

## Different patterns of corticopontine projections from separate cortical fields within the inferior parietal lobule and dorsal prelunate gyrus of the macaque

J. G. May<sup>1</sup> and R. A. Andersen<sup>2</sup>

<sup>1</sup> Smith-Kettlewell Institute of Visual Sciences, 2232 Webster Street, San Francisco, CA 94115, USA

<sup>2</sup> The Salk Institute for Biological Studies, P. O. Box 85800, San Diego, CA 92138, USA

**Summary.** Corticopontine projection patterns were studied after injections of an <sup>3</sup>H-leucine and <sup>3</sup>H-proline mixture into each of four distinct cortical fields within the inferior parietal lobule and dorsal prelunate gyrus. Different preferential patterns of pontine labeling were observed for each of the four cortical areas studied. Multiple injections across the dorsal aspect of the prelunate gyrus (area DP) yielded scattered patches of label limited to the dorsolateral pontine nuclear region. A single injection within the lateral intraparietal area (area LIP), located in the caudal portion of the lateral bank of the intraparietal sulcus resulted in a series of labeled patches across the dorsal tier of cells stretching across the dorsal portions of the dorsolateral, peduncular and dorsal pontine nuclei. Injection of the cortex on the caudal aspect of the inferior parietal convexity (area 7a) produced multiple patches of label along the lateral margin of the ventral, lateral, and dorsolateral nuclei. Injection of area 7b resulted in label along the lateral aspects of the ventral, lateral and dorsolateral nuclei, as seen with area 7a injections, as well as additional label in the ventromedial portions of the ventral, peduncular and paramedian pontine nuclei. These results provide supporting anatomic evidence for the functional subdivision of the inferior parietal lobule and dorsal aspect of the prelunate gyrus and provide new information about the organization of cortical projections to the primate pontine nuclei.

**Key words:** Corticopontine projections – Inferior parietal lobule – Prelunate gyrus – Area 7 – Intraparietal sulcus – Pontine nuclei

### Introduction

The visual cortical areas in the macaque can be divided into two major systems: one devoted to the analysis of color, form and pattern information and one involved in the analysis of the motion and spatial location of visual objects. The cortical areas processing form and pattern information lie ventrolaterally in the hemisphere where they include the ventral portions of the prelunate gyrus, the cortical regions surrounding the inferior occipital sulcus, and the inferotemporal areas TE and TEO. Dorsal to these ventrolaterally located regions lie the inferior parietal and prestriate areas which are involved in the analysis of visual motion, spatial location and visuomotor integration. These dorsomedially located areas include the dorsal portion of the prelunate gyrus, the caudal third of the superior temporal sulcus, the convexity of the inferior parietal lobule, the lateral bank and fundus of the intraparietal sulcus and portions of the parieto-occipital sulcus (Glickstein and May 1982; Mishkin 1972; Ungerleider and Mishkin 1982; Van Essen and Maunsell 1983; Wilson 1978).

Lesions within the inferotemporal cortical regions lead to severe deficits in the identification of visual objects and in the learning and retention of visual object discriminations with little impairment in visuomotor or spatially oriented behavior. Conversely, lesions of the inferior parietal and dorsal prestriate areas have little effect on visual discrimination learning but lead to impairments on a variety of visuospatial and visuomotor tasks (Buchbinder et al. 1980; Dean 1976; Faugier-Grimaud et al. 1978; Haaxma and Kuypers 1975; Lynch and McLaren 1982, 1983; Mishkin 1972; Newsome et al. 1985; Ungerleider and Mishkin 1982).

Previous anatomic investigations in the macaque suggest that the bulk of the cortical visual input to the

pontine nuclei originates in the dorsal prestriate and inferior parietal regions. The pontine projections from area 17 are relatively small arising primarily from the striate representation of the far peripheral visual field. There are only few if any pontine projections which arise in the central portions of striate cortex or from the ventral portions of the lunate sulcus, prelunate gyrus, or from the inferotemporal areas (Brodal 1978; Fries 1981; Glickstein et al. 1980, 1985).

These findings provide additional anatomic support for the division of extrastriate cortical visual regions into two functionally distinct systems. The ventrolaterally located regions involved in pattern analysis and visual object discrimination and identification do not project significantly to the pontine nuclei, whereas the dorsal prestriate and inferior parietal areas involved in visuomotor control and the analysis of visual motion and spatial information provide the major cortical visual input to the pons and cerebellum (Glickstein and May 1982; Glickstein et al. 1980, 1985).

Results from recent anatomic and physiological investigations are beginning to delineate numerous functionally distinct cortical fields within this inferior parietal and dorsal prestriate region (Andersen et al. 1985a, b; Hyvärinen 1981; Lynch et al. 1985; Maguire and Baizer 1984; Maunsell and Van Essen 1983; Van Essen and Maunsell 1983). This report describes the pontine projections from four of these cortical fields; the dorsal prelunate gyrus – DP; the lateral intraparietal area – LIP; and areas 7a and 7b on the inferior parietal convexity (Fig. 1A). We were particularly interested in whether functional differences observed in anatomic and physiologic studies of these distinct areas would be reflected as differences in their pontine termination patterns. We found different preferential termination zones in the pontine nuclei for each of the four cortical areas studied. These results provide additional support for the delineation of these cortical fields and provide new information about the functional organization of the pontine nuclei.

Preliminary results of this study have been reported elsewhere (May and Andersen 1984).

## Methods

Unilateral injections of a mixture of tritiated amino acids were made into the inferior parietal or dorsal prestriate cortex of nine *Macaca fascicularis* monkeys. Some of these animals received additional injections of fluorescent dyes for a separate investigation of cortico-cortical and pulvino-cortical connection patterns. The results of these fluorescent studies will be presented elsewhere (Andersen et al. 1985a–b; Asanuma et al. 1985).

Animals were anesthetized with sodium pentobarbital (35 mg/kg) and craniotomies were placed over the parieto-occipital area using aseptic procedures. The dura was incised and reflected permitting direct visual placement of the injection needle within the cortical area of interest.

Pressure injections of a mixture of  $^3\text{H}$ -leucine and  $^3\text{H}$ -proline (New England Nuclear, concentrated to 100  $\mu\text{Ci}/\mu\text{l}$ ) were made through a 0.02" outer diameter needle attached to a 1  $\mu\text{l}$  Hamilton syringe. The majority of cases consisted of a single injection ranging in size from 0.4 to 0.5  $\mu\text{l}$ . In one case a series of eight, 0.5  $\mu\text{l}$  injections were made across the convexity of the dorsal prelunate gyrus. Multiple injections were also made into areas 7a and 7b in one case.

After 2–7 day survival periods the animals were perfused transcardially with three solutions: (1) cold heparinized saline, (2) 10% formaline in a 0.1 M phosphate buffer (pH 7.4), and (3) an 8% sucrose, 10% buffered formaline solution. After removal, the brains were blocked and placed in 15% sucrose in phosphate buffered saline. Three of the brains were dehydrated, embedded in Paraplast and cut at room temperature while the others were cut on a freezing microtome. Sections were cut at 30 microns with every ninth section (270  $\mu\text{m}$  intervals) mounted and processed for autoradiography by the method of Cowan and colleagues (1972). Briefly, sections were mounted on subbed slides, defatted, dipped in Kodak NB-2 nuclear track emulsion and exposed for 4–12 weeks. The slides were developed in Kodak D-19, fixed, stained with 0.5% thionin at low pH, and coverslipped with permount.

