeneration method, in the rabbit (Uchida et al., 1983) and squirrel (May and Hall, 1986) by the anterograde and retrograde tracing methods with horseradish peroxidase (HRP). For the rat, however, available data are fragmentary. Three papers have been published in the rat:one described gross distribution of the projections following lesions of the entire brachium conjunctivum (Faull and Carman, 1978), another

described only the projections arising from the medial nucleus (Gonzalo-Ruiz et al., 1990), and the third described only the projections arising from the lateral nucleus (Chan-Palay, 1977). For a better understanding of cerebellotectal projections from the viewpoint of comparative neurology, it is necessary to compare data among animals with temporal eyes as well as among those with frontal eyes. In this respect, the cerebellotectal projections in the rat need to be studied comprehensively. We present the first documentation of individual tectal projections from each of the four cerebellar nuclei in the rat, using the anterograde and retrograde tracing methods with wheat-germ-agglutinin-conjugated horseradish peroxidase (WGA-HRP).

MATERIALS AND METHODS

Forty-five adult rats (200-400g) of the Wistar strain were used: 22 for the anterograde study and 23 for the retrograde study. In both studies, 5% WGA-HRP (Toyobo) dissolved in 0.9% saline was used as a tracer. Animals were anesthetized with sodium pentobarbital (35 mg/kg, i.p.) and placed in a stereotaxic head holder.

In 19 of the 22 rats for the anterograde study, a single injection of the tracer was placed in a single cerebellar nucleus, either the medial nucleus (MN), the posterior interpositus nucleus (PIN), the anterior interpositus nucleus (AIN), or the lateral nucleus (LN), using a 0.5μl Hamilton microsyringe. The volume of each injection ranged from 0.01μl to 0.015μl depending on the size of the nucleus, so that the injection site might cover fully one nucleus and yet be restricted to that nucleus. In the other three rats, three injections in the amount of 0.02μl to 0.04μl for each were made to cover fully the four cerebellar nuclei unilaterally.

In the 20 of the 23 rats for the retrograde study, a single injection of the tracer in the amount of 0.01μl to 0.03μl was placed into various parts of the superior colliculus (SC) to determine the topographical organization of the projection. In the other three rats, multiple injections (10-15 sites) in the amount of 0.03μl to 0.05μl for each were made to cover fully the SC unilaterally.

After 24 hours, the animals were deeply anesthetized with ethyl ether and perfused through the ascending aorta with 200 ml of 7% formalin in 0.1M phosphate buffer, followed by 200 ml of 0.9% saline containing 10% sucrose. The brains were removed immediately and soaked in 0.9% saline containing 30% sucrose.

Subsequently, the brains were frozen and cut serially into 70μm frontal sections. The sections were treated with benzidine dihydrochloride and hydrogen peroxide according to the method of De Olmos and Heimer (1977). In the cases with injections into the cerebellar nuclei, every second section of the cerebellum was counterstained with 0.5% Neutral Red to identify the spread of tracer in the injection site. The other sections of the cerebellum and every second section of the pons and midbrain were initially unstained to avoid fading the reaction products, which was often very light. After observation under darkfield illumination, these sections were stained, if necessary. In the cases with injections into the SC, every third section of the SC was counterstained to identify the spread of tracer in the injection site. All sections of the cerebellum were initially unstained to observe the labeled cells under darkfield illumination and stained afterward to observe the anatomical structure of the cerebellar nuclei.

RESULTS

The four cerebellar nuclei, the medial nucleus (MN), the posterior interpositus nucleus (PIN), the anterior interpositus nucleus (AIN), and the lateral nucleus (LN), were identified according to the criteria of Korneliussen (1968), but the borders between them were difficult to define. The PIN is partly continuous with the AIN at its rostral levels, and the lateral part of the MN and the medial extremity of the PIN were observed to merge with one another at some levels. Finally, the AIN and the LN form a completely continuous mass interposed with the dorsolateral hump region. While Korneliussen (1968) stated that it is uncertain whether the dorsolateral hump region belongs to the AIN or the LN, in the present study we tentatively considered it as a part of the AIN, following the usage of Goodman et al. (1963).

The present study adopted the classification of the superior collicular layers in the mouse illustrated by Wiener (1986). Although the layers in the rat have been named in various ways (Murray and Coulter,1982; Chevalier and Deniau,1984; Redgrave et al., 1986), Wiener's classification corresponds to the widely accepted terminology illustrated by Kanaseki and Sprague (1974) for the cat. Following this classification, layer IV and layer VI can be clearly identified by their characteristic large stellate cells. This classification also has been used in the squirrel (May and Hall, 1986) and therefore facilitates comparisons between these two rodent species.

Anterograde study

Before we describe the cerebellotectal projections from individual cerebellar nuclei, we will describe them as a whole, based on findings in the three cases in which the injected tracer covered most of the four cerebellar nuclei on one side without spread to the other side. The findings of terminal labeling in these cases were similar (one case is shown in Fig.1, with the injection site shown in Fig.2A). In the SC, dense terminal labeling was observed on the contralateral side (Fig.1A), but little was observed on the ipsilateral side (Fig.1B). Labeled terminals on the contralateral side were distributed mainly in layer IV and to a lesser extent in layer VI. The labeled terminals were distributed throughout the entire rostrocaudal and mediolateral extent of the SC; they were denser at the rostral than at the most caudal levels, and denser in the lateral portion than in the medial portion.

Medial nucleus (MN)

In six out of the nine animals injected with tracer into the MN, the tracer covered a large proportion of this nucleus, spreading to the undefined border with the medial extremity of the PIN (one case is shown by CN11 in Fig.2B by a photograph and in Fig.3A by a drawing). In the remaining three animals, the tracer covered only the rostral portion of the MN. Labeled terminals in the SC were found in the former group of animals, whereas they were entirely absent in the latter group.

In the six animals with large injections in the MN, the labeled efferent fibers entered the midbrain by way of the contralateral ascending limb of the uncinate fasciculus, which decussated within

the cerebellum and traversed the portion just dorsal to the contralateral brachium conjunctivum (BC). In five out of the six animals, there was an extra component of labeled fibers that entered the midbrain by way of the dorsal tip of the ipsilateral BC. These fibers were located between the ipsilateral ascending limb of the uncinate fasciculus and the fibers from the ipsilateral PIN (described later), somewhat overlapping the latter (Fig. 3B). This extra component was not labeled in the remaining one animal perhaps because the amount of involvement of the undefined border by the injection site was lighter than in the five other animals.

In the SC, terminal labeling was observed exclusively on the contralateral side (Fig.3C). The labeled terminals were distributed mainly in the deeper zone of layer IV and in layer VI and to a lesser extent in layers V and VII. The labeled terminals were distributed throughout the rostrocaudal and the mediolateral extent; they were denser at the rostral than at the caudal levels and denser in the lateral portion and the medial extremity than in the middle portion.

Posterior interpositus nucleus (PIN)

Three animals were injected with tracer into the PIN. In one, the injection site covered most of the PIN with a slight spread to the caudal part of the AIN (CN28, not shown). In another, a large proportion of the PIN was involved without spread to other nuclei (CN20, shown in Fig.2C and Fig.4A). In the third, only the caudolateral portion of the PIN was involved (CN24, not shown). The findings in these three animals were similar.

The efferent fibers labeled with the tracer entered the midbrain by way of the ipsilateral BC and occupied its dorsal part (Fig.4B). In the SC, labeled terminals were observed exclusively on the contralateral side (Fig.4C). While labeled terminals were observed from the deepest zone of layer III through layer VII, they were very dense in layer VI and the deeper zone of layer IV and sparse in the other layers. The two densely labeled bands coincided with layers containing large stellate cells (Fig.5). The bilamellar distribution of dense terminals was observed not only when the injection covered most of the PIN but also when the injection covered only the caudolateral portion of the PIN (CN24). The labeled terminals were distributed throughout the rostrocaudal and the mediolateral extent; they were denser at the caudal than at the rostral levels and denser in the lateral portion and the medial extremity than in the middle portion.

Anterior interpositus nucleus (AIN)

In one out of the five animals injected with tracer into the AIN, the tracer covered most of the AIN with a slight spread to the rostral part of the PIN. In two other animals, tracer covered a large proportion of the AIN without spread to other nuclei (one case is shown by CN21 in Fig.2D and Fig.6A). In the other two animals, tracer covered the rostral two-thirds of the AIN.