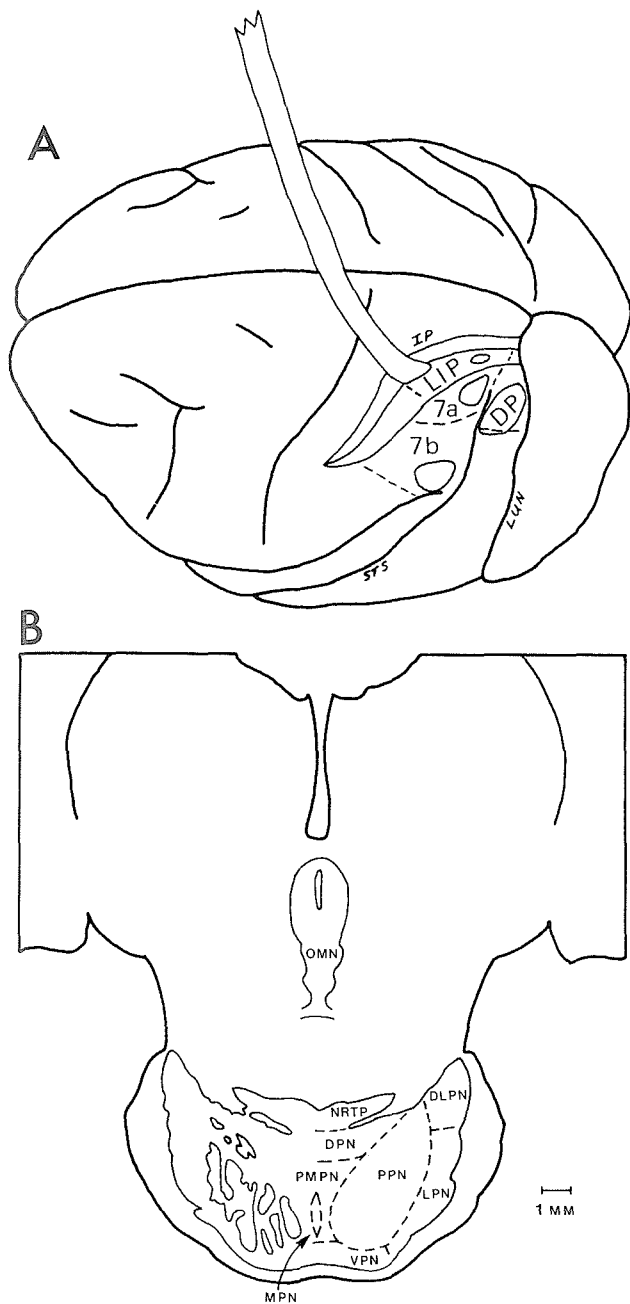
Autoradiograms were analyzed under both darkfield and lightfield conditions. The location and extent of terminal label was plotted by hand onto enlarged tracings of the counterstained section outlines. The spatial relation between regions of label and section landmarks such as blood vessels and cellular groups was determined by switching back and forth between bright and dark field illumination.

The boundaries between areas 7a, 7b, LIP and DP can be easily recognized by their patterns of cortico-cortical connections with one another and with other areas of the brain, particularly the prefrontal cortex (Andersen et al. 1985a–b; Asanuma et al. 1985). In most of the autoradiographic cases reported here, single or multiple injections of the two fluorescent dyes nuclear yellow and fast blue were also made in the prefrontal and posterior parietal cortices to aid in visualizing these borders. Area LIP projects much more strongly to the dorsolateral prefrontal cortex (comprising areas 8, 45 and 46; Walker 1940) than does area 7a, and area 7b has even weaker connections than does 7a. Injections of retrograde tracer in area 7a can be used to delineate the extent of area DP, which is the only cortical field on the convexity of the prelunate gyrus that projects to area 7a.

In those cases in which additional connective data were not available some borders could still be clearly defined on the basis of cytoarchitecture. The border between areas 7a and LIP can be distinguished by the fact that layer three of LIP has fewer cell bodies and greater neuropil than area 7a (Seltzer and Pandya 1980). This sparseness coupled with the large cell bodies in the lower part of the layer gives it a laminated appearance that is not seen for 7a. Layer 5 of area 7b is less homogeneous than 7a, with a sparse lower half and a dense large cell upper half abutting layer 4 (von Bonin and Bailey 1947). Area DP has a much denser layer 4 than LIP, 7a or 7b and layers 5 and 6 are poorly differentiated from one another.

## Results

The pontine nuclei of the macaque consist of a variable pattern of cell groups divided and separated



**Fig. 1.** **A** Location of the parieto-occipital areas studied in this report. The location of one injection site for each of the four areas studied is denoted by the circular outlines. These injection sites correspond to the cases presented in Figs. 2, 3, 5 and 6. Abbreviations: DP, dorsal prelunate gyrus; LIP, lateral intraparietal area which lies along the lateral bank of the intraparietal sulcus; 7a, area 7a on the caudal portion of the inferior parietal convexity; 7b, area 7b on the rostral portion of the inferior parietal convexity; STS, superior temporal sulcus; IP, intraparietal sulcus; LUN, lunate sulcus. **B** Anatomic subdivisions of the macaque pontine nuclei (after Nyby and Jansen 1951). Abbreviations: DPN, dorsal pontine nucleus; DLPN, dorsolateral pontine nucleus; LPN, lateral pontine nucleus; VPN, ventral pontine nucleus; PMPN, paramedian pontine nucleus; PPN, peduncular pontine nucleus; MPN, medial pontine nucleus; NRTPT, nucleus reticularis tegmenti pontis; OMN, oculomotor nucleus

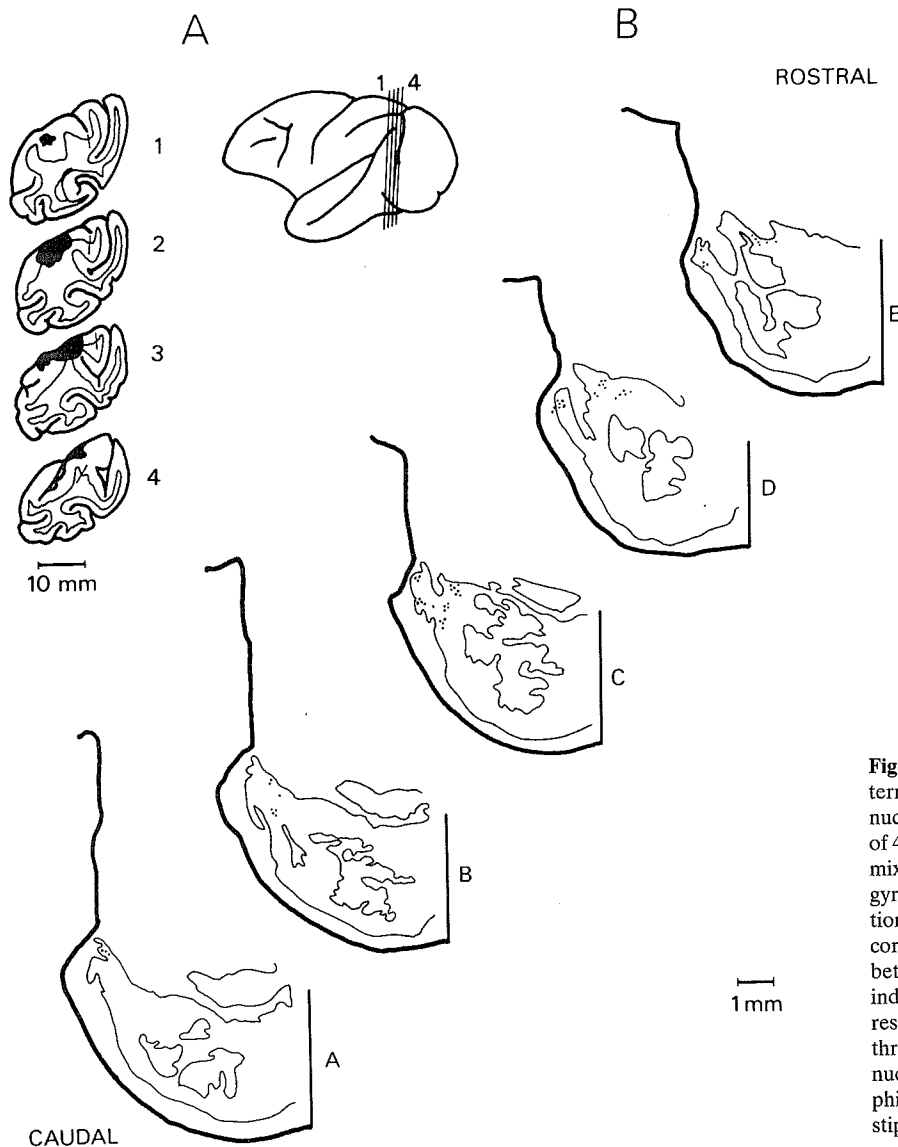
by the fiber fascicles of the descending corticobulbar and corticospinal tracts as they course through the pontine region. Labeling patterns within these scattered cell groups will be described below with references to the nuclear subdivisions of Nyby and Jansen (1951), shown in schematic form in Fig. 1B.

For all cases the terminal labeling in the pontine nuclei appeared as fragmented patches which were often scattered across more than one pontine region (see Fig. 4). These small patches of terminal label could often be traced through a series of adjacent sections, thus forming rostro-caudally oriented columns or slabs similar to previous descriptions of corticopontine terminations by Brodal (1978) and of the longitudinal clusters of retrogradely labeled pontine neurons seen after horseradish peroxidase injections in the cerebellum (Brodal 1979, 1982b). In addition to this columnar organization, labeling often occurred in either single isolated patches or as a series of loose discontinuous patches in serial sections.

In no case was there significant label in the body of the Nucleus Reticularis Tegmenti Pontis (NRTPT), although in some cases there was relatively sparse labeling within the most rostral transition zone between the NRTPT and the underlying dorsal pontine nucleus. All of the pontine labeling observed in this report was ipsilateral to the cortical injection sites.

The nomenclature used to describe cortical fields in the macaque has become complex and at times confusing. Cortical fields have been defined in terms of mylo- or cytoarchitectural variation, hodological connection patterns, as well as on functional criteria such as the response properties of single units or the effect of lesions within circumscribed regions. Some of the newer descriptive terms presently emerging for cortical fields are being defined by a combination of functional characteristics, connection patterns and cytoarchitectural features. In this report we have tried to use those terms which are commonly encountered in the experimental literature or, where appropriate, some of the newer descriptive terms which better characterize the functionally distinct cortical fields within the parieto-occipital region. Cortical fields within the inferotemporal region have typically been described using the nomenclature of von Bonin and colleagues (Bailey et al. 1950; von Bonin and Bailey 1947). In contrast, descriptions of frontal cortical areas often use Brodmann's nomenclature (Brodmann 1905) or one of its subsequent modifications such as the schema outlined by Walker (1940). The parietal regions studied in this report are gradually being subdivided into separate cortical fields based on a combination of the cytoarchitec-

DP



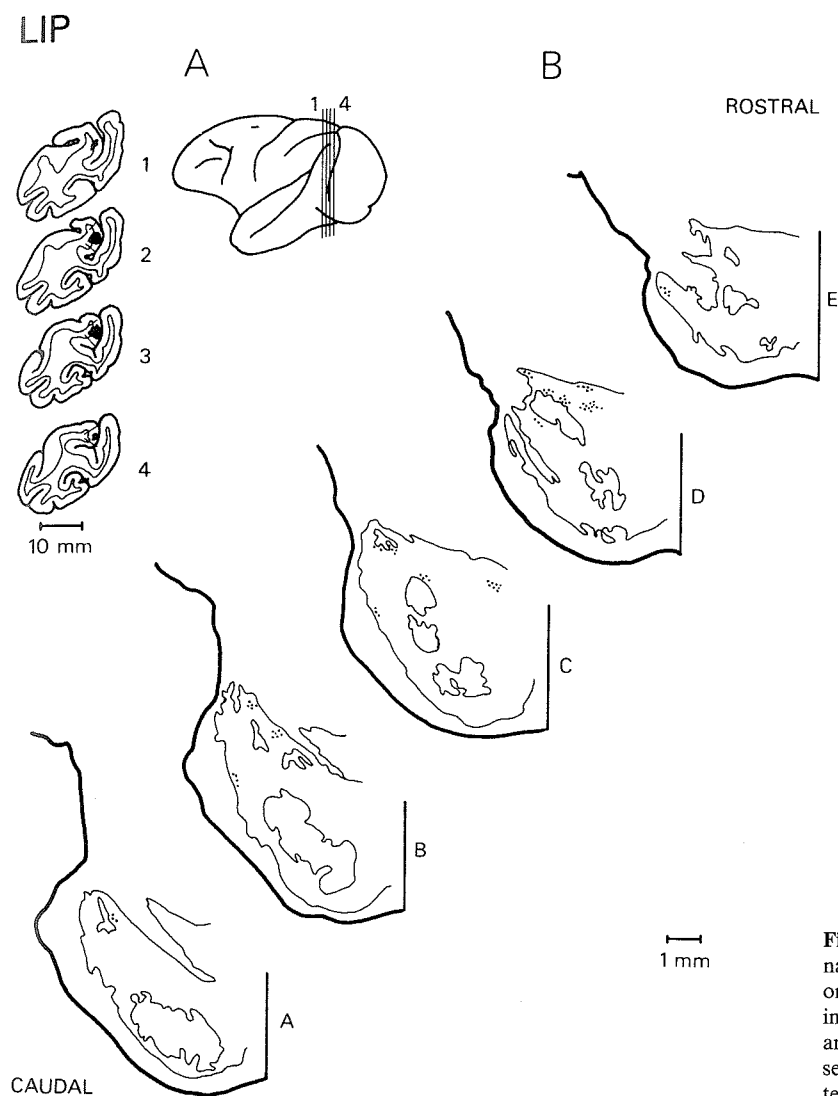
**Fig. 2A and B.** The distribution of terminal label within the pontine nuclei after multiple injections (total of 4  $\mu$ l) of a tritiated leucine/proline mixture across the dorsal prelunate gyrus (DP). **A** Selected cortical sections to illustrate the extent of the cortical injections. The border between area DP and area 7a is indicated by the slash marks. **B** Representative transverse sections through the ipsilateral pontine nuclei. The density of auto-radiographic label is indicated by the stippling

tural, connectional and functional criteria described above. Descriptions of the cortical fields studied in the report (DP, LIP, 7a and 7b) are presented in the discussion section below, whereas a description of the boundaries separating these areas is presented above in the method section.