The efferent fibers labeled with the tracer entered the midbrain by way of the ipsilateral BC; they occupied the middle part of the BC, ventral to the fibers from the PIN (Fig.6B). In the SC, the labeled terminals were sparse and exclusively contralateral (Fig.6C). The distribution pattern of the labeled terminals was different from those observed in the MN and PIN in two ways. First, labeled

terminals were observed only in the rostral three-fourths of the SC. Second, they were distributed mainly in the superficial zone of layer IV, with some extension into layers III and V in the lateral part. As in the other cases, while the labeled terminals were distributed throughout the mediolateral extent, they were denser in the lateral part and the medial extremity than in the middle portion. In the two animals in which the injected tracer covered only the rostral two-thirds of the AIN, the terminal labeling in the rostrolateral part of the SC was much lighter than in the other three animals.

Lateral nucleus (LN)

The injected tracer covered most of the LN with a slight spread to the lateral extremity of the AIN (dorsolateral hump region) in one animal and a large proportion of the LN without encroachment on other nuclei in one animal (Fig.2E and Fig.7A).

The efferent fibers labeled with the tracer joined the ipsilateral BC. At levels just caudal to the midbrain, they occupied the ventral part of the BC and partially overlapped the fibers from the AIN (Fig.7B). In the SC, labeled terminals were observed exclusively contralateral rostral three-fourths of it (Fig.7C). In the most rostral fourth portion, the labeled terminals were distributed throughout the mediolateral extent of an area extending from the deeper part of layer III through layer VII. They were much denser in the lateral part of these layers. The dense terminal labeling in the lateral part was continuous rostrally with that in the anterior pretectal nucleus. In the second rostral fourth portion, the labeled terminals were distributed densely in the lateral part in the deeper zone of layer III through layer VII and sparsely in the superficial zone of layer IV throughout its mediolateral extent; in the latter

layer they were relatively denser in the medial extremity than in the middle portion. In the next rostral fourth portion, the distribution pattern of the labeled terminals was largely similar to that in the second rostral fourth portion, but the terminal labeling of the lateral part was lighter as compared with that of the second rostral one-fourth, and it was restricted mostly to layer IV and the adjoining layers. The most caudal fourth was free of labeled terminals.

The density of labeled terminals was much higher in the cases with injection into the PIN and LN than in those with injection into the MN and AIN.

Retrograde study

In three animals with multiple injections (10-15 sites) into the SC, the injected tracer covered most of the unilateral SC (one case is shown in Fig.8 and Fig.9). In the cerebellar nuclei, a large number of labeled cells were observed contralaterally but only a few ipsilaterally. The contralaterally labeled neurons were located mainly in the PIN (Fig.9B) and LN (Fig.9C) and to a lesser extent in the MN and AIN. In the MN, labeled cells were sparsely distributed in the caudal half of the nucleus, and no labeled cells were found in the rostral half. In the PIN, while labeled cells were found in the rostrocaudal extent, they were denser at the caudal than at the rostral levels. Throughout the rostrocaudal extent, they were located largely in the ventrolateral region. At the undefined border between the MN and the PIN, labeled cells were very sparse. In the AIN, labeled cells were sparsely found throughout the rostrocaudal

extent. At the rostral levels, they were distributed almost continuously from the middle area to the lateral portion of the nucleus, however, they divided into a medial and a lateral cluster at the more caudal levels. At the most caudal levels, the lateral cluster was continuous with the cell population densely labeled in the lateral part of the PIN. In the LN, a large number of labeled cells were found throughout the rostrocaudal extent. At the most rostral levels, they were distributed except the dorsal pole and they were rather sparse. At the more caudal levels, they were distributed widely and densely. They were especially denser in the lateral part and the ventral part of the nucleus. At the most caudal levels, ventrally labeled cells were continuous with the cell population labeled in the lateral part of the PIN. At the border area between the AIN and LN, labeled cells were very sparse except at the most caudal levels.

To investigate the topographical organization of the cerebellotectal projection, a single injection of the tracer was administered into various parts of the SC in 20 animals. The sites of injection are shown in the dorsal view in Fig.10. Four representative cases (an injection to the rostrolateral part, caudolateral part, rostromedial part, and caudomedial part) are shown by the series of frontal sections in Fig.11. The topographical organization of the projection did not appear to be point to point. Among the cases whose injection sites did not overlap each other, the distribution of the retrogradely labeled cells was overlapped to a considerable extent. A gross topographical organization is schematically illustrated in Fig.12, with the SC divided into 4 sectors.

DISCUSSION

The present anterograde and retrograde studies revealed that the cerebellotectal projection in the rat originates from all four cerebellar nuclei on the contralateral side, mainly from the posterior interpositus nucleus (PIN) and lateral nucleus (LN) and to a lesser extent from the medial nucleus (MN) and anterior interpositus nucleus (AIN). The projection from the MN to the superior colliculus (SC) arose exclusively from the caudal half of the nucleus and crossed within the cerebellum to form the crossed ascending limb of the uncinate fasciculus. The projections from the other three nuclei arose from their almost entire rostrocaudal extent and formed a compact fiber bundle within the brachium conjunctivum (BC), which crossed in the brainstem constituting a part of the decussation of the BC. The origin and course of these projections in the rat are much the same as those reported for various other animal species, however, the proportion of projections from individual nuclei differs among the animal species. It appears likely that the difference is marked between the animals with extensive binocular overlap (frontally placed eyes) and those with little binocular overlap (temporally placed eyes). In species with extensive binocular overlap, such as the cat (Cohen et al., 1958; Edwards et al., 1979; Roldan and Reinoso-Suarez, 1981; Sugimoto et al., 1982; Kawamura et al., 1982; Hirai et al., 1982) and monkey (Gonzalo-Ruiz et al., 1988; May et al., 1990), a bilateral projection from the MN is the major component of the cerebellotectal projections, whereas in species with little binocular overlap, such as the hedgehog (Earle and Matzke, 1974), opossum (Walsh and Ebner, 1973), rabbit (Uchida et al., 1983), and squirrel (May and Hall, 1986), the projection from the

MN is contralateral and very sparse or even absent. In the species of the latter category, relatively sparse ipsilateral projections from the MN were observed in the opossum (Martin et al., 1974) by the degeneration method and in the rat (Gonzalo-Ruiz et al., 1990) by the anterograde tracing method with WGA-HRP. The presence of such projections, however, was doubted by the authors themselves because it was possibly caused by interruption of fibers arising from the contralateral MN (Martin et al., 1974) or uptake of tracer by injured passing fibers (Gonzalo-Ruiz et al., 1990). In fact, the present retrograde studies could seldom detect neurons sending such a projection in the rat.

In animals with frontally placed eyes, it is disputed whether the projections from nuclei other than the MN are similar or different among species. In the monkey, the projections from the PIN are much larger than those from the AIN and LN (Gonzalo-Ruiz et al., 1988). In the cat, one paper described the similar findings (Kawamura et al., 1982), but others reported differently: the projections arise much from the LN but little from the AIN and PIN (Roldan and Reinoso-Suarez, 1981), or much from the PIN and LN but little from the AIN (Hirai et al., 1982; Sugimoto et al., 1982). There is no explanation for this discrepancy at the moment. In animals with temporally placed eyes, the proportion of projections from individual cerebellar nuclei is also different among species. In the rabbit, they arise mainly from the PIN and AIN and, to a lesser extent, from the LN (Uchida et al., 1983). In the opossum, they arise mainly from the LN (Martin et al., 1974). In the squirrel, they arise mainly from the PIN and, to a lesser extent, from the LN (May and Hall, 1986). The present findings in the rat are largely similar to those reported in the squirrel.