#### *Dorsal prelunate gyrus*

In one animal a series of eight, 0.5  $\mu$ l injections were made across the dorsal portion of the prelunate gyrus. As shown in Fig. 2a, the injection spread over much of the dorsal convexity of the gyrus with very

little involvement of the underlying white matter or adjacent cortex within the lunate or superior temporal sulci. Most of the injection was contained within area DP, although some tracer also involved a portion of the prelunate gyrus just ventral to DP and a very limited portion of the intraparietal sulcus (Sect. 3, Fig. 2). The distribution of label within the pontine nuclei was restricted to numerous small patches within the dorsolateral nuclear region with the majority of label occurring in the rostral half of the pons (Fig. 2b). Small patches of label were seen in the border regions between the dorsolateral and both the lateral and the peduncular pontine nuclei. Despite the large cortical injection area, the density



**Fig. 3A and B.** The distribution of terminal label within the pontine nuclei after one 0.4  $\mu$ l injection in the lateral intraparietal area (LIP). The borders of area LIP are indicated on the cortical sections in part A by slash marks (see text for details)

of pontine labeling was relatively sparse when compared with the labeling seen after smaller injections in the other three areas.

#### *Lateral intraparietal area*

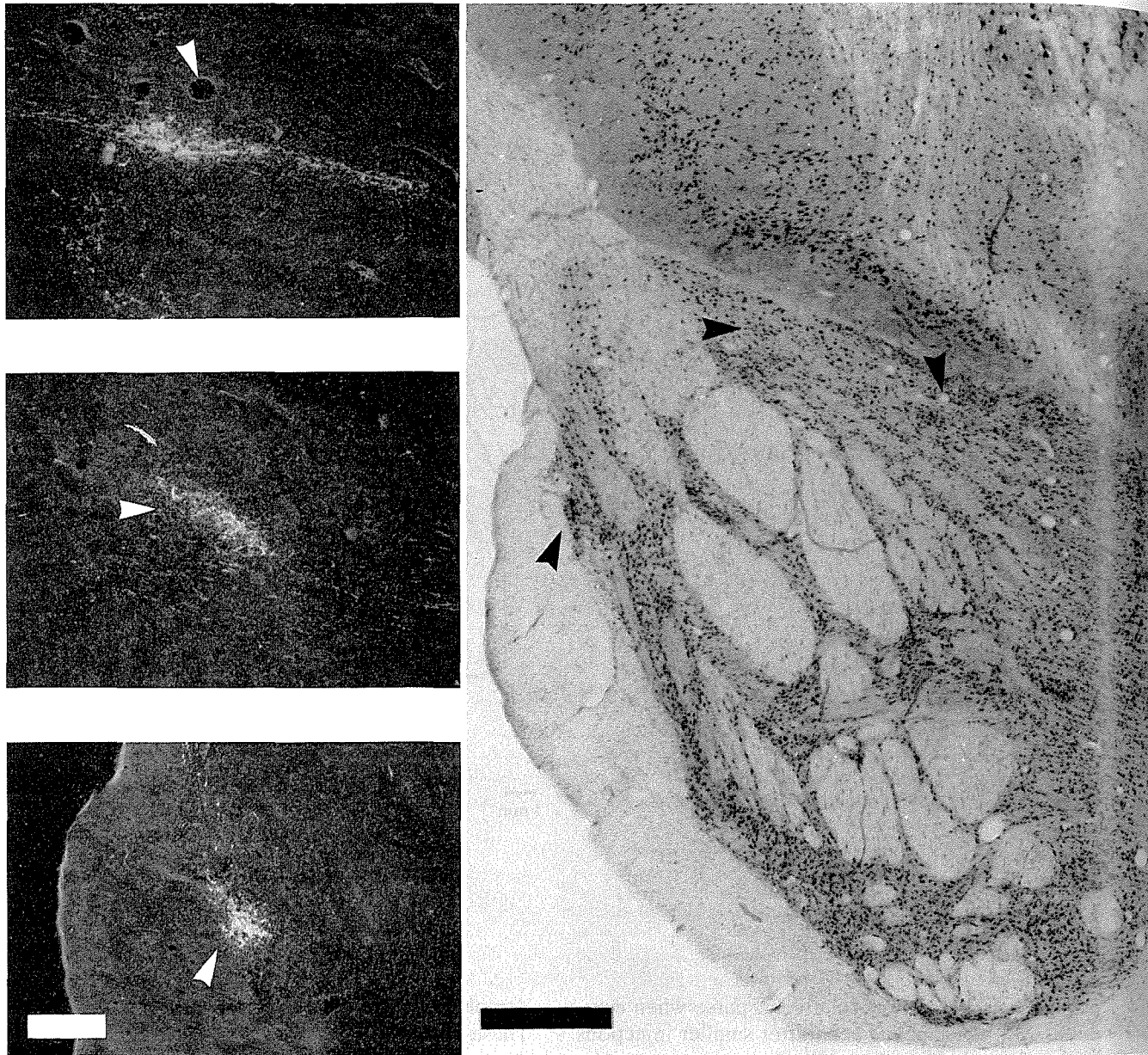
In this case a 0.4  $\mu$ l injection was placed approximately halfway down the lateral bank of the caudal portion of the intraparietal sulcus (Fig. 3a). The placement of this injection was guided by previous microelectrode recordings made in this area. There was some spread into the adjacent white matter but no spread of tracer into either the overlying convexity (area 7a) or into the medial bank of the intraparietal sulcus.

This injection produced a tier of patchy terminal label extending across the dorsal portions of the

dorsolateral, peduncular, and dorsal pontine nuclei. These patches were relatively large and particularly dense over a one millimeter region centered rostrocaudally around Sect. D in Fig. 3b. Photomicrographs of this patchy label are shown in Fig. 4 for a section falling in between Sect. C and D in Fig. 3b. This tiered pattern of label was never seen after injections into any of the other three cortical areas studied. In addition to this dorsal tier of label, small patches were also seen in the lateral and dorsolateral pontine nuclei. As in the previous case, most of the label was seen in the rostral half of the pontine nuclei.

#### *Area 7a*

Injections were placed within the caudal portion of the inferior parietal convexity (area 7a) in five ani-



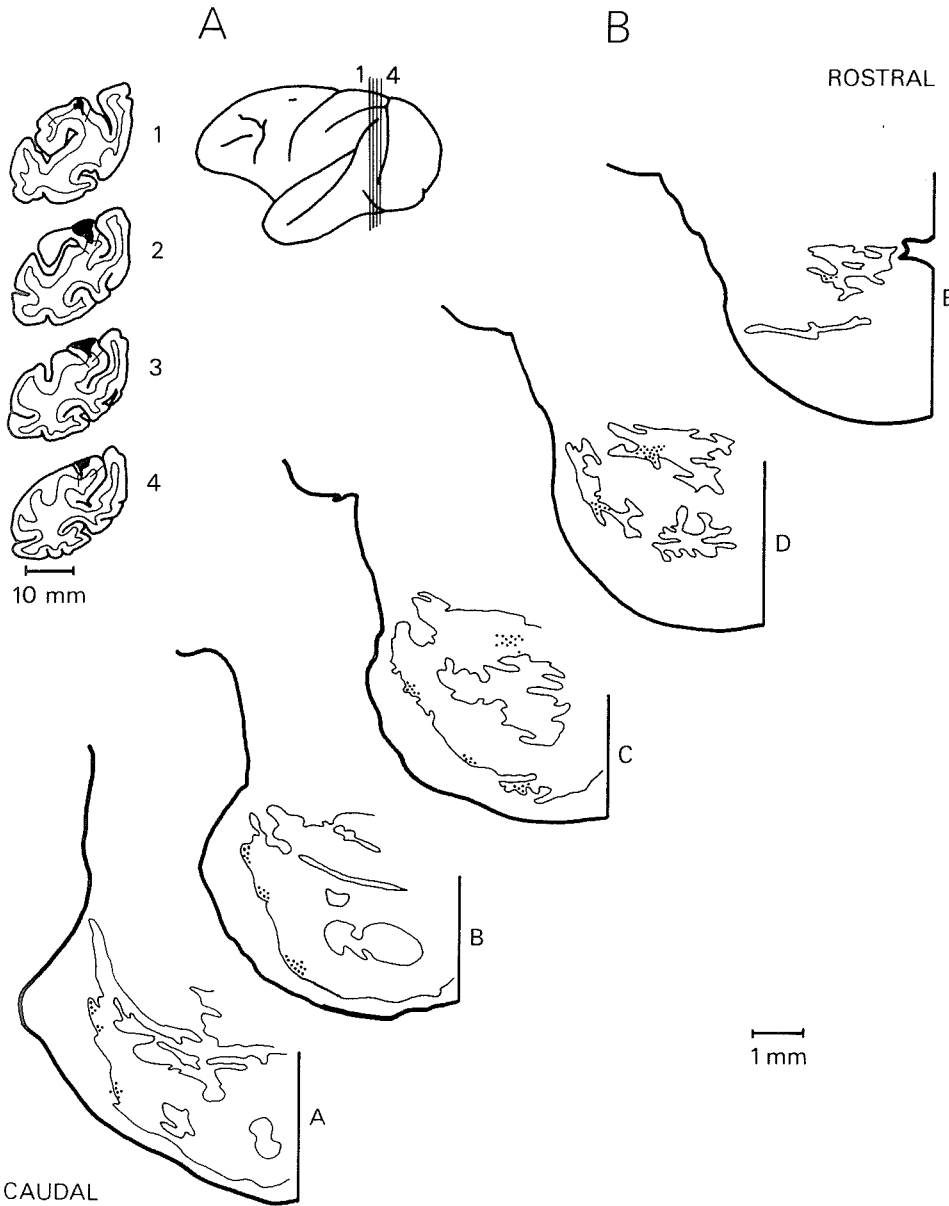
**Fig. 4.** Photomicrographs illustrating autoradiographic label along the dorsal and lateral margins of the pontine nuclei. This section falls between Sect. C and D in Fig. 3. The calibration bar on the bright field Nissl stained section represents 1 mm. The calibration bar for the darkfield autoradiograms represents 250  $\mu\text{m}$ . Arrows denote the location of the autoradiograms on the Nissl stained section

mals. The single injections ranged in size from 0.4 to 0.5  $\mu\text{l}$ . In all cases the spread of tracer was confined to that portion of area 7a occupying the convexity of the inferior parietal lobule with only limited involvement of underlying white matter or the cortex in neighboring sulci.

A representative case is illustrated in Fig. 5. This animal received one 0.5  $\mu\text{l}$  injection in area 7a which produced multiple patches of label along the lateral margin of the pons. This pattern of small discrete

patches of label along the lateral margin of the ventral, lateral and dorsolateral pontine nuclei was similar in all five cases. The actual number of patches encountered was correlated with the size and spread of the injection. Larger injection areas resulted in a greater number of discrete patches rather than an increase in patch size. These findings do not appear to result from the fragmentation of pontine cellular groups by passing fiber tracts since most of the patches of label occupy only a portion of the cellular

## Area 7a



**Fig. 5A and B.** The distribution of terminal label within the pontine nuclei after one 0.5  $\mu$ l injection into area 7a along the caudal portion of the inferior parietal convexity. The borders of area 7a are indicated on the cortical sections in part A by slash marks

groups and clusters in which they are found. The projections from area 7a occupy a larger rostro-caudal extent than those from the dorsal prelunate gyrus or lateral intraparietal area. In most cases, small patches of label were seen in both the most rostral and most caudal portions of the lateral pontine nucleus.

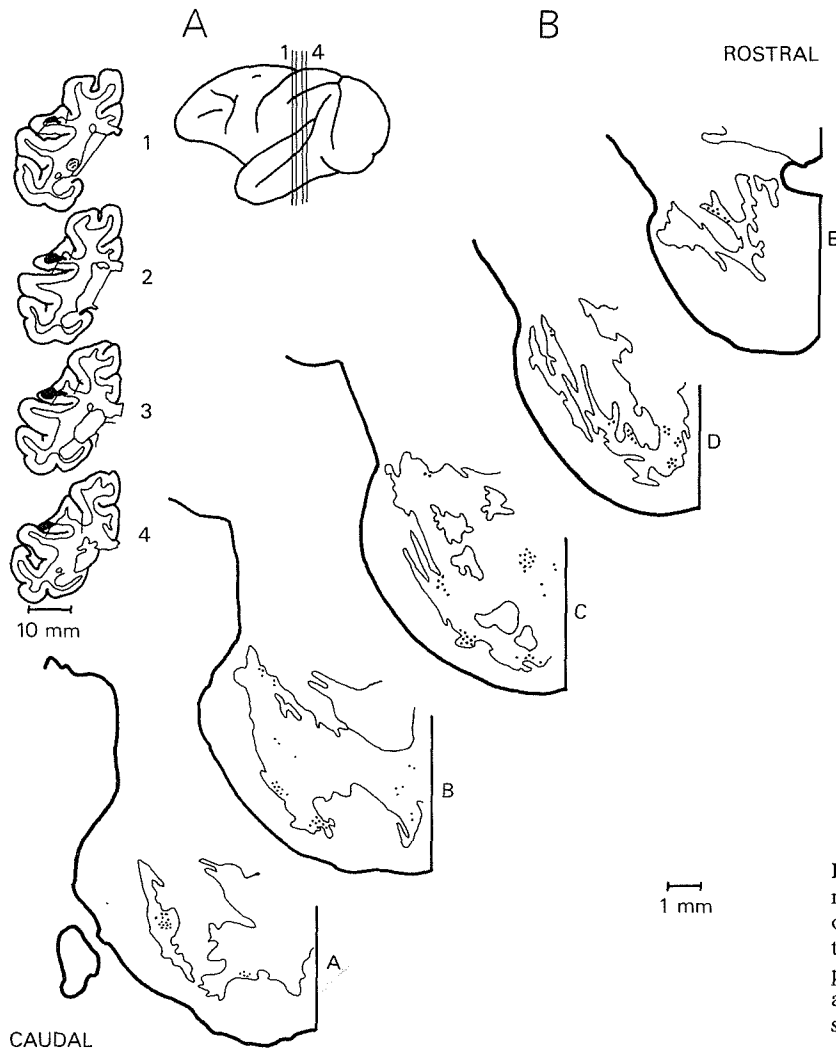
#### Area 7b

Injections in two animals involved the rostral portion of the inferior parietal convexity (area 7b). In one