The present anterograde studies revealed that the projections arising from the PIN and MN terminate mainly in the deeper zone of layer IV and in layer VI forming two bands throughout the rostrocaudal extent of the SC, and that those arising from the AIN and LN terminate mainly in the deeper zone of layer III and in the superficial zone of layer IV forming one fused band in the rostral three-fourths of the SC. The formation of two bands of terminals has been reported in the squirrel in which the projection arising from the PIN terminates in the deeper zone of layer IV and in layer VI (May and Hall, 1986). In the rabbit, the projections arising from the PIN and AIN distribute patchy terminals in the deeper zone of layer IV through layer V forming one band and diffuse terminals in layers VI-VII forming another band (Uchida et al., 1983). The formation of two bands contributed by the PIN thus appears to be a common feature of terminal distribution in animals with temporally placed eyes. By contrast, many papers on cerebellotectal projections in the monkey (Carpenter, 1959; Batton III et al., 1977; Stanton, 1980; Carpenter and Batton III, 1982; Gonzalo-Ruiz et al., 1988; May et al., 1990) and cat (Thomas et al., 1956; Cohen et al., 1958; Angaut, 1969; Angaut, 1970; Angaut and Bowsher, 1970; Edwards et al., 1979; Roldan and Reinoso-Suarez, 1981; Sugimoto et al., 1982; Hirai et al., 1982) indicate that the terminal formation of two bands contributed by the PIN is not observed commonly in animals with frontally placed eyes. It thus appears likely that the terminal distribution is markedly different between animals with frontally placed eyes and those with temporally placed eyes. This difference and that of the projection from the MN may be accounted for by evolutional changes from monocular to binocular vision.

The deeper zone of layer IV and layer VI, the recipient of projections from the PIN and MN, contain large stellate neurons that are the origins of the tecto-reticulo-spinal projection as reported for the rat (Murray and Coulter, 1982; Redgrave et al., 1986), golden hamster (Rhoades and DellaCroce, 1980), squirrel (May and Hall, 1984), opossum (Weber et al., 1979), tree shrew (Weber et al., 1979), and cat (Weber et al., 1979; Murray and Coulter, 1982). The deeper zone of layer III and the superficial zone of layer IV, the recipient of projections from the LN and AIN, contain projection neurons of the ipsilateral tecto-pontine tract as reported for the cat (Hashikawa and Kawamura, 1977; Mower et al., 1980) and rat (Redgrave et al., 1986). The tecto-reticulo-spinal projection is considered to be related to neck and body movement, while the tecto-pontine projection is considered to be related to control of saccadic eye movement because of its termination in the vision and saccade related pontine areas. In fact, systematic stimulation of layer III or layer IV of the SC in the rat produced topographically organized saccadic eye movements (McHaffie and Stein, 1982), whereas stimulation of the lateral area of the deeper zone of layer IV, which contains the large stellate neurons, induced sensory guided orienting movements of the head and body (Dean et al., 1986, 1988). Stimulation of the SC induced neck orienting movements also in the cat (Harris, 1980; Roucoux et al., 1980) but not in the monkey (Robinson and Jarvis, 1974; Stryker and Schiller, 1975). The effect of stimulation of the SC on the movements of the neck thus appears to be inversely related to the mobility of eyes, which is narrower in the rat than in the cat and in the cat than in the monkey (Guitton et al., 1980; Fuller, 1985). This is understandable because the visual orienting response is a

cooperation of eye, neck, and body movements, and it is likely that the narrower is the eye mobility, the greater is the importance of neck and body movement. As for the functional significance of the cerebellotectal projections in the rat, then, it appears reasonable to assume that projections from the PIN and MN are related to head and body movements in orientation, and projections from the LN and AIN are related to control of saccadic eye movements.

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ABBREVIATIONS

AIN	Anterior interpositus nucleus of the cerebellum
CG	Central gray
LN	Lateral nucleus of the cerebellum
MN	Medial nucleus of the cerebellum
PIN	Posterior interpositus nucleus
II	Layer II of the superior colliculus
III	Layer III of the superior colliculus
IV	Layer IV of the superior colliculus
V	Layer V of the superior colliculus
VI	Layer VI of the superior colliculus
VII	Layer VII of the superior colliculus

FIGURE LEGENDS

Fig.1. Darkfield photomicrographs of a frontal section of the superior colliculus showing terminals of cerebellotectal projections on the side contralateral (A) and ipsilateral (B) to the injection. The injection site involved the all cerebellar nuclei on one side (shown in Fig.2A). Taken from the case CN103. Bar=500μm.

Fig.2. Photomicrographs of frontal sections of the cerebellum showing the injection sites. Injections involved the all cerebellar nuclei on one side in the case CN103 (A), the medial nucleus in the case CN11 (B), the posterior interpositus nucleus in the case CN20 (C), the anterior interpositus nucleus in the case CN21 (D), and the lateral nucleus in the case 17 (E). Bar=1,000μm.

Fig.3. Drawings showing the cerebellotectal projection from the medial nucleus. A, spread of the tracer (shade) in the injection site; B, labeled fibers (shade) in and around the brachium conjunctivum; C, labeled terminals (stipple) in the superior colliculus in the framed area of the inset diagram. Taken from the case CN11.

Fig.4. Drawings showing the cerebellotectal projection from the posterior interpositus nucleus. A, spread of the tracer (shade) in the injection site; B, labeled fibers (shade) in and around the brachium conjunctivum; C, labeled terminals (stipple) in the superior colliculus in the framed area of the inset diagram. Taken from the case CN20.

Fig.5. Photomicrograph of one and the same frontal section of the superior colliculus under darkfield illumination (A) and brightfield illumination (B) to show the coincidence of the layers distributed with dense terminals and those with large stellate cells. Taken from the case injected into the posterior interpositus nucleus (CN28). Stained with Neutral Red. Bar=500μm.

Fig.6. Drawings showing the cerebellotectal projection from the anterior interpositus nucleus. A, spread of the tracer (shade) in the injection site; B, labeled fibers (shade) in and around the brachium conjunctivum; C, labeled terminals (stipple) in the superior colliculus in the framed area of the inset diagram. Taken from the case CN21.

Fig.7. Drawings showing the cerebellotectal projection from the lateral nucleus. A, spread of the tracer (shade) in the injection site; B, labeled fibers (shade) in and around the brachium conjunctivum; C, labeled terminals (stipple) in the superior colliculus in the framed area of the inset diagram. Taken from the case CN17.

Fig.8. Distribution of the cerebellotectal projection neurons. Multiple injections involved almost entirely the unilateral superior colliculus as shown on the top (shade). The retrogradely labeled cells in the cerebellar nuclei are mapped by dots on seven representative frontal sections. The cells were numerous on the side contralateral to the injection but negligibly few on the side ipsilateral to the injection. Taken from the case SC103.

Fig.9. Photomicrographs of frontal sections of the midbrain and cerebellum in case SC103 showing the injection site in the superior colliculus (A), the retrogradely labeled neurons in the contralateral posterior interpositus nucleus (B), and those in the contralateral lateral nucleus (C). Bar=1,000μm.(A). Bar=200μm.(B, C)

Fig.10. Diagrams illustrating the injection sites in the superior colliculus. Shown at the center is a dorsal view of the unilateral superior colliculus in which the injection sites are indicated with identification numbers of the animals. Tracer spread of each injection is individually shown around it (shade).

Fig.11. Drawings showing the distribution of retrogradely labeled cells in the cerebellar nuclei after injections into the rostrolateral part (SC11), caudolateral part (SC38), rostromedial part (SC36), and caudomedial part (SC32) of the superior colliculus. They are mapped by dots on seven representative frontal sections in each case with their injection sites on the top (shade). The ipsilateral cerebellar nuclei are not illustrated because the labeled cells were virtually absent.

Fig.12. Diagram showing the topographical organization of the cerebellotectal projections. A, dorsal view of unilateral superior colliculus, which is divided into four sectors. B, the contralateral cerebellar nuclei in which areas sending axons to each sector of the superior colliculus are illustrated by the same symbol.