case the injected tracer (0.4  $\mu$ l) was confined almost entirely to area 7b but with some involvement in SII. This injection produced a pattern of label along the lateral margin of the pons similar to that seen after injections in area 7a. This case also exhibited rather extensive but patchy label within the ventral portions of the peduncular and paramedian nuclei and in the medial portions of the ventral pontine nuclei (Fig. 6).

A similar but more extensive distribution of label was seen in the other animal which received relatively large injections involving both areas 7a and 7b

## Area 7b



**Fig. 6A and B.** The distribution of terminal label within the pontine nuclei after one 0.5  $\mu$ l injection into area 7b along the antero-lateral portion of the inferior parietal convexity. The borders of area 7b are indicated on the cortical sections in part A by slash marks

but definitely did not involve SII. Pontine sections in this case exhibited up to eight separate patches of label along the lateral pontine margin as well as multiple patches within the paramedian, peduncular, and ventral pontine nuclei. The similarity of the patterns of label in these two cases indicate that area 7b projects to both the lateral margin of the pons in a manner similar to area 7a and to the ventromedial portions of the peduncular paramedian and ventral pontine nuclei. Area 7b was the only area examined which projected to the ventromedial peduncular and paramedian regions.

### Discussion

The present autoradiographic study reveals different preferential patterns of pontine termination zones for

each of the four inferior parietal and dorsal prestriate areas studied. Each of these cortical areas constitutes a discrete cortical field with different functional characteristics and separate patterns of anatomic connections.

### *The prelunate gyrus*

The dorsal portions of the prelunate gyrus (area DP) contain light-sensitive neurons, many of which are responsive to the motion of visual stimuli, and have prominent connections with the lateral intraparietal area, area 7a, and a circumscribed region along the anterior bank of the caudal superior temporal sulcus (Andersen et al. 1985a, b). In contrast, the ventrolateral portions of the prelunate gyrus contain units which respond selectively to a variety of stimulus



parameters such as orientation, size and chromaticity. In addition to inferior parietal and dorsal prestriate projections, the ventrolateral prelunate gyrus maintains strong connections with the inferotemporal regions (Desimone et al. 1980; Zeki 1977).

Large multiple injections of wheat-germ agglutinin conjugated with horseradish peroxidase which involved most of pontine nuclei resulted in numerous retrogradely labeled neurons in the dorsal portions of the prelunate gyrus, though there was very little or no labeling throughout the ventrolateral portions of the gyrus (Glickstein et al. 1985).

In the present study, large multiple injections of anterograde tracer into the dorsal prelunate gyrus resulted in patchy label confined to the dorsolateral nuclear region. While some of these labeled fibers may have originated from a portion of the underlying intraparietal sulcus (see Sect. 3, Fig. 2) the involvement of intraparietal cortex was minimal and the labeling seen was similar to the sparse degeneration found in the dorsolateral pons by Glickstein and colleagues (1980) after ablation of the dorsal prelunate gyrus (case no. 9). The relatively sparse labeling seen after the ablation or injection of large cortical areas in the dorsal prelunate gyrus indicate a smaller contribution from this area to the visual corticopontine projection system than from nearby inferior parietal areas. This conclusion is supported by the diffuse distribution of retrogradely labeled neurons in the dorsal prelunate gyrus as compared with the relatively dense labeling of neurons within the superior temporal and intraparietal sulci following retrograde tracer injections into the dorsolateral pontine nucleus (Glickstein et al. 1980, 1985).

### *The inferior parietal lobule*

The inferior parietal lobule or area 7 includes the cortex along the anterior bank of the caudal superior temporal sulcus, the lateral bank of the intraparietal sulcus and the cortical convexity which lies between these two sulci. This area has been divided into a number of separate cortical fields by various investigators (Andersen et al. 1985a, b; Hyvärinen 1981; Lynch and Graybiel 1983; Seltzer and Pandya 1980; Van Essen and Maunsell 1983).

One of the cortical fields studied in the present report is the lateral intraparietal area which occupies the lateral bank of the caudal intraparietal sulcus<sup>1</sup>.

<sup>1</sup> The lateral intraparietal area has been defined based on its rich anatomic connections with the frontal eye fields, dorsal prelunate gyrus and superior colliculus (Andersen et al. 1985a-c). The LIP includes the caudal portions of the cortical field PO<sub>s</sub> of Seltzer and Pandya (1980) but is not coextensive with this cortical strip

This area is the major source of the inferior parietal projection to the superior colliculus and the major source of parietal connections with the frontal eye fields (Barbas and Mesulam 1981; Lynch and Graybiel 1983). In their microstimulation studies Shibutani and colleagues (1984) found this area to be the most effective portion of the inferior parietal lobule for the elicitation of saccadic eye movements through electrical stimulation. Recent studies using special eye movement paradigms to separate saccade-related from visually related neural activity have found that most inferior parietal neurons with saccade-related responses are found in this lateral intraparietal area (Andersen et al. 1985a, b).

The present report is the first description of the pontine projections arising exclusively from the lateral intraparietal area. The salient feature of these projections is the dense tier of terminations stretching across the rostral portions of the dorsolateral, dorsal peduncular and dorsal pontine nuclei. This termination pattern is quite different from that seen after injections placed in the inferior parietal convexity providing additional anatomic evidence for the functional subdivision of the inferior parietal lobule as suggested by previous electrophysiological and anatomic studies.

A pattern of corticopontine projections very similar to that described above for LIP has been reported for the frontal eye fields (Brodal 1979; Künzle and Akert 1977). Fibers from area 8 terminate in a series of patches across the dorsal tier of cells in the rostral portions of DLPN, PPN and DPN. Although these projections may extend more medially than those from LIP, there appears to be significant overlap or interdigitation between the termination zones of these two areas. Together these projections may constitute a relatively continuous termination zone across the dorsal margin of the rostral pontine gray. The similarity of these projection patterns is striking in light of the extensive cortico-cortical connections between the frontal eye fields and the lateral intraparietal area.

The other inferior parietal regions which were studied in this report lie on the inferior parietal convexity. Area 7a occupies the caudal-most medial portion of the convexity while area 7b lies rostral along the lateral aspect of the convexity. Andersen and colleagues (Andersen and Mountcastle 1983; Andersen et al. 1985a, b) have studied these areas in detail and find that almost all of the cells in area 7a respond to visual stimuli with a large number of them showing eye-position dependent tuning for the location of stimuli in head-centered coordinates. In contrast, the majority of units recorded in area 7b respond to somatosensory stimuli with some units

responding to both visual and somatosensory stimulation (Hyvärinen 1981; Hyvärinen and Shelepin 1979; Leinonen et al. 1979).

Injections of anterograde tracer substances into the area 7a and/or 7b resulted in multiple patches of label along the lateral margin of the dorsolateral, lateral and ventral pontine nuclei in all seven cases. These results agree well with the findings of Brodal (1978) and Wiesendanger et al. (1979) after relatively large area 7 ablations. Small punctate injections produced several small patches of label suggesting that each cortical locus sends multiple packets of information to a variety of pontine areas along the lateral pontine margin. This idea is consistent with the observation that large or multiple injections, which involve larger areas of cortex, produce a greater number of small patches rather than larger patches.

The two cases in which the injections included area 7b exhibited rather extensive label in the paramedian, ventral peduncular and medial portions of the ventral pontine nuclei. These projections have not been described previously for area 7 but fit in well with the somatic nature of area 7b since these same pontine regions receive extensive projections from premotor and motor cortex (Brodal 1978 – see projections from motor cortex hand area, case OM 324 and premotor cortex case OM 59).

In summary, visual cortical projections from the striate, dorsal prestriate, inferior parietal and frontal eye field areas terminate in a rather extensive crescent shaped region along the lateral margin of the ventral, lateral and dorsolateral pontine nuclei; and the dorsal portions of the dorsolateral, peduncular and dorsal pontine nuclei. Although different cortical areas have different preferential termination zones within this region, they all maintain some projections to the DLPN

#### *Functional studies of the dorsolateral pontine nucleus*

Functional studies of the pontine nuclei have been directed primarily at the dorsolateral pontine nucleus. This area has been classically regarded as the visual portion of the macaque pons and has recently been implicated in the control of smooth pursuit eye movement. Early descriptions of visual corticopontine projections after partial or complete occipital lobectomies report fiber degeneration distributed primarily across the rostral dorsolateral quadrant of the pontine nuclei (Brodal 1978; Glickstein et al. 1980; Nyby and Jansen 1951; Sunderland 1940). More recent anterograde tracing studies, including the present report, reveal DLPN projec-

tions from all of the prestriate and inferior parietal areas which project significantly to the pons. The DLPN is also the major recipient region in the basilar pontine nuclei for the tecto-pontine projection in the macaque (Cohen et al. 1981; Harting 1977).

Recent electrophysiological recordings from the DLPN of alert behaving monkeys have revealed a variety of neural responses related either to eye movement during smooth pursuit tracking or to the motion of visual images across the retina. Suzuki and Keller (1984) describe DLPN units with passive visual responses to the motion, in the units preferred direction, of either full field textured backgrounds, a discrete target spot or to both stimuli during periods of stationary fixation. One very interesting group of DLPN units responded to the movement of a discrete visual stimulus with a two component discharge: 1) a direction specific maintained discharge as the spot crossed a large receptive field, and 2) a transient response related to retinal image slip-velocity as the stimulus crossed a small foveal receptive field. During smooth pursuit tracking these units respond only during periods of retinal image slip in the units preferred direction, thus providing an error signal conveying the direction and velocity of target image motion across the retina.

Mustari et al. (1984) have described DLPN units whose discharge is related to eye-movement during smooth pursuit, units responsive to visual stimulation, and units which respond to both eye movement and visual stimulation. The discharge of units in the first group was modulated during smooth pursuit in the dark but did not respond to visual stimulation during fixation. If the target light was briefly extinguished (200–500 ms) during pursuit these cells continued to respond. In contrast, the strictly visual units responded to visual stimulation during fixation as well as during pursuit tracking. When the target was blanked out during pursuit, the discharge of these cells fell to spontaneous rates. This later group may correspond with the visual slip-velocity cells reported by Suzuki and Keller (1984) and may be similar to the visual motion sensitive units recorded in the visual cortical recipient regions of the pontine nuclei in the acute paralyzed cat (Baker et al. 1976). Unfortunately the acute preparation precluded the study of oculomotor related responses in the early cat studies.

Recent behavioral studies of smooth pursuit tracking performance after injections of lidocaine or the excitotoxin ibotenic acid into DLPN provide additional evidence for the involvement of DLPN in both the initiation and maintenance of pursuit. Suzuki et al. (1984) found direction specific gain reductions in eye velocity during sinusoidal tracking after lidocaine injections in the DLPN. These impair-