Fig. 1

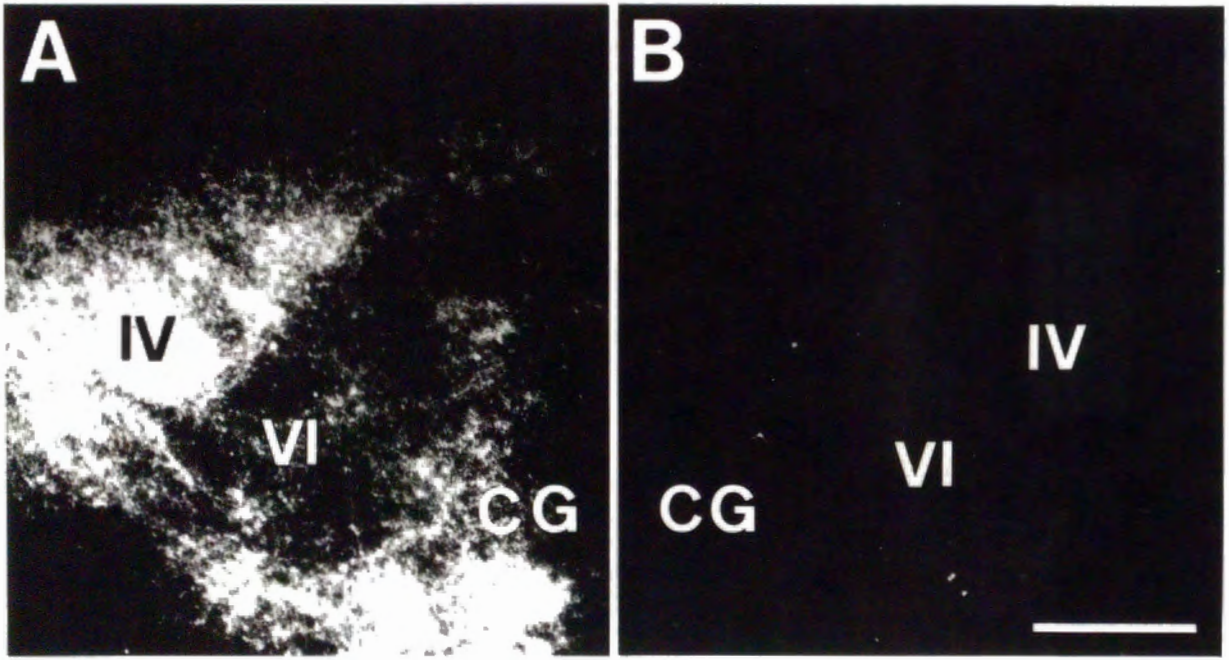
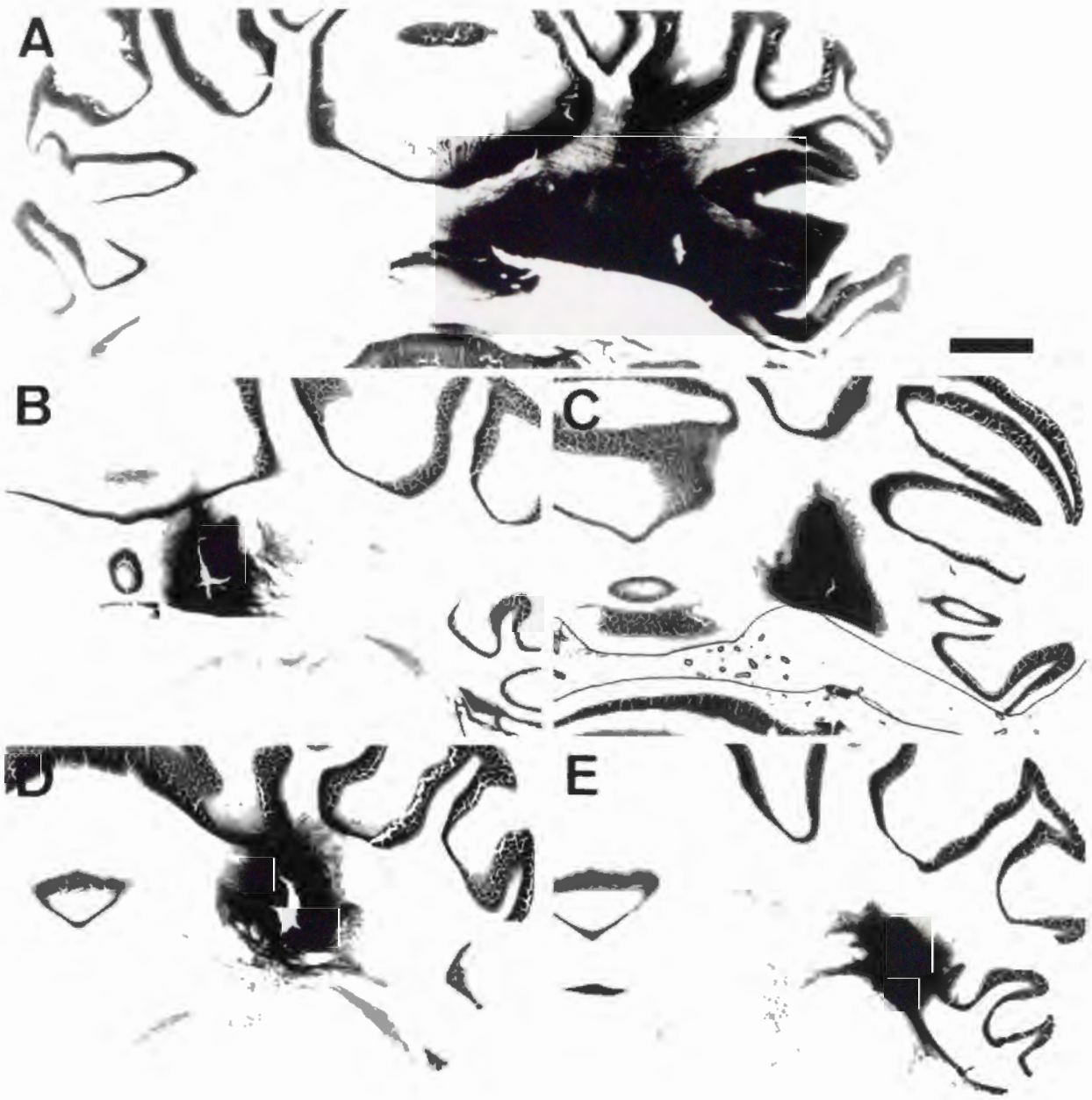
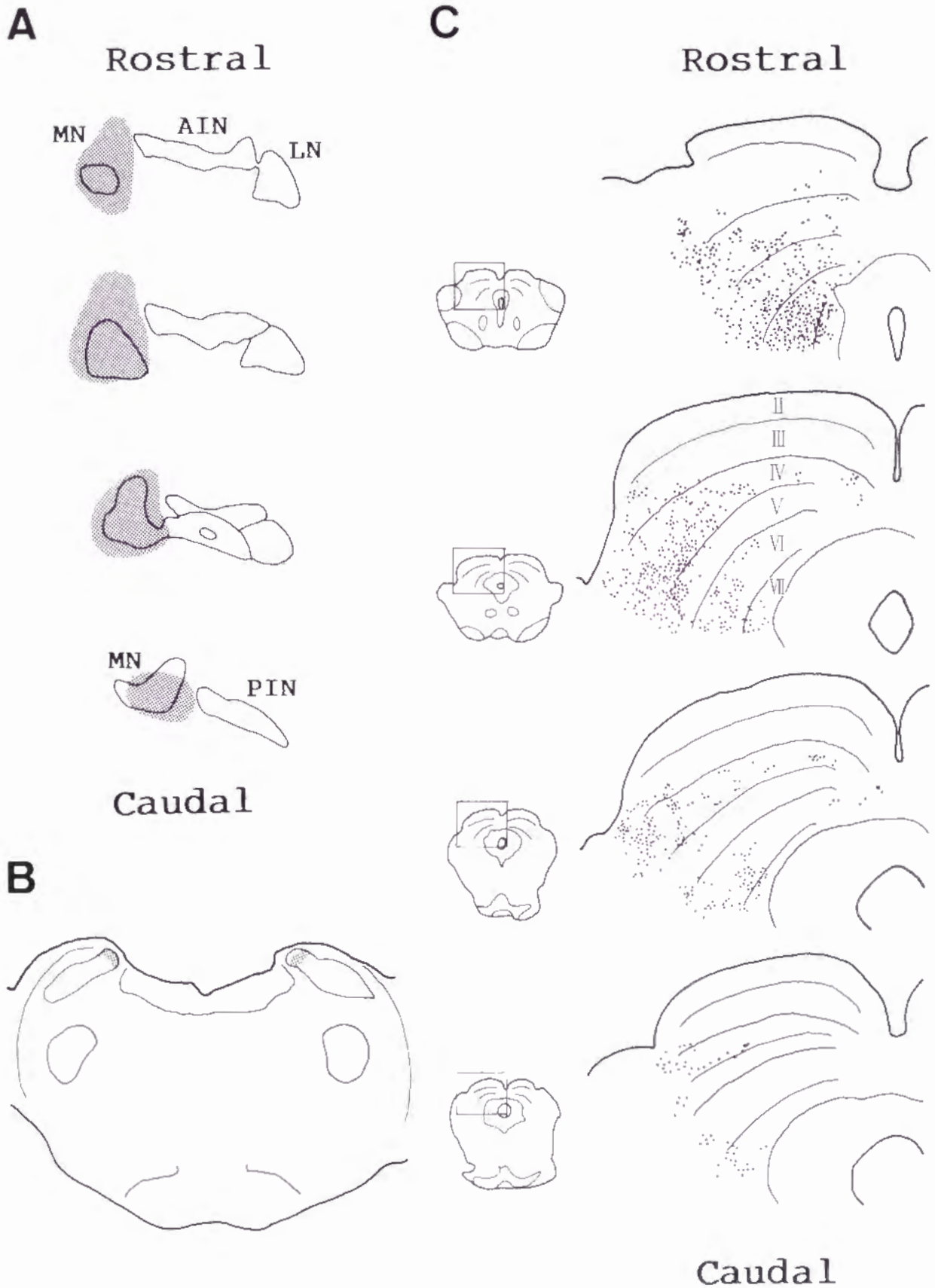