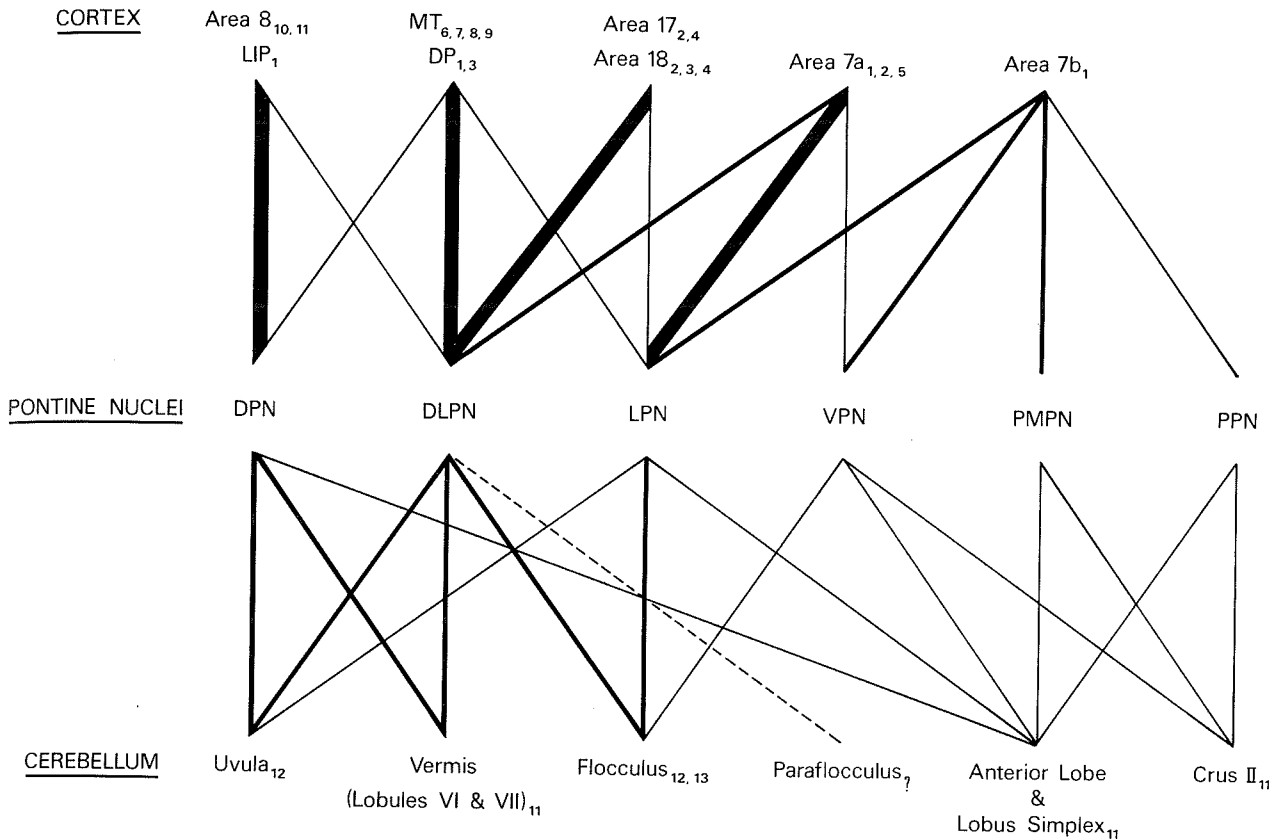


Fig. 7. Schematic representation of the cortico-ponto-cerebellar system in the macaque. Shown are some of the major anatomic connections conveying visual and oculomotor related signals from the cerebral cortex through the pontine nuclei to the cerebellum. The relative prominence of efferent projections from each area is indicated by arrow thickness. The small numbers associated with each cortical, pontine or cerebellar region refer to the following list of studies on which this figure is based. 1) May and Andersen – present report; 2) Brodal 1978; 3) Glickstein et al. 1980; 4) Glickstein et al. 1985; 5) Wiesendanger et al. 1979; 6) Fries 1981; 7) Maunsell and Van Essen 1983; 8) Galletti et al. 1982; 9) Ungerleider et al. 1984; 10) Künzle and Akert 1977; 11) Brodal 1979; 12) Brodal 1982a; 13) Langer et al. 1985

ments were reversible, disappearing within 15 to 45 min after injection. Ibotenic acid was used to produce a permanent lesion of pontine neuron somata without concomitant involvement of fibers of passage. Injections into DLPN or LPN regions containing pursuit related neurons produced impairments during the initial eye acceleration phase of pursuit tracking which lasted for 3–7 days before recovery. Pursuit deficits have also been reported following ibotenic acid injections into the dorsal prestriate area MT (Newsome et al. 1985), an area whose pontine projections include the DLPN (Fries 1981; Galletti et al. 1982; Maunsell and Van Essen 1983; Ungerleider et al. 1984). Unfortunately, there is very little information concerning the functional properties or organization of the other pontine nuclear regions other than their hodological relations with the cerebral cortex and the cerebellum. One exception to this is the most medial portion of the rostral dorsal pontine nucleus of the monkey. This

area is responsive to full-field visual stimulation but does not appear to receive a major cortical input (Keller and Crandall 1983).

#### *Pontocerebellar projection patterns*

It is difficult to accurately map the functional projections from the cerebral cortex through the pons onto the cerebellum given our current knowledge of pontocerebellar connections in the macaque and the intrinsically complex pattern of divergent and convergent connections evident throughout the cortico-ponto-cerebellar projection system.

It is not yet clear to what extent small groups of cells in the pontine nuclei represent individually distinct functional units. Due to the patchy or columnar nature of both the corticopontine and the ponto-cerebellar projection systems, adjacent cell groups within a given pontine region may receive separate

sets of afferent input and could have entirely different patterns of pontocerebellar connections. A more optimistic schema would have similar or related information extracted from each of several cortical areas and sent to particular regions of the pontine nuclei. Presumably the pontine nuclei are organized such that appropriate sets of converging inputs may be processed and relayed onto functionally specific cerebellar targets. Much of the complexity seen in this system must arise from the cerebellar requirement that different subsets of convergent inputs be distributed to various cerebellar areas, each of which may be involved in separate visuomotor functions.

Though much of the anatomic work concerned with the organization of the pontocerebellar system has been done using the rabbit, cat or rat, there are significant differences in the oculomotor abilities (Cohen et al. 1977; Collewijn 1972; Lisberger 1982); and the organization of the pontine nuclei between the macaque and these other species (Brodal 1978, 1982b). Early studies of the ponto-cerebellar connections in the macaque relied on retrograde degenerative changes after cerebellar ablations and revealed only the more global organizational aspects of this system (Sunderland 1940). More recently, modern retrograde tracing techniques have been used to study in detail the pontine distribution of retrogradely labeled cells after tracer injections in different cerebellar regions of the macaque (Brodal 1979, 1982a; Langer et al. 1985). Some of the connections revealed in these studies along with a representation of the corticopontine projections described in this report are shown in Fig. 7.

These retrograde anatomic studies have demonstrated projections from DLPN to the posterior vermis (lobules VI and VII), the flocculus, the uvula and, more diffusely, to lateral hemispheric areas. Both the posterior vermis and the flocculus have been implicated in the control of smooth pursuit and saccadic eye movements. Single unit recordings from the posterior vermis have revealed Purkinje cell activity related to saccadic eye movement (Kase et al. 1980) as well as units responsive to retinal error velocity, eye velocity, and head velocity during sinusoidal tracking (Kase et al. 1979, Suzuki et al. 1981; Suzuki and Keller 1982). When put together these latter three signals form a neural correlate of target velocity which is an important signal for the smooth pursuit control system (Robinson 1976a; Young 1971). Stimulation within the midvermal region elicits saccadic eye movements (Ron and Robinson 1973) which exhibit initial position dependent trajectories (McElligott and Keller 1984), whereas lesions of this region produce impairments in both saccadic and smooth pursuit eye movements

(Ritchie 1976; Suzuki and Keller 1983). Electrophysiological studies of the flocculus reveal a variety of responses related to saccadic eye movement (Noda and Suzuki 1979a) and to eye and head velocity during tracking or vestibular stimulation (Lisberger and Fuchs 1978; Noda and Suzuki 1979b; Waespe and Henn 1981). Microstimulation within the flocculus has been shown to elicit saccadic as well as slow, smooth changes in eye position (Belknap et al. 1983). Ablation of the flocculus produces deficits in smooth pursuit tracking, impairments in optokinetic nystagmus, as well as gain reductions and a loss of the adaptive modification of the vestibulo-ocular reflex, all of which may involve visual and oculomotor related mossy fiber input from the pontine nuclei (Optican et al. 1980; Robinson 1976b; Takemori and Cohen 1974; Waespe et al. 1983; Zee et al. 1981).

Another likely recipient of dorsolateral nucleus pontocerebellar projections is the paraflocculus. This structure receives a prominent input from the pontine areas in the cat and rat which receive visual cortical input (Burne et al. 1978; Robinson et al. 1984). Portions of the paraflocculus have usually been included in flocculus ablations and may contribute to the oculomotor deficits observed after these lesions. Another target of the DLPN, the uvula, may be involved in the visuo-vestibular interactions which lead to motion sickness (Bard et al. 1947; Siegel and Wespicek 1974). The uvula is also a major target of the pontine regions in the cat which receive input from visual cortical areas (Robinson et al. 1984).

The precise relation between the pontocerebellar projections from other pontine nuclear zones to these visual and oculomotor related areas of the cerebellum is difficult to extract from the available literature. The use of anterograde tracing techniques to study the cerebellar distribution patterns of fibers from separate pontine regions may be essential for a more detailed understanding of the functional organization of the pontocerebellar system.

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