Fig. 2

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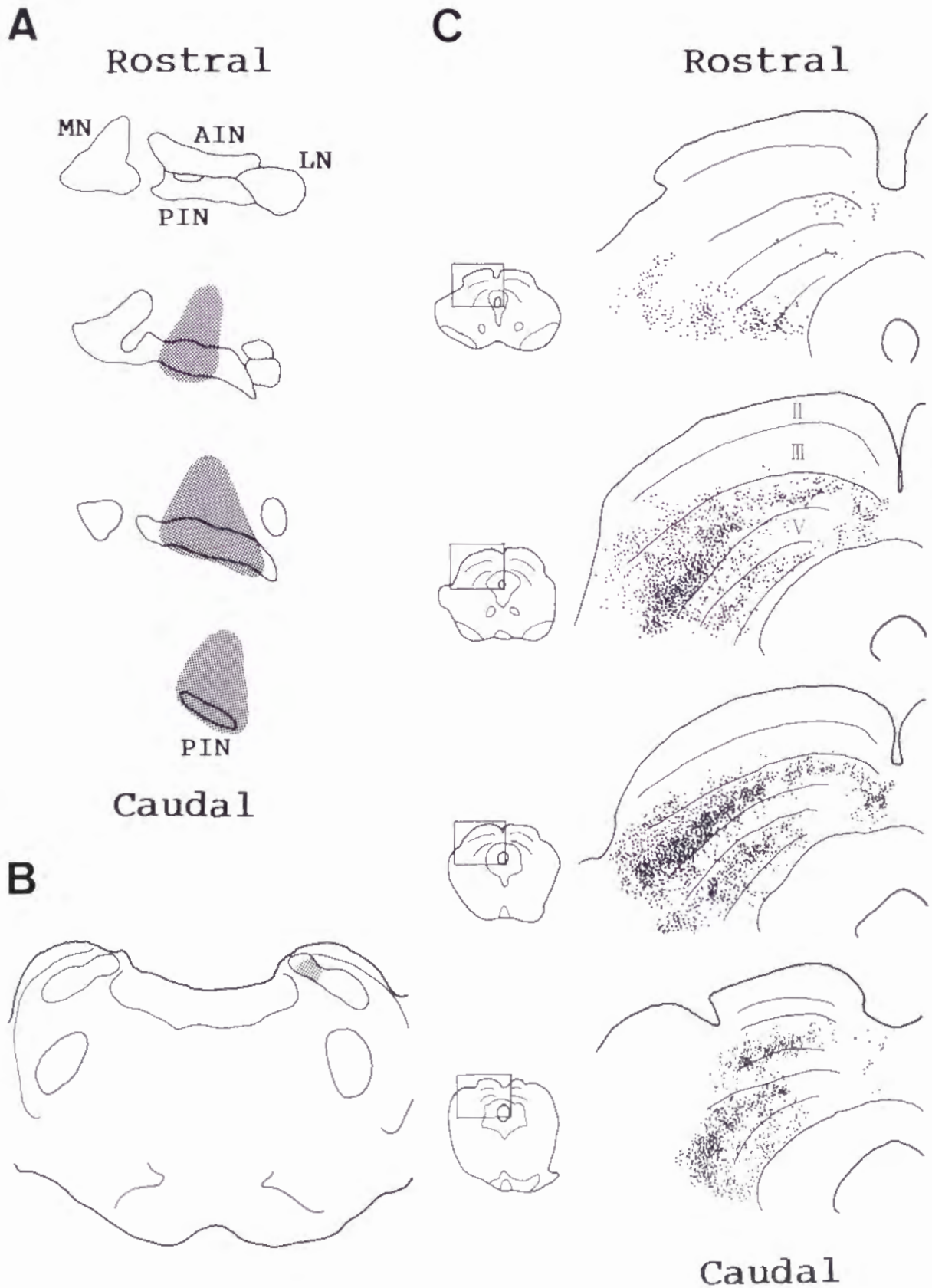
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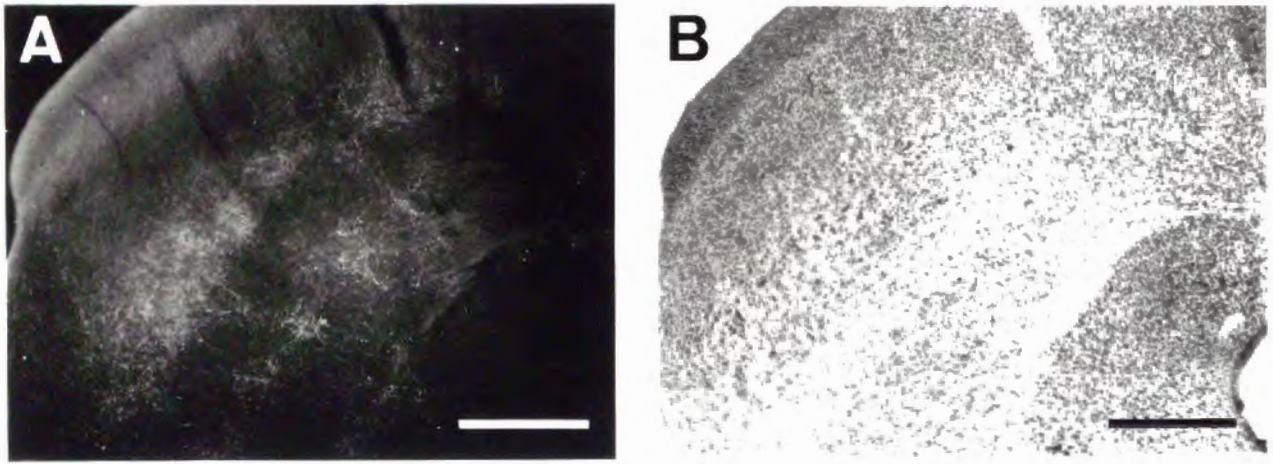
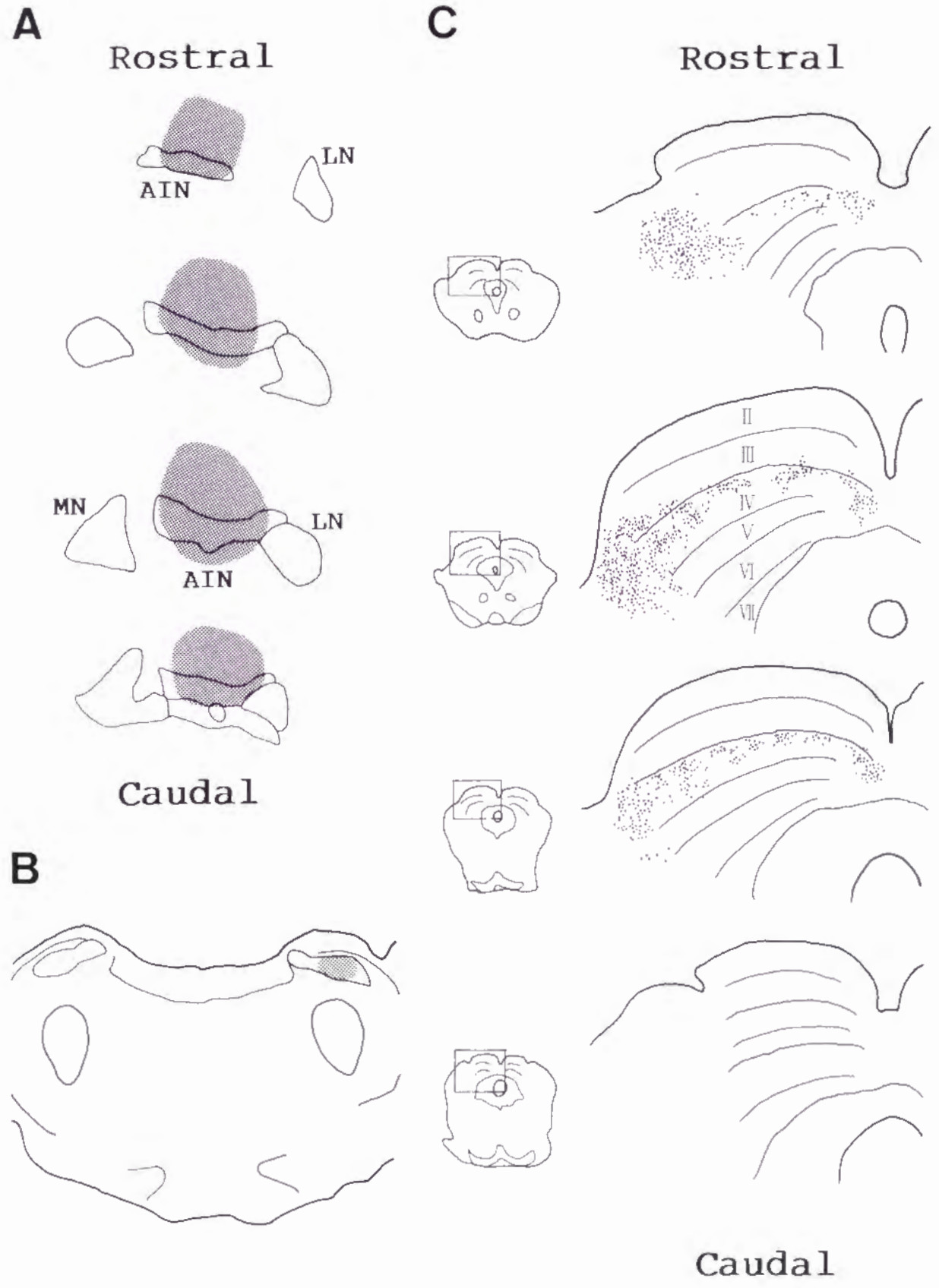
Fig. 5

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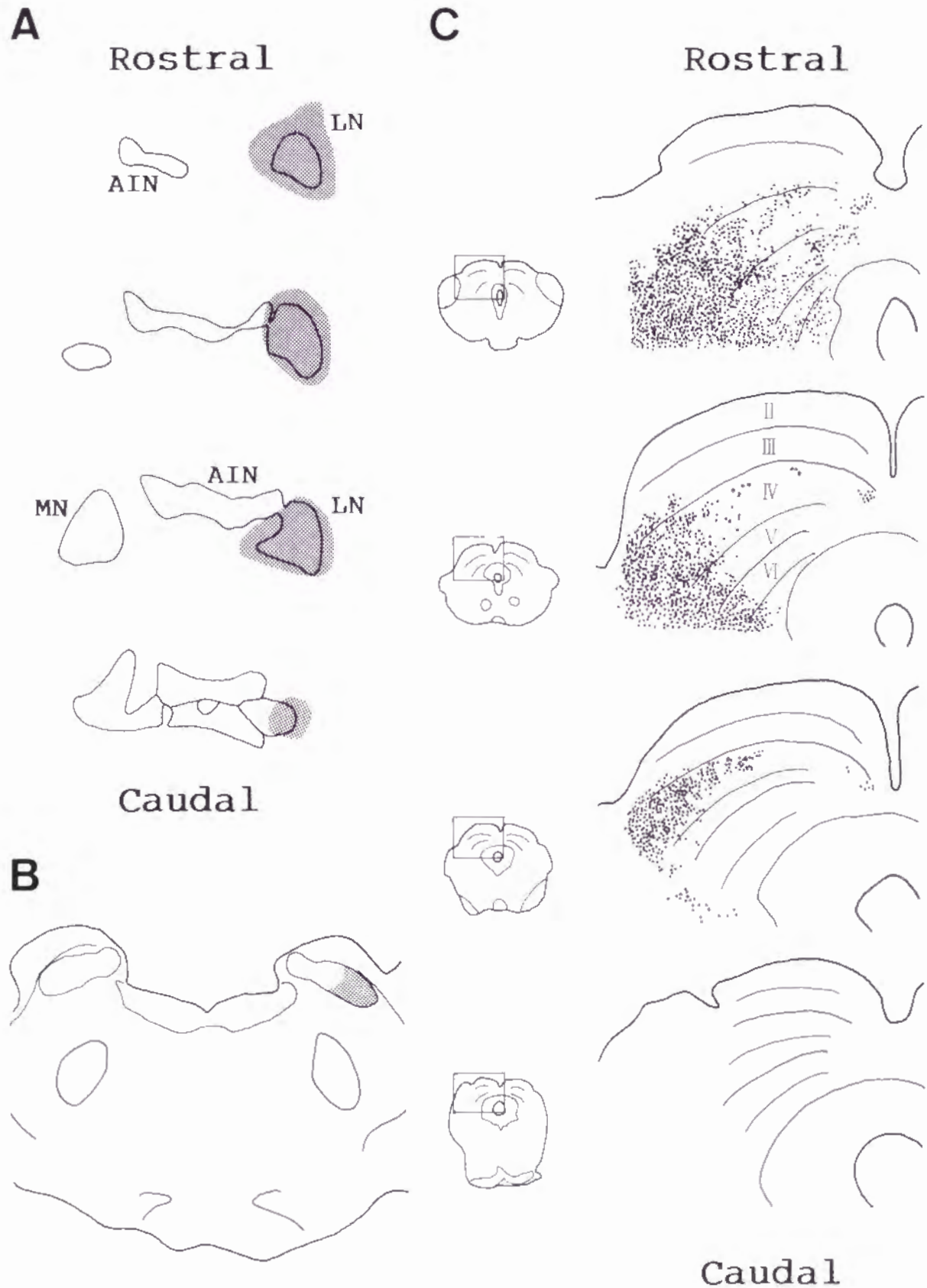
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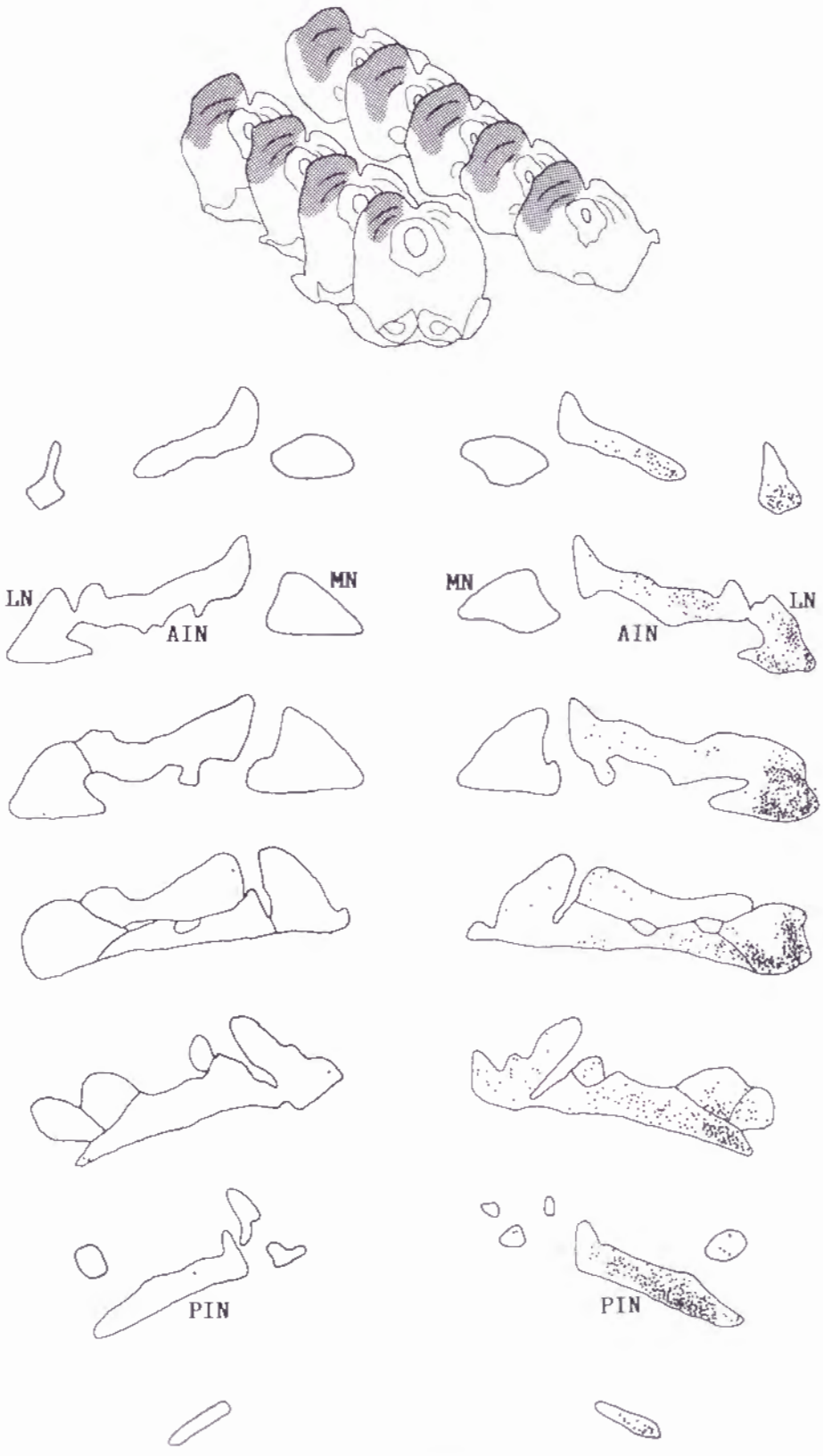

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Fig. 9

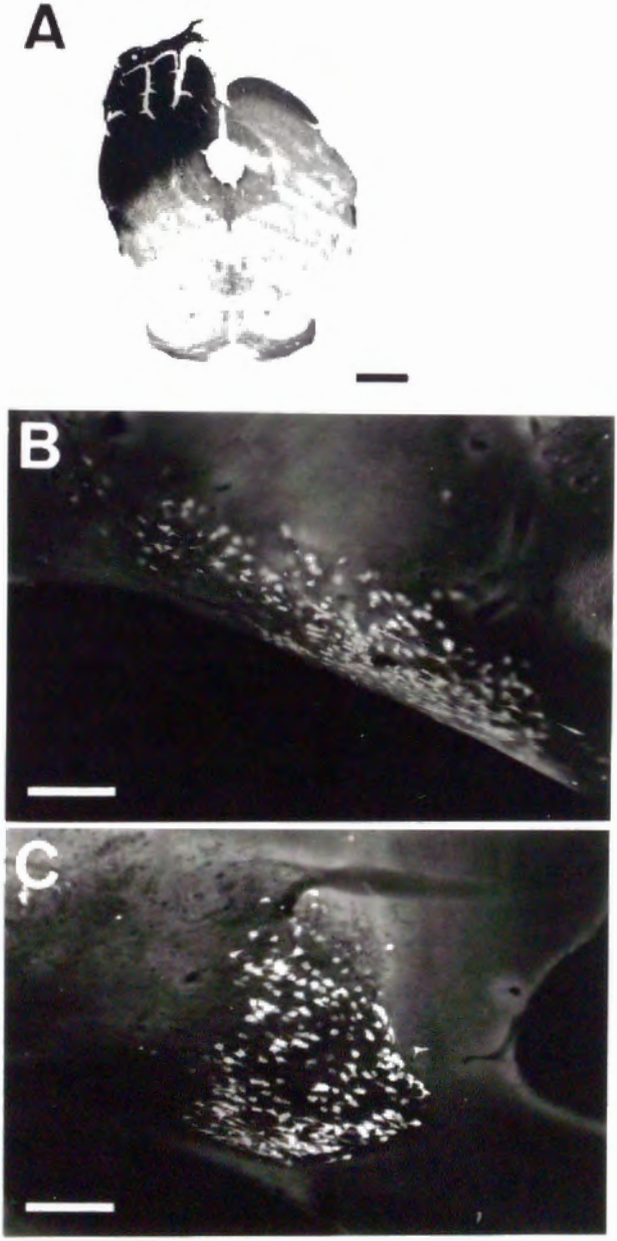

Fig. 10

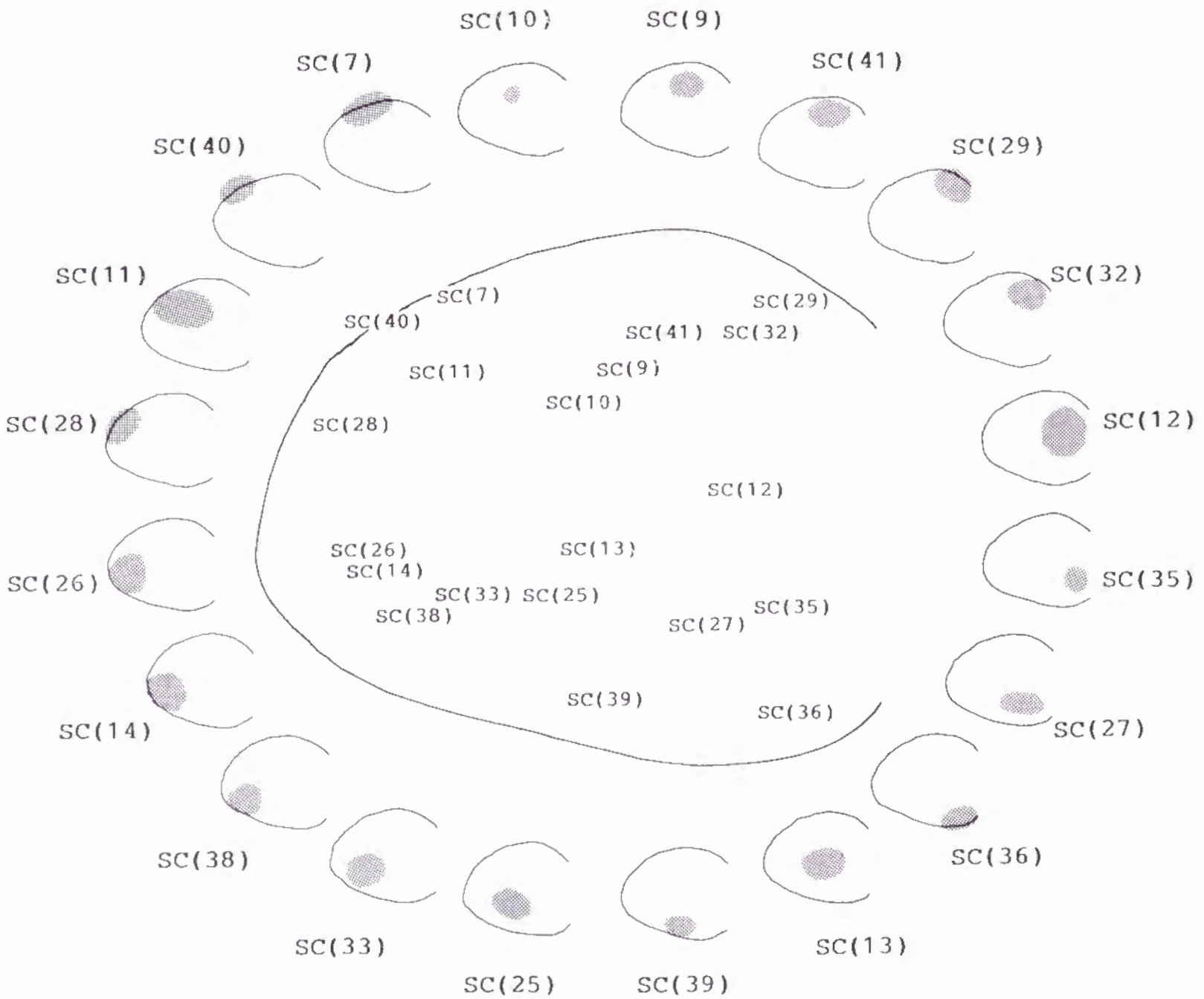
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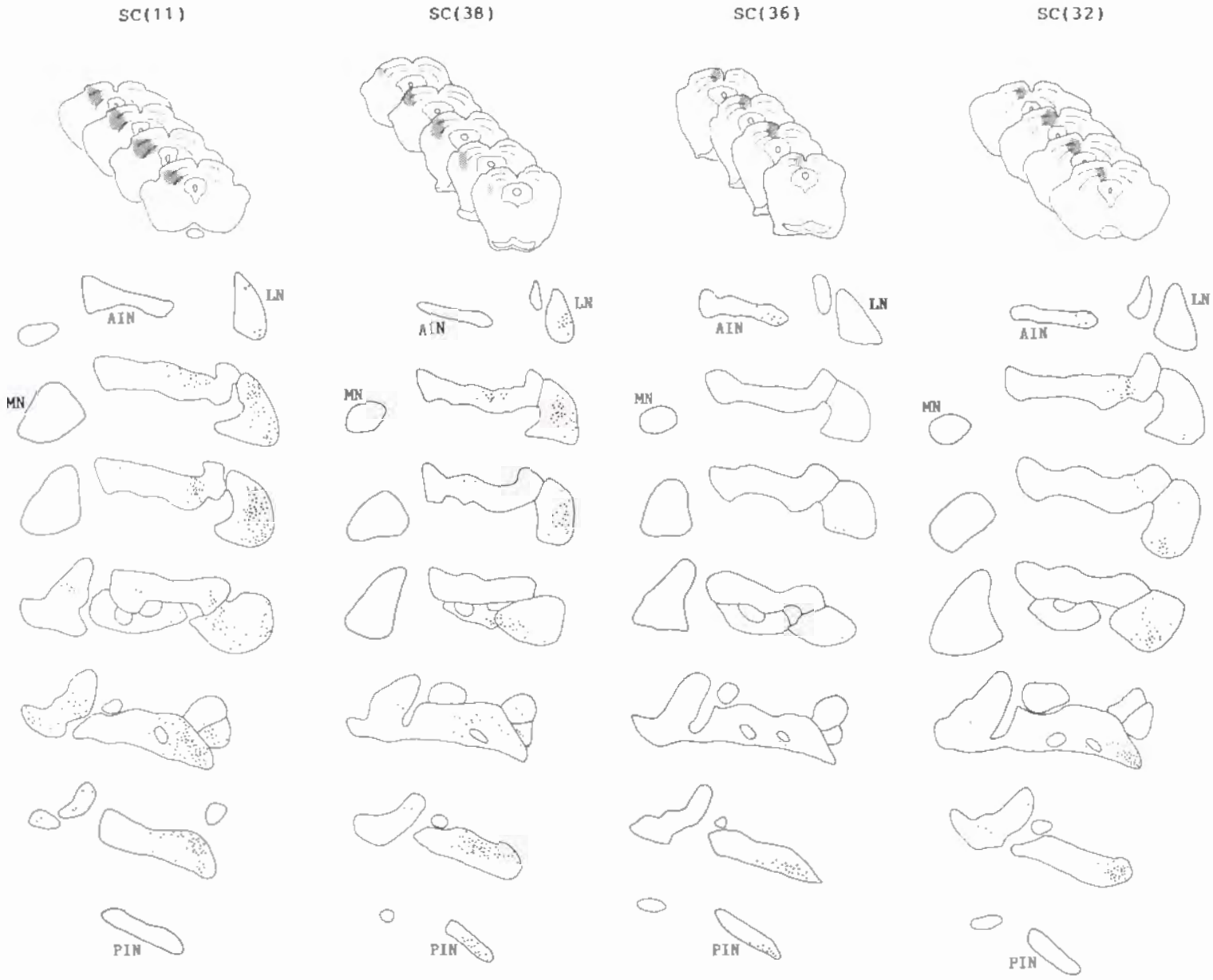
Fig 11



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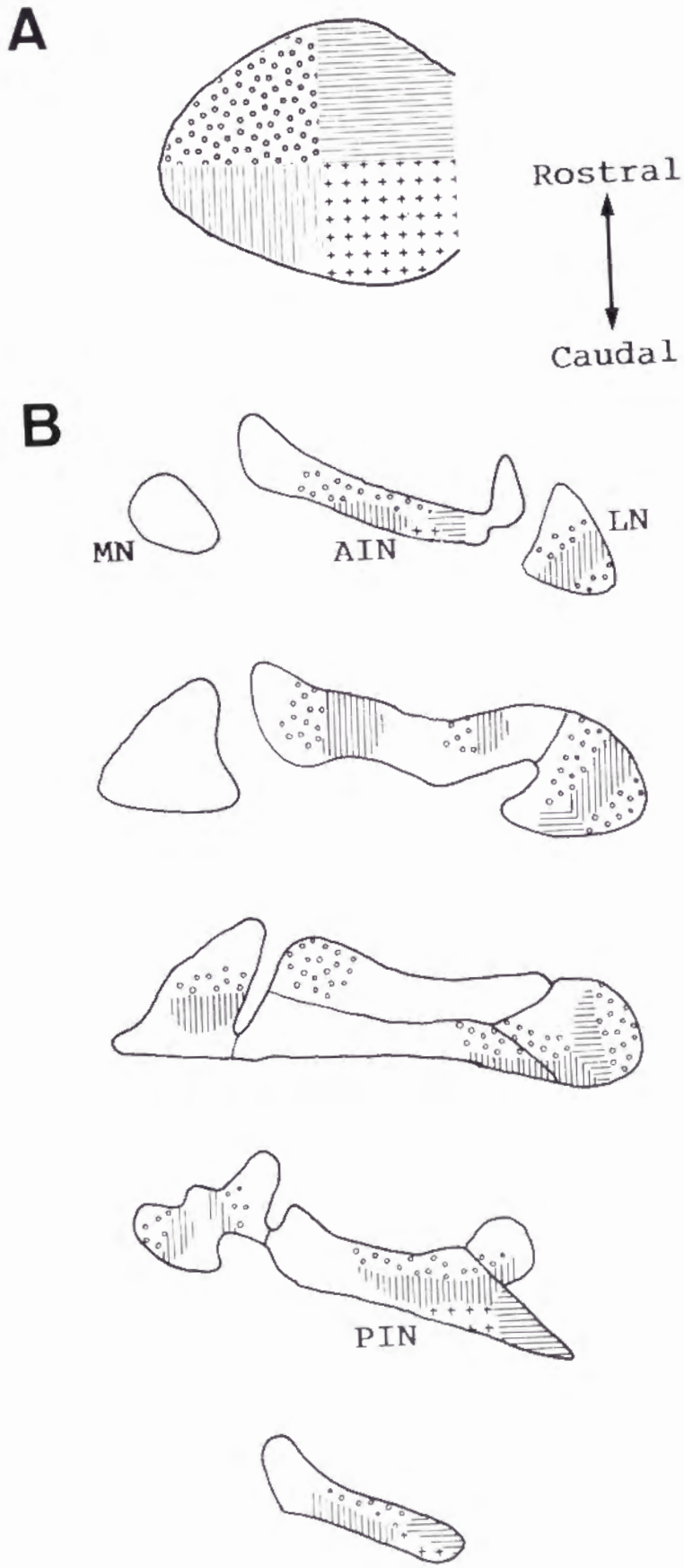
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